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Actas de la 5.ª Reunión Internacional de la Sociedad de Ortopterólogos

Proceedings of the 5th International Meeting of the Orthopterists' Society

17-20 julio, 1989
Valsaín (Segovia), España

MINISTERIO DE AGRICULTURA PESCA Y ALIMENTACION
DIRECCION GENERAL DE LA PRODUCCION AGRARIA

PORTADA:

Macho de *Podisma ignatii carpetana* (Bol. 1890) especie endémica de la Península Ibérica. Esta especie fue revisada por E. Morales Agacino 1950. (Foto de J. Gosálvez.)

Indice

CONFERENCIA PLENARIA:

SIMPOSIO:

La reciente progresión de las plagas de langostas y nuevos métodos para su manejo.
The recent upsurge of the locust plague and novel approaches to locust pest management

TRATAMIENTOS / *CONTROL*

EVOLUCION Y SISTEMATICA / *EVOLUTION & SYSTEMATICS*

ECOLOGIA Y COMPORTAMIENTO / *ECOLOGY & BEHAVIOR*

FISIOLOGIA Y GENETICA / *PHYSIOLOGY & GENETICS*

Prólogo

La Orthopterists' Society es el nuevo nombre que recibió la Panamerican Acridilogical Society tras la memorable reunión italiana de Siena (1986). Este cambio fue debido, en parte, a que América le venía pequeña y el Viejo Mundo se ofrecía como un amplio campo en el que desarrollar su juvenil e imparable actividad y que le pedía su inmediata coordinación con la serena y reposada marcha de lo que ocurría en la otra orilla del Gran Charco, a fin de que, con la conjunción de ambas energías, se afianzara y desarrollara cuanto sea pertinente a este grupo de insectos.

La Quinta Reunión de la Orthopterists' Society tuvo lugar en los aledaños de la bella sierra de Guadarrama, bajo la protectora sombra de ese gran maestro de la Ortopterología que fue don Ignacio Bolívar, gracias a los eficientes recursos que brindó la Administración española —comprensiva y generosa— y con el concurso de una Naturaleza pródiga en temas y materiales que en muy pocos lugares se muestran con tanta abundancia y diversidad. El volumen que tienen en sus manos recoge las contribuciones del casi centenar de especialistas de los cinco continentes que acudieron a la cita de Valsaín (Segovia). Las cinco secciones en que queda dividido corresponden a las que configuraron la Reunión, y además se incluye una recopilación de los resúmenes de los trabajos que no se han desarrollado como artículos.

El primer apartado («Symposium») recoge los trabajos de prestigiosos especialistas que se expusieron y discutieron en el «Symposium on locust control» organizado por el doctor Pener. En ellos se plantean nuevos interrogantes sobre el«comportamiento inquietante» que caracteriza a la naturaleza fásica de ciertas especies, las que el vulgo llama «langostas». causantes de las asoladoras plagas de ese nombre y que producen cuantiosos gastos y daños a las regiones y países que las sufren. Ligado a esta sección se encuentra el apartado dedicado a «Control». Sus conclusiones tendrán una buena acogida por los gestores de este problema.

Quizá con cierta lógica la aportación en la sección de «Systematics and Evolution» es mayoritaria en estos Proceedings. En esta ocasión, la clásica «sistemática» muestra su conocido ropaje adornado con nuevas joyas que la actualizan, ya que no puede prescindir de los favores y consejos que, la tan hoy día denostada y perenne dama sigue proporcionando a los fundamentos y al imparable desarrollo de sus olvidados retoños que siempre, por esto o por aquello, tendrán que recurrir a apoyarse en ella. Menos mal, porque de no ser así, no sabremos qué disciplinas con base firme vamos a construir.

Los insectos descritos y nominados, es decir, los hoy en día llamados «taxones», se comportan y distribuyen conforme a normas muy estrictas y diversas, que si son sobrepasadas con viabilidad, pueden incidir sobre otros aspectos relacionados, por ejemplo, con su morfología. De tal forma que a veces uno tiene que olvidarse del propio insecto y verle tan sólo como un elemento más de un todo cambiante y factor importante de un comportamiento sumamente inquietante.

Todo cuanto le rodea se refleja en ellos, cualquier modificación transitoria, estacional o de otra naturaleza que actúen donde es propio que vivan, es decir, en su «ecosistema», lo recogen, sobre todo, las especies que más dependen de él. De ahí que aquellos caracteres limitantes puedan ser considerados como «indicadores biológicos» que nos señalen con sus oscilaciones numéricas, de comportamiento y distributivas el estado de conservación o desequilibrio de un determinado biotopo o incluso del ecosistema en su conjunto; sobre todo de los enclavados de las tierras llamadas marginales y de alta montaña. Así se hace evidente nuestra preocupación por el mejor estudio y conservación de los taxones que en mayor medida se vean afectados por estos aspectos. Todo ello fue parte importante de las contribuciones de Bolívar y su escuela, que quedaron recogidas en numerosos estudios y publicaciones.

En este volumen los trabajos relacionados con dichos temas se recogen en la sección «Ecology and Behavior», donde el análisis pormenorizado del intrigante y específico canto de los acrídidos es parte sustancial.

Finalmente, en la sección «Physiology and Genetics» se analiza la estructura genética de algunas especies y queda de manifiesto el interés de estos estudios para mejor entender el proceso de divergencia de especies y, en general, los mecanismos evolutivos de estos insectos.

Si la reunión de Valsaín fue un verdadero éxito no sólo en su vertiente científica, sino también por el entorno paisajístico, cultural y humano que todos pudimos disfrutar, yo espero que este volumen también lo sea y su contenido auspicie la formación de nuevos compañeros en el estudio de los ortopteroidea.

Eugenio Morales Agacino

Bol. San. Veg. Plagas (Fuera de serie) 20, 1990

Alocuciones de apertura / *Welcoming Address*

EUGENIO MORALES AGACINO

Comité Organizador

«Sr. Director de ICONA, Sr. Presidente y Sr. Secretario de la Orthopterists' Society, señoras y señores:

Tan sólo quiero dirigirles dos palabras como pequeño comentario a las actividades que se van a desarrollar en esta Quinta Reunion Internacional de la Sociedad Ortopterológica. De hecho los que forman parte de la misma precisarán con sus intervenciones el contenido y alcance de la misma.

En primer lugar, y como simple detalle histórico, debemos recordar que en la reunión de Siena (Evolutionary Biology of Orthopteroid Insects, 1987) se acordó que la Panamerican Society of Acridology, que tenía un ámbito restringido a las Américas, ampliara su misión para ser universal y se transformara en la Orthopterists' Society.

Ahora debiera celebrarse la Quinta Reunión de la Panamerican, que en esencia es la Primera de la Orthopterists' Society, y nuestros buenos amigos Stan (Gangwere), el Secretario General que ha pasado largas temporadas en España, y muchos otros de Europa pensaron que uno de los sitios ideales para la ortopterología, por los problemas que tiene de tipo puro y de tipo aplicado, es España. Por ello la primera reunión que se celebra en Europa, es en España.

Todo el mundo sabe que en cuestión de Entomología siempre los que han «mandado» (pudiendo decirlo de esta manera un poco fuerte) han sido los de Coleóptera y Lepidóptera, que han tenido grandes plagas. Y nadie se ha acordado nunca de las plagas que causaban los ortópteros. Pero, desgraciadamente o afortunadamente, estaba la langosta. Un problema que nos ha condicionado en nuestro trabajo de dos maneras.

Porque no es sólo lo que se puede hacer en favor de la langosta con estudios básicos de mayor o menor transcendencia. Es que nos encontramos con una nueva visión con la vigilancia de muchas tierras marginales donde el ortóptero, sobre todo endémico, puede ser un buen indicador biológico que bien estudiado y seleccionado dé una guía o una orientación a la Administración para las medidas que ha de tomar *a posteriori.*

Este planteamiento para nuestra investigación puede constituir un pilar para el futuro y son líneas de trabajo que no conviene olvidar.

Además, en esta reunión se estudiarán otros temas de tipo genético, sistemático o filogenético que son los que clásicamente se han abordado.

Yo tengo muy poco más que decir y le ruego a nuestro Director General de ICONA, cuya comprensión por estos problemas ha permitido disponer de todas estas facilidades, que nos dirija dos palabras que nos lleven a la apertura de esta Reunión. Muchas gracias.»

SANTIAGO MARRACO SOLANA

Director, ICONA

«Sr. Presidente y Sr. Secretario de la Orthopterists' Society, querido amigo y compañero Morales, señoras y señores:

Quiero darles a todos ustedes la bienvenida en nombre de D. Carlos Romero (Ministro de Agricultura Pesca y Alimentacion) y en nombre, también, de ICONA a estas instalaciones de Valsaín donde a lo largo de estos días van a celebrar su Quinta Reunión Internacional. Esperamos que éste sea un ambiente propicio para la exposición y dicusión de sus trabajos.

Cuanto afecta a la Zoología y a la Entomología tiene un enorme interés para el Ministerio de Agricultura y, sobre todo, para ICONA. En este caso, los ortópteros, tal como acaba de comentar Eugenio Morales, tienen un doble interés: por una parte, como grupo zoológico y, por otra, por su incidencia económica. Si bien ha sido esta incidencia económica la que, históricamente, le ha dado mayor relevancia al grupo; desde ser un plaga bíblica, e incluso una de las interpretaciones de lo que pudo ser el maná, hasta su incidencia dañina como plaga en el rendimiento económico de diversas regiones.

Esta es, sin duda, una de sus características más singulares y la que, en gran medida, ha propiciado que se haya profundizado más en el estudio de estos insectos. En este sentido, me van a permitir que haga un par de reseñas de trabajos científicos, ya históricos. En tiempos de nuestro rey Felipe III, Juan de Quiñones, alcalde de El Escorial, publicó su célebre *Tratado de las langostas, muy útil y necesario* (Madrid, 1620) donde, entre otras cosas, aparece por primera vez un minucioso grabado que representa a una langosta depositando correctamente su puesta, canuto u ooteca; pormenor biológico que muchos años más tarde se daría como nuevo, cuando ya había sido descrito en estas fechas del inicio del siglo XVII.

Más tarde, un paisano mío, el aragonés Ignacio de Asso publica en Amsterdam (1785) un *Discurso sobre la langosta* que, junto con las páginas y dibujos que a ellas dedica en su *Introductio in Oryctgraphiam et Zoologiam Aragoniae,* aporta datos muy valiosos, sistemáticos y biológicos, sobre las langostas que viven en las tierras del viejo Reino de Aragón. Y a finales de la ilustración, Guilermo Bowles, en su *Introducción a la Historia Natural y a la Geografía Física de España* (Madrid, 1782), dedica un largo capítulo a los daños de la langosta de 1754 a 1757 que asoló diversas provincias españolas.

Este interés histórico que tienen los ortópteros, se une, en este momento, a otros referidos a las especies que pueden considerarse indicadores biológicos y a las que están en peligro de extinción. Por ello la clásica división de los seres vivos, desde un punto de vista antropocéntrico, en útiles y perjudiciales ya no tiene valor. Ahora somos conscientes de que esta simplificación carece de sentido y la totalidad de los seres vivos tienen un enorme valor como compañeros del hombre, también especie biológica, en el espacio que todos compartimos: la biosfera. Por ello, estamos obligados a mantener el equilibrio ecológico lo que exige asegurar también la diversidad biológica.

ICONA, que tiene entre sus obligaciones la conservación de la fauna, publicó en su momento *El libro rojo de los ortópteros ibéricos,* una monografía cuya finalidad era llamar la atención sobre estas especies que en este momento están en peligro de extinción.

Esperamos de sus conclusiones todo aquéllo que pueda sernos útil como elementos para entender mejor el equilibrio biológico y saber defender especies que deben tener su sitio en la biosfera y cuya desaparición sería una nueva señal de alarma de que algo no está funcionando bien en el conjunto.

Agradezco, por tanto, su presencia y, en nombre del Ministro de Agricultura, abro esta Quinta Reunión Internacional de la Sociedad Ortopterológica y cedo la palabra al Dr. Vickery, Presidente de la Orthopterists' Society. Muchas gracias.»

V. R. VICKERY

President, Orthopterists' Society

"Sres. Marraco, and Morales, distinguished members and guests of the Orthopterists' Society, ladies and gentlemen, is for me a great pleasure to welcome all of you to this fine institution on this occasion. We hope that all that we do here will have a significant impact on the world in general, that is, to assist the world in lessening starvation, which is our Society's general aim. Each of you here who is presenting a paper or simply attending the meeting will no doubt agree.

"I do not intend to say very much this morning. My comments will be made later at the Conference Dinner at Torrecaballeros. I just want to welcome you here and point out that our hosts are in large measure responsible for this meeting, and without them it could not have been done.

"Now I would like to introduce our Keynote Speaker, Dr. Nick Jago, a man who is truly a world traveler. He tells me that he is no more African than English, but he spends most of his time in Africa. I have no doubt that what he is going to say will bear on his work in Africa at the same time as it addresses 'The future of Orthopterology.'

"I think that, with a man as well known as Nick Jago is, I should not need to say anything else before giving the microphone to him. Thank you."

S. K. GANGWERE

Executive Secretary and Meeting Organizer, Orthopterists' Society

"President Vickery, Sres. Marraco, and Morales, distinguished members and guests of the Orthopterists' Society, ladies and gentlemen, I take immense pleasure in addressing you on this auspicious occasion, the opening of the 5th International Meeting of the Orthopterists' Society. Longer ago than I care to admit, I first came to Spain to work in the orthopterological laboratories of Eugenio Morales Agacino, the same scientist who today is our host. Ricardo Ronderos, Carlos Carbonell, Alejo Mesa, and other orthopterists who visited Eugenio's laboratory at the same time and still others whom I met in my travels provided a series of relationships that proved to be the genesis of the Pan American Acridological Society, the precursor organization of the Orthopterists' Society. PAAS ostensibly started in San Martín de los Andes, Argentina, in 1976 when a small group of orthopterists met and planned the organization that took its formal inception in 1978 upon adoption of a Constitution and By-Laws. However, we must look to earlier times in Madrid for PAAS' real origin.

"However modest my personal research contributions may be, I like to think that perhaps some day my colleagues (some of whom I see in the audience today) and I who participated in creation of the Society will be remembered for our foresight. How our organization has burgeoned in numbers and stature! How bright and limitless is its future! I think it especially appropriate, therefore, that this, the first meeting of our new global organization, the Orthopterists' Society, convenes in Spain.

"I thank our hosts of the Spanish Government for excellent facilities provided. I thank

Sres. Jaime Gosálvez and Carlos García de la Vega and Sra. Carmen López Fernández, and so many others of the Organizing Committee for their hard work on our behalf, work that comes into fruition over the next few days. Above all, I thank my friend of so many years and our host, Eugenio Morales.

"I wish us a successful meeting such as will strengthen relationships among us and further our discipline."

Bol. San. Veg. Plagas (Fuera de serie) 20, 1990

Reunión del Consejo de Dirección / *Minutes of the Board Meeting*

Presiding Officer: V. R. VICKERY
Recording Secretary: S. K. GANGWERE
Present: T. J. COHN, S. K. GANGWERE, N. D. JAGO, W. P. KEMP (for J. E. HENRY), D. A. NICKLE, and V. R. VICKERY
Absent with Notice: R. G. BLAND and D. OTTE
Absent: N. E. SÁNCHEZ

The meeting was called to order by President V. R. Vickery at 9:10 am (July 17). He welcomed the officers with a few well-chosen remarks following which there was a motion from the floor that business be handled informally, i.e., without formal recorded motions, seconds, and votes, with only the result of the deliberations (approval/denial/tabling) recorded. The following minutes are prepared accordingly.

Editor's Report and Editorial Matters

Editor D. A. Nickle noted that Metaleptea Vol. XI, No. 2 is in press, having been completed but not run off in time for distribution to the Valsain participants. He mentioned the delays experienced in printing and mailing the newsletter and discussed reasons for these delays. He asked for the Board's suggestions toward elimination of these problems. Following extended discussion, it was decided that all Society notices, ballots, and billings should be mailed separately from the newsletter mailings, making the Secretariat and the Editorial Office responsible each for its own mailings.

Editor Nickle's report was accepted as read. Because of schedule conflicts, D. Otte was unable to attend the meeting, but his motion was brought to the Board's attention by S. K. Gangwere. Otte recommends that the Board replace the infrequently issued Occasional Papers Series with a Bulletin Series to be issued regularly and that a Bulletin Editor and several Regional Editors be named to prepare this projected high quality refereed publication. There followed extended discussion of the motion, but action on it was tabled. It was decided that an *ad hoc* committee be constituted to investigate the matter further with particular reference to whether the new journal is needed. This committee, consisting of N. D. Jago, D. A. Nickle, and D. Otte, was directed to report back to the Board at its early convenience.

Secretary's Report and Recommendations

Secretary S. K. Gangwere discussed the current financial state of the society. He described it as generally satisfactory owing to the recently implemented dues increase to $15 (US currency) per year for Active Members and $7 for Student Members. However, he caution-ed that this favorable status could change overnight if the society were to embark on any overly ambitious programs involving accelerated expenditures. Questioned about the society's main areas of expense, he indicated they include mailing, publications, and meeting costs and that the society's main sources of revenue stem from dues, publications receipts, and donations. For details, he referred the Board to the formal Financial Report issued each year in Metaleptea.

The next item discussed was membership. Gangwere indicated that his staff updates the membership rolls upon each mailing. The current, 40th List includes a total of 247 persons from 36 countries, with the USA, Spain, Canada, and England, followed by the Federal Republic of Germany, Australia, and Italy, represented most fully. He reminded the Board of the Society's goal to represent orthopterists and orthopterological interests throughout the world. If this objective, embodied in Article II of the Constitution, is to be met, new membership initiatives seem indicated. The last formal membership drive took place about four years ago. Since then, the society has routinely enclosed membership applications with each mailing in hopes that members will bring the organization to the attention of colleagues, students, and others who, by virtue of their orthopterological interests, should be encouraged to join. This word-of-mouth approach is insufficient. There is need for a formal membership drive.

In response, the Board requested that strategically placed members from various regions of the world be named to a Membership Committee to help with membership solicitation. The identity of this committee is left to the President's discretion though the names of N. D. Jago (for Africa), S. Sakai (for Japan), R. A. Farrow and D. C. Rentz (for Australia and southeast Asia), B. Baccetti (for Italy and western Europe) were suggested for the President's consideration.

Gangwere discussed the Society's two-part Training Program being readied for submission to FAO (United Nations) for possible support. The first part of the project involves preparation of a field-guide to the locusts and grasshoppers of the world. This guide, under the editorship of V. R. Vickery and for which Vickery has already received a grant of $45,000 (Canadian currency), is well underway. The second part, under Gangwere's coordination, consists of a course of field studies for would-be locust and grasshopper control officers. The course is already in late stages of preparation by W. P. Kemp, of Bozeman, Montana, USA, and A. B. Ewen, of Saskatoon, Saskatchewan, Canada. When questioned about the program, Gangwere indicated that it had received Board approval and had been announced to the membership in Metaleptea on at least two occasions and was going forward as an initiative of the Vickery administration. However, the Otte administration is obliged to make its own decision as to whether it should be continued in future years. A committee consisting of A. B. Ewen, S. K. Gangwere, N. D. Jago, W. P. Kemp, J. Mark Ritchie, R. Skaf, and V. R. Vickery was constituted to oversee the project and advise the President on matters relative to it.

Gangwere announced the results of the Feb. 1, 1989, election as follows: proposed revisions of the Constitution and By-Laws accepted; dues increase for Active and Student Members approved; Reginald F. Chapman elected President-Elect for the 1989-1992 term; Baccio Baccetti, Aola M. Richards, and A. B. Ewen elected Board Regional Representatives for 1989-1992; and Drs. Baccio Baccetti, Felice Capra, Kurt Harz, and Eugenio Morales Agacino approved for Honorary Membership. The Board certified these results.

Finally, Gangwere discussed the need for a thorough reevaluation of the Constitution and By-Laws in light of the way in which they have served the Society since the last (1986) revision when the Orthopterists' Society was created. He mentioned the desirability of naming an Executive Director in place of the Executive Secretary. This projected change of title reflects the reality of the Secretariat's operation and, if approved, promises to streamline the organization enabling the officer in question to handle his/her responsibilities more efficiently. He also asked for needed revisions in the nominating mechanisms for President-Elect and Regional Representatives and suggested the need for reexamination of the current standing committees.

Executive Secretary Gangwere's report was accepted as read.

Amendments and Resolutions Committee

It was determined that the Society's amendments and resolutions functions should be handled by a single committee rather than by separate committees as has been the past practice. President Vickery nominated the following individuals to serve on this dual committee: S. K. Gangwere, Vicenta Llorente, J. Mark Ritchie, and D. R. Ragge (Chairperson). The Board approved the nominations and asked the committee to begin its deliberations immediately. Without discussion, the Board remanded to the committee's attention a motion by D. C. Rentz.

Other Business

There being no other business brought forward, the meeting adjourned at 9:45 am.

Reunión de la Sociedad de Ortopterólogos / *Minutes of the Business Meeting*

The Orthopterists' Society

Presiding: V. R. Vickery
Recording Secretary: S. K. Gangwere
Present: L. L. Barrientos, C. Bonet Betoret, T. J. Cohn, S. B. Gaines,
S. K. Gangwere, M. J. González, J. Gosálvez, J. C. Hartley,
R. D. Hawkins, T. L. Hopkins, S. Ingrisch, N. D. Jago,
D. K. K evan, V. Llorente, C. López Fernández, D. Otte,
B. Nagy, D. A. Nickle, S. Y. Paranjape, F. Pascual, J. J. Presa,
D. R. Ragge, D. C. Rentz, J. M. Ritchie, R. Skaf, V. R. Vickery, F. Willemse
Guest: J. Cohn

The meeting was called to order by President-Elect Otte (acting temporarily on behalf of President Vickery) at 17:30 (July, 19). The agenda was as follows.

Editor's Report and Editorial Matters

Editor D. A. Nickle noted that Vol. XI, No. 2, of Metaleptea will be mailed in August. It will be the final issue in the old format. He discussed the new format to which incoming President Otte and he have agreed. It will be such that it can be mailed lst class rather than 3rd class, greatly accelerating receipt by the membership. The 5th Proceedings are under a strict publication deadline of September 1989. They have to be edited and submitted almost immediately, which will be done with the help of Secretary Gangwere. Nickle finished his report with mention of the possibility of a peer reviewed Bulletin to be issued on a regular basis. This journal remains under committee (N. D. Jago, D. A. Nickle, and D. Otte) consideration, with a report to be issued to the Board in the near future.

Acceptance of Editor Nickle's report was moved (T. J. Cohn), seconded (N. D. Jago), and approved unanimously.

Secretary's Report and Secretarial Matters

Secretary S. K. Gangwere read the report that he submitted earlier at the Board Meeting (see Minutes of Board Meeting). Acceptance of his report was moved (N. D. Jago), seconded (T. J. Cohn), and approved unanimously.

Host's Report

Host E. Morales Agacino was unavailable for the meeting. He asked S. K. Gangwere to offer brief comments on his behalf. Morales' main concern is length of meeting. Perhaps the

Society should consider making the next meeting a five-day affair rather than the four-day gathering that has been past practice. There was discussion as to whether this recommendation is sound or whether it might be best to schedule concurrent sessions and more poster and in-title presentations such as might enable more effective use of the shorter (four-day) time. The desirability of a questionnaire to participants was explored but then tabled without recommendation. Inasmuch as no formal host report was submitted by Morales, formal acceptance was ruled unnecessary.

Amendments and Resolutions Committee Report

D. R. Ragge read the report of the Amendments and Resolutions Committee consisting of S. K. Gangwere, Vicenta Llorente, J. Mark Ritchie, and himself as Chairperson. He noted that the "A & R Committee was asked to reexamine the Society's Constitution and By-Laws and did so at several sessions. The Committee felt, however, that in the time allowed by its members' commitments to conference activities, it was not possible to prepare definitive recommendations to this meeting. The Committee asks, therefore, for approval to continue its reexamination of the Constitution and By-Laws after the conference and to submit its recommendations to the Executive Secretary as soon as is reasonably possible." Acceptance of this recommendation was moved (T. J. Cohn), seconded (N. D. Jago), and approved unanimously.

Chairperson Ragge then read the following resolutions:

Resolution I. "The Meeting affirms the importance of Orthoptera in ecological, behavioral, cytological, anatomical, and physiological research, and their increasing importance in biodiversity studies, especially in the diminishing tropical forest ecosystems, and requests the Governing Board to arrange for brief accounts of the significance of Orthoptera, suitable for scientific and non-scientific audiences, to be sent to selected national and international sponsoring agencies concerned with the biological sciences."

T. J. Cohn questioned the agencies, institutions, and other groups to which Resolution I might be directed, and Ragge indicated that, among others, IUBS, EEC, *etc.*, are likely recipients. D. Otte suggested the need that any resolution sent be accompanied by a strong set of arguments presented in essay form by various specialists who know whereof they speak. Only in this way, he argued, will it be possible to convince agencies, who usually regard such proposals, with suspicion to change their practices. After additional discussion, acceptance of Resolution I was moved (D. C. Rentz), seconded (D. A. Nickle), and approved unanimously.

Ragge then read Resolution II:

"The Amendments and Resolutions Committee proposes a vote of thanks to the following institutions and individuals:

1. To our hosts and sponsors, the Universidad Autónoma de Madrid, ICONA, and especially CENEAN, for the provision of excellent facilities at Valsain;
2. To Dr. E. Morales Agacino, Chairman of the Local Committee, for the leading part he played in making the local arrangements;
3. To the other members of the Organizing Committee: Dr. D. Cadahía (Editor of the Boletín de Sanidad Vegetal, in which the 5th Proceedings will be published); Dr. J. M. Ruiz Dana (Director of CENEAN at Valsain), Sr. J. Velasco Cabas, also of CENEAN Valsain, Drs. C. García de la Vega, J. Gosálvez, and C. López Fernández, of the Universidad Autónoma de Madrid, and their excellent staff (Luis Cintas, Sofía Moro, Alicia Rodríguez, Elena Rodríguez, Lourdes Serrano, and Patricia Vázquez) for the prominent part they played in the arrangements;
4. Drs. F. Pascual and J. J. Presa for arranging the post conference field excursion;
5. To the moderators of sessions (T. J. Cohn, S. K. Gangwere, J. Gosálvez, G. M.

Hewitt, W. P. Kemp, E. Morales Agacino, B. Nagy, D. Otte, F. Pascual, M. P. Pener, D. R. Ragge, R. Skaf);

6. To the city authorities of Segovia and La Granja and to all the staff concerned with transport and the clerical, catering, and audiovisual facilities;

7. To Mrs. Muriel Vickery, who personally designed and embroidered the book marks distributed to all participants; and finally

8. To our retiring President, Dr. V. R. Vickery, and to our hard-working Executive Secretary, Dr. S. K. Gangwere, for their contributions to the meeting."

Vicenta Llorente then read the Spanish-language version of Resolution II.

Acceptance of Resolution II, the Resolution of Thanks, was moved (T. J. Cohn), seconded (D. A. Nickle), and approved unanimously.

Other Business

There being no other business brought to the floor, it was moved (N. D. Jago), seconded (T. J. Cohn), and approved unanimously that the meeting be adjourned. Adjournment was at 19:30 pm.

Bol. San. Veg. Plagas (Fuera de serie) 20, 1990

Alocuciones de clausura / *Presidential address*

VERNON R. VICKERY

President, Orthopterists' Society
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Since the organization of this Society, each meeting has been held in a different country. This meeting, our 5th, is in the 5th country and is the first meeting held outside the Americas. This is indicative of our expanded role, and the setting in Spain is significant as it represents a bridge between the Americas and Europe and also between Europe and Africa. The original intention was to have triennial meetings but this has not been found to be practical. None of the meetings have been held three years after the preceding one. In fact, all but one meeting has been held 4 years after the preceding one. This was because we did not want to compete with an International Congress of Entomology, that could siphon off potential delegates to our meeting. Few of us have sufficient funds to attend more than one major meeting in a given year.

I wish to extend my thanks, personally and for all of you, to Eugenio Morales Agacino and to his lovely wife for all they have done to make this meeting a success. I wish also to thank the officials of the Spanish government for their interest, their active and financial support, and allowing us the use of the excellent facility in Valsain. Their efforts have resulted in this most informative and highly enjoyable meeting.

Thanks are due to the people on the Local Arrangements Committee, chaired by Sr. Morales: Drs. C. García de la Vega, J. Gosálvez, C. López Fernández, V. Llorente, F. Pascual and J.J. Presa. There are others too that have served us well, though their names do not appear on the program. They are: Patricia Vázquez, Lourdes Serrano, Luis Cintas, Sofía Moro, Alicia Rodríguez and Elena Rodríguez. If there are others whose names I do not have, I thank them too.

Our sincere thanks are due to Dr. N.D. Jago, our keynote speaker, whose talk set the stage for our deliberations. Drs. David Ragge and Mark Ritchie are doing a masterful job of amending our constitution to suit our greater role. My thanks too to Dr. Rafik Skaf, consultant with FAO, Rome, for his participation in the planning session on training programs. I wish to thank all those who acted as moderators at the scientific sessions. Their efforts added much to the proceedings. Also, I want to offer my congratulations to the speakers for the excellence of their presentations. Finally, I want to thank especially our untiring (but tired) Executive Director, Dr. Stan Gangwere. Only those people who have worked closely with him realize how much the Society owes him.

Many of you are attending our meeting for the first time, so for your information I will outline briefly the purposes for which the Society was founded and the history of its progress.

In the beginning the Society was limited to the Americas. In December, 1976, a group of about 50 dedicated orthopterists were invited to a meeting in San Martín de Los Andes, Argentina. The founders were Dr. Stanley K. Gangwere, of the United States and Dr. Ricardo Ronderos of Argentina. The result of that very interesting meeting was the formation of the Pan American Acridological Society (PAAS). The Constitution and By-Laws were adopted in 1978. The Society was granted tax-exempt status as a non-profit organization in the United States.

The stated purposes were, and still are, to facilitate communication between workers; to encourage research, first in Acridoidea but now in all Orthopteroidea; and to disseminate information in order to promote research and related activities. Training programs for worthy candidates were organized, subsidized by a philanthropic organization, that enabled 17 individuals from South American countries to study at various research centres, including museums, in North America.

The second meeting of the PAAS was held in Bozeman, Montana, U.S.A. in 1979; the third in Maracay, Venezuela in 1981; and the fourth in Saskatoon, Saskatchewan, Canada in 1985. The proceedings of each of these meetings were published.

Dr. John Henry, my predecessor as President, suggested and laid the groundwork for expanding the Society, as many orthopterists of note from other parts of the world were outside our sphere (as well as our hemisphere). It was agreed that global status, both geographic and systematic, was desirable and probably essential for the growth and usefulness of the Society. The meeting in 1985 approved the necessary changes so that the Society is now open to orthopterists of all countries working on any orthopteroid group. The name chosen for the expanded Society is Orthopterists' Society. As the reorganization progressed it turned out that I was not only the last President of the Pan American Acridological Society but also the first President of the Orthopterists' Society.

We live in a period of time in which the mission of orthopterological research has become not only important but urgent. The news media world-wide has reported on the dire effects of the locust hordes in Africa. It would appear, however, at this time, when additional research is essential, that actual research is declining, at least in some areas.

During the past decade, a number of prominent orthopterists have died and others have retired. Retirement has not always meant cessation of activity but inevitably a decrease of activity occurs as the years go by. Some of the workers on Orthoptera and related Orders were not replaced upon retirement or were replaced by persons whose orientation was not on these insect orders. As a case in point, when Dr. Kevan and I retired in 1986, we were replaced by a biotechnologist and one taxonomist, who specialized in Hymenoptera.

The research on Orthoptera by some organizations has declined. The former Anti-Locust Research Centre (ALRC), in London, England, became the Centre for Overseas Pest Research (COPR), with a declining emphasis on orthopteroid insects as other pests came to the fore. The name changed again to Tropical Development and Research Institute (TDRI), with further erosion of activity on orthopteroids. Now it is Overseas Development Natural Resources Institute (ODNRI), and has moved to Chatham, Kent. The work on orthopteroids has not come to a halt, as Dr. Jago is still working very intensively in Africa, but is much less than when ALRC was active.

These facts indicate a decline in the active research on orthopteroids but the outlook is not as bleak as it might appear to be. The CIRAD/GERDAT organization in Montpellier, France, is very active and is doing excellent work in the fight against locust and grasshopper problems in the Sahel region of Africa.

The very successful symposium organized by Professor Baccetti in Siena, Italy in 1986, brought together orthopterists from all over the world. In addition to the programmed papers, I was able to chair a half-day session devoted to the Orthopterists' Society. A suggestion was made that the Society should undertake a project. I will have more to say on that later.

There is another item that makes the situation appear brighter. At each of the last two annual meetings of the Entomological Society of America, a full day session, organized by some of our younger members, was devoted to orthopteroid insects. I managed to attend both of these "workshop" sessions, in Boston, Massachusetts in 1987, and in Louisville, Kentucky, in 1988. The plans for a similar session at the ESA meeting in San Antonio, Texas, are well underway. I am pleased to take this opportunity to congratulate Drs. Lockwood, Kemp, and Bellinger, and others that assisted them, for their enthusiasm and excellence. The younger scientists, with their ability and willingness to carry the load ensure a bright future.

Now I want to turn to the role of our Society, what we have done, what we are doing and what we hope to do.

First, we wanted to reinstate a training program. Funds from the Tucker Foundation, the organization that had underwritten the PAAS training programs, were no longer available to us. Dr. Gangwere and I came to a decision to discuss the problem with the locust control people of the Food and Agriculture Organization (FAO) of the United Nations in Rome. We travelled to Rome and met with Drs. Skaf, Roffey and Brader. We received much encouragement and advice from them as well as their tacit agreement to select and cover expenses of prospective candidates to travel to North America for training. The training courses were to take place at research centres, specifically at government research centres at Bozeman, Montana, U.S.A., and Saskatoon, Saskatchewan, Canada. Specialists at these centres have experience gained on several continents. Since that time we have taken steps to organize the training programs in minute detail and hope and expect that this will be finalized very soon.

Early in our planning we visualized the need for training literature. The original intention was to prepare something quickly to be used in conjunction with the training sessions. It soon became apparent that preparation of a "Field Guide" would of necessity be more comprehensive than a bulletin or pamphlet dealing with the problems of a particular region. This, however, is precisely what is needed, not only for one region or continent but a series to cover the entire globe. This has resulted in considerable expansion of the "Field Guide" to the extent that publication of a single volume would be well beyond the concept of such a guide. At present, we have outlined a series of papers: general topics; papers on specific locust and grasshopper pests; and papers on the most serious pests of each region. I expect a total of 32 to 36 papers. An outline of the series appeared in a recent issue of Metaleptea (Volume 10, No. 1) but is now out of date.

As the size of the prospective completed work increased, it was decided to publish each paper separately in a numbered series, each to be punched with three holes to fit in one (or more) loose-leaf binders. This lessens the editorial chore by spreading the load over time; publication can proceed without waiting for the last paper in the series; and there is an economic advantage in that complete sets of papers will not be necessary for most people.

I have many of the papers on hand and I expect others very soon. The group in Montpellier, France, have been very cooperative and several of the papers on hand have been written by the workers at that institution. My thanks as well to all of the others who have written or are writing papers for the series.

Those of you who attended the Orthopterists' Workshop session in Louisville, Kentucky, last December, will remember that I reported that I had obtained funds for publication. I had hoped to show this gathering some of the published papers. Unfortunately, bureaucratic bungling delayed receipt of the funds but I can now report that funds from the Canadian International Development Agency are in an account for use by this project and publication will begin soon. I have agreed to continue as coordinator of this project until it is completed.

I will conclude with a few remarks regarding some changes within the Society. The position of Secretary-Treasurer has been split. Dr. Roger Bland, Central Michigan University, Mount Pleasant, Michigan, is now Treasurer. This was done to lessen the work load on Dr. Gangwere. Dr. Gangwere has contributed more time and effort to this organization than anyone else, much more than most of you realize. His title is now Executive Director, as this is, in fact, the capacity in which he serves. I extend my sincere thanks to him. He has carried the load for me and for all of us.

I extend my thanks for the support of the governing board and committee members, particularly to Dr. David Nickle, our editor, who, with his committee, produced the Proceedings of the Saskatoon meeting, and has prepared the issues of Metaleptea for the past few years.

During my term of office, we found it necessary to increase membership dues. Much as we disliked doing this, it was necessary to increase the annual dues of active members to $15.00 and of student members to $7.50, U.S. funds. Because of the difficulty that prospective members in some countries have in paying this amount or of sending funds out of their countries, a new class of membership was instituted, that of Sponsored Members. This has been well accepted by the membership.

We have with us tonight only one Past-President, Dr. S. K. Gangwere, though that number will be increased to two very shortly.

There has been a change in selection of Honourary Members so that two eminent people can be chosen every two years instead of in the former four year interval. We have with us tonight only one of our Honourary Members, Dr. D. Keith McE. Kevan, and I ask that he stand and be recognized.

The four individuals that we honour at this time were listed in a late issue of Metaleptea (Volume 10, No. 2). They are Baccio Baccetti of Siena, Italy and Felice Capra of Genoa, Italy, neither of whom is with us tonight. Their certificates will be forwarded to them. Kurt Harz of Steinsfeld, West Germany, unfortunately was injured upon arrival in Spain and has been unable to attend the meeting. Dr. Gangwere and I presented him with his certificate in his hotel room this afternoon. The fourth recipient is our friend and benefactor, Sr. Don Eugenio Morales Agacino, of Madrid, and I take pleasure in presenting his certificate.

Our new President, Dr. Otte, will be assisted by the newly elected President-Elect, Dr. R.F. Chapman, and Regional Representatives Dr. B. Baccetti (Italy), Dr. A.M. Richards (Australia) and Dr. A.B. Ewen (Canada). He will appoint other officers and committees as he wishes.

Finally, I wish to thank the members of the Society for electing me to the office of President. It has been an honour to serve you.

Now it is my great pleasure to introduce to you a man who needs no introduction, our new President, Dr. Daniel Otte. I have every confidence in the future of the Society under his capable direction. I have no gavel to turn over to him but greet him with a handshake and my word to support him in any way I can.

JULIO BLANCO

Director General de la Producción Agraria, Ministerio de Agricultura, Pesca y Alimentación.

«Distinguidos señores:

Es para mí un honor, pero sobre todo un gran placer, el clausurar esta Quinta Reunión Internacional de la Sociedad Ortopterológica que tan fecundos resultados ha tenido, como en realidad era de esperar, dada la alta categoría científica y técnica de los ponentes y conferenciantes.

No voy a caer en la tentación de intentar sintetizar todo lo discutido estos días, porque es labor, por cierto ardua y difícil, del Presidente de la Sociedad, pero no quiero dejar pasar esta ocasión sin felicitarles por el alto nivel con el que se ha desarrollado toda la Reunion.

Todos los temas tratados: ecología, evolución, sistemática, fisiología, genética, etc., han sido muy útiles, pero hay uno, la langosta, que tanto por el cargo que ocupo, como por mis aficiones personales me ha interesado más que los demás.

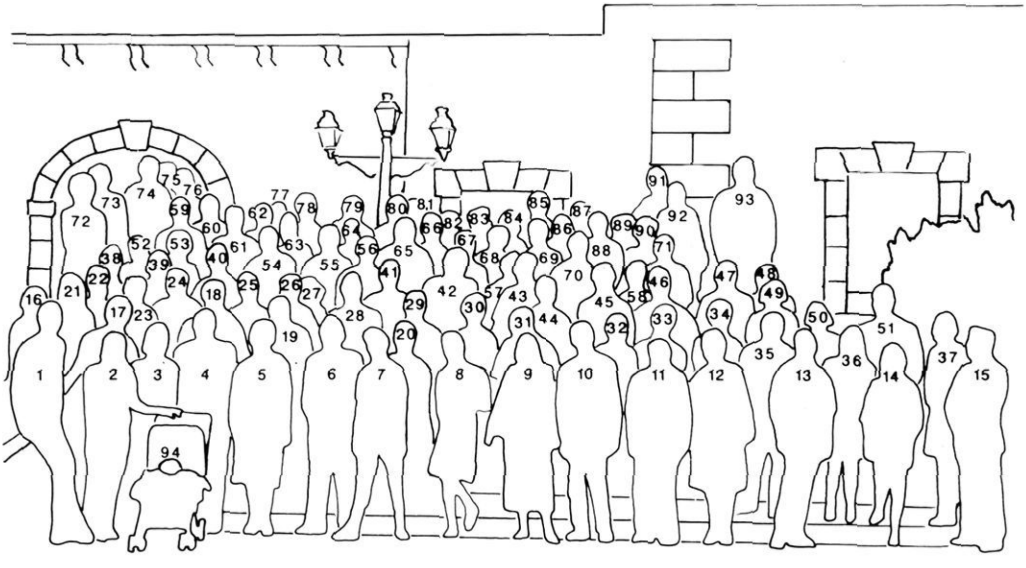
No podemos olvidar que España es país que, desde siempre, sufre plagas de langosta (*Dociostaurus maroccanus*), como ya recordó en la inauguración el director de ICONA, con tres zonas endémicas en el Valle de la Serena (Extremadura), Valle de Alcudia (Ciudad Real) y los Monegros (Aragón), que nos obligan a realizar tratamientos anuales de unas 85.000 hectáreas, con una inversión, también anual, de 150 millones de pesetas (más de un millón de dólares).

Por otra parte, España sigue muy de cerca la situación de nuestra vecina Africa, con intercambio constante de informacion tanto bilateral con los países afectados, como a nivel supranacional a través de FAO y otras instancias internacionales; también la CEE, a la cual pertenecemos, ha colaborado en el combate de la explosión actual de langosta de modo que, por medio de ella, y, sólo por parte española, se han enviado 300 millones de pesetas (cerca de dos millones y medio de dólares) en ayuda para aviación y, 120 millones de pesetas (aproximadamente un millón de dólares) en productos fitosanitarios tanto en la zona del Magreb, como al Sahel. Estas cifras nos dan un índice claro de la gran importancia económica que este grupo de insectos presenta en las economías agrarias de muchos países del mundo.

No me queda nada mas que felicitar a todos los participantes y, en especial, al comité organizador; esperar que su estancia en España haya sido tan agradable como fructífera, desear que nos volvamos a encontrar en situaciones tan agradables como la presente, y darles la más cordial despedida en mi nombre, en el de la administración y, en definitiva, en el de España, rogándoles sigan haciendo crecer la ciencia, como aquí, para bien de toda la humanidad.»

Participantes

Conference Members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1. J. A. Lockwood (USA), **2.** Nancy Lockwood (USA), **3.** P. A. Fard (Irán), **4.** V. R. Vickery (Canadá), **5.** Muriel Vickery (Canadá), **6.** L. Herrera Mesa (Spain), **7.** A. Herrera (Spain), **8.** Dolores García García (Spain), **9.** Eulalia Clemente (Spain), **10.** U. Carlberg (Sweden), **11.** S. Sakai (Japan), **12.** Vicenta Llorente (Spain), **13.** J. Velasco (Spain), **14.** Patricia Vázquez (Spain), **15.** S. K. Gangwere (USA), **16.** Lisa Vawter (USA), **17.** E. Morteza (Iran), **18.** D. C. Rentz (Australia), **19.** A. Mesa (Brasil), **20.** Christine Amegdenato (France), **21.** Sonia Virdee (United Kingdom), **22.** Magda Charalambous (United Kingdom), **23.** M. Duijm (Netherlands), **24.** S. Ingrisch (Fed. Rep. Germany), **25.** Esther Viseras (Spain), **26.** J. C. Hartley (United Kingdom), **27.** Daphne Hartley (United Kingdom), **28.** L. L. Oudman (Netherlands), **29.** R. Skaf (Italy), **30.** Xin Bau Jin (Peoples' Republic of China), **31.** J. García García (Spain), **32.** Hanna Harz (Fed. Rep. Germany), **33.** Toshiko Sakai (Japan), **34.** M. Victoria Peinado (Spain), **35.** J. Mateos (Spain), **36.** Elena Rodríguez Iñigo (Spain), **37.** Joaquina de la Torre (Spain), **38.** J. Dagley (United Kingdom), **39.** Jean Cohn (USA), **40.** T. J. Cohn (USA), **41.** Arlene Hopkins (United Kingdom), **42.** G. H. Schmidt (Fed. Rep. Germany), **43.** H. J. Ferenz (USA), **44.** S. Masaki (Japan), **45.** B. Nagy (Hungary), **46.** C. C. Hsiung (Canadá), **47.** E. Seno (Japan), **48.** C. Millán (Spain), **49.** Carmen López Fernández (Spain), **50.** Sofía Moro (Spain), **51.** C. García de la Vega (Spain), **52.** R. A. Nichols (United Kingdom), **53.** Binky Ragge (United Kingdom), **54.** K. C. Shaw (USA), **55.** L. E. Pedersen (Denmark), **56.** R. D. Hawkins (USA), **57.** S. Y. Paranjape (India), **58.** J. M. Rubio (Spain), **59.** D. R. Ragge (Spain), **60.** F. Pascual (Spain), **61.** J. Gosálvez (Spain), **62.** H. Tingskov (Denmark), **63.** J. L. Bella (Spain), **64.** Sarah Gaines (USA), **65.** D. D. Yager (USA), **66.** W. P. Kemp (USA), **67.** T. L. Hopkins (United Kingdom), **68.** A. W. Harvey (United Kingdom), **69.** G. M. Hewitt (United Kingdom), **70.** M. D. Greenfield (USA), **71.** E. Morales Agacino (Spain), **72.** S. N. Visscher (USA), **73.** J. Visscher (USA), **74.** M. G. Ritchie (United Kingdom), **75.** D. A. Nickle (USA), **76.** Diane M. Nickle (USA), **77.** M. G. Ritchie (United Kingdom), **78.** P. L. Mason (United Kingdom), **79.** M. P. Pener (Israel), **80.** N. D. Jago (United Kingdom), **81.** J. Rey (Spain), **82.** Consuelo Sanz de Bremond (Spain), **83.** A. Piedrahita (Spain), **84.** J. González (Spain), **85.** J. J. Presa Asenio (Spain), **86.** Alicia Rodríguez (Spain), **87.** L. Cintas (Spain), **88.** W. J. Reynolds (United Kingdom), **89.** Josefina Isern-Vallverdú (Spain), **90.** Amalia Oñate (Spain), **91.** F. Willemse (Netherlands), **92.** M. Lourdes Pulido (Spain), **93.** C. Bonet (Spain), **94.** Erin Lockwood (USA), **95.** Lourdes Serrano (Spain) (Absent).

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The present and future roles of the Orthopterist

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ABSTRACT

The present and future roles of the Orthopterist.

1. The decline in orthopterology is linked to a decline in the credibility of locust and grasshopper control, coupled with its very high cost.

2. The Orthopterists, Society derives strength from our common interest, our educational role and the importance of practical and environmental aspects of the subject. The educational role of the Society is in its infancy, but the Society can do much by encouraging Membership from developing countries. Examples are given of orthopterological research important to environmental and conservation programmes.

3. Examples are given of the cost of recent locust and grasshopper control campaigns. The global expenditure of roughly US $200 million for the years 1986-1988 cannot be justified unless campaigns are proved to be more effective relative to other investments for the same money (three are mentioned).

4. Crop protection and preventive control strategies (PCS) are not mutually exclusive but are compared and contrasted. PCS is in practice rarely achieved for many different reasons and may be applicable, in a species such as Locusta, only in part of the area of distribution. Campaigns should finance parallel socioeconomic studies to evaluate the effectiveness of PCS and crop protection approaches, the equipment used and the reduction in crop loss.

5. A brief review of the family economy of the Sahelian millet farmer shows that he has little to invest in chemical pest control and that grasshoppers and locusts are only one of the insect pests to be considered. The risk factor in Sahelian agriculture makes chemical pest control a high risk investment. Other use of farmer time, or investment in fertiliser or resistant millet varieties are strong contenders for the resources available.

6. Seven main points are outlined, each covering a facet of orthopterology which should be actively promoted by the Society.

Key words: locust, control, strategy, economics.

We are privileged to meet in Segovia, which marks the contact made historically between the great cultures of Christianity and Islam. Mathematicians tell us that Islamic scholars amazed their Christian counterparts with concepts such as "zero". Our Society brings together Orthopterists from all over the World. We too started from "zero" in the beautiful surroundings of Bariloche and since then we have held four Symposia. The paradox is that while the Society has flourished orthopterology has not. Our Society has spread rapidly from a focus on the Americas to one with a global perspective, while the number of active orthoperists has diminished.

The success of orthopterology and particularly acridology in the fifties lay squarely on the concensus that locusts represented an economic problem meriting a large investment in research. Many of us at that time received financial support at home and overseas. Those days are past and it is pertinent to ask why acridology in particular has been losing credibility over the past decade. This decline is reflected in fewer workers entering the field and less support for operational or basic research. If the trend continues there will be an inevitable effect on the Society.

This having been said, among the Founding Fathers of the Society we must thank Dr. Stanley Gangwere for his persistence and vision which inspired the first meeting in Argentina and whose subsequent devotion has been crucial to its success. I am pleased to see that the Society now draws members not only from the museum fraternity but increasingly from the unspeakable ranks of applied acridology — locust and grasshopper control in all its aspects.

It is the balance between theory, basic research and application which I wish to address today. If our Society gets this right it will be the key to its future. At the same time, I would like to address the current credibility of orthopterology.

The Society derives its strength from three influences:

1. a brotherhood in our particular and peculiar specialism.
2. our educational role — our yearning to share our specialist knowledge with peoples world-wide.
3. our practical and, in popular current parlance, our environmental roles — where we use our knowledge in the service of Mankind and the Earth we live on.

These premises do not imply arrogance. At bottom they demonstrate that we love our subject and can see great good arising from the understanding it reveals.

I have just arrived from my current host country Mali in West Africa where we are once again at the onset of another grasshopper campaign season. The confrontation with the locusts and grasshoppers brings us together round the camp fires and to the homes of men and women in a very different society from our own. Through the commonly agreed aim of curbing the numbers of acridids which threaten food production we discover common humanitarian qualities in each other and gain a new respect for the intelligence and tenacity of the people who have worked those hard lands down the millenia. It is this humanitarian spirit which inspires loyalty among us in the Orthopterists'Society.

The educational role of the Society is in its infancy, but is of utmost importance. Western technology owes much to a sense of history and traditions which go back to the sciences and mathematics of the Middle East and Asia which have been passed on to be nurtured by us. Scientific philosophy in the west has been eager to absorb enlightenment from whatever source; its roots do not lie exclusively in western Europe. In turn the success of science has generated the Learned Societies of which our own is but one of the newest. One of their functions is to act as places where dialogue and praise can generate enthusiasm and where new discoveries can be published. It is often forgotten that Western Science is a foreign import into many parts of the developing world and that it impinges on countries which are ready to accept the technology without the innovative thinking that lies behind it. To encourage a more positive creative approach their graduates require their own Learned Societies which can act as a mirror to their discoveries, but these are as yet very rare. Our Orthopterists'Society should consider ways in which it can help initiate such Societies and a good first step would be to encourage more membership among scientists from tropical regions of the World, particularly Africa. With the great renewed interest in locusts generated by the locusts themselves since 1986, this makes the present moment a good time to act.

I have touched upon the usefulness of the Society. This in turn depends on the utility of studying the Orthoptera themselves. I do not for one moment, for example, dismiss the aesthetic importance and the beauty of the arboreal fauna of South America as revealed by members of this very Society. This is a starting point for many of us. There is immense intellectual satisfaction to be derived from understanding such faunal complexity, and its integration with floral elements in space and time (Amedegnato and Descamps, 1980a, b; Rowell, 1985a, b). But add to this the importance of this knowledge in our bid to conserve the World's most complex and threatened land ecosystem, the tropical lowland rainforest, and its importance takes on a new dimension. Such studies should also play an important role in managing tropical grassland ecosystems where we are seeking to maintain maximum floral and faunal diversity. Management of National Game Parks (Harvey & Ritchie, in prep.), studies of the use of pesticides to have minimal environmental impact (Ottesen and Somme, 1987; Mathys and Metzger, 1986) and monitoring of the best use of fire in tropical grassland ecosystems (Gillon, 1978; Le Pelley, 1952), could also use Orthoptera as indicator species. By encouraging our Members to take up consultancies, the Orthopterists'Society can play a part in promoting the importance of Orthoptera in such programmes.

In the current climate of accountability and shortage of financial and other resources it is dismaying, but not surprising, that we are being asked to justify our work in the face of more and more stringent budgets. The high cost of locust and grasshopper control is an immense burden for "front-line" Sahelian states with small GNPs. Mali is typical of the Sahelian states and in 1986 estimated US $150,000 would be needed to scout and treat some 100,000 ha (Request for emergency aid Mali PP service, O.P.S.R. Aug. 1986). The FAO donors meeting (May 7 1986) estimated that the nine Sahelian front-line countries (not including Sudan or Ethiopia) would require US $11,482,000 for the 1986 grasshopper control campaign. The just completed 1988 campaign against *Schistocerca gregaria* (FAO data 10.4.1989) used a total budget of US $21.75 million to cover 19 countries. Just over half this sum is pesticides and the sum excludes capital equipment and depreciation.

Chemical control on this scale can be justified only if it can be demonstrated to be:

1. effective in achieving its avowed aims.
2. can be shown to have a priority over other methods of crop protection and yield improvement.
3. does not have a dangerous impact on the parts of the ecosystem which come under the category of non-target organisms.

Let us examine each of these three points more closely.

EFFECTIVENESS

Effective treatment of locust and grasshopper populations can be achieved in two ways:

1. the control is directed at protecting crops against economically unacceptable damage, or
2. a preventive control strategy (PCS) is directed at globally reducing the population of the pest species thereby preventing major, economically unacceptable, outbreaks.

In practice the first could be achieved without resort to the latter. In fact, due to limited resources, campaigns are usually thought successful if they have achieved the first objective. There has never been a careful analysis of the economic success of a campaign compared with all the different alternative investments which might have achieved similar if not better results.

We need well documented data to replace the often anecdotal estimates of economic loss due to these insects. If this is not done, investment in applied or basic orthopterological research will dwindle because the claims for its utility to Mankind will fall into disrepute. We must remember that the great expansion of our knowledge in orthopterology during the 1940s and 1950s was financed on the back of the generally accepted economic importance of the locusts.

In the case of millet, the money might have been better spent on distributing faster developing varieties whose vulnerable period did not coincide with the periods of major attack by last generation grasshoppers (say *Oedaleus senegalensis*), or building anti-feedent qualities into the millet genome, or in providing road transport to convey marketable grain from areas unaffected by grasshopper attacks to those suffering heavy loss in a given year. Economists would argue that this would also reinforce the local agricultural economy. In most years for example the areas suffering major grasshopper attack are limited and geographically near to areas capable of producing excess grain to needs. This is true of the clay plains areas of Nigeria's Lake Chad basin and the Kayes region of Mali as a potential source of grain for rainfed areas of N.W. Mali. The factors preventing this are the frequent absence of effective roads or commercial vehicles. While in some areas grasshopper initiated crop losses are chronic, in most of the millet growing areas a crop loss of 70% and upwards caused by these insects is experienced only once every 4-5 years. Given minimal attack by other pests this would allow for years of recovery and argue for investment in grain redistribution by commercial means rather than mass spraying campaigns. In areas hit more frequently this tactic would not work and greater emphasis should continue to be placed on grasshopper control.

The second aim is also rarely achieved. Over 25 years of research into the African Migratory locust, culminating in 7 years of the O.I.C.M.A./UNDP research programme in the Middle Niger Delta of Mali, it has been shown that due to the special needs of the insect that 2 of its 5 annual generations are restricted to limited eco-zones in the Delta during the dry season. A light scouting/chemical control system enables these concentrated populations to be reduced at this ecological bottleneck to such a degree that a true "preventive control strategy" (PCS) can be devised. One should note, however, that *Locusta* in the Lake Chad basin offers an entirely different problem. Here PCS is unnecessary because of the nature of the breeding area, which is ecologically (area, latitude, nature of soils and flood draw-down area, etc.) unlikely to become a dangerous "outbreak area" like the much larger Mali Niger floodplain. Overwintering sites are such as to prevent winter generations (Batten, 1974). Batten's hypothesis about failure of winter breeding in the Chad basin in outbreak years was fully confirmed in 1981 when without any effective chemical intervention the populations died out of their own accord at the return of the following spring rains. Here is a case where had there been an all-out control campaign the decline would have been attributed to intervention by man. It is also evident that in the basin *Locusta* should be tackled as a crop protection problem. The Red Locust (*Nomadacris septemfasciata*) is another pest species which can be controlled by a PCS strategy, providing small highly trained ground teams carry out dry season scouting to discover the location of the adults undergoing dry season adult diapause.

On the other hand, there is little evidence that the Desert Locust or the Senegalese Locust (*Oedaleus senegalensis*) can be controlled by a PCS using existing ULV chemical methods once their breeding zones expand and conditions become really favourable (see analysis of effectiveness of control at different stages in the upsurge and decline of the 1967-69 plague by Bennett, 1976). The natural decline of the *Schistocerca gregaria* populations and the effect of natural genetic or parasite pressure is almost always underrated (see Bennett, 1976 p. 542 *et seq.*). A statement to the effect that population expansion in Niger outran all reasonable available aerial control efforts was made recently by Duranton (1987). He said that after October 1987, and in spite of a hitherto effective "PCS" campaign in northern Niger, populations outstripped the resources available and many swarms escaped from northern Niger into Mali, Mauritania and Morocco. Moreover, we can clearly see that once *Schistocerca gregaria* gains the upper hand more than 90% of the infested area consists, as it did in 1988 in Mali, of solitariform insects spread over thousands of square kilometers which do not afford a viable target for chemical spray methods. The failure of chemical PCS in these cases is a strong argument for urging greater long-term investment in non-chemical control methods of all kinds and in more economic and effective crop protection using currently acceptable chemical pesticides. I urge the Orthopterist's Society to champion this aspect of orthopterology. Extended field trials over the next decade will be required to prove and perfect these techniques.

PRIORITY AND ECONOMICS

Finally I will turn to the Environment and the Economics of pesticides. We have already seen that the financial cost is great. With the greater awareness of damage to the environment by pesticide, there is a strong argument for the chemical control to be applied as accurately as possible to the target crop or adjacent infested habitats. At Koussi in Mali in 1987 I have seen considerable mortality to grasshoppers from ULV aerial spraying (Fenitrothion 50), which had been carried out the previous day 10 km west wind of the village. Topical application will be best achieved by putting the front-line effort into the hands of the farmers themselves. The methods should be simple, safe and cheap, so that as far as possible, the farmers or their low-budgetted Plant Protection services, can support the cost of the system themselves. This implies much better study of the economics of the farmer family economies in developing countries and development of suitable equipment. It implies in-depth study of crop losses.

The Scale of Crop Losses and Attacks

The current Mali Millet Pest Control Project operates in about 15,000 km^2 of N. W. Mali, just below the frontier with Mauretania. We are interested in methods of pest control on a range of insects, among which grasshoppers rank as number two. The east-west line of greatest grasshopper infestation changes seasonally and from year to year. As a rough estimate, 10% of villages within the high infestation belt lose between 70%-90% of the millet crop annually. With the shift in the high infestation belt, following the cycles of drought and average to good rainfall, any particular village in the Project area gets high crop loss due to grasshoppers every 5-7 years.

In the west of our study area in 1988, farmers in 10 villages lost millet and sorghum to grasshoppers valued at between £ 300 and £ 400 (US $450-US $600), which is half to two thirds of an average family annual income (Average family income US $900 per annum or per capita US $60). In 1986 the farmers in 350 km^2 of Mourdiah region lost 25% of planting area to early season (July) grasshopper attack by bands of *Oedaleus* at a density of 16/m^2. By August-September (Jago, 1986) an area of 1,450 km^2 between 14°30'N and 15°15'N had been 20% decimated by late hopper instars (50:50 *Kraussaria*/*Oedaleus*) at 10,000-50,000/ha and young adults at 10,000-30,000/ha. North of 15°15'N III-IV hopper instars covering 800 km^2 had not yet entered cultivations but were concentrating along field margins. The limited aerial support which arrived on September 10 concentrated first on these populations. A massive southward movement of young adults took place throughout September down to the level of 13°50'N, leading to crop losses on the ripening grain. This gives you a quick picture of the scale of these massive attacks.

THE CUSTOMER

Locust and grasshopper control in developed countries will continue to be to the advantage of the big grower or government projects where big investment has been made. Thus the value of crops in the Souss valley of Morocco is estimated at US $270 million (Magor, pers. comm.). However, contrary to popular belief the longterm customer in Sahelian Africa is not the big control campaign but the African farmer in one guise or another. Malian farmers are my example in this respect, because we are currently working there on millet crop protection. The problems are, however, typical of the sub-Saharan belt. Methods must take into account the risk factor in semi-arid farming. In 1988, with average to better than average rains, 87% of families in the Mourdiah area produced sufficient for 12 months grain supply. In contrast, in 1987, a poor rains year with an August drought, 65% produced less than 3 months supply (Lock *et al.*, unpublished).

The rainfed area in which we operate in N. W. Mali contains about 151,000 inhabitants (1983 census) in an area of 30,000 km^2 (density 5/km^2). A family in Mali might consist of 15 people, requiring about 2,500 kgs of millet per annum. The farm will be about 5 ha and an average yield in a bad year between 300 and 500 kg/ha, while in a wet year the yield (as in 1988) may be 300-940 kg/ha (average 650 kg/ha.). Large families do better than small ones and in poor rains years produce 3.2-4.4 months of grain supply or nearly twice that of the smaller ones. In good years the small families produce 7.7 months of grain supply, while the large families produce 8.6-11.2 months supply (Lock *et al.*, unpublished). Investment in their fields amounts to about F.CFA500/year/ha, or US $1.5/year/ha. This is, however, an average figure. In 1988 (Lock *et al.*, unpublished) only 20% of the cultivated area in 3 study villages was farmed by families who invested more than F.CFA2500/ha. (US $7.5/ha), and 50% of families invested nothing except to purchase sowing seed. The price of the crop varies from 45F.CFA/kg-145F.CFA/kg during the year, with a mean about 75F.CFA (15p or US $0.23).

The most optimistic view in the drought year of 1986 was that farmers using a ULV treatment mainly against *Heliocheilus albipunctella* (millet head miner moth) won an average improvement of 170 kg/ha with a market value of 12,750F.CFA (£ 24 or US $38). If a stringent 2:1 benefit/cost ratio is applied, the maximum investment would be say US $19 per ha. Note that the farmer might still opt to spend the money on rock phosphate (at a total cost of US $13/ha) or resistant millet varieties (at a total cost of US $3.25/ha) rather than purchase pesticide. Just one treatment with ULV Cypermethrin costs (with labour, etc.) F.CFA5,740/ha. (£ 11.50 or US $17.2). However, when using ULV Cypermethrin against millet head miner in 1988, only 25% of farmers reached or surpassed the 2:1 benefit/cost threshold. This is because in good rains years the improvement in yield due to the treatment fell from 170 kg/ha to only 120 kg/ha, although average yields per non-treated plot rose to about 650 kg/ha.

If pesticides were adopted we can assume that, judging by our trials in 1985, a farmer would be able to apply dust formulations against about 10 ha/day, given that his whole family cooperated. In bad grasshopper years he would have to repeat this several times in July or early August. So even if the dusts were free his valuable time would be used. His choice would be to do this or push on with ploughing and sowing further fields. Later, usually at the end of August and beginning of September (incidentally the time to treat millet head miner also) one ULV machine would treat about 30 ha/day (swath widths 10 meters). His "time window" would be reduced because of rainy periods, unfavourable wind, rest for food, etc. Unfortunately late season treatment probably requires at least 2 applications. This is not economically possible unless a 1:1 benefit/cost ratio is accepted on his investment.

Aerial application of pesticides against millet pests must always be a last resort and in the case of Sahelian Mali is neither economically viable nor proven to be environmentally safe. Aerial spraying of grasshopper millet pests has, heretofore, been funded by outside agencies and realistically will not be guaranteed from year to year. Like other forms of chemical pest control on millet it may still be advocated by Sahelian governments as a means of reducing the drift of rural communities to the towns or for other political reasons relating to the need to demonstrate regional inter-state solidarity. Control of *Schistocerca gregaria* often falls into this category.

CONCLUSIONS

The future customer for grasshopper and locust pest control is not the traditional one of the high budget locust control organisation. A new look needs to be taken at the farmer customer, who has very little to invest in chemical control. Chemical control methods are currently inappropriate much of the time and larger scale use must be accompanied by environmental studies.

There are seven main points I would like to make in summary:

1. Orthopterology will survive in a viable state by virtue of its demonstrable success in applied areas such as pest control.

2. A radical rethink over control strategy is required and claims for success need to be backed by good positive evidence.

3. Better use of pesticides should be promoted so that smaller quantities of active material are directed more effectively onto their target. This implies more farmer participation in control and a choice between fixed wing aircraft or helicopters to ensure environmental safety when aerial application becomes essential.

4. The farmer customers should be offered carefully researched techniques, which are realistically sustainable within the budgets of the family or groups of families by accurate targetting.

5. Long term efforts should be supported with great vigour to find alternative methods to current chemical control.

6. Orthopterological research should be a basic part of conservation and faunistic studies, and should be properly budgetted for. Terrestrial ecology in the tropics should include support for orthopteran taxonomy. This is particularly true of Tropical Central and South America where so few groups have had recent taxonomic treatment.

7. More long term environmental studies are required to study the effect of chemical and other control methods against Orthoptera. This implies longer periods of study of the untreated populations so that we understand the cycles of "natural" population fluctuation.

I respectfully request that our Society takes a leading role in restoring the reputation of orthopterology by enlarging Society Membership and strengthening the lines of communication between scientists and technicians involved with the Orthoptera throughout the World. In particular, it should promote an emphasis on research directed at the seven points I have listed.

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SIMPOSIO:
La reciente progresión de las plagas de langostas y nuevos métodos para su manejo

The recent upsurge of the locust plague and novel approaches to locust pest management

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The 1985-1989 grasshopper/locust upsurge in sub-Saharan Africa: the usage of conventional pesticides and equipment

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ABSTRACT

The 1985-1989 grasshopper/locust upsurge in sub-Saharan Africa; usage of conventional pesticides and equipment.

1. A brief account is given of the upsurge in grasshopper and locust activity in Africa north of the equator and south of the Sahara desert since 1984, with special emphasis on species other than *Schistocerca gregaria* (for that species see R. Skaf elsewhere in this symposium volume). A general ecological amelioration seems to have occurred with regard to rainfall since 1984 throughout a belt from Senegal to Ethiopia. The timing of different parts of the rainfall pattern has given a favourable sequence of habitats for successive generations of *Schistocerca gregaria*.

2. The control of acridid pests is, in practice, largely a crop protection exercise and involves stepped-up response as population pressure increases. At the lowest level farmers apply dust formulation pesticides or baits to hopper stages in the form of security belts around cultivation. When this begins to be inadequate hand-held ULV equipment is used to lay down wider swaths of liquid pesticide. Plant Protection Services will be required to intervene with vehicle borne ULV equipment. Later and finally aerial ULV methods are required using helicopters or fixed-wing aircraft.

With some species, such as *Schistocerca gregaria, Locusta migratoria* and *Nomadacris septemfasciata* control of populations remote from crops is part of a preventive control strategy. Decline in upsurges is often attributed to such strategies without much supporting technical or economic evidence.

3. The conventional chemical methods and materials for control are briefly outlined as a background to other Conference papers which describe biological methodology. All chemical means have their advantages and disadvantages. There is, moreover, a worrying lack of analysis of the environmental impact of chemical campaigns and still less incentive to analyse the economics of acridid control. The very large sums of money used annually for this chemical control should be justified, given the need for development of roads, resistant crop varieties and integrated pest management strategies involving biological control. The «new generation» pesticides have not been in use long enough for us to be able to claim that they are environmentally safer, especially as they have to be applied several times to counteract their short persistence. It is also unfortunate that only a small part of large acridid populations afford practical targets for chemical methods and that global reduction of population as a strategy is rarely an acceptable aim.

Key words: Sahel, grasshoppers, locuts, 1984-1989 outbreaks, chemical pesticides, methodology.

INTRODUCTION

The current outbreak of both locusts and grasshoppers has been one of the most dramatic within historical times, culminating in enormous swarms of the Desert Locust crossing the Atlantic from western Africa and reaching the West Indies on a broad front in three waves (Ritchie & Pedgley, 1989; L. McComie, eyewitness accounts, unpubl., 1989). An outline of the current plague to date is summarised succinctly in Pedgley (1989). He traces the beginnings of the current *Schistocerca gregaria (S. g.)* outbreak to good winter rains from November 1985 to April 1986 on both sides of the Red Sea but concedes that earlier breeding in Chad, Niger, Mali and Mauritania may have gone unreported. I will try to follow the story with a Malian perspective, year by year, to demonstrate that the upsurge was due to a generalised improvement in the levels and distribution of rainfall, not only in the *S. g.* breeding area but in the Sahelian zones to the south of it also. Good rains in southern Africa have led to major outbreaks of *Locustana pardalina* and *Locusta migratoria* during the same period. I will emphasise species other than *Schistocerca gregaria* because this species is covered by Skaf elsewhere in this volume.

1984

Having experienced the drought period 1981-1984 I would set the break in the drought at late in 1984. Various authors have shown that *Oedaleus senegalensis (Oe. s.)* egg pods are capable of accumulating unhatched in dry soils over drought periods (Cheke, Fishpool & Ritchie, 1980; Cheke, Fishpool & Forrest, 1980; Fishpool & Cheke, 1983; Launois-Luong, 1980). There is little doubt that this occurred over the drought period 1981-84 in Sahelian Mali. Heavy late rains fell at the end of October so that high density eclosion leading to marching bands of IV and V instar hoppers were observed in the first week of November (area N and W of Dilli in two areas of 4 km^2 and 20 km^2). *S. g.* was not reported.

1985

Rains (June-September) were locally good though still below the long-term monthly averages. The moisture caused heavy hatching of *Oe. s.* so that by end August millet was being invaded by marching hopper bands over an area of 1,700 km^2 in N.W. Mali alone. Emergency intervention by aerial and terrestrial means in early September was inadequate and in Mali represented the swan song of OICMA. The Inter Tropical Convergence Zone (ITCZ or in French literature the FIT) collapsed rapidly southwards carrying enormous numbers of young last generation adults as deeply south as 13°50′ N (see migratory capacity of *Oe. s.* —Rainey, 1976; Riley & Reynolds, 1979; Riley & Reynolds, 1983; Reynolds & Riley, 1988; Lecoq, 1978; 1980). Massive egg fields were laid throughout the zone between the Mauritania border and 13°50′ N.

Some breeding of the Desert Locust took place prior to November leading to small swarms in Mauritania. The species was under-recorded because regular scouting had died with the financial collapse of the West African regional locust control organisations.

1986

The monsoon was characterised by below average but extensive rains. The rains of August were weak, causing near drought in many places, but rains started precociously in an irregular patchwork. Mass hatching of *Oe. s.* was caused at places near the Mauritania border and as far south as 13°50′ N. The seasonal unfolding of populations followed the model of Launois (1976, 1977) and the observations covered by Lecoq (1978, 1980) like a textbook. A first generation of young adults (Jago unpubl. report Nov. 1986) moved northwards and settled at roughly 14°30′ N during the first week in July. Their laying coincided with the hatching of immense numbers of pods laid the previous year. Two waves of high density populations were produced. In the Mourdiah area alone we experienced 300 km^2 of hoppers at a density of $16/m^2$, in a gregarised state, and they developed from instar I to late V in an astonishing 15 days (normally 21 days). Their presence had reduced the area under cultivation by 25% by damage to seedlings. Their marching and colour indicated that *Oe. s.* is a true locust. All adults of this generation were miniaturised. By the end of July the entire latitude at 14°30′ N had emptied and the two superimposed generations departed northwards to 15°00′ N and into Mauritania.

By the end of August a Project-launched survey in N.W. Mali (Nara cercle) revealed that another generation of hoppers and adults had developed interspersed with V instar hoppers and young adults of the univoltine *Kraussaria angulifera*. South of 14°30′ N fallow was moist enough for entry to cultivation to be minimal. Between 14°30′ N and 15°15′ N populations contained fewer adults (10-30,000 adults/ha; 10-50,000 hoppers/ha over 1,450 km^2) and had already entered fields causing some 20% of millet loss. North of 15°15′ N the populations were entirely hoppers (instars III-IV dominant) massed along field margins over an area of 800 km^2. By the end of September young adults moved south by night migration, but heavy rains at the end of September kept the main populations further north than in 1985. Areas in Mali 600 km further east, in ancient lake beds, were nearly 1 month developmentally behind the N.W. Mali populations. Drought there in August and early September had caused delay in hatching so that eclosions occurred right through into October.

A report by Launois (1986) shows that an analogous situation occurred in all the Sahelian states from Senegal to Chad. Populations in western Niger were more successful than in the eastern half of the country. In the east the southerly adult movement took place after harvest and the insects were badly affected by the August drought.

During the summer rains breeding was highly successful along the whole of the Sahel. Solitariform *S. g.* were noted in north-western Mali from time to time, but plant protection services were totally preoccupied with *Oe. s.*, witness the Malian request for aid 1986 (Aug.) which did not mention *S. g.* Again the SAS 1986 Surveillance des Acridiens au Sahel newsletter noted westward movement of *S. g.* for the first time in its 8 September issue, showing intrusion and breeding in Central Sudan, northern Chad, N.E. Niger, S. Algeria and N.E Mali.

1987

As observed by us in Mali and as witnessed by SAS newsletters between May and September, *Oe. s.* met with mixed success. In western Mauritania and Senegal for example, dry intervals during the monsoon held populations in check. No early season crop losses were noted south of 14°30′ N in N.W. Mali and the bulk of major populations developed at or about 15°15′ N and upwards. The ITCZ also remained at northerly latitudes very late so that there was no major end-of-season descent of young adults. What Popov (1980, 1988) has described as the centre of gravity of the late season diapause egg-fields remained much further north than in 1986, at or about 15° N. September populations in such areas, however, caused major crop damage and remained highly gregarised. IV and V instars often marched in bands and young adults often showed spontaneous low altitude daytime flight activity for hours at a time.

Excellent winter rains in the Red Sea area led to the first Desert Locust swarms crossing west into Sudan in May. Pedgley cites swarms entering Niger by June. The process of population build-up, which finally overwhelmed the small antilocust teams in Niger, is graphically described in an on-the-spot report by Duranton (1987).

1988

The scale and distribution of generations of *Oe. s.* was much as we had seen it in 1987. In N.W. Mali, for example, areas north of 15° N were locally devastated by last generation V hoppers and mobile young adults in early September. Near the latitude of the Mauritania border attack and population density was higher than in 1987 and marching columns of gregarised *Oe. s.* covered bigger surface areas in savanna and cultivation. The areas below 15° N received much less grasshopper damage than in previous years and no early season seedling damage at all. The rains in 1988 were at or above the average in practically every month, rainfall reaching levels not seen throughout the whole course of our Project since 1983. The ITCZ remained strongly north causing late rains to extend into southern Mauritania and preventing a heavy southward descent of young adults. In most areas south of 15° N harvest was completed before last generation adults descended. The end of season centre of gravity of egg-fields was further north than in 1987, with alarming implications for crop damage in 1989 on the latitude of the southern Mauretania border and southern Mauretania. However, local last generation adults and V hoppers caused 70-90% crop loss on headed millet and late planted sorghum in villages principally north of 15° N. This seems to have had serious short term effects on family displacements in some areas and will be dangerous if 1989 sees a repeat of events. So far (up to first week of August 1989) the Senegalese Locust has demonstrated some first generation populations at or about 14°30′ N which required local control to protect young millet. The scattered rains of July have given place to heavy August rains, and more generalised hatching of final generation *Oedaleus senegalensis* is expected at latitudes just below and north of the Mauretania border.

Favourable monsoon rains led to reports of enormous hopper bands of *Schistocerca* in southern Mauritania in August-September. Good rains were general and a second and third generation followed.

By September a westward movement of swarms was in progress. In mid October (Ritchie & Pedgley, 1989; McComie, 1989 pers. comm.) the now famous trans-Atlantic movement took place and on a less dramatic scale S. g. also arrived in southern England. End of November-December migrations took swarms into the southern circuit down to Guinea and the Gambia, return movements up through Mali having been reported recently. Other winter swarms reached the Red Sea coast where breeding started. Swarms from Central Saharan Africa penetrated the Middle East, reaching Syria and Turkey. The Adrar des Iforas Mts. and Tamesna have had good rains and successful breeding would be a reasonable forecast (T. Diallo, SNPV Mali, pers. comm.).

Overwintering adults on the ‘southern circuit’ are still immature and moving N.E. and E., but losing coherence (Popov, pers. comm. June 1989).

A disturbing feature of the *S. g.* populations in 1988 was the enormous population of very low density solitariform adults, which in N. W. Mali may have constituted 90% of the population. The gregarised elements of the population would have constituted only a small proportion of the total biomass, and yet they were the only portions which were appropriate targets for chemical control. Most workers admit that with the available resources and with the environment in mind, that the campaign in late 1988 became a crop protection exercise and not one targetted at global reduction of the *S. g.* population. Low density populations with solitary appearance (density 200/ha) have been noted recently (June 1989) over several areas of Mali north of the inland Niger delta.

CHEMICAL METHODS OF CONTROL CURRENTLY IN VOGUE

Control of grasshoppers and locusts takes place at three different lavels.

1. Farmer level

Organised at village (ton villageois) or family levels this takes different forms in a scale of escalation:

A. Intervention against hatchlings and small groups of hoppers in or along the margins of fields. This is best achieved with the dusting bag which is cheap, easy to use and economical with dust formulation pesticide. Normally about 1 kg of dust is required per ha of cultivated land. Hatchling clusters within the field are killed independently and a 5 m security belt created round the field. Currently 5% Lindane dust is not being used for environmental reasons. In spite of claims for its efficacy based on residual properties, in practice heavy rains nullify this advantage. Instead, for example, 2% propoxur, 1% bendiocarb, 5% choropyriphos or 5% fenitrothion dust are being used.

The main problem with the dust formulation is that stocks deteriorate in storage. Experience with fenitrothion and propoxur is that new stock should be acquired every year. Once applied the active ingredients (a.i.) break down within 3-5 days. This means repeated applications. In June-July this means diverting hands who might otherwise be increasing the area under cultivation. The method works in late August against grasshoppers in wild vegetation and fallow until the grasses are consumed or dry out. Economically important older hopper populations mixed with young alates then everrun the security zones, so that a moment is always reached when dusting no longer suffices. In August-September, however, pesticide application does not compete dangerously with other farming activity.

B. Use of ULV drift spraying. This is the next step after dusting. Although now not acceptable in Europe, *e.g.* Germany, at farmer-level in Africa in areas of low reinfall and with lack of abundant water or means for its transport to site, the method is all we have at our disposal. The "Electrodyn" type of equipment is impractical in crops such as millet, so we must rely on mainly electrically-operated or motor-operated back-pack sprayers. The swath width is usually something in the order of 10 m. Most machines, and especially motorised knapsack types, appeared to have been created for the "European market" and field testing in the tropics by the manufacturers has been inadequate. In practice dosage rates should be altered by changing the speed of walking not by changing the nozzles. This requires cooperation with the pesticide manufacturers to adjust the amount of a. i./litre so this can be achieved. Each type of machine has its own particular hazards and disadvantages. Locally in the Sahel and southern Sahara where treatment is near bodies of clean standing water, etc., Norwegian aid has advocated pressurised back-pack sprayers and an emulsifiable Codacide oil-based mixture. This is said to be safer than other ULV concentrates, since it is supplied to the farmer as a 50/50 oil/pesticide mix which is then further diluted by the farmer with water. Containers wash out more easily. The disadvantage will reside in the high cost of the Codacide oil and the clumsy equipment.

The motor back-pack sprayers have temperamental motors and a two-stroke mixture must always be used. Even the best machines have their Achilles heels, *e. g.* rubber petrol feed pipes, etc., which break or get cut. Some dual purpose machines, which can be used as dusters, have reservoirs which leak their liquid contents into the blower fan. They are all heavy and exhausting to use at temperatures which often exceed 80° F and the shoulder harness is bad over tropical weight shirts. They are seldom strictly ULV and the droplet spectrum is often very wide (greater than 60-100 μm).

The electric spinning disc type suffers from being fragile and uses say 8 standard torch batteries every two days. We have found no economic or technical advantage, however, using solar rechargable batteries. Standard machines carry their batteries in the machine which makes it too heavy. A small modification with a battery pack on the shoulder is an enormous improvement. Refilling the ULV bottle is a major hazard, but can be overcome with some redesign. The improved version (Shah, 1989, unpubl. rep.) would be much better for European markets also, but in Africa is essential. A simple tool called a Vibratak is used to test the disc speed and hence state of the batteries. A single machine can treat about 30ha/day.

In practice farmers will treat throughout all the daylight hours regardless of temperature, so carrier oils must take this fact into account. Only very high wind or none at all, or rainstorms, will prevent treatment. The usual precautions apply with all machines regarding washing, overalls, face protection and time between treatment and harvest.

It is essential that, as with treated seed, all pesticides, including baits, be marked as poisonous. Pest control must be accompanied by study of the local people, whilst agents give hands-on training. Thus, in the south of our region, children were discovered to be eating heading millet like sugarcane. This affected tactics regarding spraying until residue analysis had confirmed that health risks were negligible.

2. Ground based teams using ULV man-carried and vehicle-borne equipment.

While farmers help in this the operatives are professionals from the Plant Protection services. The methodology has changed little since the early post-war days. Equipment reflects the urgency of the problem in terms of the area infested:

A. Up to 1,000 ha. Man-carried ULV equipment of the type used in 1B above. The rotary atomiser type of equipment is perfectly acceptable since the team can work a staggered pattern with say 5 units to a team. Each machine has roughly 11 litres of ULV pesticide, enough for treating a swath of 11 to 22 ha dependent on the pesticide. A team of 5 could treat about 150 ha a day. The motor knapsack sprayer will treat about the same area per day but is greedier on pesticide and there will be delays due to refilling. A 10 m swath in open country would be conservative; for *S. g.* country 20 m might be nearer the figure.

B. 1,000 to 10,000 ha. The vehicle mounted system is only appropriate to open country. It is useful for early to middle season treatment of millet. There are two main types:

1. Those **without** an autonomous motor system like the famous exhaust nozzle sprayer. This is still an excellent machine but depends for its efficiency on the vehicle engine and exhaust system being in good condition. Its adverse effect on the engine has been exaggerated. It requires a vehicle heavier than a Landrover for maximum confidence.

2. Those **with** an autonomous motor.

a) the simplest is the "Popov quinquireme" in which one or more operators sit in the back of a Unimog and each aims his motor knapsack sprayer at right angles to the direction of travel of the vehicle but downwind. A small vehicle like a Landrover can also take this system. Noise is a problem.

b) the Tifa type machine with its own petrol driven system. These are essentially foggers with an adaptor for "ULV". In our experience the machine suffers from fantastic weight and excessive noise. It has to be mounted on a heavy all-terrain vehicle since Toyota or Landrover simply get bogged down by the weight. The ULV droplet spectrum is very poor. The good feature is the direct aspiration from the chemical drum so that no decanting is required. Fogging is not effective against *S. g.* and other grasshoppers and involves an immense amount of drift.

c) light electrically-operated machines with atomisation to give ULV using spinning cages and discs. The best of these run off the vehicle battery and are controllable from within the vehicle cab. When empty the reservoir and sprayer mast are light enough to be lifted off the vehicle by two men. Unfortunately all these machines suffer from "prototyposis" and 1989 models will, we hope, have benefitted from tropical field trials.

All these machines give swath widths in the order of 50 m under good spraying conditions. In difficult bushy terrains and around village cultivations it takes two, driver and observer, to safely operate these machines because of constant changes in vehicle direction, changes in wind direction, presence of domestic animals etc.

3. Aerially applied systems
Above 10,000 ha

These are well known to most of us and fall into two groups:

A. those driven by the airstream of the aircraft.

B. those atomising pesticide using spinning discs or cages driven by independent electric motors.

The first in my opinion is most suitable in open terrain like those occupied by *S. g.* where marking the infested area is relatively easy. Unfortunately *Oe. s.* and other species living in more complex Sahelian environments cannot be so easily treated. A helicopter has the advantage that it can touch-down and the crew discuss in some detail the area and terrain to be treated "surgically". The cost is often said to mitigate against the helicopter, but the value of working near to the bowser and better contact with ground teams probably cancel the time wasted with fixed wing aircraft getting lost and not applying the ULV pesticide on target.

PESTICIDES

Table 1 shows the results obtained from the use of various pesticides with comments on their effectiveness and any deleterious side effects. Some idea of prices and dosages is also instructive and these are listed in Table 2.

CONCLUSIONS

Current chemical methods confront us with a number of intractable contradictions. In most cases, when the areas threatened are favourable to massive upsurges the intervention by chemical methods is insufficient to protect the crops. If sufficient chemical was applied the damage to the non-target organisms in the ecosystem would be unacceptable. It is often the case that dense populations which offer acceptable targets represent only a small proportion of the global population and the low density majority population will be easily concentrated later in crop areas. The current grasshopper and locust upsurge has not finished. It was not foreseen and the response by donors and plant protection services in the first two years was slow and did little to avert crop damage. The extent of the damage and the sociological and economic justification for the chemical pest control has not been scientifically presented. Unbiased discussion is desperately needed to decide on alternative ways or improved ways of tackling the problem.

Table 1.—Pesticides used for locust and grasshopper control with comments on performance based on Popov (pers. comm. 1988-89 campaign) with some of my own notes.

Pesticide	Results	Observations
Sumithion super 100% + 5% Esfenvalerate	90% kill after 6 hours	Damages sorghum
Fenitrothion 96%	75% kill after 6 hours on *S. g.*; 0.251/ha 95% kill *Oe. s.* in 2 hours.	Damages sorghum
Fenitrothion 50%	68% kill after 48 hrs to *Oe. s* using 0.251/ha. IV-V **a** few young ads α 8-10/m^2 6 ha treated.	Almost no damage to sorghum. Old stock polymerises blocking filters.
Volaton 300	85% kill *S. g.* after 24 hrs.	Rather slow
Volaton 930	85% kill *S. g.* after 6 hrs.	Not recommended due to blockages.
Deltamethrin	95% kill *S. g.* after 20 mins. Low toxicity to vertebrates.	
Lamdacyhalothrin 10% (Karate)	90% kill *S. g.* after 6 hrs 10 g a.i./ha	Dermal irritation in humans.
Karate 8 g a.i./litre	95 + % kill *Oe. s.* after 24 hrs. IV-V hoppers α mean 27/m^2. 3.3 ha treated in 60 mins. starting 1,700 hrs. Kills millet head miner also.	Immediate knockout effect on many nontarget insects, *e.g.* ants. *Oe. s.* 90% kill in 1 hr.
Cypermethrin 12 g a.i./litre	90% kill in *Oe. s.* after 24 hours; III-V hoppers *a* mean 29/m^2. 5.2 ha treated in 60 mins starting 15:30 hrs; millet head miner also killed.	Adults disperse to die in shade down holes, etc.
Bendiocard (Ficam) ULV 20%	95% kill in 10 mins. Persistent 1 week+ Aerial or ground use. *S. g.* or *Oe. s.*	
Carbosulphan (Dursban) 24%	50% kill after 6 hrs. *S. g.*	Slow: skin irritant. Danages Sorghum.

Table 2.—1986-87 prices and dosages for some pesticides used in locust and grasshopper control.

Product	Recommended dose (litres or kg/ha)	Price/litre:kg (££ sterling; $$ US)	
Lindane dust 25%	0.7-1.0 kg/ha	0.95	1.45
Ripcord 12 g a.i. /litre	3 litres/ha	2.12	3.18
Fenitrothion 500 g a.i./litre	0.5 litres/ha	8.16	12.25
Sumithion 500 (Fenitrothion)	0.5 litres/ha	4.56	6.84

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Microbial control of locusts and grasshoppers in the semi-arid tropics

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ABSTRACT

Most of the attention on biological control of locusts has focused on pathogens. Several viral and protozoan pathogens have been identified for evaluation as locust control agents. Furthermore, the demonstration of a lethal disease in locusts by a lepidopteran nuclear polyhedrosis virus suggests the need for a more comprehensive screening of insect pathogens against locusts. Certainly only a small fraction of the acridid pathogens present in the environment have been isolated and identified. Further exploration and screening must be conducted to provide additional pathogens for evaluation as potential biological control agents of locusts.

Key words: Biological control, entomopathogens, Orthoptera, pathogens.

INTRODUCTION

During the latter part of the 19th century and the first half of the 20th century, numerous efforts were made to control locusts and grasshoppers with microbial agents. Most of the attempts were with the fungus now known as *Entomophaga grylli* (Fresenius), but known then as *Empusa grylli.* Among the earliest reports were those by Kunckel d'Herculais and Langlois (1891) and Brongniart (1891) on the effects of this fungus on locusts. A few years later Edington (1848), in South Africa, and Bruner (1901), in the United States, reported natural epizootics among Acrididae. During this same period, Kunckel d'Herculais (1900) reported on the natural and artificial propagation of fungi in Argentina. The efforts, reported in a review by Charles (1965), continued well into the present century. However, the most interesting and possibly the most controversial attempt to achieve microbial control of Acrididae began with a report by d'Hérelle (1911) of an epizootic among Acrididae in Mexico caused by the bacterium then called *Coccobacillus acridiorum* d'Hérelle. Later, d'Hérelle (1914a, b) reported positive results when he used the bacterium to kill locusts and grasshoppers in Argentina and Africa. Subsequently other workers in Africa, particularly Sergent and L'Heritier (1914), Béguet (1915, 1916), and Sergent (1916), reported highly variable results and a lack of effectiveness in some cases. The work on *C. acridiorum* was virtually discontinued, but investigations of other bacteria, and of their potential applied use, have continued.

It now is apparent that early efforts to use bacteria and fungi for control of Acrididae failed because the microorganisms generally require specific climatic conditions, such as high humidity, for growth and development. These microorganisms play a significant role in regulating the densities of Acrididae in the tropical and subtropical parts of the world; however, because of dependence on high humidity, they are not sufficiently dependable in the arid and semi arid regions of the world where grasshoppers and locusts are pests. Microorganisms that are developed for applied use must be infective under a variety of conditions.

Locusts and grasshoppers are hosts to numerous microorganisms that are not restricted to narrow temperature and moisture regimes for growth and development. Protozoa and viruses are particularly promising in this respect and, are therefore excellent prospects for applied use. There are also some species of bacteria and fungi that could be manipulated to minimize their dependence on specific climatic conditions. The following is a discussion of those organisms that could be involved, either naturally or applied, in the regulation of locusts and grasshoppers in the semi-arid tropics.

BACTERIA

Bacillus thuringiensis Berliner: The commercialization of various strains of *B. thuringiensis (Bt)* as microbial insecticides against Lepidoptera, Coleoptera, and Diptera pests has provided justification to search for strains that would be pathogenic to Orthoptera. Many strains of *Bt* that have been isolated from Lepidoptera and Coleoptera have been tested against grasshoppers; however, pathogenicity has never been evident. *Bt* has also been isolated from moribund and dead grasshoppers. Some of these were pathogenic to nymphs, but active dosages were in the range of 10^{11} spores per grasshopper (Henry, personal communication). Because of these prohibitively high dosages, very little research has been conducted on *Bt* in Orthoptera.

It is likely that *Bt* does occur extensively in locusts and grasshoppers. Although the natural isolates may not be sufficiently toxic for immediate use against locusts, the emerging technology for genetic engineering for enhancing virulence warrants a reconsideration of the potential value of these bacteria. Consequently, surveys for *Bt* isolates should be conducted in locust and grasshopper populations for the specific purpose of developing an engineered microbial insecticide.

FUNGI

Beauvaria bassiana (Bals.): There have been many instances of isolation of *B. bassiana* from locusts and grasshoppers, but very few published reports. Efforts to artificially propagate the fungus in grasshoppers have largely been disappointing, undoubtedly because of moisture level requirements. In recent years, however, there has been renewed interest in *B. bassiana*. Several commercial firms in the U.S. and Europe have developed improved culture techniques which have led to the selection of strains that are more active against grasshoppers. These strains should be evaluated as microbial insecticides against locust bands.

Unidentified fungi. Henry *et al.* (1985b) reported the isolation of a yeast-type fungus from *Oedaleus senegalensis* (Krauss), *Aiolopus thalassinus* (Fab.) and *Anacridium* sp. from West Africa. The pathogen was very similar to another fungus that had been isolated from grasshoppers in the U.S. and proved highly infective to grasshoppers in the laboratory. These fungi are highly pleiomorphic and very difficult to grow on defined media; therefore, their taxonomic status has not been fully determined. Nevertheless, they should be tested against locusts and grasshoppers.

PROTOZOA

Malameba locustae (King and Taylor):

This amoeba infects the epithelia of the malpighian tubules and midgut of a variety of Orthoptera, including Acrididae, Tettigoniidae, and Gryllidae. It has also been reported from silverfish (Thysanura) that inhabited a room in which locusts were reared (Larsson, 1976). *M. locustae* can be a very serious pest in laboratory cultures of locusts and grasshoppers (Henry, 1968; Donaldson, 1971; Davies, 1973; Henry and Oma, 1975; Hanrahan, 1984; Braun *et al.* 1988.)

Very little information is available on the natural occurrence of *M. locustae* in locusts and grasshoppers. Lea (1958) reported a high prevalence of infection in the brown locust *Locustana pardalina* (Walker) in South Africa, and Venter (1966) suggested that the parasite prevented an outbreak of this locust. Ernst and Baker (1982) reported natural field infections in the Australian grasshopper *Pardillana limbata* (Stål) and cricket *Pteronemobius* sp. Henry *et al.* (1985b) reported *M. locustae* infections in *O. senegalensis* and *Diabolocatantops axillaris* (Thunberg) in West Africa.

M. locustae infects a wide range of hosts, including the locusts *Locusta migratoria migratorioides* (Reiche and Fairmaire), *Schistocerca gregaria* (Forsk.), *L. pardalina,* and *Nomadacris septemfasciata* (Serville) and causes debilitative infections that appear to reduce fecundity. Venter's (1966) suggestion that the parasite was responsible for preventing an outbreak of the brown locust may indicate some applied potential. Augmentative releases of cysts into solitary or nonswarming hopper bands may prove effective in reducing gregarization.

Nosema locustae Canning: Canning (1953) originally described *N. locustae* from *L. m. migratorioides* and later (Canning, 1962a) extended the host range to include *S. gregaria.* Henry (1969) reported that 58 species of Orthoptera were susceptible to infection, including a gryllid and tetrigid. Later, Henry *et al.* (1985a) reported infection of seven species of West African grasshoppers, including *O. senegalensis* and *Oedaleus nigeriensis* Uvarov. It now appears that all species of Acrididae may be susceptible to infection.

Nosema locustae has been registered for applied use against grasshoppers in the U.S. When *N. locustae,* a moderately virulent pathogen, is applied in the field on wheat bran it will cause significant mortality within four weeks of treatment and infection among the surviving grasshoppers. The infections cause reduced fecundity (Ewen and Mukerji, 1980) and develop an inoculum reservoir for infection of the subsequent generation (Henry and Onsager, 1982).

Because of the moderate virulence of *N. locustae,* and the resulting long lethal time, its value against locusts has been considered as minimal. Although Canning (1962b) was able to infect *L. m. migratorioides* rather easily, infection of *S. gregaria* was more difficult. Also, by conjecture, it is possible that *N. locustae* would not persist in bands of migrating hoppers or adults because infected individuals probably would be left behind. However, *N. locustae* might be useful against these insects when they are non-gregarized and restricted to localized areas, such as to rainfall recession areas. Certainly, *N. locustae* should be tested against locusts in the field.

Other Microsporidia: Three other microsporidia have been described from grasshoppers *(Nosema acridophagus* Henry, *Nosema cuneatum* Henry, and *Perezia dichroplusae* Lange), and a number of other probable species have been isolated. *Nosema acridophagus* is the most virulent of the described species (Henry *et al.*, 1979) and was described from *Schistocerca americana* (Drury) (Henry, 1967). Consequently, this species should be a promising candidate for evaluation against African locusts. *Nosema cuneatum* is moderately virulent and also should be tested. *Perezia dichroplusae* infects the malpighian tubules, causing debilitative affects, but usually not mortality (Lange, 1987). Purrini (personal communication) has also reported the isolation of microsporidia from locusts in Tanzania. Accordingly, there exist a number of described and undescribed microsporidium species for evaluation against locusts.

VIRUSES

Entomopoxviruses: Henry and Jutila (1966) first reported isolation of an inclusion body virus from grasshoppers which was later (Henry *et al.*, 1969) characterized as an entomopoxvirus. Since then, six other entomopoxviruses, identified by restriction enzyme (REN) analysis, have been discovered in grasshoppers from the U.S., Africa, and Canada (Oma and Henry, 1986). In addition, there have been entomopoxviruses reported from a grasshopper in China (Farrow, personal communication), among *S. gregaria* and a *Chortipes* sp. from the Yemen Arab Republic (Purrini and Rohde, 1988), and among *L. m. migratorioides* from Tanzania (Purrini *et al.*, 1988). It now appears that entomopoxviruses are the primary viral group associated with Acrididae.

Generally, entomopoxviruses appear to be moderately pathogenic to grasshoppers. However, the host ranges of specific isolates appear to be restricted to particular groups of grasshoppers. The limited host ranges are not important in Africa where outbreaks usually involve a single species. However, development of these viruses as microbial control agents of North American grasshoppers may be more challenging, where outbreaks include complexes of 12-15 species.

Structurally, these viruses appear similar to the poxviruses of vertebrates and are assigned to the same family, Poxviridae. Nevertheless, DNA hybridization studies have demonstrated no genetic relatedness between the grasshopper viruses and vaccinia (see review by Streett, 1987). Safety tests conducted according to the Environmental Protection Agency Tier I requirements have been completed for two of the viruses without evidence of infectivity to non-target vertebrates and invertebrates.

Two of the six isolates that have been characterized by REN analysis and DNA hybridization came from African grasshoppers. The *Oedaleus* entomopoxvirus (OsEPV) was isolated from *O. senegalensis, O. nigeriensis,* and *Kraussaria angulifera* (Krauss) while the *Cataloipus* entomopoxvirus (CcEPV) was isolated from *Cataloipus cymbiferus* (Krauss), *Cataloipus fuscocoerulipes* (Krauss), and *Heteracris annulosus* (Walker). OsEPV appears to have a fairly wide host range, including a number of grasshoppers in North America. In the absence of molecular studies of the viruses reported by Purrini and Rohde (1988) and Purrini *et al.* (1988) it is impossible to evaluate their relatedness with the more fully characterized viruses, including those from the North American grasshoppers. Certainly the viruses reported by Purrini and coworkers need to be compared to these characterized viruses, primarily to prevent duplication of effort on the same viruses.

In any event, the entomopoxviruses appear to be excellent prospects as microbial control agents of locusts. Studies in North America have demonstrated that they can be mass produced in quantities sufficient for field evaluations. They seem to have a stable shelf life, indicating a potential for prolonged storage. Pathogenically, they cause three rather distinct symptomatic processes; grasshoppers may become moribund and subsequently die within eight days of infection, may become stunted and remain as second and third instar nymphs, or may appear normal and become adults. All of these processes are of value in a biological control program. Accordingly, research directed at the eventual applied use of these viruses should be given high priority.

Other viruses: Jutila *et al.* (1970) reported isolation and characterization of a highly virulent picornavirus from a grasshopper in North America. The virus was infective to various North American *Schistocerca,* which indicates some potential use against African locusts. However, because of similarity to other picornaviruses, it must be tested extensively for safety to non-target animals before it could be evaluated as a biological control agent.

Recently Bensimon *et al.* (1987) reported experimental lethal infection of *L. m. migratorioides* by a nuclear polyhedrosis virus (NPV) from the lepidopteran *Spodoptera littoralis.* This is a very interesting report simply because it suggests a need to screen locusts against a wide variety of insect pathogens.

RICKETTSIA

Vago and Meynadier (1965) first reported isolation of *Rickettsiella schistocercae* from the desert locust, *S. gregaria,* and transmission to *L. m. migratorioides.* Prior to that Martoja (1964) had transmitted *Rickettsiella grylli* to both species of locusts. Henry *et al.* later (1985b) reported isolation of a rickettsia from the African grasshopper *Zonocerus variegatus* (L.) which was subsequently considered a strain of *R. grylli* (Henry *et al.* 1986). Since the isolate named *R. schistocercae* has been lost and because it was not characterized ultrastructurally, its relationship to *R. grylli* remains unknown. However, based on the infectivity of the *R. grylli* isolate from *Z. variegatus* for a wide range of grasshoppers, as well as other insects and vertebrates, it appears likely that *R. schistocercae* might also be *R. grylli.*

While the rickettsia from *Z. variegatus* was highly virulent to grasshoppers, the possibility that it infects vertebrates would preclude its use in grasshopper control.

CONCLUSION

A number of pathogenic microorganisms are available for evaluation against grasshoppers and locusts in Africa. Priority should be given to the entomopoxviruses, because they appear to be moderately virulent and are stable for prolonged periods of storage and application. Two species of microsporidia, *N. acridophagus* and *N. cuneatum,* also appear potentially useful. However, priority should also be given to an extensive survey of grasshoppers and locusts in Africa for other useful microbials. Previous efforts have demonstrated that these insects serve as natural hosts to many pathogenic organisms. Particular emphasis should be placed on the isolation of *Bacillus thuringiensis* strains which might be improved genetically and used as microbial insecticides against gregarized locusts.

Concerned African countries and several donor agencies have expressed interest in the potential use of biological control strategies in recent years. The interest is probably an outcome of our inability to manage locusts with traditional chemical insecticides and has prompted the initiation of several projects to explore the potential value of microbial organisms. Assuming some degree of success with these current efforts, it is quite likely that a very large and intensive project for ultimately using microbials against locusts and grasshoppers in Africa will be underway within the next 2 to 3 years.

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Locust pheromones — basic and applied aspects

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ABSTRACT

Synthetic chemical pesticides are the basis of present Desert Locust control measures. In order to reduce environmental damage caused by such chemicals it is suggested to use locust pheromones as part of environmentally acceptable integrated locust pest management. Among the locust pheromones under discussion those responsible for phase transition and oviposition seem to be suitable candidates for future new locust control strategies. Thus studies of their biology and chemistry should be given a high priority.

Key words: Locusts, pheromone, locust control.

INTRODUCTION

The current Desert Locust plague is the worst in over 25 years. In 1985 Desert Locust swarms originating from small areas near the Red Sea started to invade East and West Africa as well as the Arabian peninsula. The Desert Locust has a vast invasion area of some 29 million square kilometres, affecting 57 countries. This is more than 20% of the total land surface of the world inhabited by about a tenth of the world's population. Damage caused by locusts can be very severe. Each one eats its own weight of food (ca. 2 gm.) every day; and a Desert Locust swarm can measure hundreds of square kilometres and contain thousands of millions of locusts. Analysis of Desert Locust damage shows that hoppers cause 8%, immature and maturing swarms 69% and mature swarms 23% of the damage (Steedman, 1988). The recurring nature of locust outbreaks, their devastating effects on the economies of semi-arid tropical and subtropical countries and their psychological and socio-political impact on the affected populations have stressed the need for effective and acceptable methods of managing this pest.

Existing control measures for Desert Locusts rely heavily on chemical pesticides. The most effective of these, dieldrin, is no longer acceptable. Persistent organochlorine insecticides are probably accumulated in the environment and gradually absorbed into the food chain. The replacement compounds are non-persistent but also less effective and more expensive requiring multiple applications. There is an increasing concern about the dangers of environmental pollution and the threat to wildlife and man. The banning of persistent organochlorine compounds may actually have increased the threat of environmental damage since larger quantities must be used. In addition chemical pesticides are non-selective, leading to destruction of natural enemies which probably hasten the decline of plagues. It is therefore essential to pay attention to more acceptable, non-chemical alternatives.

Several years ago we have proposed a new strategy based on the concept of preventing or interfering with the formation of locust swarms and with their reproduction by using behaviour-modifiying chemicals. The intention is to retain locust populations within their primary breeding sites and to suppress mass reproduction. Such chemicals, called pheromones, are target-specific, harmless to the environment and may form an important component of a future integrated locust management system. However, enthusiasm about the use of pheromones to control locust populations has slowed down because very few studies on pheromone-relevant and -dependent locust behaviour and development exist until today. A much more intensive effort is required now in the areas of locust pheromone biochemistry and neurobiology to solve problems of their biosynthesis, perception, transduction and metabolism. It is clearly understood that much more of this and other basic research has to be done before pheromones can be used in the field for locust control.

LOCUSTS AND PHASE POLYMORPHISM

Locusts belong to the family of short-horned grasshoppers (Orthoptera, Arcrididae). They are defined as grasshoppers which meet two criteria: (i) they can form dense groups of hoppers (bands) or winged adults (swarms) which migrate; (ii) they can occur in two phases —solitaria and gregaria— which differ in morphology, colour, ecology, physiology and behaviour. This polymorphism in locusts was first described by Uvarov (1921) and subsequently many details have been added (reviews *e.g.*, Uvarov 1966, 1977; Cassier, 1974; Pener, 1983; Hardie and Lees, 1985).

In Africa there are mainly four Acridid species of economical importance which show this phase polymorphism very clearly: the Desert Locust *Schistocerca gregaria*, the Red Locust *Nomadacris septemfasciata* (both of Cyrtacanthacridinae), the African Migratory Locust *Locusta migratoria* (with various subspecies) and the Brown Locust *Locustana pardalina* (both of Oedipodinae). These locusts are not a significant pest when occupying their semi-arid recession areas where they exist as dispersed, solitarious individuals. The damage they can do in this phase —if at all— is minimal. Very probably locusts play a useful role in the desert ecosystems and food chains as herbivores. Favourable climatic factors, however, induce increase in population size and density. The sequences of rain in time and space needed to initiate a plague are rare and are somewhat different for each plague. Solitarious animals generally adapt to the colour of their surroundings, either green or homochrome as in *L. migratoria* or different yellow-brown or reddish colours as in *S. gregaria.* In opposition to this the colour of gregarious locusts seems to be unrelated to that of their surroundings. This phase polychromatism is influenced by high population density, but also by temperature and humidity (Dudley, 1964). Usually homochrome adaptation is never total in any large locust population. Various intermediate colourations can be observed. Uvarov (1966) also noticed differences in morphometrics between solitarious and gregarious phases. Measuring the length of the hind femur (F) and the maximum width of the head (C) it was found that the F/C ratio is higher in the solitary phase (Dirsh, 1953).

Furthermore there are differences in the reproductive potential between locust phases. Solitarious females esp. in *L. migratoria* have more ovarioles, produce more eggs per eggpod and deposit more eggpods (Norris, 1952; Albrecht, *et al.* 1959; Injeyan and Tobe, 1981a). These differences may be associated with titres and appearance of juvenile hormone which regulates vitellogenesis (Injeyan and Tobe, 1981b).

Differences in behaviour and activity between the two phases are obvious. Gregarious locusts have a strong tendency for group formation. Hoppers form bands that march together and gregarious adult locusts aggregate to a swarm and fly together. Experimental analysis of the aggregation behaviour clearly demonstrated that gregarious locusts *actively* aggregate while solitarious animals do not. However, when exposed to gregarious ones, solitarious locusts change their behaviour rather rapidly within hours and days (Ellis, 1962, 1963; Gillett, 1972, 1973).

LOCUSTS AND PHEROMONE BIOLOGY

There are indications that volatile chemical signals may be involved in induction and promotion of phases and other aspects of locust behaviour. Like many other insect species locusts seem to communicate to a large extent by the exchange of chemical compounds termed "pheromones". Pheromones are defined as substances produced by one or several individuals of a species which cause particular behavioural and/or developmental reactions when received by another individual of the same species. They are species specific chemical messages effective in minute amounts *between* animals in much the same way as hormones *within* an individual. Thus in earlier literature they were usually referred to as "ectohormones". Since 1959 the more accurate term "pheromones" has widely been adopted (Karlson and Luescher, 1959). Pheromones may be single compounds or mixtures of compounds. The mode of influence can take either of two general forms (Wilson, 1963): if the pheromone acts upon the nervous system to evoke immediate and reversible behaviour changes it is said to have a releaser effect. Examples are alarm and sex pheromones. If it causes more permanent physiological changes in the recipient such as inhibition of gonad development in worker bees by the queen substance it is called a primer pheromone. Pheromone compounds are usually transmitted in the vapour phase as air-borne odours, but some are transmitted directly, and are then called surface or contact pheromones. Many insect species have developed this chemical communication system to a uniquely high level of sophistication and importance, so that pheromones are involved in many aspects of their life. Pheromonal communication including sensory physiology and behavioural mechanisms involved in the responses have been studied most closely in moths. Despite the recent 30th aniversary of pheromone research for many animal species including locusts the knowledge of chemical communication is still at a rather early stage. However, a rapid solution of many interesting problems can be expected in the near future, since new sensitive and sophisticated techniques in analytical chemistry combined with perceptive studies of animal behaviour are available now.

Little progress in locust pheromone biology has been made since the sixties. The reasons for this negligence seem to be related to the long-term recession of locust outbreaks and subsequent lack of proper funding for necessary expensive research. Research on the physiology and behaviour of locusts suggested that the following pheromones may occur: (i) Gregarisation pheromone is involved in gregarisation of solitarious locust hoppers and probably prepares them for aggregation and swarming in adult life; (ii) Solitarisation pheromone promotes some solitary characteristics and may be useful for dispersing locusts; (iii) Maturation pheromone accelerates and synchronizes sexual maturation in both sexes; (iv) Oviposition pheromone aggregates females of both phases to a common oviposition site and stimulates egg-laying, or attracts females to substances previously used by egg-laying locusts.

THE GREGARISATION AND SOLITARISATION PHEROMONE

Several attempts to identify and characterise the gregarisation pheromone system have been reported, but, unfortunately, none were based on analytically sound techniques and interpreted with sufficient caution. A gregarisation pheromone was identified in locust larvae faeces and termed "locustol". Nolte and associates extracted this locustol by steam distillation followed by solvent extraction and purified it by thin layer chromatography. The resulting major component with reported biological activity was described as 5-ethyl-2-methoxy phenol (Nolte *et al.* 1970, 1973; Nolte, 1976). It was postulated that this and other phenolic compounds were degradation products of lignin ingested in grass or shrubs. However, Gillett (1983) has recently corroborated the basic observations concerning the inductive effect of faeces, but was unable to elicit similar effects with the synthetic locustol. Most of the data published by Nolte are unreliable or wrong because of lack of suitable controls and/or poor statistical tests. In a recent study Fuzeau-Braesch *and associates* (1988) have identified phenol, guaiacol and veratrole as olfactory attractants in the air surrounding locusts. Ongoing research studies do not fully support these results (Applebaum and Ferenz, unpublished data). There are indications that volatile factors act in combination with visual and tactile stimuli. The gregarisation pheromone seems to be perceived by receptors at the antennae; amputation of antennae had solitarizing effects (Mordue, 1977).

There is also experimental evidence for a solitarizing pheromone excreted by gregarious adult locusts. This pheromone seems to promote anti-social behaviour in the immature stages of *S. gregaria* (Gillett and Phillips, 1977; Gillett, 1983, 1988). The existence of this solitarizing stimulus of the adult faeces is supported by the observation that adult gregarious locusts show lower levels of grouping than do young gregarious nymphs. However, then the question arises which factors keep a locust swarm together? It is clear that the identification of pheromone(s) regulating gregarisation and additional factors contributing to gregarisation must be carefully re-evaluated.

Little is known about perception and transduction of this pheromonal information. As mentioned the antennae are involved in the perception of the gregarisation pheromone, but more research is necessary to support this finding and to understand the receptor system involved. The importance of other sensorial information for phase transition such as visual and tactile stimuli needs further clarification, too.

The pheromonal information seems to be translated into neurosecretory signals by the locust brain. Since juvenile hormone plays a dominant role in locust development, reproduction and presumably also in the regulation of some phase characteristics the study of the control of juvenile hormone biosynthesis by the brain appears to be important. However, despite intensive studies little is known about the regulation of juvenile hormone biosynthesis (Feyereisen, 1985). Juvenile hormone biosynthesis in locusts is stimulated by a cerebral allatotropin, a peptide hormone transported to and released from the neurohaemal corpora cardiaca (Ferenz, 1984; Gadot and Applebaum, 1985). Currently this neuropeptide is further characterized and the stage within the biosynthetic pathway identified where allatotropin exerts its stimulating effect. We suspect that one of the effects of the gregarisation pheromone on the endocrine system could be to suppress production and/or release of allatotropin. Undoubtedly juvenile hormone promotes solitary phase characteristics: implantation of active corpora allata or administration of exogenous juvenile hormone cause green colouration and solitary morphometrics in *L. migratoria;* allatectomy results in opposite effects. However, despite many experiments it is not clear whether many phase characteristics are solely related to juvenile hormone. Pener (1983) admirably discussed these endocrine aspects of phase polymorphism in a recent comprehensive review (see also his contribution in this volume).

PHEROMONAL CONTROL OF MATURATION

There are several reports proposing the existence of a maturation pheromone which hastens and synchronizes the maturation of immature adult female *S. gregaria.* It is secreted by the epidermal cells of the gregarious male at maturity but not of solitary males nor of either solitary or gregarious females. Epidermal cells are almost completely absent in females or in solitary males. In gregarious males they differentiate in the pharate fifth instar and the first two days of overt fifth instar in the presence of ecdysone and absence of juvenile hormone. Initially these glands are inactive but during maturation they acquire responsiveness to juvenile hormone and then produce the pheromonal factor which regulates female sexual maturation. The persistence of juvenile hormone in the critical period of the fifth instar of solitarious *S. gregaria* depresses the differentiation and development of these epidermal gland cells (Norris, 1954, 1962; Loher, 1960; Cassier and Delorme-Julie, 1976). Attempts to identify chemically this volatile compound from mature male *S. gregaria* failed (Blight *et al.*, 1969).

OVIPOSITION PHEROMONE

The initiation of the gregarious phase of locusts and subsequent swarming is dependent on the population density of the hoppers. Usually each individual female locust oviposits a batch of 50 to 80 eggs and if one assumes that most of them hatch under optimal climatic conditions the number of resulting hoppers within a grouping is initially dependent on the distribution of the eggpods in a given breeding area. In fact it was repeatedly observed that the majority of eggpods are clustered in a common egglaying ground. Although the soil quality influences this distribution, it seems that environmental factors are not sufficient to explain the clustered distribution of eggpods (Popov, 1958; Norris, 1970). Experiments with sand in which locusts have laid eggs repeatedly show that this sand strongly attracts mature females and these females preferentially deposit their eggpods in it. This sand has no effect if washed with detergents and sulfuric acid (Lauga and Hatte, 1977, 1978). It is postulated that egglaying locusts produce an oviposition pheromone attracting other gravid females to an eggfield. This phenomenon could have direct effects on the development of gregariousness in following generations.

LOCUST SEXUAL BEHAVIOUR AND PHEROMONES

Insects communicate between sexes of their own species prior to and during their mating. Chemical communication involving sex pheromones is vitally important for many of them. Most insect sex pheromones are secreted by females and act as odorous stimuli for males. Receiving the message of the presence of a female males are aroused, locate the female by upwind orientation, initiate a mating procedure and finally copulate. Many sex pheromones have been chemically identified and some of them are already used as tools in integrated pest management.

There is no clear evidence that locusts use any sex pheromones for finding and stimulating their sex partner. However, solitary locusts are quite dispersed and it might be a problem to a find a sex partner. Gregarious locusts probably would not need such a long distance communication system. Prior to copulation locusts exhibit a more or less intensive courtship behaviour (Uvarov, 1966). The males seem to be very excited, and show a lot of palpation when close to the receptive female. This might indicate a short distance chemical communication. However, nothing is known about it. For several locust species it has been shown that juvenile hormone can control male sexual behaviour (Pener, 1974, 1976), but the relationship between pheromones, juvenile hormone and sexual behaviour is not clear. Locusts also use audible acoustic signals for communication. Sexually mature males make use of such signals quite often. These signals may be of importance for attracting females over a longer distance. Obviously more research is necessary to understand the sexual behaviour of locusts. If sex pheromones are present the possibility of using them for disruption of mating behaviour or as attractants should be explored.

PROBLEMS IN LOCUST PHEROMONE RESEARCH

Because of the extreme nature of the crowding-induced behavioural and physiological changes, the high mobility and the deficient ecophysiological knowledge, locusts are uniquely difficult to study. In the laboratory it is not easy to breed truly solitary locusts. Although locust pheromones are only present in very small amounts techniques like gas chromatography combined with mass spectrometry have become available over the past three decades to analyse such compounds. Methods developed for the study of pheromones in other insect species can easily be adopted. The main problem seems to be the development of behaviourally interpretable laboratory assay methods for screening and identifying pheromone compounds which influence the behaviour or physiology. In particular the identification of pheromones responsible for phase transition may cause problems because the change of phase is a slow and multifactorial process. For future insights it will be essential to possess assays and methods of analysis which also allow the quantitative assessment of the phase-status of individuals as indicated by their behavioural characteristics. Reliable screening of compounds can be achieved only when the methods used are based on the knowledge of the insect's behaviour. Such detailed knowledge is also essential for the design of future field trials and for optimising the way in which new pheromone based methods are applied. Locust pheromone research is a complex subject necessitating the cooperation of pheromone biochemists, insect physiologist and experts on insect behaviour and ecology.

LOCUST CONTROL BY PHEROMONES

In recent years pheromones have become very powerful tools to control pest insects. They are used (i) to bait traps with attractants to trap pest insects and reduce their population, (ii) to bait traps with sex-pheromones to remove one sex of the target insect population, (iii) to bait traps with aggregation pheromones *(e.g.,* in the bark beetle) and (iv) to disrupt mating communication in a population *(e.g.,* in the pink bollworm). More recent approaches explore the possibilities to use pheromones for monitoring insect population densities and for making baits containing toxic substances or pathogens more attractive.

In a similar way locust pheromone research can help to develop methods of control which will reduce reliance on the use of conventional insecticides, which are poisonous and harmful to the environment. The use of synthetic pheromones (and also insect hormones) which influence development, behaviour and phase transformation is attractive, as such compounds are likely to be specific to insects and perhaps selective between species. High priority should be given to the question of whether manipulation of the gregarisation process is possible. As stated earlier, the knowledge of the physiological basis of phase transformation is deficient. The question of the feasibility of manipulating locust phase transformation should be answered in the course of the studies. Preferably the locusts should be retained in their solitary stage within their primary breeding sites which are usually far away from cultivated areas. Since juvenile hormone plays an important role in phase transition the additional application of juvenile hormone analogues may enhance the development of solitary phase characteristics, or, alternatively, anti-juvenile hormones may interfere with the development of some important phase characteristics.

Also the suspected oviposition pheromone might be a very good candidate for controlling locust populations at an early stage. With this pheromone aggregations of gravid females on egg-fields can be generated which then could form targets for control measures. However, it seems that the oviposition pheromone might act only over a short distance. Hence, the degree to which it will be able to attract and concentrate oviposition would depend on the searching behaviour of the females before selecting an oviposition site.

Present evidence suggests that the Desert Locust and other locust species do not possess a volatile sex pheromone system to which either sex responds at a distance. Thus locust sex pheromones —if present— will probably not be a powerful attractant system as in some moth species. Future research should answer the question whether short range sex pheromones exist which could be used to disrupt locust mating. Maturation pheromones are also not promising candidates for locust control. Adult locust populations are highly mobile and thus are unattractive targets for manipulation. Since in general little is known about locust pheromones only speculations about their possible use can be made at present.

CONCLUSIONS

Synthetic chemical insecticides are the basis of present Desert Locust control campaigns and remain the only practical means available today and in the near future. There is limited data on the environmental impact of these synthetic pesticides that have been used for locust control under tropical conditions, but the deleterious effects of these chemicals on the environment, wildlife and human health are obvious. Thus their use should be minimized. New technologies and methods have to be developed to limit the environmental stress and health hazards associated with pesticides. In addition pesticide control measures have become very costly. Research activities to develop alternative control strategies require a long term commitment of the international community to finance the necessary research and to support high quality professional scientific endeavours in developed and developing locust affected countries. Although locust pheromone research is at an early stage very interesting results can be expected which will form an important part of future integrated locust management. It is assumed that pheromones can efficiently help to retain locusts in their solitary phase and in their primary breeding sites or recession areas. Thus research on pheromones regulating phase transition and oviposition should be given a high priority. However, future application of pheromones can only be successful if locust ecology is much better understood and logistics for field work in remote desert areas are considerably improved.

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Endocrine effects on locust phase changes; basic and applied aspects

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ABSTRACT

Locusts are short-horned grasshoppers which form, at irregular periods, dense migrating groups, bands of hoppers and/or swarms of adults, and exhibit density-dependent phase polymorphism. They appear in two forms, or "phases", gregarious and solitary, widely differing in many features collectively termed "phase characteristics". Density is the primary extrinsic factor that affects locust phase change, but the intrinsic factors underlying the physiological/molecular basis of phase change are insufficiently known. Some authors claim that the corpora allata (CA) and their product, the juvenile hormone (JH) constitute the primary physiological causal factor in phase change, and specifically timed JH excess induces the solitary phase. JH undoubtedly promotes many solitary characteristics, the induction of the green solitary color being the most thoroughly demonstrated one. However, green color is not a necessary characteristic of the solitary phase and color polymorphism characterized by absence or presence of the green color is widespread in non-locust acridids. Some phase characteristics are not affected by CA/JH and in some cases CA/JH promote gregarious characteristics. In one instance the target organ responds differently to JH in crowded and isolated locusts and this difference does not depend on previously experienced JH titer. CA activity and JH titers seem to be higher in isolated than in crowded locusts, but when such differences are clear and considerable, they may just reflect differences in the rate of sexual maturation of isolated and crowded *Locusta* adults. Probably, therefore, differences in CA activity and JH titers do not constitute the primary physiological causal factor in phase change; these differences may stand somewhere in the middle, but not in the beginning, of a complex chain of physiological events leading to phase change.

Ecdysteroid titers are similar in crowded and isolated locusts. Therefore, ecdysteroids do not seem to play a major role in locust phase transformation. Some early reports on effects of the ventral glands (VG = prothoracic glands of other insects, the source of ecdysteroids in hoppers) on phase are largely unexplainable today and open to speculations.

Research has been neglected on possible role(s) of neurohormones and/or of hormones originating from the corpora cardiaca (CC) in phase change. For example, in spite of the vast literature on the adipokinetic hormones (AKH) that mobilize lipids as necessary fuel for intense migratory flights in crowded (gregarious) locusts, there are no data whatsoever on AKH in solitary (isolated) locusts. A chemically unidentified neurosecretory factor promotes the black patterns characteristic to gregarious hoppers, but this factor may not be restricted to locusts and their phase changes.

Further investigations are urgently needed from both basic and applied standpoints. The subject has been rather neglected since it was realized over 30 years ago that phase change does not precede but follows changes in population density. Nevertheless, if present or future insect growth regulators (IGR), such as hormone analogs and anti-hormonal agents, can prevent the change from solitary to gregarious phase, especially the associated development of aggregation behavior, marching behavior of hoppers and/or swarming behavior of adults, locusts would not aggregate actively and would not emigrate from localized areas. Such locusts would be easy targets to limited conventional or integrated control measures.

Key words: Locust phase changes, corpora allata, juvenile hormone, ventral (=prothoracic) glands, ecdysteroids, neurohormones, aggregation behavior, marching behavior, swarming behavior.

INTRODUCTION

The theory of locust phases was formed by Uvarov (1921) in a taxonomic revision of the genus *Locusta*. He concluded that *L. migratoria* and *L. danica*, formerly regarded as two distinct species, are respectively the swarming and the solitary forms, or "phases", of the same species. These forms are capable of transforming into one another and there are intermediates between the two forms. The phase theory was soon extended to other locusts, such as *Locustana pardalina, Schistocerca gregaria, Nomadacris septemfasciata* and some further species, for example, *Dociostaurus maroccanus* and *Chortoicetes terminifera* (for details and vast literature, see Uvarov's, 1966, 1977 and Albrecht's, 1967, books).

I defined locusts as such short-horned grasshoppers (Acrididae) "...that meet two criteria: 1) They form at some (rather irregular) periods dense groups comprising huge numbers, bands of hoppers and/or swarms of winged adults which migrate; and 2) they are polymorphic in the sense that individuals living separately differ in many characteristics from those living in groups" (Pener, 1983, p. 379). Different species of locusts belong to several different subfamilies of acridids.

According to current views, typical locust species show density-dependent phase polymorphism. A large number of characters, collectively termed "phase characteristics", change with the change of the phase. Such phase characteristics are found in morphology, morphometrics, anatomy, coloration, reproduction, development, physiology, biochemistry, molecular biology, cytology, behavior, and ecology. The extreme phases are usually termed "gregarious" and "solitary" (or "solitarious"). Full scale phase differences seem to be limited to the field. In the laboratory, locusts kept under crowding and in isolation respectively approach gregarious and solitary characteristics. Locust phase polymorphism is continuous and endless intermediates can be found between the extreme gregarious and extreme solitary phases. Moreover, phase change itself is continuous and induction of phase change is not instar-specific. Phase characteristics are shifted to either (solitary or gregarious) direction and the direction of the shift is reversible in any stage, all in response to appropriate changes in density. Some phase characteristics, for example certain behavioral patterns and some components of adult coloration, respond in the same instar to changes in density. Others, such as hopper coloration, show changes in the next and/or subsequent instars. Some phase characteristics of the hatchlings are affected by parental density. Phase transformation is cumulative, a shift starting in an instar progresses in the next instars and also in the next generation; a full scale phase transformation may take several generations. Different locust species may show somewhat different phase characteristics and the amplitude of the change may be species-dependent and sometimes even sex-dependent. Many density-dependent phase characteristics, such as color and morphometrics, are also affected by abiotic environmental factors, especially by humidity and temperature. Locust phase polymorphism, therefore, is an extremely complex phenomenon. It is comprehensively surveyed by Uvarov (1966, 1977) and Albrecht (1967) and more recently, though less comprehensively, by me (Pener, 1983).

The complexity of the phase characteristics and their changes may constitute major difficulties in evaluation of experimental results obtained from studies on endocrine effects on phase. An endocrine manipulation may induce appreciable shifts in some phase characteristics and leave others unaffected. Change of one or of a few phase characteristics does not necessarily mean that phase transformation has been accomplished. Thus, extreme caution is needed in the evaluation of the experimental findings. This point is often neglected by insect endocrinologists not having firm knowledge of locusts and the complexity of the phase change. Such negligence leads to oversimplification at best and to confusion in worse instances. On the other hand, lack of absolute correlation in the change of different phase characteristics may have applied advantages. If an IGR is capable of changing some phase characteristics that are important from the practical standpoint, lack of changes of some other phase characteristics may be considered as unimportant. As a hypothetical example, an IGR that would suppress active aggregation behavior or swarming flight behavior of gregarious locusts may have applied value, even if it does not affect other phase characteristics such as morphometrics or coloration.

A comprehensive review of the phase characteristics is outside of the scope of the present article. Only those used as indicators or parameters in experimental endocrine studies and those with apparent applied importance will be dealt with here.

THE CORPORA ALLATA (CA) AND THE JUVENILE HORMONE (JH)

The CA/JH undoubtedly affect many phase characteristics and so play a role in locust phase change. Implantation of extra CA or administration of JH or JH analogs induces green color which is a solitary characteristic (P. Joly and L. Joly, 1954; P. Joly *et al.*, 1956; L. Joly, 1960; Staal, 1961; P. Joly, 1962; Novák and Ellis, 1967; P. Joly and Meyer, 1970; Němec *et al.*, 1970; Roussel and Perron, 1974; Couillaud *et al.*, 1987; and many others). Solitary or isolated *Schistocerca* and *Nomadacris* usually undergo one more hopper instar than conspecific crowded locusts (Albrecht, 1955; review: Uvarov, 1966); thus, the metamorphosis of the solitary phase may be regarded as retarded. Lower values of the E/F morphometric ratio are characteristic to solitary adults and P. Joly and L. Joly (1954) and P. Joly (1956, 1962) reported that implantation of CA into crowded *Locusta* hoppers results in a decrease of the E/F ratio. These authors even obtained "hypersolitary" values. The CA/JH control vitellogenin synthesis in the fat body and vitellogenic oocyte growth in adult females (L. Joly, 1960; Highnam *et al.*, 1963; Pener, 1965, 1967; Girardie, 1966; Lazarovici and Pener, 1977; Chen *et al.*, 1979; and many others) and isolated locusts show higher fecundity than crowded ones (Norris, 1950; Albrecht, 1959; Papillon, 1960; Cassier, 1965a, 1966a, 1966b).

Some of these early results led Kennedy (1956, 1961, 1962) to assume that solitary locusts are somewhat neotenous or juvenile and the physiological mechanism underlying locust phase differences and phase change is based on more active CA, secreting more JH, in isolated locusts. This view is rather deeply rooted in the literature and even a relatively recent review (Nijhout and Wheeler, 1982) firmly holds it, claiming that the solitary phase is induced by specifically timed JH excess. The reason for this situation may be related to the facts that most of the cases in which CA/JH promote (or are assumed to promote) solitary characteristics were discovered and recognized earlier, received more attention, as well as wider publication, than those cases in which CA/JH promote (or are assumed to promote) gregarious characteristics. However, almost three decades ago, P. Joly (1962, p. 77) had already concluded that the

"...problem of physiological determination of locust phases cannot be explained on the basis only of differential activity of the corpora allata". Rowell (1971) advocated a similar conclusion.

The opinion that the CA/JH play an all-encompassing role in locust phase determination was criticized by me (Pener, 1983). Some other recent reviews (Hardie and Lees, 1985; Dale and Tobe, in press) also outlined the difficulties in accepting without restrictions this presumably oversimplified view. Table 1, summarizing investigated effects of CA/JH on phase characteristics clearly reveals that CA/JH promote several solitary characteristics, but some other phase characteristics are not affected by CA/JH and in some instances CA/JH promote gregarious characteristics. A full discussion of the data compiled in Table 1 is impossible within the page limitations of the present article. Here I limit myself to deal with two points only, both related to coloration: one is the green color inducing effect of CA/JH in hoppers and the other is the yellow color inducing effect of CA/JH in adult males.

Many research articles have firmly demonstrated that CA/JH promote the solitary green color (see some references above). However, solitary hoppers and subsequent adults of *Locusta* and *Locustana* exhibit the so-called green/brown color polymorphism (Faure, 1932; and many others; reviews by Uvarov, 1966; Rowell, 1971; Pener, 1983; Fuzeau-Braesch, 1985). Under high humidity the hoppers become green, but under low humidity they show "homochromy". Such non-green "homochrome" hoppers are often called the "brown" form (the term "green/brown polymorphism" is derived from this usage), but actually the color is not restricted to brown shades and the "brown" hoppers are capable of adjusting their color, whitish, straw-yellow, beige, buff, brown, grey, black, or almost any intermediate shade between these colors, to match the color of the underlying background. The very existence of homochrome solitary locusts demonstrates that the green color is not a necessary characteristic of the solitary phase. Injection of JH into isolated non-green (homochrome) *Locusta* hoppers induces green color (Nicolas, 1977). On the other hand, precocene-induced chemical allatectomy (cf. Pener *et al.*, 1978) of isolated *Locusta* hoppers leads to disappearance of the green color, but the resulting coloration is similar to that of the "brown" homochrome hoppers and so markedly different from the gregarious color (Pener and De Wilde, unpublished). Therefore, in isolated *Locusta* hoppers endocrine manipulations involving the CA/JH just shift one solitary characteristic to another (from homochrome to green, or *vice versa*). Promotion of the "brown" homochrome color by experimentally induced CA/JH excess in crowded hoppers has never been observed (cf. Pener, 1976b).

On the other hand, green/brown color polymorphism is not restricted to solitary locusts and it occurs in many acridids that show no density-dependent phase polymorphism (see Uvarov, 1966; Rowell, 1971). The CA/JH promote green color also in these species. Implantation of extra CA into hoppers of *Acrida turrita* induced green color (P. Joly, 1952) and similar treatment led to similar results in *Humbe tenuicornis, Gastrimargus africanus* and *Acanthacris ruficornis* (Rowell, 1967). In *A. ruficornis* even green adults were obtained, despite the fact that such adult coloration has not been observed in natural populations. Moreover, CA/JH also promote green color in some non-acridid insects (review by Raabe, 1983). In conclusion, the green color inducing effect of CA/JH is not specific to locust phase transformation.

Phase polymorphism is much less frequent in acridids than green/brown polymorphism and every major locust species is taxonomically closely related to many acridids which exhibit the latter. It is feasible to hypothesize that some not necessarily simple mechanism which controls green/brown polymorphism by CA activity and/or JH titers was "coapted" during evolution to play a partial role in a more complex locust phase polymorphism.

Gregarious adults of locusts, especially the males, become yellow with sexual

Table 1.—Effects of the CA and/or JH on locust phase characteristics. Phase characteristics for which no experimental findings nor circumstancial evidence are available in relation to an effect of CA/JH, are not included in the table (modified after Pener, in press).

Phase characteristic investigated (in parentheses: difference between phases*)	In relation to the given phase characteristic, the CA/JH**			References ǂ	Remarks, notes, doubts
	Promote solitary feature(s)	Promote gregarious feature(s)	Do not exert an effect, or the effect is not clear		
1. E/F morphometric ratio (higher in G).	+			1, 2, 3, 4,	Effect may be related to disturbed metamorphosis
2. F/C morphometric ratio (higher in S).	+?		+?	3, 4	Different authors draw somewhat different conclusions.
3. Shape of pronotum (convex in S, straight or concave in G).			+	2, 5	
4. Sternal hairs (longer in G).	+			4	Effect may be related to disturbed metamorphosis.
5. Thickness and number of gland cells in epidermis of adult male (more numerous in G).	+			6, 7	Effect may be related to disturbed metamorphosis.
6. Green color (absent in G, may be present in S).	+			1, 3, 4, 5, 8, 9, 10, 11, 12, and many others; review: 13	Green color is not a necessary characteristic of the solitary phase, effect is not restricted to locust phase polymorphism.
7. "Homochrome" coloration (absent in G, may be present in S).			+	14	CA/JH induce green color in homochrome hoppers, thus shift one solitary characteristic to another.

Phase characteristic investigated (in parentheses: difference between phases*)	In relation to the given phase characteristic, the CA/JH**			References †	Remarks, notes, doubts
	Promote solitary feature(s)	Promote gregarious feature(s)	Do not exert an effect, or the effect is not clear		
8. Black patterns in hoppers (present in G, absent in S except in black homochromy).	+?			4	Effect may be due to green color induction, or due to interactions with a black color promoting neurosecretory factor.
9. Yellow color in adults (present in G, absent in S except on hind wings of *Locusta*).		+		15, 16, 17 and many others	Target organ (epidermis) of isolated and crowded adults reacts differently to CA/JH.
10. Intensity of male sexual behavior (more intense in G).		+		18	Target organ (nervous system?) of isolated and crowded adults may react differently to CA/JH.
11. Fecundity of adult females (higher in S).	+?		+?	19, 20, 21	Results are open to different interpretations.
12. Adult life span (longer in S).		+		18, 19	
13. Adult reproduction; effects "transmitted" to the progeny***.	+?			19, 20, 21, 22, 23, 24	Conclusion is open to slight doubts; not all experimental data support the conclusion.
14. Number of hopper instars = number of eye stripes in some species (higher in S of some species).	+?		+?	25	The claim that CA/JH may induce an extra hopper instar is entirely theoretical; some experimental data do not support this claim.

Phase characteristic investigated (in parentheses: difference between phases*)	In relation to the given phase characteristic, the CA/JH**			References †	Remarks, notes, doubts
	Promote solitary feature(s)	Promote gregarious feature(s)	Do not exert an effect, or the effect is not clear		
15. Rate of O_2 consumption (higher in G).		+?	+?	3, 26, 27	
16. Heartbeat frequency (higher in S).			+	28, 29, 30	CA/JH do affect heartbeat frequency, but this effect is not responsible for phase differences.
17. Fat content (higher in G).	+?			31 as compared to 32, 33.	Evidence is entirely circumstantial.
18. Isoenzymes in hoppers (some qualitative and quantitative differences between G and S).			+?	34	JH treatment did not induce insoenzymes which were induced by isolation; as a "negative" result, it is not entirely conclusive.
19. Adult flight and/or spontaneous locomotor activity (higher in G).		+?	+?	35, 36, 37; review on flight: 38	Experimental data and evidence are not clear.

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* G = gregarious or crowded locusts; S = solitary or isolated locusts.

** Although every effort was made to present an objective picture, this task is practically impossible when results are conflicting or open to different interpretations. Some other authors may prefer removal or insertion of a question mark (which reflects some uncertainty) in relation to some effects.

*** These include: weight of hatchlings (higher in G), color of hatchlings (differences between G and S), number of ovarioles in female hatchlings (higher in S) and morphometrics of hatchlings (hatchlings of S are smaller and morphometrical analyses show differences between G and S).

†References: 1. P. Joly and L. Joly, 1954; 2. P. Joly, 1956; 3. P. Joly, 1962; 4. Staal, 1961; 5. P. Joly *et al.*, 1956; 6. Cassier and Delorme-Joulie, 1976; 7. Cassier, 1977; 8. P. Joly and Meyer, 1970; 9. Němec *et al.*, 1970; 10. Couillaud *et al.*, 1987; 11. Novák and Ellis, 1967; 12. Roussel and Perron, 1974; 13. Rowell, 1971; 14. Nicolas, 1977; 15. Loher, 1961; 16. Pener, 1976b; 17. Pener and Lazaroviçi, 1979; 18. Pener, 1976a; 19. Cassier, 1965a: 20. Cassier, 1966a; 21. Cassier, 1966b; 22. Lauga, 1976; 23. Lauga, 1977; 24. Cassier and Papillon, 1968; 25. Kennedy, 1956; 26. Roussel, 1963a; 27, Roussel, 1963b; 28. Roussel, 1975a; 29. Roussel, 1975b; 30. Roussel, 1975c; 31. Matthée, 1945; 32. Odhiambo, 1966a; 33. Strong, 1968; 34. Colgan, 1987, 35. Cassier, 1965b; 36. Odhiambo, 1965, 37. Odhiambo, 1966b; 38. Pener, 1985.

maturation (see Uvarov, 1966; Pener, 1983). This yellowing absolutely depends on the CA/JH. Allatectomy results in complete absence of the yellow color, but reimplantation of CA or administration of JH restores yellowing (Loher, 1961; Pener, 1965, 1967; Girardie, 1966; Pener *et al.*, 1972; Pener and Lazarovici, 1979; and others). Isolated adult male locusts never turn yellow, except on the hind wings of *Locusta*. In this case, therefore, CA/JH promote a gregarious characteristic. Were these facts discovered and widely publicized before the green color inducing effect of CA/JH, the conclusion that crowded adult males have more active CA or higher JH titers than isolated ones would have been easily reached. Such a conclusion, however, is unjustified. I performed some comprehensive experiments on the subject (Pener, 1976b) and found that implantation of extra CA into isolated adult *Locusta* males does not induce yellowing, whereas simple transfer of the isolated adults to a newly formed crowd does, even without implantation of extra CA. Thus, although yellowing is completely controlled by the CA/JH, the competence of the integument of the adult male to become yellow is governed by some density-dependent unknown intrinsic factor(s). The lack of response of the isolated adult males to the yellow-color inducing effect of the CA/JH cannot be explained by the assumption that the relevant competence of the integument was already fixed by JH titers (or other endocrine events) experienced during previous hopper instars, because simple transfer of the isolated adult males to a crowd changes the competence and leads to yellowing. Thus, the target organ (integument) responds differently to JH in crowded and isolated adult males.

JH biosynthetic activity of the CA of crowded and isolated locusts was compared by radiochemical assay *in vitro* (for details and references in relation to the method, see Tobe and Stay, 1985) only in a few studies. The major findings are summarized in Table 2. The literature on comparison of JH titers in crowded and isolated locusts is also rather limited, and investigations were carried out only on *Locusta*. These are summarized in Table 3. Undoubtedly, JH biosynthetic activity of the CA and JH titers were found to be higher in isolated than in crowded adults of *Locusta*. However, the relevant investigations of Dale and Tobe (1986) were carried out only up to day 8 after fledging and so it is difficult to decide whether the differences reflect a genuinely higher gland activity and JH titer, or just an earlier increase associated with the shorter period of sexual maturation of the isolated adults in this species (cf. Norris, 1950). For a more meaningful comparison of isolated and crowded adults, CA activity and/or JH titers should be related not to chronological age but to physiological events, such as percent of increase in oocyte length during at least the whole first gonotrophic cycle and preferably during several consecutive cycles, Unfortunately, no such reliable data are available for *Locusta*. Neither the *Galleria* bioassay used by L. Joly *et al.* (1977), nor the radioimmunoassay employed by Fuzeau-Braesch *et al.* (1982) may be considered as completely reliable for JH titer determination.

In *Schistocerca* the period of sexual maturation, i.e., the time elapsing between fledging and first oviposition, is shorter in crowded than in isolated adults (Norris, 1952; Papillon, 1968), a situation opposite to that found in *Locusta*. Interestingly, in *Schistocerca* the differences between CA activity of crowded and isolated adult females were mostly temporal (Injeyan and Tobe, 1981) and less marked than in *Locusta*. The CA of isolated adult *Schistocerca* females showed relatively higher rates of JH biosynthesis earlier in the first gonotrophic cycle. This earlier activity correlated well with a shorter period from fledging to first appearance of vitellogenin in the oocytes of the isolated locusts. However, in spite of the initially higher CA activity and earlier onset of vitellogenesis, vitellogenic oocyte growth was slower in the isolated females and eventually the crowded females completed the first gonotrophic cycle earlier than the isolated ones. Were the CA/JH the only factor involved, the initially higher

Table 2.—JH biosynthetic activity of the CA in crowded and isolated locusts assessed by radiochemical assay *in vitro*.

Species and instar	Major finding(s)	Reference	Remarks
Schistocerca; last two nymphal-instar females.	Activity is higher in isolated than in crowded hoppers.	Injeyan and Tobe, 1981.	
Schistocerca; adult females, first gonotrophic cycle.	Activity is slightly higher in isolated than in crowded females.	Injeyan and Tobe, 1981.	The differences in activity are mostly temporal.
Locusta; adult females, up to day 8.	No difference up to day 5-6; higher activity in isolated females on day 8.	Dale and Tobe, 1986.	Higher activity in isolated females may just reflect earlier activation of CA.

Table 3.—Comparison of JH titers in crowded and isolated *Locusta*.

Instar	Major finding(s)	Method	Reference	Remarks
Last two hopper instars.	Higher titers in isolated than in crowded hoppers.	*Galleria* biossay.	Joly *et al.*, 1977.	
Adults.	Higher titers in isolated than in crowded adults.	*Galleria* bioassay.	Joly *et al.*, 1977.	Differences may just reflect an earlier increase of titer in isolated adults.
Last-instar hoppers and adults.	No clear cut differences between isolated and crowded locusts.	RIA*.	Fuzeau-Braesch *et al,* 1982.	
1-day old and 4-day old adult females.	No differences in 1-day-old adult females. Higher titers in isolated than in crowded females on day 4.	GC-MSM**.	Dale and Tobe, 1986.	Differences may just reflect an earlier increase of titer in isolated adults.

* RIA = Radioimmunoassay.

** GS-MSM = Gas chromatography-mass spectrometry.

gland activity would have resulted in an earlier completion of the cycle in the isolated females. The fact that this did not occur may indicate the existence of a density-dependent factor that influences oocyte growth beside the CA/JH.

In conclusion, it seems that there are some differences in CA activity and JH titers between isolated and crowded locusts. These differences, however, may just constitute an additional physiological phase characteristic, though at the same time these differences may also cause appropriate changes in some but not in all phase characteristics. If so, CA activity and JH titers do not constitute the primary physiological causal factor in phase change and they probably stand not at the beginning, but somewhere in the middle of a complex chain of physiological events and causal factors leading to phase transformation. Thus, the hypothesis that the solitary phase is just a neotenous form induced by permanent or even specifically timed JH excess, seems to be at best an oversimplification.

THE VENTRAL GLANDS (VG) AND ECDYSTEROIDS

The VG of acridids are at least analogous to the prothoracic glands of other insects; they are located in the posterior part of the head (P. Joly *et al.*, 1956; Staal, 1961) and they constitute the source of ecdysteroids (molting hormone) in the hopper stages (cf. Hirn *et al.*, 1979; Reichhart and Charlet, 1986).

Solitarizing effects of the VG were advocated by Ellis and Carlisle (1961) and Carlisle and Ellis (1962) who claimed to find a positive correlation between the size of the VG and the F/C morphometric ratio in *Schistocerca* and reported that partial extirpation of the VG promotes gregarious color in *Schistocerca,* though not in *Locusta.* The same authors (Carlisle and Ellis, 1963) also reported reduced marching activity in crowded *Locusta* hoppers after injection of VG extracts, and Michel (1972) observed that implantation of presumably active VG decreased flight activity in *Schistocerca* adults. On the other hand, Staal (1961) found no appreciable effect of implanted VG on color, nor on morphometric ratios in *Locusta,* and Girardie and Joly (1968) reached similar conclusions.

Later studies, carried out in several independent laboratories, clearly demonstrated that ecdysteroid titers are quite similar in crowded and isolated *Locusta* (L. Joly et al., 1977; Ismail *et al.*, 1979; Fuzeau-Braesch *et al.*, 1982) and *Schistocerca* (Wilson and Morgan, 1978). Therefore, it seems to be improbable that ecdysteroids play a major causal role in locust phase transformation. This conclusion leaves the reports of Ellis and Carlisle (1961), Carlisle and Ellis (1962, 1963) and Michel (1972) unexplained and open to speculations. One line of such speculation would be that the VG produce some other hormone(s) beside ecdysteroids (cf. L. Joly *et al.*, 1969; Hoffmann and Weins, 1974; Charlet *et al.*, 1988; see also discussion by Wilson and Morgan, 1978).

Carlisle and Ellis (1959) reported that the VG degenerate in crowded adults of *Locusta* and *Schistocerca,* but persist in isolated adults of these species. Later work somewhat modified this conclusion at least for *Locusta* (Cassier and Fain-Maurel, 1968, 1969; Fain-Maurel and Cassier, 1969). In isolated green adults kept under high humidity the VG persist, but the glands degenerate in non-green isolated adults maintained under low humidity. Moreover, under long days the VG degenerate but under short days persist in crowded *Locusta* adults. The persistence or degeneration of the VG seems to be influenced, therefore, by both density and abiotic factors and the physiological importance of this phenomenon and its relation to phase change is unclear.

CORPORA CARDIACA (CC) NEUROSECRETORY CELLS (NSC), AND NEUROHORMONES

The activity of the CA is affected by neurosecretory and nervous signals from the brain (reviews by Raabe, 1982; Tobe and Stay, 1985) and an allatotropic neurohormone was partially purified from brains of *Locusta* (Gadot *et al.*, 1987). The activity of the prothoracic glands is also controlled by the brain, primarily by the prothoracicotropic hormone(s) (reviews by Raabe, 1982; Bollenbacher and Granger, 1985), and in accord with this concept, Reichhart and Charlet (1986) have found that brain-CC extracts exert a prothoracicotropic effect on the VG of *Locusta in vitro.* Thus, any effect on phase polymorphism which may be related to differential activity of the CA and/or the VG in gregarious and solitary locusts, may eventually be governed by the regulatory effects of the brain or brain and CC. Since neurohormones play a major role in the regulation of CA and VG activity (see above), they may be as much involved in the regulation of locust phase polymorphism as the CA or VG themselves, though the effect(s) of such neurohormones on phase may be considered as indirect. Possible phase related differences in allatotropic, allatostatic, and/or prothoracicotropic neurohormones have never been investigated.

Extensive studies on locust adipokinetic hormones (AKH) revealed that AKH, produced by the glandular lobes of the CC, promote mobilization, transport and possibly also utilization of lipids as necessary fuel for sustained long-time migratory flights characteristic to gregarious locusts (reviews by Stone and Mordue, 1980; Goldsworthy, 1983; Beenakkers *et al.*, 1985; Orchard, 1987). Locusts deprived of the glandular lobes of the CC and of AKH are unable to make long flights because of lack of adequate fuel supply. Despite the extensive studies and hundreds of research articles, all AKH related investigations were carried out on crowded locusts; there is not a single publication devoted to AKH in isolated ones! Nothing is known, therefore, on possible AKH related differences between gregarious and solitary locusts. These possible differences may be qualitative (there are two AKH in *Locusta* and also in *Schistocerca*) and/or quantitative and should be explored from various aspects, such as AKH content of the CC, rate of release of the AKH, and AKH titers. The adipokinetic responses, that is the responses of the target systems to AKH, may also be qualitatively or quantitatively different between gregarious and solitary locusts.

Staal (1961) obtained an increase of the black patterns after implantation of extra CC into hoppers of *Locusta* and this effect was traced back to some NSC in the protocerebrum (Girardie and Cazal, 1965; Girardie, 1974). However, this chemically yet unidentified NSC-CC factor, or a factor of similar origin, also promotes black color (though in less defined patterns) in isolated *Locusta* (Nicolas and Ismaïl, 1978), being probably involved in the control of the black homochrome response. Moreover, a factor from the same organs is responsible for the black homochrome response of *Oedipoda coerulescens* (Moreteau, 1975) which exhibit marked homochromy but neither green/brown, nor phase polymorphism. Thus, like the effect of JH on green color (see above), the black-color-promoting effect of this NSC-CC factor may not be restricted to locusts or their phase polymorphism. Perhaps again an existing hormonal mechanism was "coapted" during evolution to constitute a part of more complex phase-controlling physiological mechanisms. Possible effects of this NSC-CC factor on other phase characteristics remain to be investigated.

Bernays (1980) has suggested that a factor from the CC reduces locomotor activity in crowded hoppers of *Locusta.* The role of this putative factor in behavior related phase differences has not been investigated, though it may well be assumed, as a working hypothesis, that this factor promotes the more sedentary solitary behavior.

The relationships, if any, between biogenic amines which may function as neurohormones and locust phase polymorphism is unclear. Fuzeau-Braesch and David (1978), Fuzeau-Braesch *et al.* (1979) and Benichou-Redouane and Fuzeau-Braesch (1982) reported that octopamine content of whole heads and of various parts of the nervous system is higher in isolated than in crowded Vth-instar hoppers and adults of *Locus-*

ta. In contrast, Morton and Evans (1983) obtained no differences in octopamine levels of nervous tissue, muscles, or whole heads between crowded and isolated *Schistocerca* adults and strongly criticized the work of Fuzeau-Braesch and David (1978) and of Fuzeau-Braesch *et al.* (1979). In conclusion, even if phase-dependent differences exist in some biogenic amines, their causal role and mode of involvement in phase change remain to be clarified.

Yet unknown or unindicated neurohormones may also be involved in locust phase change. The search for such unknown hormones is difficult because they cannot be straightforwardly bioassayed. Nevertheless, pilot experiments, aimed to reveal possible existence of neurohormones affecting phase, should be carried out.

APPLIED ASPECTS

According to present concepts, induction of the gregarious phase is a result of increased population-density. In other words, phase change follows and does not precede changes of density. Theoretically, strict conventional control that prevents population increase may be sufficient to prevent locust outbreaks. However, the very existence of the current locust plague indicates that such conventional methods are not always sufficient. The present broad-scale application of toxic chemicals results in pollution, endangers the fragile ecosystem of semi-arid zones of the Old World and may lead to unselective destruction of beneficial insects, including natural enemies of other pests. Thus, alternative non-conventional or integrated locust pest management should be sought.

If the change from the solitary to the gregarious phase, especially the appearance of aggregation behavior of hoppers and adults, marching behavior of hoppers and/or swarming flight behavior of adults can be prevented despite increase of densities over critical levels, the locusts may not be able to escape from localized areas. Present and future IGR, such as hormone analogs and anti-hormonal agents seem to be reasonable candidates for such prevention of gregarization and gregarious behavior. Locusts which would not aggregate actively and would be unable to make large-scale collective emigrations from localized areas, would be easy targets to limited conventional or integrated control measures. Most of the locusts may meet death even without any interference because of starvation imposed by food limitations in such localized areas. Moreover, if the appropriate IGR are not toxic to Vertebrates, the locusts may be used as food for domestic animals or for human beings.

Keeping these points in mind, the following subjects should be studied from the applied standpoint.

1. *Effects of JH.* JH is probably not the key factor that controls locust phase transformation; nevertheless, it affects certain phase characteristics (see above) and it may affect aggregation behavior and/or marching behavior of hoppers. These subjects have not been explored at all. In regard to the effect of CA/JH on flight activity of crowded adults the data in the literature are somewhat controversial (see Pener, 1985). However, this controversy itself indicates that CA/JH may not have a crucial effect on migratory locust flights.

2. *AKH.* As already outlined, nothing is known on AKH content and adipokinetic responses in solitary adults. Although such solitary adults fly and even make longer night flights (see Uvarov, 1977), their flight performance is much inferior to that of gregarious adults. Knowledge and understanding of possible AKH-related differences between gregarious and solitary adults may yield novel applied approaches, such as interference with AKH production (synthesis and/or release) or with adipokinetic responses. Development of IGR with anti-adipokinetic mode of action should eventually be sought.

3. *Endocrine effects on marching behavior and/or on marching related fuel metabolism in hoppers.* Gregarious hopper bands march intensely for long periods in the field (see Uvarov, 1977). However, fuel

mobilization and fuel metabolism, presumably necessary for the marching, and possible endocrine effects on marching behavior or on marching related fuel metabolism have not been explored despite the fact that it was demonstrated over 40 years ago that marching can be induced and studied even in the laboratory (Ellis, 1951). It is highly desirable to study the possible hormonal background of marching behavior and of related fuel metabolism. If endocrine factor(s) turn(s) out to be involved in the control of marching, development of IGR with "anti-marching" effect should be sought.

4. *Possible roles of neurohormonal factors and of biogenic amines in phase transformation and gregarious phase related behavior.* As already outlined, investigations aimed to explore possible roles of such factors in phase change and gregarious behavior have been much neglected. It is highly desirable to study possible roles of known or indicated neurohormones (such as allatotropine(s), allatostatin(s), the NSC-CC black-pattern-promoting factor, and the postulated "locomotor-depressing" factor), as well as of yet unknown neurohormones on phase characteristics, especially in relation to behavior. If a neurohormone that plays a major role in these respects is found, it may constitute the starting point for the development of appropriate IGR.

5. *Hormone-pheromone interrelations.* Gregarizing and solitarizing pheromones seem to be involved in locust phase changes (see Ferenz in this volume). Possible hormonal control of the production of these pheromones has not been investigated, though it is known that the production of a maturation accelerating pheromone is controlled by CA/JH (Loher, 1961). If the production of a pheromone with major effect(s) on phase or on gregarious behavior is controlled by endocrine factors, appropriate IGR to be developed may have considerable applied value.

Among the relevant potential IGR presently known only JH analogs are produced commercially and employed for practical pest control. Anti juvenile agents are also available (Staal, 1986), but the currently known compounds do not seem to be suitable for practical usage. IGR interfering with insect neurohormones (peptides) are not yet available, but probably they will become available in the near future because many institutes, laboratories and commercial firms are engaged in relevant applied research. It may be estimated that such IGR will be developed within a few years. By this time locust biologists should be ready to pinpoint the targets for these IGR.

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Tratamientos

Control

Bol. San. Veg. Plagas (Fuera de serie) 20: 59-66, 1990

The development of a new plague of the Desert Locust *Schistocerca gregaria* (Forskål) (Orthoptera; Acrididae) 1985-1989

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ABSTRACT

The period summer 1985 to summer 1989 was marked by frequent and successful breeding in the Central and Western Regions of the Desert Locust invasion area. The plague developed because suitably timed rains fell in areas which were reached rapidly by increasingly gregarious populations which in 1987-88 allowed virtually continuos breeding in West and Northwest Africa. Due to the inaccessibility of certain areas, the lack of adequate control measures in some parts of the infested area and the use of non-persistent pesticides, the locust situation was not brought under full control in spite of very large scale operations. However, the latter continued through 1988 and no winter-spring breeding 1988/89 occurred in West Africa. In 1989 there was a dramatic decline of the plague. Residual populations now (July 1989) exist in most Sahelian countries, and if the 1989 summer rains are good, there could be a rapid resurgence of the plague. Otherwise there is a good chance to terminate the plague by the end of 1989.

Key words: Band, breeding, generation, gregarious, hopper, invasion, migration, swarm.

1. There were good summer rains in the interior of Sudan and adjacent areas of northern Ethiopia in summer 1985, which resulted in a local upsurge of the Desert Locust in eastern Sudan. Day-flying adults were seen from a fishing trawler 40 kilometres west of Jizan in early November and in early December patchy gregarious breeding commenced in the Lith and Qunfidah Tihamas of western Saudi Arabia. Breeding also started on the Red Sea coast of Sudan in early November and in addition two swarms from the interior reached the Red Sea coast between Port Sudan and Tokar in early January 1986. Control operations were mounted in Saudi Arabia, Sudan and Egypt. Egypt was invaded in early February but there were some escapes and swarms and subsequently hopper infestations occurred in the interior of Saudi Arabia between March and August 1986.

2. In early June there were reports of swarms moving south in the Yemen Arab Republic and later of gregarious breeding in the People's Democratic Republic of Yemen. There were also several reports of adults in Oman, Pakistan and India indicating that at least some adults had moved east.

3. Migration to the west was, however, much more significant. A swarm was seen at Musmar in the Red Sea Province in late June and in early July 1986 an airborne observer reported flying through locusts for 40 minutes between Mersa Teclai and Halibai in northern Eritrea. Subsequently there were numerous unconfirmed reports of swarms in Eritrea and in late August fifth instar hopper bands began to enter Sudan east of Kassala. In the interior of Sudan, where the main control efforts were concentrated on controlling grasshopper infestations in the cultivated areas, the first generation of Desert Locust breeding to the north of the cropping areas was virtually missed until, in September, late instar hopper bands and swarms were found in a broad belt extending from the Red Sea Province to Northern Darfur. Aerial and ground control operations were mounted against these populations and against a second generation of breeding but, again, control was not sufficiently effective and there were numerous reports of swarms in November and December which were moving east and reached Red Sea coastal areas of Sudan, Eritrea, Saudi Arabia and Yemen Arab Republic. Control operations in Saudi Arabia completely controlled the infestations by the third instar in mid-January 1987. In Sudan control continued until late April but in Eritrea breeding continued on the coast until July giving rise to swarms which invaded the interior of Sudan in late May and the highlands of northern Ethiopia between May and July.

4. In Western Africa in 1985, adults produced as a result of first generation summer breeding in Niger, Mali and Mauritania increased rapidly in numbers in southwest Mauritania in October 1985, and bred giving rise to gregarising populations. Control was undertaken but some swarms were produced. These subsequently scattered but considerable numbers of adults overwintered in the southern Sahara; in September and October 1986 mixed populations of gregarised and partially gregarised individuals were found in Niger, Mali and later Mauritania on a scale which suggests that the indigenous populations had been augmented by large numbers of locusts from the east. But, as in the Sudan, the presence of large-scale grasshopper infestations in the crop-growing areas meant that the first-generation infestations in the southern Sahara were not monitored or controlled. Medium-scale control operations were mounted against the second generation and it seemed likely that no significant gregarious populations survived at the end of the 1986 summer breeding season in West Africa or western Sudan. However, in May 1987 swarms were seen in Northern Darfur.

5. Unusually early rains in western Sudan and northeastern Chad at the end of May 1987 provided excellent breeding conditions for the onset of unusually early summer breeding and permitted two generations of summer breeding to occur. Aerial and ground control operations were mounted up to about 16° N but in the more northern areas no survey or control operations were possible due to lack of security; in view of subsequent developments it appears that this breeding was on a very large scale. In Darfur a number of swarms were produced in October and November and some were controlled but the extent of the escapes is unknown. Breedind on a smaller scale also occurred in Aïr in Niger.

6. In early October 1987 numerous swarms from northeastern Chad moved rapidly west and then northwest across northern Niger and the extreme south of Algeria, reaching Tindouf on 17 October and, later, northern Mauritania, southeastern and southwestern Morocco. An intensive aerial and ground control campaign was mounted against them, particularly in Morocco where some 200,000 hectares were treated, but some swarms laid in northern Mauritania, which had received very heavy rainfall in September. Other swarms laid in southwest Morocco which also provided favourable conditions for breeding. Another westward migration in October resulted in swarms reaching northeast Mali and central Mauritania, and breeding also commenced in both areas.

7. Large-scale control operations were mounted against all these infestations but the total area treated, some 500,000 hectares, was certainly only a small proportion of the total area actually infested because in late January 1988 new generation swarms began to form. Some of these moved north and northeast into southern Morocco and later across northern-central Algeria reaching Tunisia and northwest Libya in early March and Egypt in late April and May. In Morocco the swarms remained south of the Atlas. In Algeria most swarms remained south of cultivated areas in western and in central-eastern parts of the Atlas Saharien but in Tunisia some swarms did reach cultivated areas. Very large scale aerial and ground control operations were launched against the swarms but many laid and young hoppers started to appear in late March. Further very large scale control operations were mounted against the hoppers but new generation adults started to appear in Morocco in early May. By mid-June some 4,800,000 hectares of hopper and adult infestations had been treated in Morocco, Algeria, Tunisia, Libya and Mauritania. In southeast Algeria and southwest Libya there were several reports of swarms and, later, breeding but its extent was unknown.

8. Other swarms, however, remained to breed again in southwest Morocco and northern Mauritania and, although these second generation hopper infestations were partially controlled, new swarms began to appear in the sub-region in mid-March. Under the influence of an Azores anticyclone these moved south and southwest to invade southern Mauritania, Senegal and Cape Verde, which was reached on 22 March, and on the 26th flying locusts were seen from a ship about 800 kilometres southwest of the Cape Verde islands.

9. In early April 1988 the swarms moved southeast, invading western Mali on about 10 April, causing considerable local damage, and Gambia in mid-April. These were joined by other swarms moving south through eastern Mauritania and by yet others moving south across eastern Mali, which reached the Gao area in mid-April. By 28 April a number of swarms had coalesced to form one reported to measure 120 km by 25-30 km near Niafunke. The swarms continued to move south, invading Guinea and Burkina Faso in early May. Yet another wave of swarms reached western Mauritania from the north in early May.

10. The invasion of the Western Sahel from winter-spring breeding further north on such a scale and so early is unprecedented. After good rains in late April and early May, there was a dry period and the number of swarm reports declined, probably as the swarms split up prior to laying.

11. Further east, Niger was invaded in early April, when swarms were reported from Aïr, but later there were several reports from eastern oases, while other swarms moved south towards Zinder and Niamey. In late May swarms were reported from Chad and western Sudan.

12. Western Egypt was invaded in late April, and again in late May from the southwest; these events raise the possibility that very considerable numbers of adults may have over-wintered in the Sahara.

13. There was rather widespread breeding in western, central, and eastern Sudan during the summer of 1988. This was partially controlled but sufficient adults escaped to commence winter breeding on the Red Sea coast of Sudan and in southeastern Egypt. This is again an area difficult of access and the breeding was thought to be on a rather small scale but in April 1988 several swarms escaped to the southeastern Desert of Egypt and northern Saudi Arabia, where they laid and were being controlled.

14. The situation in the rest of the Near East and Southwest Asia remained calm until June 1988.

15. In July, swarms coming from West Africa continued to move eastwards and invaded northern Ethiopia and The Yemen Arab Republic in late July. By August Northwest Africa was finally clear of swarms.

16. 1988 summer rains were heavy and widespread throughout the Sahel from Mauritania to Sudan. The swarms matured rapidly and laid so that many bands were present from July onwards in the west, and from August onwards in the east. These in turn produced swarms which matured with great speed giving rise to a second generation of breeding in Mali, Niger and western Chad during late September and early October. At that time some swarms from the Sahel started to migrate northwards across Algeria reaching Morocco by 10 October. Immediately afterwards a much larger invasion arrived from Mauritania. These necessitated another very rigorous aerial and ground campaign during which a further 1,700,000 hectares were controlled in Morocco including up to 100,000 hectares a day in early November. In Algeria 150,000 hectares were treated. Swarms from central and western Sudan and from northern Ethiopia moved first to the Red Sea plains in late September and then across the Red Sea to the Central Tihama of Saudi Arabia where a large aerial and ground control campaign was mounted.

17. Swarms from western Sudan and Chad and areas to the west moved west during October 1988. Many continued to move in that direction into the Atlantic Ocean so that during mid October locusts crossed the Altlantic and invaded the eastern Caribbean and northern coastal areas of South America on a front of some 1,500 km. Such a crossing is without known precedent. An enormous number of locusts must have perished. The locusts which reached the Caribbean were reported to have died quickly but there has been a recent report ot hoppers in Dominica, which may be of Desert Locusts. There were several other unusual migrations out to sea during 1988 including invasions of Italy and Greece in March and May, and of the British Isles in October-November. It is not as yet known whether these unusually frequent and large-scale offshore movements were caused by exceptional weather conditions or exceptional swarm flight behaviour.

18. Swarms continued to form in the Sahel until late November and to migrate from there to Northwest Africa. Swarms also continued to move eastwards in Sudan and across the Red Sea; some spread into central Saudi Arabia with a few swarms reaching southern Jordan and the eastern coastal areas of the Arabian Peninsula, southern Iraq, Kuwait and southwest Iran in late October-early November. During late November a small number of swarms moved rapidly northwards across Chad and Libya and then swung east across the Eastern Mediterranean. As a result swarms were reported in Libya, Egypt, the coast of Syria and Lebanon, and for the first time on record, in southwestern Turkey.

19. By the end of 1988 swarms were effectively restricted to four areas Northwest Africa and especially Morocco; the Red Sea coastal plains on both sides of the Red Sea and the interior of Arabia; the southern Sahara where breeding continued throughout the winter in northwest Niger and northeast Mali, and in southern Mali, Senegal and extreme southern Mauritania. In West Africa the swarms which moved south with the retreating Inter-Tropical Convercence Zone (ITCZ) in late 1988 spread even further south in early 1989, reaching Guinea Bissau and Guinea during February and March. There were confirmed reports of swarms from southern Cameroon 300 kilometres south of the limit of the invasion areas known from previous plagues.

20. The winter and early spring of 1988-89 was, by contrast with 1987-88, exceptionally dry. A blocking high pressure system over Southern Europe persisted from December until late March forcing rain-producing depressions to track northwards. Conditions were unfavourable for breeding in Northwest Africa, on the Red Sea coastal plains and in the northern interior of the Arabian Peninsula. Virtually no breeding occurred in those areas. The combined effect of unfavourable conditions and vigorous control campaigns rapidly reduced the locust populations although a few swarms did reach the United Arab Emirates, Qatar and Kuwait before being destroyed. By March no substantial infestations were known to exist in Arabia. Heavy rain occurred during late March and April in Northeastern Africa and Arabia. The occurrence of some hopper bands in Djibouti in late May, however, indicated that some pockets of gregarious locusts persist in the Central Region.

21. Since the end of January only a small amount of control has been carried out. The number of swarm reports remained low in April but in May there was a rapid increase in the numbers of immature swarms reported in southern Mali, Burkina Faso and southwest Niger as the swarms became active with the return of the ITCZ. In June there were no more reports of swarms but only of scattered populations.

22. The largest populations at present are probably those recently reported in Niger, Mali, Burkina Faso and Mauritania. These have two origins: those in southern areas are the result of late 1988 summer breeding in the western Sahel and those in the north are the result of 1988-89 winter and spring breeding in the southern Sahara. Populations to the north of the ITCZ are likely to continue to move southwestwards and those to the south to move eastwards, possibly reaching as far east as western Sudan.

23. The main concern is now to be on the alert for the start of a chain of events which could, if unchecked, lead to the resurgence of the plague. Such a resurgence will require substantial rain and consequent successful breeding, in a sequence of areas within the normally arid recession distribution area. Every past sequence has been different so it is not possible at present to predict where and when the next sequence will occur. The main survey effort should be concentrated in the southern fringes of the Sahara and in the Sahel, the central belt in Sudan, the southern parts of the Arabian Peninsula and the Indo-Pakistan desert and surrounding areas in the Eastern Region.

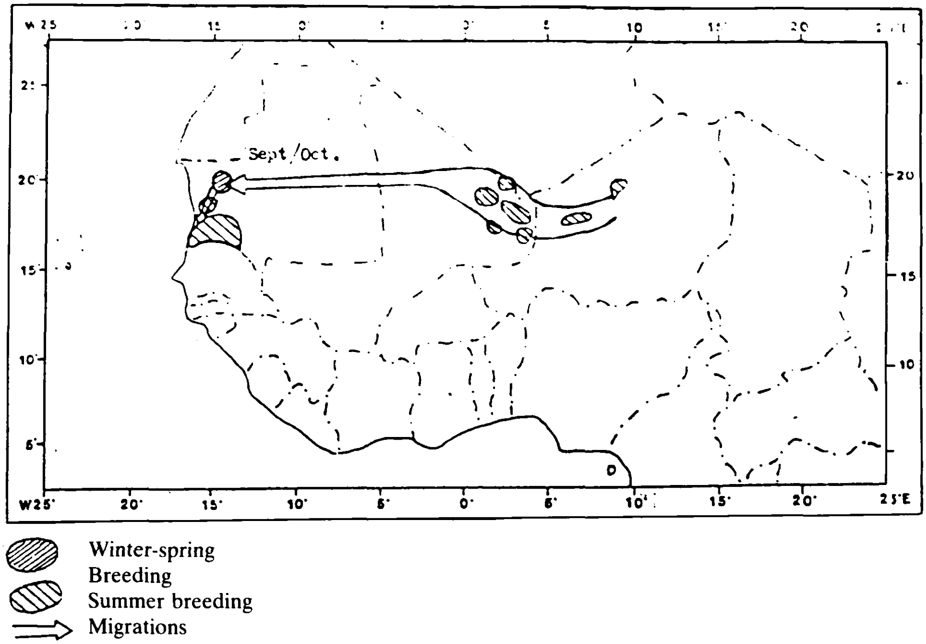


Fig. 1.—1985 Campaign.

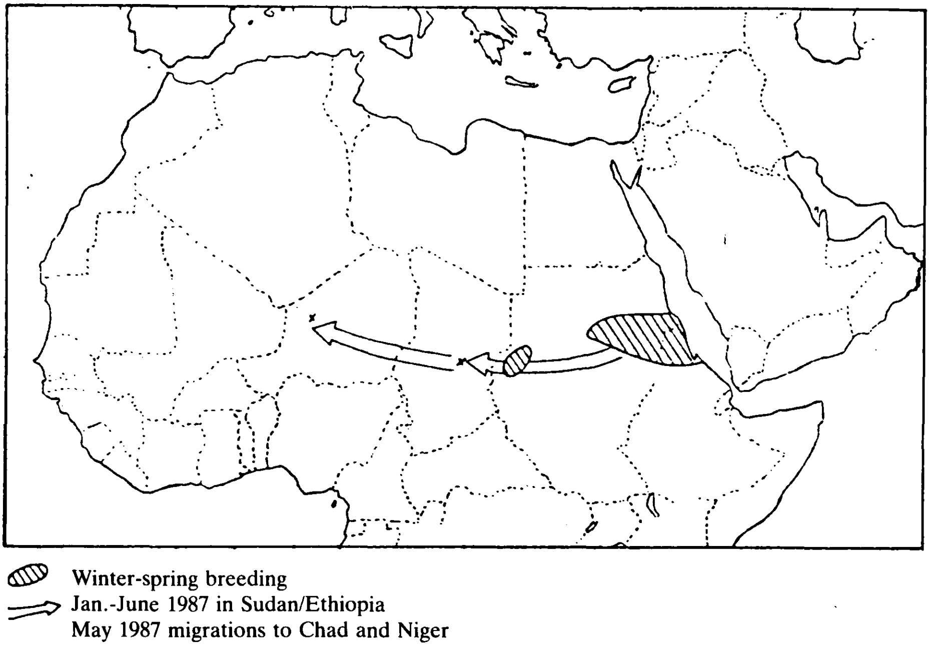
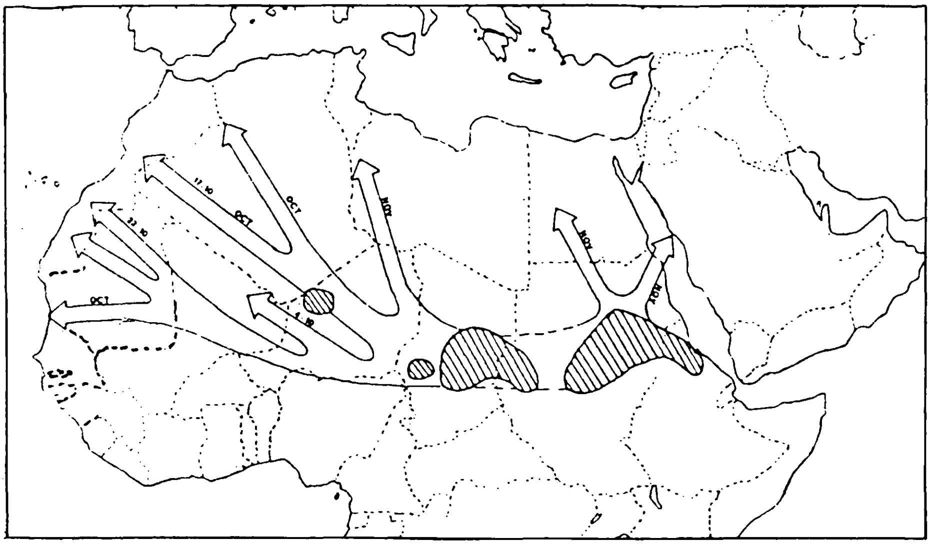
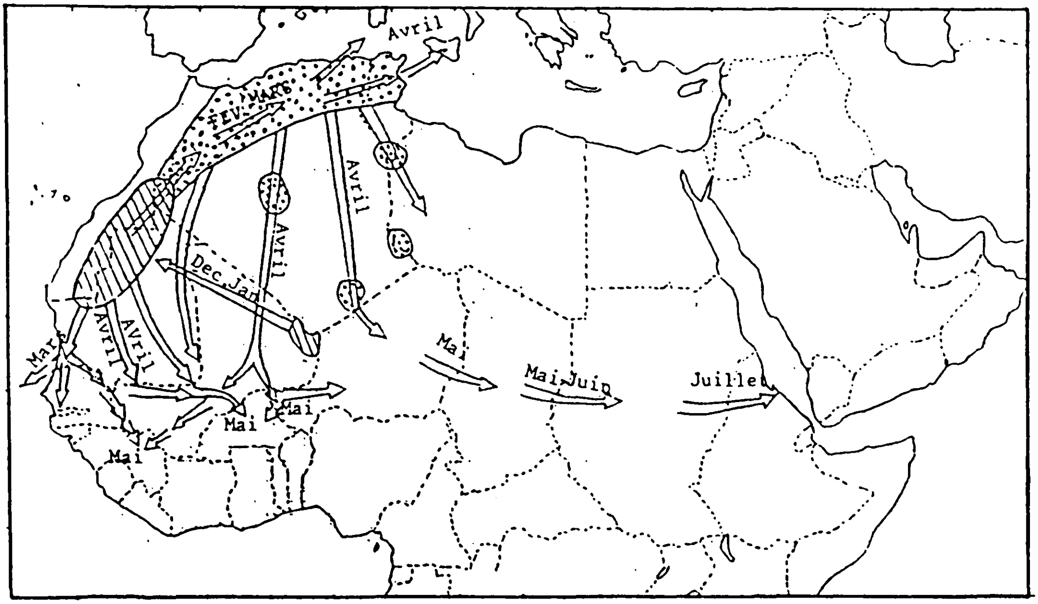


Fig. 2.—1986/87 winter-spring breeding.



▨ Summer breeding
(June-Oct.) 1987
⇨ Migrations

Fig. 3.—1987 summer breeding.



▨ ' breeding
Nov. 1987-March 1988
⁘ Breeding
April-June 1988
⇨ Migrations

Fig. 4.—Winter-spring breeding 1987/88.

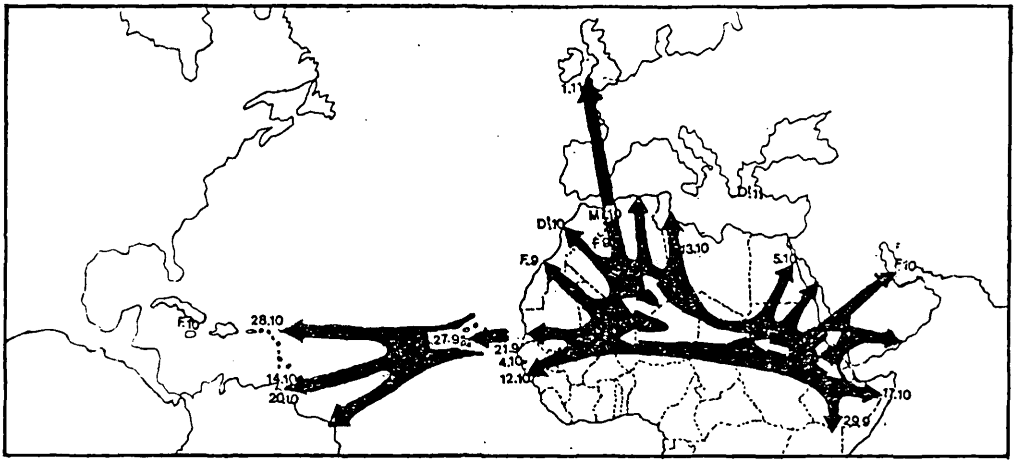


Fig. 5.—Movements of swarms following 1st summer generation (June-Sept. 1988).

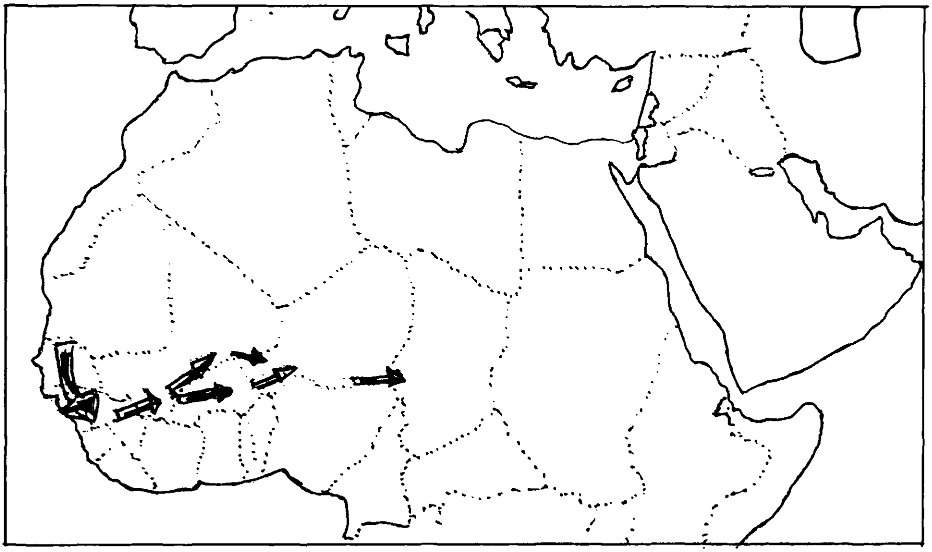


Fig. 6.—Movements of swarms following 2nd summer generation (Oct. 88-May 89).

Bol. San. Veg. Plagas (Fuera de serie) 20: 67-74, 1990

A hundred years of the Moroccan Locust, *Dociostaurus maroccanus* Thunberg, in the Carpathian Basin

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ABSTRACT

The appearance of the Moroccan Locust, *Dociostaurus maroccanus* Thunberg, was not detected before 1888 in the Carpathian Basin, but during a 60-year period after this date six massive invasions developed mainly in the Great Hungarian Plain, each lasting 2-5 years. These populations have to be considered the most northern ones in Europe.

Intervals between invasions lasted 8-13 years. During the last four decades the Moroccan Locust has become a faunistic rarity in Hungary. Diminishing availability of alkaline steppe pastures and more intensive agriculture might be important factors in the disappearance or at least low population density of the Moroccan Locust in Hungary and Northern Yugoslavia; however, the last century's climatic factors seem worth evaluation as well.

Key words: *Dociostaurus maroccanus*, Moroccan locust, Hungary, population history, invasions, habitats.

INTRODUCTION

The Moroccan Locust, *Dociostaurus maroccanus* Thunberg, is a characteristic pest of the Old World, especially in the Mediterranean and MiddleAsian countries (Fig. 1). Outbreaks used to occur first of all in three subdistricts: a) the Mediterranean part of Europe, b) the Near East, c) Middle-Asia.

The economic importance of the Moroccan Locust has decreased in the last 3-4 decades. This is clear in the summary of bibliographical items from the periodical *Review of Applied Entomology,* dealing with the Moroccan Locust (Fig. 2). This statement is especially valid for the Carpathian Basin, and on the occasion of the centennial of the Moroccan Locust in this area, it is appropriate to offer a short review and evaluation of the correlating bioecological events. Some important and detailed studies were already published earlier (Jablonowski, 1926; Adamovic, 1959; Nagy, 1964).

FIRST APPEARANCE AND LATER OCCURRENCES

The first appearance of the Moroccan Locust in the Carpathian Basin was reported by scientists at the Hungarian National History Museum in 1888. At that time there were no specimens of this locust originating from the Carpathian Basin in the insect col-

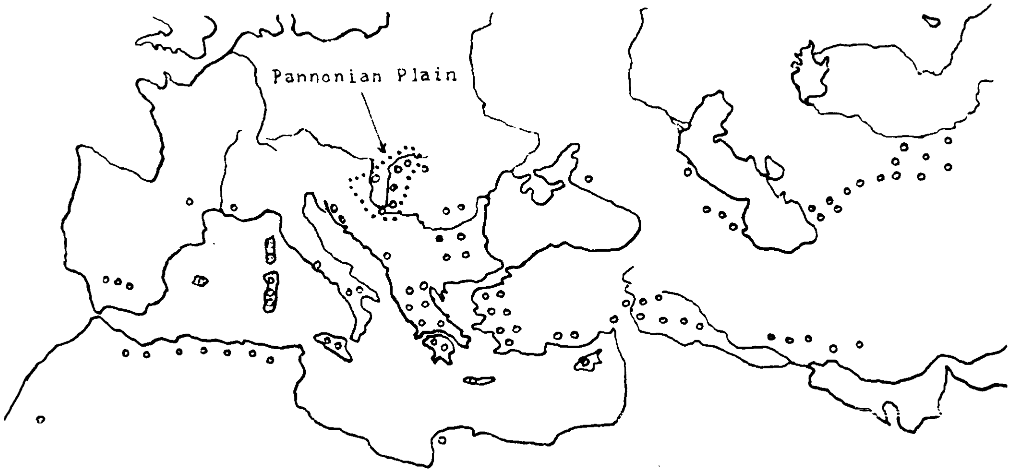


Figure. 1.—Dispersion area of the Moroccan Locust (modified from Uvarov, 1977).

lection of the Museum; assistance in the final determination was given by C. Brunner von Wattenwyl in Vienna, the well known specialist of orthopteran insects.

The monograph of Frivaldszky (1867) on the Hungarian Orthoptera (at that time Hungary meant the entire Carpathian Basin) makes no mention of *Dociostaurus (Stauronotus) maroccanus:* it does describe and illustrate, however, the near relative *Stauronotus brevicollis* Eversmann. The occurrence of *D. maroccanus* was reported before 1888 in the Carpathian Basin only in 1862, just at the extreme south at the Basin's border: at Báziás (today in Northern Serbia, Yugoslavia), about 70 km east of Belgrade (Fig. 3).

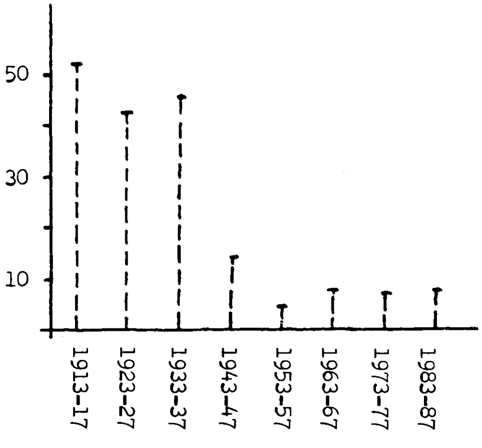


Figure. 2.—Number of publications dealing with Moroccan Locust based on data compiled from the Review of Applied Entomology.

The appearance of the Moroccan Locust in 1888 had two features making it hard to observe: firstly, it began suddenly without earlier precedents and, secondly, it happened in the very center of the Basin, only a few kilometers east of Budapest (Mocsáry, 1888; Sajó, 1889). This location was at that time some hundred kilometers north of the known distribution limit of the Moroccan Locust.

After this time -- mainly between 1889 and 1950 -- a series of localities became infested by the locust (Sajó, 1894; Jablonowski, 1926; Kadocsa, 1952; Nagy, 1964). Unfortunately, the majority of the specimens from these outbreaks was destroyed, partly by the 2nd World War (in the Institute for Plant Protection, Budapest) and partly at the time of the popular uprising in 1956 (in the Zoology Department of the Hungarian National History Museum, Budapest).

Therefore, exact inquiry into the validity of the earlier distinction between *D. maroccanus* and *D. brevicollis* is not possible today. In connection with this problem, we can mention the latest infestation in 1948, when *D. maroccanus* (0.7 %) was outnum-

Figure. 3.—Carpathian Basin area († peripheral occurrences of Moroccan Locust ... boundary of the Pannonian Plain).

bered by *D. brevicollis* (48.3 %) (Nagy, 1951). Contemporary descriptions of the flying habit of the locust itself provide unquestionable evidence of the Moroccan Locust.

The number of swarms grew rapidly during the next one or two decades after 1888, restricted mostly to the deepest part of the Pannonian Plain (*i.e.*, the Great Hungarian Plain, "Nagy-Alföld") along the Tisza River (Fig. 4).

Habitats of the Moroccan Locust in the Mediterranean and Middle East region can be found mostly in hilly, rocky areas (Dempster, 1957; Uvarov, 1977), but this habitat is not at all characteristic of the Carpathian Basin. The reasons for this are partly climatic, partly pedologic, and partly botanic. We were unable to make detailed investigations due to the lack of material of this species during the last three decades in the Carpathian Basin.

Until now, of several hundred recorded localities in the Carpathian Basin, only two points lie in mountainous areas, namely, Buda Mountain at Nagykovácsi and the Bükk Mountain at Szentlélek (Nagy, 1964). Both may be considered temporary fringe settlements, because we have not found any sign of the continued presence there of the Moroccan Locust. Both are on the northern boundary of the distribution area at this geographical longitude.

The area and the occurrences inside it are subject to continuous change, and this is especially typical of the Moroccan Locust. In spite of heavy outbreaks in Hortobágy-puszta (today, Hortobágy National Park) between 1903 and 1925, we found *D. maroccanus* specimens only in scattered samples taken between 1943-1944 and in 1948 (Nagy, 1944, 1964, 1983).

It is interesting that, at the start of the 1888-89 outbreaks at Pécel and Maglód, we found only one male specimen in July, 1988, and none in June of 1989. We had

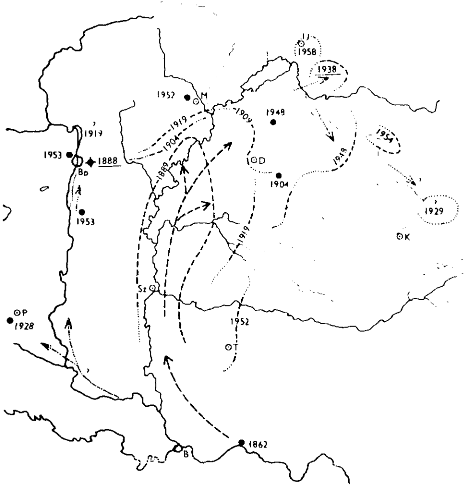


Figure. 4.—Places of occurrences and expansion of the Moroccan Locust in the Carpathian Basin and years of the first discoveries (Nagy, 1964).

other similar experiences in Hungary indicating that extensive areas infested earlier by the Moroccan Locust were later free or nearly free of it. Therefore, reports of previous occurrences need in every case to be reconfirmed; in other words, an occurrence does not always mean a permanent breeding area.

HABITAT REQUIREMENTS

Short grasses and a low vegetational cover on sodic soil are characteristic of the most important habitats of the Moroccan Locust in the Pannonian Plain; for example, the mosaic-complex of *Achilleo-Festucetum pseudovinae and Camphorosmetum annuae* in the middle of the Pannonian Plain, serving usually as pasture for cattle and sheep (Nagy, 1964). Adamovic (1959) found also. a high probability of the occurrence of the Moroccan Locust in the *Staticeto-Artemisietum monoginae, Trifolietum subterranei, Ranunculetum pedati,* and *Festucetum pseudovinae* plant communities in the southern part of the Pannonian Plain. These statements are valid for non-swarming situations, but habitat-types were extended during outbreaks also to places covered by weedy associations *(Matricario-Chenopodion albi, Consolido-Eragrostidion poidis)* and then stands of cereal crops such as wheat and barley.

The occasional appearance of small gregarious adult-groups might lead to temporary persistence on atypical habitats, as was the case at the most northern and highest point of occurrence in the Carpathian Basin, an old clearing in a *Carpineto-Fagetum* forest, really a pasture with a plant community of *Festucetum rubrae-Cynosuretum* (Nagy, 1964).

Important changes have occurred during the last 3-4 decades with respect to the extension and nature of habitats discussed above. Pastures on the sodic steppe soil have diminished. The number of grazing domestic animals has declined, and herds

Table 1.—Companion ("constant") species +/ of *Dociostaurus maroccanus* in the Orthoptera assemblages in the Pannonian Plain under non-gregarious conditions.

Middle (Nagy 1964)	South (Adamovic, 1959)
Dociostaurus maroccanus	*Dociostaurus maroccanus*
Dociostaurus brevicollis	*Dociostaurus brevicollis*
Glyptobothrus brunneus	*Calliptamus italicus*
Dirshius haemorrhoidalis	*Oedaleus decorus*
Chortippus albomarginatus	*Oedipoda caerulescens*
Stenobothrus stigmaticus	
Aiolopus thalassinus	
Oedaleus decorus	
Oedipoda caerulescens	
Celes variabilis	

+/ Species comprising 66% or more of the samples studied.

have become concentrated. These changes had begun or intensified by the late 1940's. Since that time, outbreaks of *D. maroccanus* have rarely if ever occurred in the Pannonian Plain; the connections among these phenomena, however, are not clear.

GRASSHOPPER ASSEMBLAGES

Evaluation of grasshopper assemblages containing *D. maroccanus* provides valuable information concerning the specific composition, dominance relations, and the possible indicator role of the insects. It is a pity that we have so few evaluations of grasshopper assemblages originating from the "great, old swarms" in the Carpathian Basin. Detailed studies relatig to grasshopper assemblages were mostly made after the 1940's, when *D. maroccanus* had few conspicuous outbreaks (Nagy, 1944, 1951, 1964; Adamovic, 1959).

In the middle part of the Pannonian Plain nine species have proven to be the most significant and frequent companions of *D. maroccanus* in those assemblages (Table 1).

The situation in the southern part of the Pannonian Plain proved to be very similar (Adamovic, 1959). One conspicuous difference may be found in the more southern districts only, *e.g.*, on the Dalmatian coast, where *Acrotylus patruelis* Herrich-Schaeffer, *Dociostaurus genei* Ocskay, and *Aiolopus strepens* Latreille are members of the assemblage. These species are characteristic to the Damatian coast (Adamovic, 1968).

POPULATION HISTORY 1888-1988

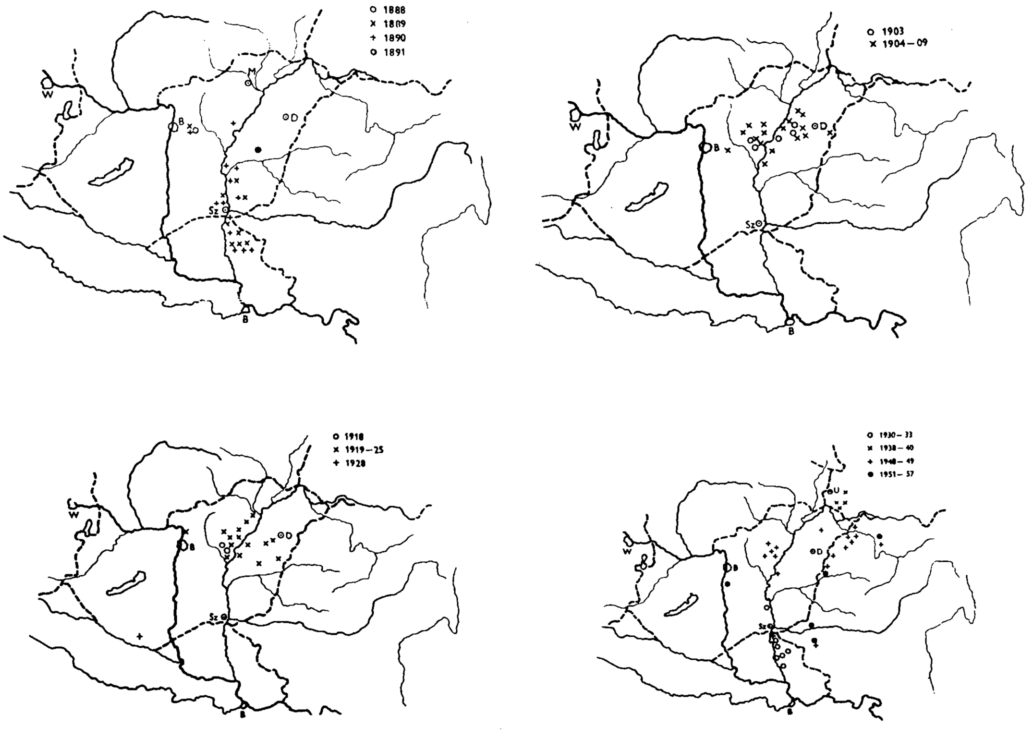
The chronology of the Moroccan Locust swarms in the Carpathian Basin is relatively well documented (Jablonowski, 1926; Kadocsa, 1952; Nagy, 1964, 1988). The mode and time of entry of the locust into the Basin is disputable. The lack of data has obscured the population history of the last 3-4 decades.

The main events may be summarized as follows:

1862: only known occurrence at the southern edge of the Carpathian Basin at Báziás (Frivaldszky, 1867, Fig. 5).
1888: sudden appearance in the middle of the Carpathian Basin at Pécel (Sajó, 1889).
1888-91: heavy outbreaks in the middle of the Pannonian Plain (Sajó, 1891, 1894).
1903-09: extensive outbreaks in the mid-north of the Pannonian Plain (Jablonowski, 1911, Fig. 6).
1918-25: extensive outbreaks in the mid-north of the Pannonian Plain (Jablonowski, 1930, Fig. 7).
1928: an isolated swarm in the southern part of Transdanubia (the only known gregarious occurrence in Transdanubia) (Kadocsa, 1952).
1930-33: restricted outbreaks in North Yugoslavia, in the lower Tisza alluvial plain (Kadocsa, 1952; Adamovic, 1959, Fig.8).
1938-40: small swarms along the northeastern edge of the Pannonian Plain (Czechoslovakia and today USSR) (Kadocsa, 1952).
1948-49: restricted swarms mostly in the northeastern (today, Rumania) and northern parts of the Pannonian Plain (Kadocsa, 1952; Nagy, 1951).
1951-57: sporadic increases mostly in the eastern zone of the Pannonian Plain (Manolache *et al.*, 1949-1959).
1951-52-53-55-56-58-59: scattered specimens occasionally in the Pannonian Plain and in the peripheral mountain districts (Grebenschikov, 1949; Likovic, 1959; Nagy, 1964; Adamovic, 1971).
1988: one male specimen only, collected at the location of the first appearance of the Moroccan Locust in the Carpathian Basin (Nagy, 1988).

Many intensive collecting trips by the author at different places in the Carpathian Basin between 1942 and 1989 produced negative results, also confirming the rarity of the Moroccan Locust in this period.

Summarizing the centennial population history of the Moroccan Locust in the Carpathian Basin, we can state that in the first 60 years it expanded nearly everywhere



Figures. 5-8.—Outbreaks of the Moroccan Locust in the Carpathian Basin (Nagy, 1964).

throughout the Pannonian Plain, causing three massive and five minor outbreaks (Fig. 9). In the last three decades (1958-1988), however, swarms have not occurred, and only scattered specimens have been detected.

DISCUSSION AND CONCLUSIONS

The alterations of the landsurface by man in the Carpathian Basin has brought about conspicuous changes in the population dynamics of two major orthopteran pest species. The drainage of the Pannonian Plain through the damming of rivers and other waterways in the 19th century greatly restricted the habitat of *Locusta migratoria* Linné while, at the same time, expanding habitats suitable for *D. maroccanus.*

There is an interesting but secondary question: when and how did the Moroccan Locust enter the Carpathian Basin? We cannot, I believe, answer this question definitively. Adamovic (1959) expressed the view that the Moroccan Locust is an ancient member of the Pannonian fauna, having arrived in a warm period after the ice age about 7500-9000 years ago. In fact, several observations indicate the possibility of a latent presence of this locust. On the other hand, the possibility of a relatively late invasion from the Balkans is also an acceptable supposition. In both cases the drainage of the Pannonian Plain caused by flood control work increased the extent of suitable habitats for the Moroccan Locust about 100-150 years ago.

It is also important to analyze the drastic, sudden retreat of the Moroccan Locust population in the last three decades, halting the periodic threats to agriculture in the Pannonian Plain. An exact evaluation of this matter is lacking; I think, however, that the regression of the locust population in this case was mainly caused by more inten-

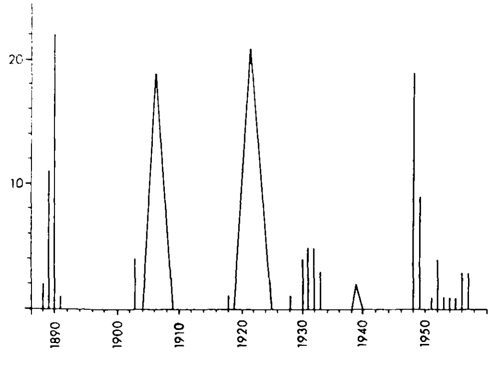


Figure. 9.—The number of villages affected by the Moroccan Locust in the Carpathian Basin in chronological order (Nagy, 1964).

sive agriculture, the decrease of seminatural sodic pastures with grazing animals, the improvement of soil cultivation, the increasing use of insecticides, etc.

A possible relationship between the continuing decrease of temperature in the Northern Hemisphere in the last four decades (Miles, 1978) and the decreasing swarms of the Moroccan Locust needs evaluation.

The centennial history of the Moroccan Locust in Hungary is reflected in interesting social relations as well. During the periods of the heavy outbreaks, mainly between 1888-1925, many thousands of agricultural workers in Hungary and Yugoslavia were forced into the control measures. Over threehundred horsedrawn "locust-killer machines" (developed by J. Jablonowski) worked for years before the age of organic insecticides, both in Hungary and Yugoslavia (Fig. 9).

The heavy outbreaks of the Moroccan Locust in 1888-89 forced the agricultural leadership to establish the Royal Hungarian Entomological Station at Budapest in 1890, one of the oldest entomological institutions in the World and the legal predecessor of the Zoology Department of the Plant Protection Institute in Budapest.

Also noteworthy are the lively scientific debates concerning the role of entomophagous birds in controlling locust plagues.

The Moroccan Locust has become an interesting and important landmark in the history of plant protection in the Carpathian Basin and especially in Hungary.

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Locust control in Africa

The new role of Malathion

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ABSTRACT

The 1988 locust control campaign has been based on large scale aerial and ground application of insecticides. This effort has been largely successful in terms of few reports of severe crop damage compared to the magnitude of the actual Desert Locust plague. The choice of insecticides has changed compared to earlier campaigns. The use of organochlorine compounds like Dieldrin has been reduced whereas organophosphorous compounds have continued to play a major part in the campaign. Amongst the latter Malathion has become one of the most important chemical control measures. The efficacy, availability, and toxicology of this insecticide are discussed.

Key words: Desert Locust, Dieldrin, Malathion.

INTRODUCTION

Locust plagues have been a recurrent menace to human welfare in Africa through the history of civilisation (Gutsch, 1987). Invasions by swarms of the Desert Locust *Schistocerca gregaria* (Forskål, 1775) are part of the ecology not only in the Sahara zone but also in much wider areas. The invasion area covers more than 20% of the total land surface of the globe (Steedman, 1988). A recent transatlantic flight to the Caribbean Islands illustrates the extraordinary migration power of the Desert Locust (SAS, 1988). Evidently the potential for crop destruction by the Desert Locust is very substantial. Although hard data are rare, estimates indicate that locust plagues constitute a very serious threat to agriculture in the affected areas (Skaf, 1986; Musuna, 1988; Steedman, 1988).

THE PRESENT PLAGUE

Due to favorable climatic conditions since late 1985 Desert Locust breeding in the Red Sea area led to substantial swarm formation and continued breeding across Africa during 1987. In 1988 the situation developed into a large scale infestation affecting among others the Sahel and Maghreb regions. (Brader, 1988; SAS, 1989). With regard to the outlook for 1989, swarms have been detected in the Sahel, Morocco, and Sudan. Despite the decreased intensity of locust attack, *Schistocerca gregaria* is presently considered the major pest in many African countries (CILSS, 1989).

In 1988 the plague attracted the attention of the world community to an extent leading to an unprecedented pan-African control effort (Brader, 1988; SAS, 1989).

CHEMICAL CONTROL

In areas plagued by locusts and grasshoppers chemical control is used frequently to control the pest population. A variety of insecticides have been used with different preferences in the different regions (McEwen, 1982; Symmons, 1984; USDA, 1987; Brader, 1988). Over the last decade or longer the general trend has been a shift away from persistent organochlorine compounds to less toxic and less persistent insecticides. Several products are generally acceptable for use in locust and grasshopper control (Launois-Luong *et al.*, 1988) and at irregular intervals FAO issues a list of products in use in well organized control operations. The insecticide Dieldrin has played a central part in locust control over many years. This insecticide has proven extremely efficient in the barrier spraying techniques developed in the 1950's for the control of hopper bands.

High toxicity to mammals, long persistence in the environment, and a large potential for bioaccumulation have led to an almost general ban on Dieldrin, making it unacceptable to the major donor agencies during the 1988 campaign. The fact that a limited initial outbreak had quickly developed into a more or less general pan-African plague in 1988 has led to speculations whether usage of Dieldrin could have stopped the invasion in due time (Skaf, 1988a, 1988b). Other important elements played their part in the initial control failure: deterioration of the local locust control organizations, inaccessibility of key areas and civil war hampered the control effort significantly (Brader, 1988).

During the 1988 control campaign, which was heavily supported by the international community, emphasis has been placed on chemicals that degrade readily in the environment (Brader, 1988). Among the insecticides presently used, Malathion has gained a dominant role in African Desert Locust control (SAS, 1988; Pedersen, 1989). This insecticide is relatively new in large scale locust control in Africa. It is among the very few insecticides registered for and extensively used for control of grasshoppers in the USA, where the product is well-known for its efficacy (USDA, 1987). Malathion is now considered a standard insecticide for use against grasshoppers as well as locusts in Africa, (SAS, 1988; Launois-Luong et al., 1988). Control practice in Africa has proved that it is not only very successful against the Senegalese grasshopper (Walsh, 1986a, 1986b), but also against the Desert Locust. In the Maghreb countries in northwestern Africa the locust control campaign has been outstandingly well organized (Lorelle, 1989). During the massive spring campaign of 1988 against the Desert Locust in Morocco, Algeria, and Tunisia, Malathion has become the preferred insecticide (Pedersen, 1988). In this area the spray operation has been particularly successful: in spite of a very heavy locust infestation little crop damage has been reported. In Mali and Senegal Malathion spraying has also played a central part and in these countries, the control effort has been considered successful (CILSS, 1989). According to the authorities in the affected countries, the main reasons for the increasingly important role of Malathion among several effective acridicides are:

1. The product has a very low mammalian toxicity. This is very important in terms of protecting the pest control operators in large scale campaigns, where safety precautions may not always be up to international standards.
2. The product is inexpensive (despite its being a highgrade technical chemical of more than 96% purity) and is one of the most widely used insecticides in agriculture and public health and therefore readily available from reliable sources.

Additionally, it is well known that Malathion ULV formulations are easy to handle, and that the product is a non-persistent, non-bioaccumulating chemical. During the control campaign in 1988, 14-15 million ha. were sprayed with insecticides (SAS 1989). This unprecedentedly large effort has raised the following key questions:

1. How do we prevent locust plagues? How can locusts be controlled at an early stage, before the situation develops into a disaster?

2. What is the impact of the anti-locust chemical control measures on human health and the environment?

The answer to the first question obviously is related to improved surveillance, early warning, and international collaboration, all based on strong and efficient local control organizations (Brader 1988, Steedman 1988). This is uncontroversial in theory but very hard to practice continously in Africa. A further discussion along these lines is beyond the scope of the present paper. Concerning the second question, as a result of the overwhelming toxicological and environmental concern in the Western community, pesticides have been subject to a very thorough test scheme. This makes pesticides one of the best scrutinized group of chemicals - often more information is generated for pesticides than for cosmetics and food additives (Cedar, 1987). Since Malathion has been in use in crop protection and public health for more than three decades, a substantial amount of experience on the safety of this product has accumulated.

To answer the question of the effects on human health and the environment, the properties of Malathion are reviewed below in relation to locust and grasshopper control in general.

MAMMALIAN TOXICITY

As mentioned already, the acute oral and dermal toxicity of insecticides plays a very important part in the selection of products for locust control. It appears from Table 1 that Malathion is among the safest insecticides used in the 1988 campaign. In chronic and subchronic studies where technical grade Malathion was fed to rats for various periods of time, no significant adverse effect on growth and food intake was observed at dose levels up to 4000 ppm in the feed (EPA, 1975; FAO/WHO, 1967). In the past, several chronic feeding studies in rodents have been conducted to evaluate the carcinogenic potential of Malathion. The conclusion is that there is no evidence that Malathion or its metabolite malaoxon are causing cancer in experimental animals or in the human population (Oshima, 1982; WHO, 1983).

ENVIRONMENTAL EFFECTS

Evaluation of potential adverse effects on non-target species caused by pesticide usage is often accomplished by the use of laboratory data (McEwen, 1982). Although application of these data to complex ecosystems is basically questionable, laboratory data offer the advantage of comparability and reproducibility. For locust control insecticides relevant laboratory data on soil degradation and acute toxicity to non-target species have been compiled. From Fig. 1 it appears that the persistence of Malathion in soil is very short (Rao and Davidson, 1980). A quick disappearance from the treated surfaces is a favorable quality in terms of protecting non-target species. Also the low octanol/water partition coefficient for Malathion (781) strongly indicates that Malathion has no significant potential for bioaccumulation in the environment (Freed *et al.*, 1979). Summarizing acute toxicity data on aquatic species, Table 2 indicates that pyrethroids and to some extent Malathion are toxic to fish and that insecticides are toxic to aquatic invertebrates. For obvious reasons the toxicity of insecticides to aquatic species is not very relevant to locust control in Africa. Of more relevance are the bird toxicity data appearing in Table 3. From the available data, it seems very unlikely that Malathion presents any toxicological risk to birds and mammals under normal spray conditions. A variety of species belonging to various taxa of terrestrial organisms like plants, worms, snails, centipedes, millipedes, soil mites and reptiles are relatively tolerant to Malathion, whereas insects and scorpions are sensitive. (Pimentel, 1971; Mulla *et al.*, 1981; Russel and Clark, 1982). A review of the rangeland grasshopper management in the USA concluded that repeated control activities with Malathion might have local indirect impacts on wildlife ,but most individual animals would not be seriously affected. (USDA, 1987).

Table 1.—Toxicity of insecticides used for locust control.

	Oral LD50 rats mg/kg	Dermal LD50 rats mg/kg
	Organophosphates	
Malathion (FYFANON®)	5500	>2000
Fenitrothion	800	890-1200
Dichlorvos	56-108	75-210
Chlorpyrifos	160	2000
Diazinon	400	>2000
	Carbamates	
Carbaryl	850	>4000
Bendiocarb	40-156	566-600
Propoxur	90-128	800-1000
	Pyrethroids	
Deltamethrin	135-5000	>2000
Lambdacyhalothrin	56-477	632
Esfenvalerate	75	>2000 (rabbit)
	Organochlorines	
Dieldrin	37-87	60-90
Lindane	88-270	900-1000

(Kynoch, 1986; Worthing, 1987; Farm Chemicals, 1988)

Half-lives in soil (days).

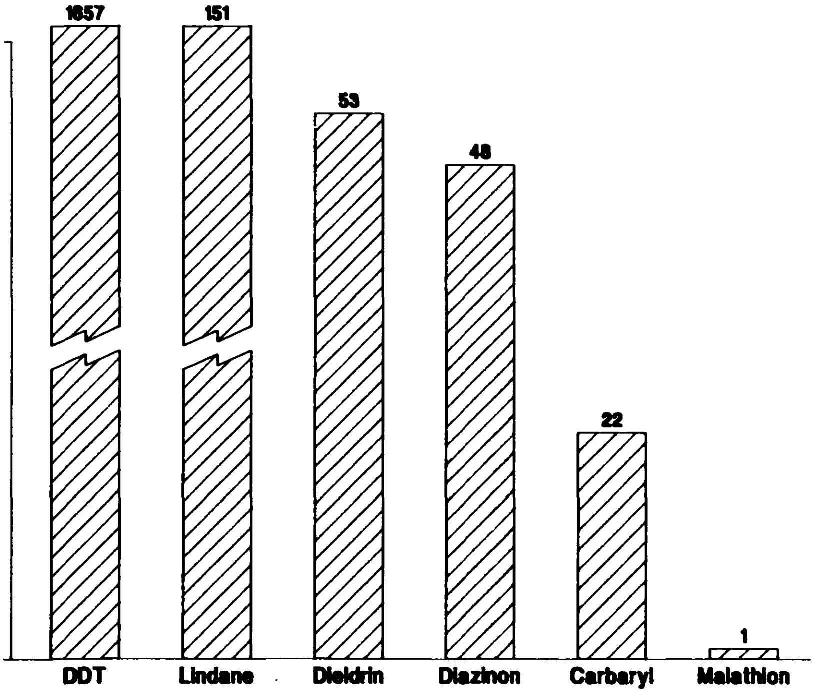

Table 2.—Toxicity (LC50 μg/1.96h) of insecticides to aquatic species.

	Rainbow trout (Salmo gairdneri)	Carp (Cyprinus sp.)	Bluegill (Lepomis-macrochirus)	Amphipod Gammarus lacustris)	Stonefly (Ptheronar sp.)
Malathion	200	6,590	103	3.8a	10
Fenitrothion	2,400	12,000	3,800		4
Dichlorvos			869	0.5	0.1
Chlorpyrifos	7.1		2.4	0.1	10
Diazinon	90	7,600-23,400	168	800a	25
Carbaryl	1,950	5,280	6,760	22	4.8
Bendiocarb	1,550				
Propoxur	8,200		4,800		
Deltamethrin	1-10				
Lambdacyhalothrin	0.5				
Esfenvalerate	3.6b				
Dieldrin	1.2		3.1	1,400a	0.5
Lindane	27	90	68	88	4.5

a: 24h
b: Fenvalerate

(Pimentel, 1971; Johnson and Finley, 1980; USDA, 1987)

Table 3.—*Bird Toxicity* 5 days Diet test LC$_{50}$ppm ai in diet and (Acute oral LD$_{50}$ mg/kg).

	Mallard Anas platyrhynchos		Phesant Phasianus colchicus		Japanese Quail Coturnix japonica	Bobwhite Colinus virginianus	Redwinged blackbird Agelaius phoeniceus
Malathion	>5000	(1489)	2639	(167)	2962	3497	(400)
Fenitrothion	2482	(1190)	453	(56)	440	157	(25)
Diazinon	191	(4)	244	(4)	47	245	(3)
Chlorpyrifos	940	(112)	553	(18)	299	—	(13)
Dichlorvos	>5000	(8)	568	(11)	298	—	(18)
Dieldrin	169	(381)	58	(79)	62	37	(18)

(Schafer 1972, Schafer *et al.* 1983, Hudson *et al.* 1984).

CONCLUSION

Locust and grasshopper infestations constitute a tremendous problem for the welfare of human beings in Africa. The environmental effects of insecticide usage in arid and semiarid zones have not been thoroughly investigated. However, judging from the favorable general properties of Malathion the possible ecological side effects of this insecticide are not at all likely to match the potential impact of locust swarms on the ecology of the semiarid regions.

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A synthesis paper on the use of insecticides formulated as baits for grasshopper control in Canada and the USA

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ABSTRACT

Over the past decade, in Canada and the U.S.A., considerable research effort has been expended on examining the efficacy, cost, and environmental safety of dry, edible, bait formulations of insecticides for grasshopper pest management. The chemicals tested have been selected from all three major groups of insecticides: organophosphates, carbamates, and synthetic pyrethroids. Some organophosphate and carbamate insecticides have proven to be useful when formulated as a bait. If efficacy of an insecticide can be defined as the reduction of a pest population to levels that are no longer economically important, then some baits are as efficacious as the spray formulations. Because considerably less active ingredient per unit area is needed as a bait compared with spray, to reduce a grasshopper population to non-economic levels, baits are less expensive. And because the insecticide is more closely targeted to the pest insect when formulated as a bait, environmental hazards are reduced: there is little, if any, insecticide drift; there is little, if any, insecticide residue on crops being attacked by the pest. This paper summarizes previous work published on the subject and includes results from 1986, 1987, and 1988 field evaluations of three additional chemicals (fenitrothion, cloethocarb, and malathion) formulated as baits.

Key words: grasshoppers, control, insecticide baits.

INTRODUCTION

Although poison baits were used during the 1930's and 1940's to protect crops from grasshoppers (Paul, 1942; Shotwell, 1942), their use was discontinued in North America following introduction of organochlorine insecticides in the late 1940's. Sprays provided extremely effective grasshopper control but were costly, both in terms of investment (ground or aerial application equipment, cost of materials, etc.) and environmental risk. Environmental hazard, in particular chemical residue in food and fibre and toxicity to non-target organisms, stimulated research into safer methods of grasshopper population suppression. The use of pathogenic organisms, particularly *Nosema locustae* Canning, formulated as edible baits, is one such method that has been incorporated into grasshopper pest management systems in the U.S.A. and

Canada (Henry, 1971; Henry *et al.*, 1973; Ewen and Mukerji, 1980).

Edible bait is a selective method of exposing grasshopper populations to pathogens or toxicants. However, not all grasshopper species accept and feed upon baits to the same degree. Two important studies by Onsager *et al.* (1980a,b) which have tended to be overlooked by subsequent workers, demonstrated clearly that grasshopper species differed markedly in their acceptance of insecticidal bait, but that mortality did not differ significantly among individuals that consumed it. It would appear that differences among grasshopper species in their response to insecticidal bait are due to differential acceptance of the bait itself and not due to differential toxicity of the chemical. Fortunately, the most economically-important grasshopper species to cereal crop production in Canada and the U.S.A. are all "acceptors" of baited bran; these include *Melanoplus sanguinipes* (F.), *M. packardii* Scudder, and *M. bivittatus* (Say), with *M. infantalis* Scudder and *M. confusus* Scudder of lesser importance. *Camnula pellucida* Scudder also is an economically important species but is a "rejector" of bran bait (Onsager *et al.*, 1980a). This may explain why the population reduction of *C. pellucida* was significantly lower, compared with melanopline species, in an evaluation study of *N. locustae* in Canada (Ewen and Mukerji, 1980).

The purpose of this paper was to review previous work which used dry, edible bait for grasshopper population management and to report the results of field tests using fenitrothion, cloethocarb, and malathion baits conducted during 1986 through 1988.

MATERIALS AND METHODS

Fenitrothion, Cloethocarb, Malathion. Experimental methods, including design, sampling procedures, and statistical analyses were as described by Mukerji *et al.* (1981). The tests were conducted on short-grass pasture at different locations in Saskatchewan. Three different locations, each with at least two sites, each site with two replicates (plots), were used for every dosage of the three insecticides. The plots, each 100 by 100 m, were arranged in a randomized block design. Treatments were applied beyond the plot margins by at least 25 m on all sides. The grasshopper populations were predominantly in the third nymphal instar when the applications were made. Predominant among the species present were *M. sanguinipes, M. packardii,* and *M. infantalis,* with a few *Aeropedellus clavatus* (Thomas), *C. pellucida, M. confusus,* and other miscellaneous species. Only the predominant species were included in the data analyses.

The bait was prepared by applying five different amounts of active ingredient (AI) to 1.0-kg batches of dry, flaky wheat bran with an aerosol jet spray. The bait was broadcast at a rate of 3.0 kg per ha to the experimental plots using a truck-mounted spreader (Peacock Industries, Hague, Sask.), to give final dosages as follows: for fenitrothion (Technical), 50, 100, 150, 200, and 280 g AI per ha; for cloethocarb (48% flowable), 12.5, 25.0, 50.0, 70.0, and 100.0 g AI per ha; for malathion (50% E.C.) (1988 only), 250, 400, 550, 700, and 850 g AI per ha. Sprays of fenitrothion (50% E.C.) were applied at five dosages (700, 560, 400, 280, and 200 g AI per ha) with a boom sprayer fitted with 800067 nozzle tips spaced to give 40 L per ha at 280 kPa. The fenitrothion and cloethocarb studies were conducted during 1986, 1987, and 1988; malathion was tested only in 1988.

Sampling methods and sorting and counting procedures were as described by Mukerji *et al.* (1981) and all mortality estimates were corrected for natural mortality using Abbott's (1925) formula. There was no appreciable natural mortality (less than 5%) within the 5-day sampling period nor any significant difference ($P = 0.05$) (Duncan's Multiple Range Test) in mortality estimates due to species, year, or site and so these data were pooled to calculate mortalities of the grasshopper populations.

RESULTS AND DISCUSSION

Organophosphates. - Previous studies showed that dimethoate bait was effective in reducing third instar grasshopper populations (Mukerji *et al.*, 1981). For example, 70 g AI per ha of dimethoate reduced the population by 49% within the first 24 h, and by 71% 5 days after application. Subsequent studies have shown that population reduction in the range of 70 (Johnson and Henry, 1987) to 80% (unpublished data) could be expected within 4 days after application of the bait at 80 or 70 g AI per ha, respectively. These and other data showed that between four and six times as much dimethoate would be required as a liquid formulation to reduce grasshopper populations by ca. 90% (420 g AI per ha) (Burrage *et al.*, 1976). It is doubtful that the increased mortalities reported in the liquid formulation studies are worth the cost of the active ingredient needed. In most cases, a population reduction of ca. 70% would be sufficient to protect the crop. Dimethoate is registered for use in Canada against grasshoppers at a recommended spray rate of 210-490 g AI per ha and as a bait at 110-165 g AI per ha.

The dosage of dimethoate needed to reduce an adult grasshopper population was considerably higher than that needed to reduce a mainly third instar population to the same level over the same period (Mukerji *et al.*, 1981). For example, 130 g AI per ha was necessary to reduce an adult population by 70% within 4 days after application. Younger grasshoppers are more easily killed than older ones with sprays of dimethoate (McKinlay, 1974); a dosage of 140 g AI per ha killed 90% of second instar grasshoppers but only 14% of adult males.

Pyridaphenthion also was tested as part of the Mukerji *et al.* (1981) studies. At 6.5 g AI per ha, a rate selected from laboratory LD95 determinations, pyridaphenthion reduced third instar grasshopper populations by only 18% 24 h after application, and by only 35% 5 days after application. Obviously, not all organophosphate insecticides are effective when formulated as edible baits.

The results of the 1986 through 1988 field trials with fenitrothion are shown in Table 1. The species complex and age distributions were similar in each of the 3 years, and the pre-treatment population density ranged from 15-38 grasshoppers per square metre in each year. Within 2 days after application even the lowest dosage of fenitrothion bait (50 g AI per ha) resulted in ca. 70% population reduction; mortalities increased slightly over the next 3 days, to ca. 75-80% 5 days after application. Spray application resulted in higher mortality 1 day after application at 700, 560, and 280 g AI per ha dosages as compared with the baits. However, over the length of the experiment, the two highest spray dosages resulted in somewhat higher mortalities, but not markedly different from even the lowest bait dosage.

The 1988 field trial results with malathion bait are shown in Table 2. Although based on only 1 year's data, the results show that malathion gave good control of a third-instar grasshopper population 1 day after application even at the lowest dosage used. At all five dosages, the malathion bait resulted in at least 70% population reduction 5 days after application.

As with dimethoate (Mukerji *et al.*, 1981), the dosage of fenitrothion and malathion required to reduce the grasshopper populations to non-economic levels was considerably lower when formulated as bait than when used as a spray. The results show that dosages of fenitrothion as low as 50 g AI per ha reduced grasshopper populations by ca. 70%, 3 days after application. For most infestations, a 70% population reduction would be satisfactory for crop protection purposes. Fenitrothion is not registered for use against grasshoppers in Canada but BASF Canada, Inc. suggested that 560 to 700 g AI per ha as a spray should be efficacious in field trials. The results with malathion bait, although encouraging, are based on only 1 year's data. Malathion is registered for use on grasshoppers in Canada as a spray, at 850 g AI per ha.

Table 1.—Mortality (percent) of third-instar grasshoppers at selected times after exposure to different dosages of fenitrothion applied as a spray or as a bait in Saskatchewan, 1986 through 1988.

Spray	Time (h) after application				
g AI/ha	24	48	72	96	120
700	96	96	94	96	96
560	83	91	91	85	86
400	61	54	76	73	68
280	78	76	77	76	68
200	55	56	61	45	53

Bait	Time (h) after application				
g AI/ha	24	48	72	96	120
280	33	69	68	72	79
200	41	76	62	76	84
150	39	77	77	76	82
100	38	87	73	75	77
50	53	83	79	76	75

Table 2.—Mortality (percent) of third-instar grasshoppers at selected times after exposure to different dosages of malathion applied as a bait in Saskatchewan, 1988.

	Time (h) after application				
g AI/ha	24	48	72	96	120
850	95	87	77	97	96
700	93	86	95	95	92
550	84	90	86	93	84
400	82	58	66	79	70
250	77	86	69	78	84

Table 3.—Mortality (percent) of third-instar grasshoppers at selected times after exposure to different dosages of cloethocarb applied as a bait in Saskatchewan, 1986 through 1988.

g AI/ha	Time (h) after application				
	24	48	72	96	120
100.0	72	70	82	81	81
70.0	78	81	85	76	81
50.0	76	80	83	74	76
25.0	54	54	54	45	77
12.5	73	73	34	81	77

Note: The same control plots were used for the cloethocarb and fenitrothion tests.At least two control plots, and usually three, were used at each site and each year.

Carbamates. - Field test results on bait applications of propoxur (Mukerji *et al.*, 1981), carbofuran (Ewen and Mukerji, 1987), and carbaryl (Onsager *et al.*, 1980a,b; Mukerji and Ewen, 1984; Capinera and Hibbard, 1987; Johnson and Henry, 1987; Quinn *et al.*, 1989), have been published.

Propoxur, a chemical which is not registered for use in Canada for grasshopper control, provided a population reduction of only ca. 40%, 5 days after application. The dosage used, based on LD95 in 24 h studies in the laboratory, was 8.0 g AI per ha.

Carbofuran is registered for use in Canada at a recommended spray rate of 140.0 g AI per ha. As a bait, field tests showed that as little as 35.0 g AI per 3 kg bran per ha would reduce grasshopper populations by ca. 70%, 3 days after application. In the 2nd year of this study, the population reduction was somewhat lower in the first 3 days, perhaps due to lower daily maximum temperatures that year, which resulted in the grasshoppers feeding less than they would at higher temperatures (Ewen and Mukerji, 1987).

Field test results with carbaryl have been variable. Onsager *et al.* (1980a,b) tested carbaryl bait at three rates (1.96% at 0.58, 1.12 or 1.68 kg bran per ha) near Sheridan, WY. Many of the grasshopper species in their studies were those that are not generally considered as economically-important to cereal crop production, but the melanopline species were reduced by ca. 66-75% by the highest dosage of carbaryl bait. Mukerji and Ewen (1984) reported only limited success, with a population reduction of only ca. 46%, 5 days after application at the highest dosage tested (200 g AI per ha). As a spray, carbaryl reduced the grasshopper population by over 90% during the same time interval, at 700 g AI per ha; population reduction was inconsistent at lower spray dosages. Capinera and Hibbard (1987) compared spray and bait formulations of carbaryl on grasshoppers kept in pens in Colorado. Both formulations were prepared so that the final effective dosage was 305 g AI per ha. In three separate trials, the average corrected mortalities were: spray, 83.8, 87.1, and 90.1%; wheat bran bait, 54.4, 69.3, and 78.1%, on days 1 to 3 after treatment. Johnson and Henry (1987) reported a 76% mortality with carbaryl bait containing 4% (80 g) active ingredient per ha 4 days after treatment. Quinn *et al.* (1989) tested carbaryl bait (5% on 1.7 kg per ha) in South Dakota. They found the densities of all grasshopper species combined were reduced by ca. 47% by the carbaryl bait treatment, but if they considered only the populations of "bran-acceptor" species, the reduction was ca. 65%. Populations of "bran-rejector" species were reduced by only ca. 9% in these studies. Their population reduction data were collected 48 h after treatment. One possible explanation for the differences in the recent American and early Canadian data with carbaryl bait may be that the American studies used a different formulation of the insecticide (Sevin XLR). The XLR formulation is reported to be easier to mix and apply to bran, and adheres better than does the older, wettable powder formulation of the insecticide. Carbaryl (XLR) is registered for use in Canada as a spray for grasshopper control at a dosage of 550-1100 g AI per ha.

Results from the 1986 through 1988 field trials with cloethocarb are reported in Table 3. The species complex, age distributions, and pre-treatment population density were the same as for the fenitrothion tests reported earlier. At the three highest dosages, cloethocarb bait was very effective, reducing populations by at least 70%, 1 day after application increasing to over 80%, 3 days after application, and then declining somewhat over the next 2 days. At the lowest two dosages, 12.5 and 25.0 g AI per ha, the results showed population reductions that were somewhat inconsistent over time. Cloethocarb is not registered for use against grasshoppers in Canada.

Synthetic pyrethroids. - Fenvalerate and cypermethrin baits have been tested against third instar grasshopper populations, predominantly melanopline species, in two separate tests in Saskatchewan (Mukerji *et* *al.*, 1981; Mukerji and Ewen, 1984). Fenvalerate was applied at 10 g AI per ha (LD95 in 24 h in lab bioassays) and cypermethrin was applied at five dosages, 4, 5, 8, 15, and 30 g AI per ha. Both synthetic pyrethroids proved to be less effective in reducing grasshopper populations over time than most of the other insecticides that were tested in the field. Approximately 55% mortality was attained at the highest dosage of cypremethrin, 120 h after application; at lower dosages, the time-response data showed that mortality never reached 50%. The rates of mortality for fenvalerate were similar to those for cypermethrin over time.

CONCLUSIONS

Laboratory experiments at the Rangeland Insect Laboratory (USDA), Bozeman, MT, in 1949 tested the response of the adults of several grasshopper species to wheat bran treated with chlordane or toxaphene (cited in Onsager *et al.*, 1980a). Among "bran acceptor" species, mortality ranged from 52-93%, 3 days after the grasshoppers had been fed the treated bait. These studies were unreported in the literature until 1980, but the results are in general agreement with more recent work. Collectively the studies show that some insecticidal baits are very effective in suppressing grasshopper populations. Specifically, baits of dimethoate, fenitrothion, carbofuran, cloethocarb, and possibly carbaryl reduce grasshopper populations equally as well, or almost as well, over time as they do when formulated as sprays. Based on one test, malathion also may be effective as a bait, but further field work is needed to corroborate this conclusion.

Capinera and Hibbard (1987) have shown that vegetation density has little effect on bait efficacy; bran baits were effective in suppressing grasshopper populations in the presence of high or low levels of competing vegetation.

There is considerable benefit in using dry, edible baits of insecticides, because significantly less active ingredient is needed to achieve a desired population reduction as compared with their liquid formulations. Environmental hazards from toxic crop residues, spray drift onto non-target areas, mortalities among the natural predators of grasshoppers, and mortalities among non-target beneficial insects like leaf-cutter and honey bees, is much reduced when the insecticides are applied as bait formulations. Hazards to the applicator are minimized with insecticidal baits.

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Hybridization studies of subspecies of the African grasshopper *Acanthacris ruficornis* (F.) (Orthoptera: Acrididae)

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ABSTRACT

Hybridization experiments were carried out to test the validity of the subspecies of *Acanthacris ruficornis* (F.) established by conventional morphological taxonomy. Material of *A. r. citrina* from Mali was reciprocally crossed with *A. r. ruficornis* from Kenya. Hybrid F_2 crosses and backcrosses to parent stocks showed that egg pod size, hatching success, egg viability, and homogeneity of sex ratios were not adversely afected in any experimental hybrids. The morphometrics of F_1 hybrids were found to be intermediate between those of wild material of the two parent subspecies and similar to those of material of *A. ruficornis* from Ethiopia. It is concluded that the subspecies are valid and that the Ethiopian population may be of hybrid origin.

Key words: *Acanthacris ruficornis,* subspecies, hybridization, morphometrics.

INTRODUCTION

Uvarov (1924) recognised *Acanthacris citrina* (Serville) as a subspecies of *A. ruficornis* (Fabricius). Mungai (1987) showed that the nominate race, *A. r. ruficornis,* occurs along a thin coastal strip in West Africa but is found throughout eastern and southern Africa from Eritrea to the Cape, avoiding only the most arid areas. Conversely *A. r. citrina* is largely restricted to the Sudan savanna of West Africa, with an isolated population in Morocco. The two taxa appear therefore to be allopatric throughout their range (Fig. 1).

In appearance the two races are strikingly dissimilar (Plate 1). *A. r. citrina* is generally light brown with the eyes pale and striped and the hind tibia flushed with pink, whereas *A. r. ruficornis* is dark brown with uniformly black eyes and its hind tibiae are usually bluish or greyish. Total body length in both sexes is larger on average (by about 7 mm) in *citrina* than in *ruficornis* and the prozona of the pronotum is more arched in the former than in the latter.

These striking superficial differences are as great as or greater than those which serve to separate many sibling species of grasshoppers but nonetheless Mungai (1987) could find no significant differences in male genital morphology between the two taxa of the kind which clearly separate the four recognised species in the genus. He therefore accepted Uvarov's division of *A. ruficornis* into two geographical subspecies.

Mungai noted the variability in some populations of *A. r. ruficornis* and in particular the problem posed by material from Ethiopia which had been described by Finot (1907) as a variety *subimmaculata* of *A. ruficornis* and was later synonymised under *A. r. citrina* by Uvarov (1924). He discussed the colour patterns and pronotal morphology of this population and transferred the variety *subimmaculata* from synonymy under *A. r. citrina* to synonymy under *A. r. ruficornis.*

The conflicting indications of systematic status and affinity afforded by external morphology and male genital structure did not provide a satisfactory basis for a stable taxonomy. Accordingly the opportunity was taken during a study visit to Mali by one of us (M.N.M.), to obtain live material of *A. r. citrina* which could be crossed in the laboratory with Kenyan material of *A. r. ruficornis.* It was anticipated that hybridization experiments might clarify the true relationship between the two taxa as they had so successfully done in the case of the *Schistocerca americana* complex (Jago *et al.*, 1979; Harvey, 1979, 1982).

MATERIALS AND METHODS

The culture of *A. ruficornis citrina* (CIT) was derived from adult specimens collected at Bamako, Mali, in September 1983. The culture of *A. r. ruficornis* (RUF) was collected from the lower slopes of the Aberdare mountains in Kiambu District, Kenya.

The cultures were maintained at the National Museum in Nairobi in standard 50 litre aluminium locust cages (Hunter-Jones, 1966) heated by 60W electric light bulbs to provide a daytime temperature of 28-34°. At dusk the heating was switched off and cage temperatures dropped to the ambient night-time temperature. Humidity was increased by providing a Petri dish with moist cotton wool inside each cage. The insects were maintained on fresh leaves of kale (*Brassica* sp.) locally known as "Sukuma Wiki".

At the final nymphal instar males and females were separated to avoid any mating by fledglings. Aluminium egg tubes filled with moistened sterilised sand were provided for laying females. These were checked for laying daily and tubes with egg pods were labelled and removed to an incubator under the same temperature regime as the cages. Egg tubes were checked daily for hatching and hatchlings were sexed and counted after anaesthetizing with CO_2. When hatching was complete the pods were dissected to ascertain the number of unhatched eggs with embryos and the number of non-viable eggs.

In cases where two pods had been laid in one tube the resulting eggs and progeny could not be used for comparing size of pod, viability or hatching success of the individual pods. They were used however in the analysis of sex ratio (Table 10). For this reason the figures for total numbers of hatchlings in this table do not match those presented in the earlier tables.

RESULTS AND DISCUSSION

Observations of cultures

The incubation period of eggs of both pure stocks and hybrids was very variable. In *A. r. ruficornis* extremes of 25 and 93 days were recorded, the longer period being associated with lower incubation temperature. Nymphal colouration was found to be similar in both pure stocks and in hybrids. Newly hatched nymphs were green with small dark rings all over the body. From the third instar nymphs occurred in green, yellow-green, pink and mottled brown colour forms which persisted until the final moult.

Cannibalism was prevalent in the nymphal stages. Wounded individuals were quickly attacked and eaten by other hoppers. It is possible that the diet of kale was deficient in some way. Dense field populations of locust hoppers are known to engage in similar behaviour when food and water are scarce (Uvarov, 1977).

No special pre-mating behaviour was observed. Males simply jumped onto females. The female initially might attempt to dislodge them by kicking before cooperating. Once mounted on the back of the female the male would bend the tip of his abdo-

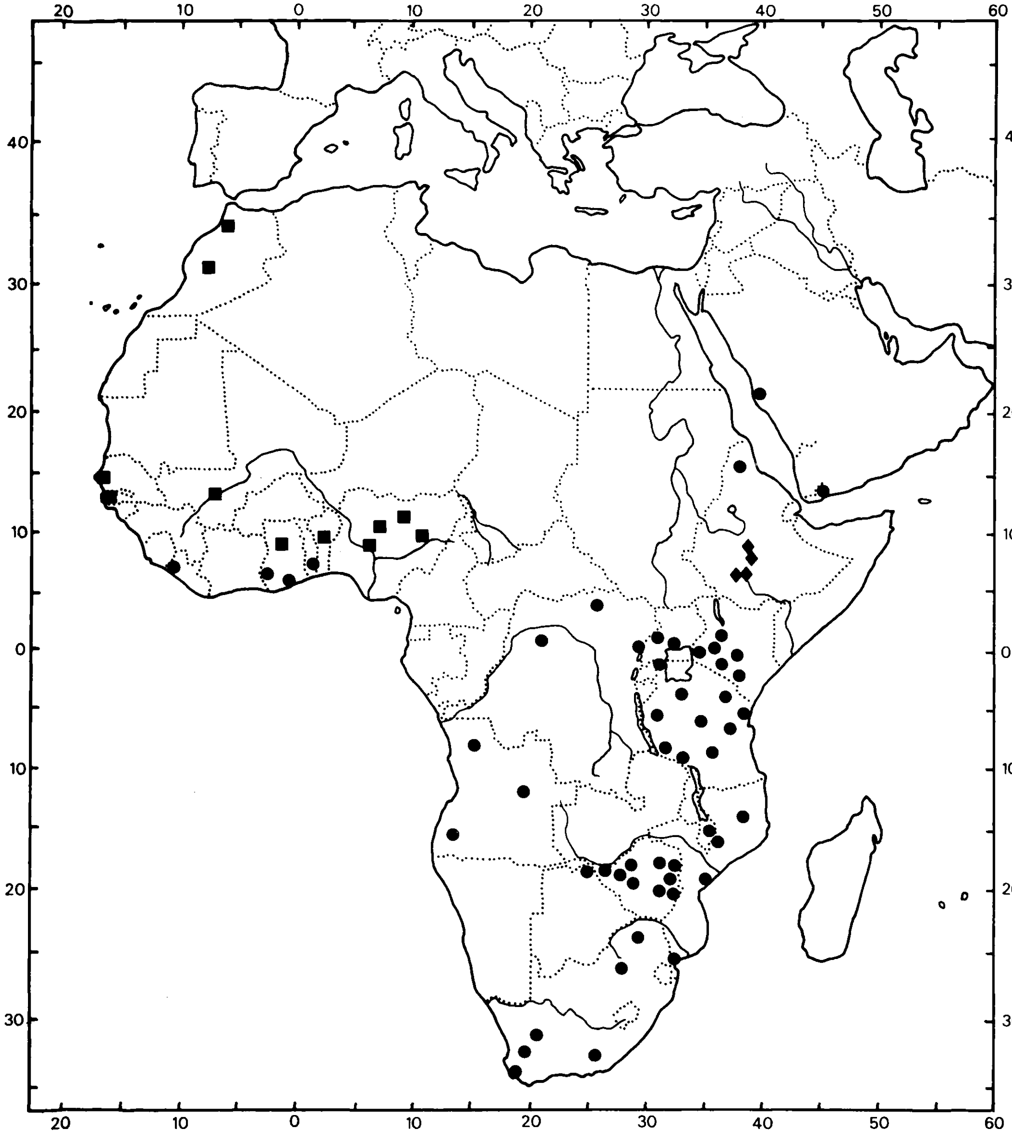

Figure 1.—Geographical distribution of *Acanthacris ruficornis* populations. Circles, *A. r. ruficornis;* squares, *A. r. citrina,* diamonds, Ethiopian putative hybrid population.

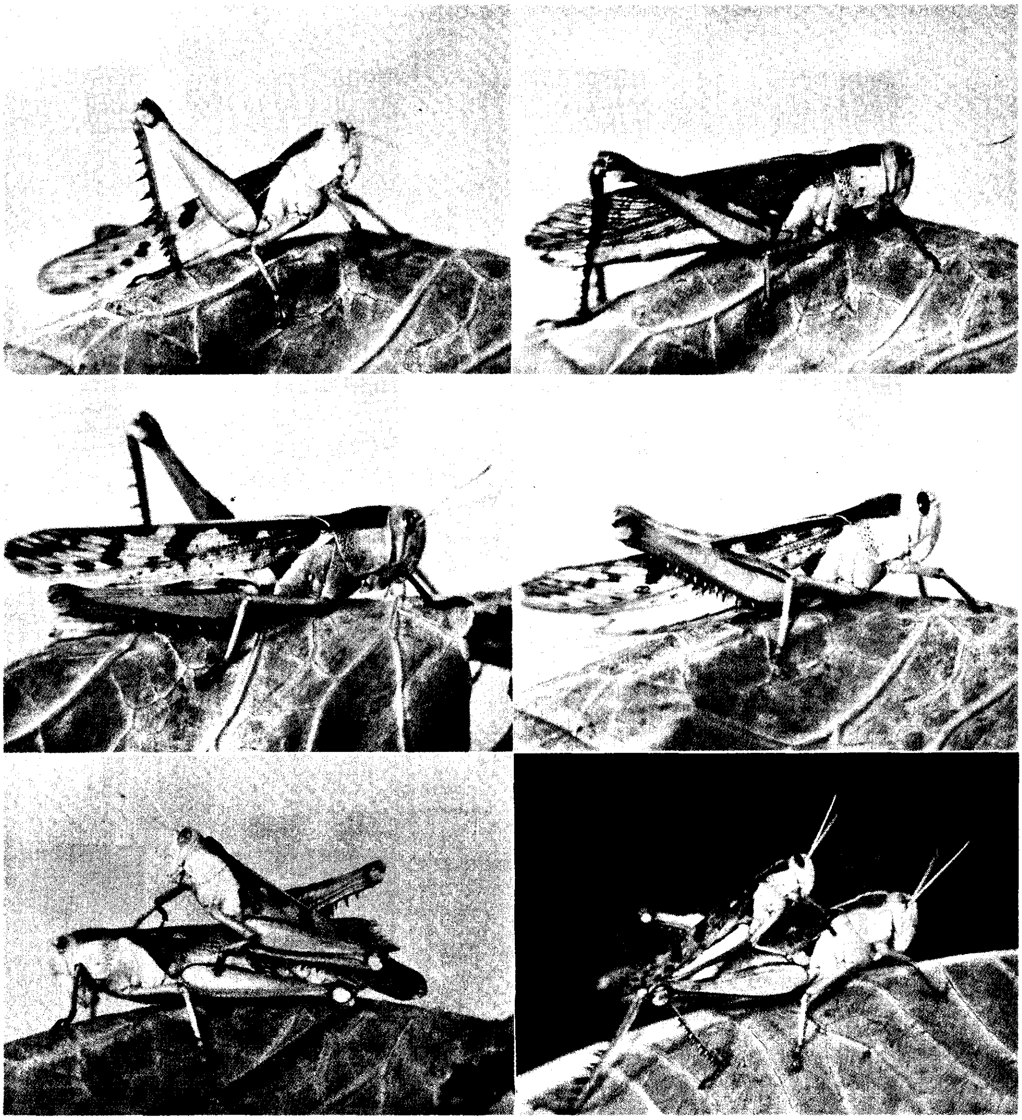

Plate 1. Top row, left, *A. r. citrina;* right *A. r. ruficornis*. Middle row, *ruf* × *cit* female hybrids, left, striped eye, right, dark eye. Bottom row, left, *cit* × *ruf* female and *citrina* male in copula; right, *citrina* female and *ruficornis* male in copula.

men to grasp the female ovipositor. If the female was unresponsive the male would move its hind legs rapidly as if stridulating, but without audible sound, until the female presented the tip of her abdomen to him.

Particular females seemed to be more attractive than others to males at certain times. On several occasions three or four males were seen trying to mount a female which was already mating, despite the presence of other available females in the same cage. From time to time females were observed to evert the Comstock-Kellog gland. This gland is said to play a part in attracting males (Hubbell & Cantrall, 1938; Laub-Drost, 1959; Thomas, 1965). It was observed that adults chewed each other's wings so that older individuals eventually had only stubs of wings.

Two mature pairs each of *A. r. ruficornis* and *A. r. citrina* were introduced into the same cage and observed for two months to establish whether males showed any preference for mates. Both species mated indiscriminately with females of either subspecies and no preference by males for females of either race was detected. However there was some indication that males of *A. r. ruficornis* mated more frequently than those of *A. r. citrina*. This might be because the latter subspecies was adversely affected by being kept at temperatures rather lower than those in its natural environment in Mali.

Egg pod size

The number of eggs per pod in pure stocks of *A. r. ruficornis* and *A. r. citrina* and their reciprocal crosses, back crosses and hybrid F_2 selfcrosses are shown in Table 1. A single factor analysis of variance for completely randomised designs (Bailey, 1959) was carried out on these data (Table 2). Mean egg pod sizes are ranked in ascending order of size with their standard errors in Table 3. The difference (t) column in Ta-

Table 1. Egg pod size in pure stocks of *A. r. ruficornis* (RUF) and *A. r. citrina* (CIT) and their reciprocal crosses, back crosses and hybrid - hybrid F_2 crosses.

Parents		No. of eggs/pod	No. of egg pods	Totals	Means
RUF	RUF	140, 161, 88, 151, 159, 109, 152, 145, 168, 127, 66, 180, 181, 38, 146, 173, 145, 156	18	2485	138.0556
CIT	CIT	90, 164, 73, 115, 122, 140, 130, 181, 179	9	1194	132.6667
RUF	CIT	162, 172, 243, 174, 222, 183, 179, 155, 168, 172	10	1830	183.0000
CIT	RUF	211, 205, 188, 227, 194, 159, 176, 133, 93, 176, 175, 163, 171, 165	14	2436	174.0000
(CIT×RUF)	(CIT×RUF)	193, 191, 175, 182, 133, 148, 162	7	1184	169.1429
(RUF×CIT)	(RUF×CIT)	170, 175, 182, 173, 180, 180, 178, 176, 173, 176, 183	11	1946	176.9091
(CIT×RUF)	RUF	173, 156, 239, 121, 184, 156, 174	7	1203	171.8571
(RUF×CIT)	CIT	173, 179, 181, 180	4	713	178.2500
Totals:			80 (N)	12991 (G)	162.3875 (G/N)

Correction factor C= G^2/N = 2109576.01
Sum of squares of deviation about general mean = 98896.9875
Sum [(total eggs/cross)^2/no of pods]-C = 29016.6697

Table 2.—Anaysis of Variance of Table 1 for completely randomised designs (Bailey, 1959) (k = number of crosses).

Source of Variation	Sum of squares	Degrees of freedom	Mean squares	Observed Variance ratio (F)
Between crosses	29016.67	(k-1)= 7	4145.24	4.27
Residual	69880.32	(N-k) = 72	970.56	—
Total:	98896.99	(N-1) = 79	—	—

Minimun significant Variance ratio F test (2-tailed)
2% i.e. 1% table = 2.95

Table 3.—Mean egg pod sizes of *Acanthacris* crosses ranked in ascending order with their standard errors.

Parents		Mean ± S.E. (s = $\sqrt{970.56}$ = 31.15)	Difference (in SDs) 't'	Significance level normal distribution (2-tailed)
CIT	CIT	132.67 ± 10.38	—	—
RUF	RUF	138.06 ± 7.34	0.42	NS
(CIT×RUF)	(CIT×RUF)	169.14± 11.78	2.24	10%
(CIT×RUF)	RUF	171.86 ± 11.78	0.16	NS
CIT	RUF	174.00 ± 8.33	0.15	NS
(RUF×CIT)	(RUF×CIT)	176.91 ± 9.39	0.23	NS
(RUF×CIT)	CIT	178.25 ± 15.58	0.07	NS
RUF	CIT	183.00 ± 9.85	0.26	NS

ble 3 gives a measure of the difference between the means of successive pairs in standard deviations.

The Significance Level is the significance of the difference between one mean and the next. Thus all hybrid crosses produced significantly more eggs than pure stocks at the 10% level. However this result is not shown to be significant at the 2% level. Clearly however there is certainly no decline in egg number in F_1 hybrids, F_2 hybrids or back crosses to parent stocks, and there is even some suggestion of improved performance.

Since hybrid females are somewhat larger than *A. r. ruficornis* females on average (Fig. 2), it is probable that they have a slightly larger number of ovarioles since ovariole number is proportional to body length in acridids (Waloff, 1954). The relatively low numbers of eggs per pod in *A. r. citrina* pure stocks may be attributable to the insects' health being adversely affected either by the diet or by the lower temperature and humidity of the cages relative to their normal tropical environment.

Hatching success

Hatching success for pure stocks and all crosses is summarised in Table 4. An analysis of variance is given for these data in Table 5. The mean percentages of eggs hatching per pod for all crosses are ranked in ascending order with their standard errors in Table 6. Since the variance ratio (F) of between crosses variation and residual variation was not significant, no signi-

Table 4.—Hatching sucess in pure stocks of *A. r. ruficornis* (RUF) and *A. r. citrina* (CIT) and their reciprocal crosses, back crosses and hybrid × hybrid F_2 crosses.

Parents		No. of egg pods	Total % ages hatching	Mean %age hatching per pod
RUF	RUF	18	1370.7	76.15
CIT	CIT	9	539.8	59.98
RUF	CIT	10	759.3	75.93
CIT	RUF	14	946.4	67.60
(CIT×RUF)	(CIT×RUF)	7	480.2	68.60
(RUF×CIT)	(RUF×CIT)	11	725.9	66.00
(CIT×RUF)	RUF	7	647.0	92.43
(RUF×CIT)	CIT	4	214.2	53.55
Totals:		80 (N)	5683.7 (G)	71.05 (G/N)

$C = G^2/N = 403799.70$

Sum of squares of deviation about general mean = 66666.70

Sum [(total eggs/cross)^2/no of pods]-C = 6723.08

Table 5.—Anaysis of Variance of Table 4 for completely randomised designs (Bailey, 1959) (k = number of crosses).

Source of Variation	Sum of squares	Degrees of freedom	Mean squares	Observed Variance ratio (F)
Between crosses	6723.08	(k-1) = 7	960.44	1.15
Residual	59943.62	(N-k) = 72	832.55	—
Total:	66666.70	(N-1) = 79	—	—

Minimun significant Variance ratio F test (2-tailed)
2% i.e. 1% table = 2.95, therefore result not significant.

Table 6.—Mean percentage hatching sucess of *Acanthacris* crosses ranked in ascending order with their standard errors.

Parents		Mean ± S.E. ($s = \sqrt{832.55} = 28.85$)	Difference (in SDs) 't'
(RUF×CIT)	CIT	53.55 ± 14.43	—
CIT	CIT	59.98 ± 9.62	0.37
(RUF×CIT)	(RUF×CIT)	66.00 ± 8.70	0.46
CIT	RUF	67.60 ± 7.71	0.14
(CIT×RUF)	(CIT×RUF)	68.60 ± 10.91	0.08
RUF	CIT	75.93 ± 9.12	0.52
RUF	RUF	76.15 ± 6.80	0.02
(CIT×RUF)	RUF	92.43 ± 10.91	1.27

ficance levels have been established for the differences between successive means. Hatching success of pure stocks and crosses do not differ significantly from each other.

Egg viability

Egg viability for pure stocks and all crosses is summarised in Table 7. An analysis of variance is given for these data in Table 8. Mean percentage viability figures for all crosses are ranked in ascending order with their standard errors in Table 9. Again since the variance ratio was not significant, no significance levels have been given for the differences between successive means. Mean viability of eggs of pure stocks and all crosses do not differ significantly from each other. Interestingly *A. r. citrina* pure stock viability is about as high as that of *A. r. ruficornis*, despite the somewhat lower egg pod size noted above.

Table 7.—Viability of eggs in pure stocks of *A. r. ruficornis* (RUF) and *A. r. citrina* (CIT) and their reciprocal crosses, back crosses and hybrid × hybrid F_2 crosses.

Parents		No. of egg pods	Total %ages viable	Mean %age viable per pod
RUF	RUF	18	1606.7	89.26
CIT	CIT	9	799.6	88.85
RUF	RUF	10	932.6	93.26
CIT	RUF	14	1239.2	88.52
(CIT×RUF)	(CIT×RUF)	7	639.0	91.29
(RUF×CIT)	(RUF×CIT)	11	977.1	88.83
(CIT×RUF)	RUF	7	687.8	98.26
(RUF×CIT)	CIT	4	308.7	77.18
Totals:		80 (N)	7190.8 (G)	89.88 (G/N)

$C = G^2/N = 646336.29$
Sum of squares of deviation about general mean = 16179. 29
Sum [(total eggs/cross)^2/no. od pods]-C = 1319.61

Table 8.—Analysis of Variance of Table 7 for completely randomised designes (Bailey, 1959) (k = number of crosses).

Source of Variation	Sum of squares	Degrees of freedom	Mean squares	Observed Variance ratio (F)
Between crosses	1319.61	(k-1) = 7	188.52	0.91
Residual	14859.68	(N-k) = 72	206.38	—
Total:	16179.29	(N-1) = 79	—	—

Minimun significant Variance ratio F test (2-tailed)
10% i.e. 5% table = 2.17, therefore result not significant.

Table 9.—Mean percentage egg viability of *Acathacris* crosses ranked in ascending order with their standard errors.

Parents		Mean ± S. (s = $\sqrt{206.38}$ = 14.37)	Difference (in SDs) 't'
(RUF×CIT)	CIT	77.18 ± 7.18	—
CIT	RUF	88.52 ± 3.84	1.39
(RUF×CIT)	(RUF×CIT)	88.83 ± 4.33	0.05
CIT	CIT	88.85 ± 4.79	0.00
RUF	RUF	89.26 ± 3.39	0.07
(CIT×RUF)	(CIT×RUF)	91.29 ± 5.43	0.32
RUF	CIT	93.26 ± 4.54	0.28
(CIT×RUF)	RUF	98.26 ± 5.43	0.71

Sex ratio

The sex ratio of hatchlings derived from pure stocks and the crosses is compared and analysed for homogeneity in Table 10. Chi square was calculated using Brandt & Snedecor's formula (Bailey, 1959) and found to be below the level of significance. The null hypothesis, that the sex ratio of hatchlings in all crosses is not significantly different from 50:50, is therefore confirmed, indicating that normal fertilisation is taking place in all crosses.

Colouration and morphology

Adult F_1 hydrids were intermediate in colour and size between the parent stocks (Plate 1). RUF×CIT hybrids were slightly paler than the reciprocal hybrid and had paler tibiae. Out of 53 adult males examined 21 had pale striped eyes and 32 unicolourous dark brown eyes. CIT×RUF hybrids had darker colouration and out of 12 adult males examined 11 had dark brown eyes. Adult F_2 hybrids of the (RUF×CIT)×(RUF×CIT) cross were still intermediate in size and colouration between *A. r. ruficornis* and *A. r. citrina,* with moderately raised pronotal crest and pale tibiae.

Figure 2 shows the relative size of adults of both sexes of the two races and the F_1 hybrids using the proportions of the hind femur as an index of overall size. For comparison measurements of six specimens from southwestern Ethiopia (between Sodo and Boreda; Awasa; Adis 'Alem) have been included which are clearly similar to those of the hybrids and intermediate between those of the parent stocks. Tibial colour in this

Table 10.—Chi squared analysis of the sex ratio of hatchlings in pure stocks of *A. r. ruficornis* (RUF) and *A. r. citrina* (CIT) and their reciprocal crosses, back crosses and hybrid × hybrid F_2 crosses (crosses numbered in order of listing as in Table 1).

Sex of offspring	Reference numbers of crosses								Totals
	1	2	3	4	5	6	7	8	
Male	1493	368	1174	985	412	685	736	197	6050
Female	1299	334	1085	858	385	601	704	185	5451
Totals	2792	702	2259	1843	797	1286	1440	382	11501

k = 0.526 1-k = 0.474 Chi^2 = 3.6867 (NS)
Degrees of freedom = 7

material also shows a tendency to be purplish rather than clear blue as in pure *ruficornis* specimens. Ethiopia has a large proportion of grasshopper species of West African faunal affinities (Jago, 1976). At the present day there are no records of *A. r. citrina* from any localities east of Lake Chad. However it seems probable that *citrina* from West Africa have reached Ethiopia during some past period when conditions were more suitable in the intervening area. Here they interbred with *ruficornis*, producing a hybrid population which is today probably largely isolated from pure *ru-*

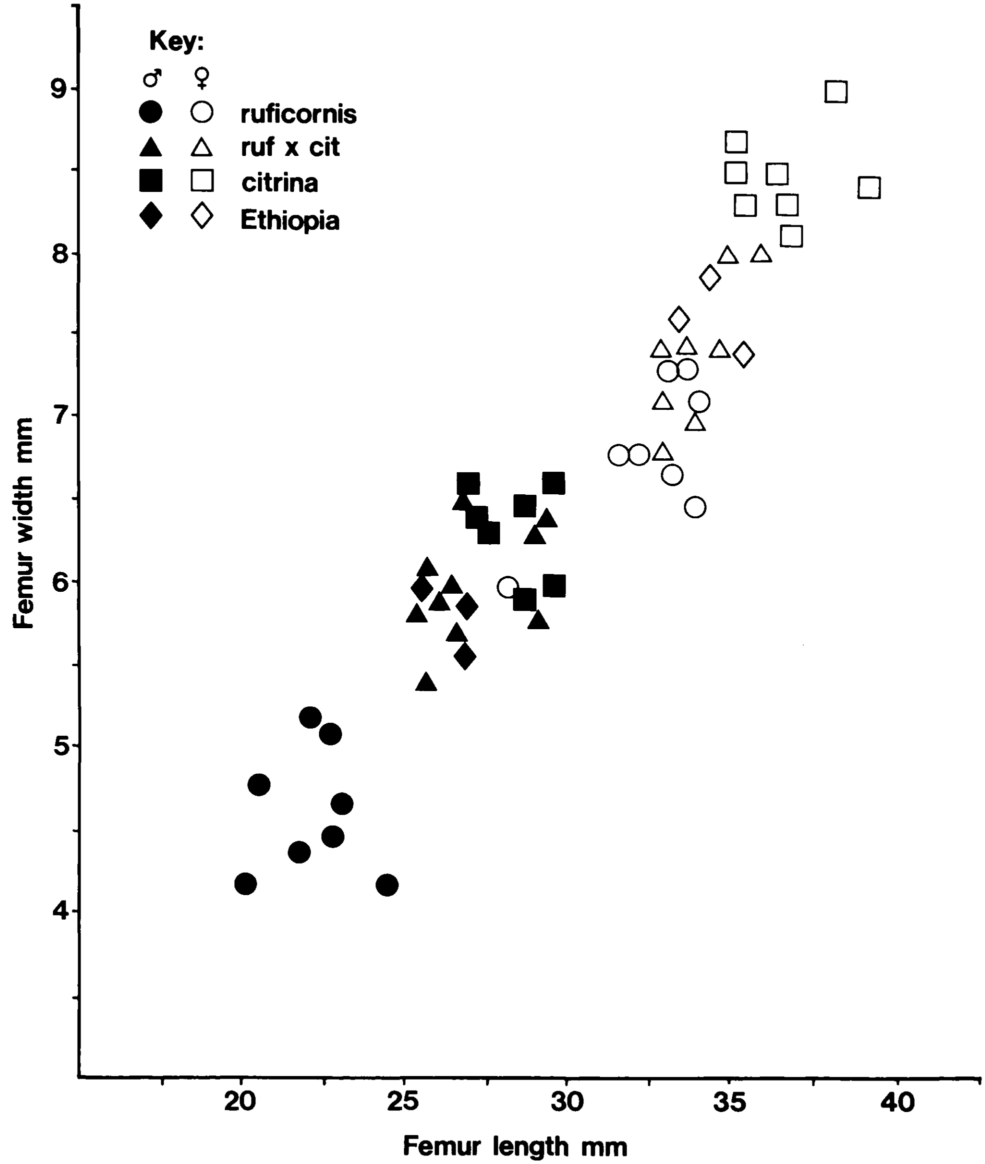

Figure 2.—Scatter diagram showing femur width plotted against femur length in *Acanthacris ruficornis* subspecies and hybrids. Males, shaded symbols, females unshaded symbols; ruf, *A. ruficornis;* cit, *A. citrina* ruf × cit, laboratory hybrids; Ethiopia, Ethiopian putative hybrid population.

ficornis populations further south by the desert of the Ogaden, northern Kenya and Somalia.

Mayr (1963) asserted that "cross-fertility does not prove conspecificity". He argued that sensory stimuli are a more important factor in correct intraspecific mate selection. These laboratory studies of *A. r. ruficornis, A. r. citrina* and their hybrids have indicated that there is no detectable premating obstacle to interbreeding and there is no post-mating obstacle to interbreeding. It further appears likely that in one area at least hybridization has occurred in the wild, giving rise to a population of intermediate characteristics. Where the two races have broadly parapatric ranges, in West Africa, they are perhaps prevented from interbreeding by differences in the timing of the onset of the rains. They may also be segregated by their different ecological requirement, *ruficornis* preferring shaded environments while *citrina* frequents more open habitats.

Several recent studies (Jago *et al.*, 1979; Harvey, 1979, 1982; Jago & Grunshaw, 1987) have utilized hybridization experiments as a tool to separate morphologically indistinguishable sibling species. In the present study the technique has demonstrated that populations which appear distinct on the basis of external morphology and colouration are in fact members of the same species. The result also enhances the importance of critical examination of the morphology of the male genitalia, which in this case indicated that the populations were conspecific (Mungai, 1987).

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Introduced grasshoppers and crickets in Micronesia

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ABSTRACT

A recent synopsis of the saltatorial orthopteroid fauna of Micronesia (Kevan, 1987) lists about 90 species. Of these, some 20 or more have been introduced by human agency, either into Micronesia or from one region within it to another. Human-assisted dispersal may be considered in four arbitrary categories: (a) early, by primitive means; (b) by sea during the "foreign trade and colonization" period (up to the late 1930's); (c) about the time of the Second World War and shortly afterwards (mostly by sea, though possibly some by air); and (d) more recently (post-1960; probably largely by air). It is also possible that one introduced species of tettigonioid may have been spread from Micronesia to the Hawaiian Islands (rather than vice versa). The latter seem to have been the source of several of the pre-1960 introductions, but direct importation from the Philippines has probably been the more recent route. Guam appears to have been the chief entry point from both directions, and several introduced species are not yet known to have spread further afield. Of recently introduced species, certain acridoids alone give cause for concern as potential pests, but evidence from elsewhere suggests than none presents a serious threat. The Philippine Taro grasshopper, *Gesonula mundata zonocera* (Navás), might possibly prove to be of some local significance, but more than a dozen years after its first known occurrence in the Marianas, this has not happened.

Key words: Grasshoppers, crickets, Micronesia, introduced.

1. Preamble

Micronesia constitutes a far-flung, rather ill-defined, heterogeneous assemblage of small islands and atolls scattered throughout the western Pacific Ocean. It does not form a discrete geographical, topographical, geological, biogeographical, ethnic, or even administrative, entity. Indeed, "Micronesia" is but a term of convenience for the islands falling within a particular near-rectangle of the Pacific Ocean (Fig. 1). The faunas of its different parts are more related to those of less distant adjacent regions than to those of more distant parts within itself. For an extensive, entomologically oriented account of Micronesia, see Gressitt (1954). Esaki (1940, 1943), Oakley (1946), Townes (1946) and Gressitt (1956) give briefer summaries of Micronesian insects. For an entomological bibliography, see Esaki *et al.* (1955). More recently, Kevan

Table 1.—Systematic list and synoptic information on species of Tettigoniodea (Katydids and allies) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Gryllacridoidea Gryllacrididae							
Gryllacris appendiculatus Brunner v. W.	Bismark Archipelago Samoas	Miscellaneous shrubs & forbs	None known.	E. Carolines Marshals	29-I-1904 (Griffini, 1908) [Pohnpei] 7-XI-1900 (Griffini, 1908) [Jaluit Atoll]	—	Possibly native to E. Carolines. Introduced status for Marshalls suggested by Schnee (1904), as *Gryllacris* n. sp.
Tettigonioidea Phaneropteridae							
Phaneroptera furcifera Stål	Philippine Is. only	Miscellaneous shrubs, forbs & grasses	? Little, if any, but will feed on tobacco, eggplant, peppers, etc.	Marianas (Guam, Saipan, Tinian, Rota, Aguiguan) Marshalls (Kwajalein, Lib.). Volcano or Kazan Is. (Iwo Jima) E. Carolines (Pohnpei)	1911 (Swezey, 1946) [Guam] 31-XII-1952 & 23-X-1953 10-VI-1958 Recent§ .	First record 15-IV-1957 (Gurney, 1958); well established by mid-1960's	Spread in Pacific probably from Guam. Earlier misidentifed as *Ph. brevis* (Audinet-Serville). *Ph. gracilis* Burmeister (?) possibly native to Bonin or Ogasawara Is.
Elimaea punctifera (Walker)	S.E. Asia*	Shrubs & miscellaneous low vegetation	Minor pest on buds & flowers of *Hibiscus*, etc.	Marianas (Guam)	1950's (28-VI-195-)	Considerably before 1882‡ (when already common)	Probably reached Guam from Hawai'ian Is. rather than directly from S.E. Asia. Unkown if still present.
Holochlora fuscospinosa Brunner v. W.	Phillippine Is. only	Trees & shrubs	None known	Marianas (Guam)	8-XI-1971	—	Became established (records to 10-X-1974 available). *H. nawae* Matsumura & Shiraki occurs (? naturally) in Bonin (Ogasawara) Is. *H. japonica* in Hawai'ian Is.

Table 1 (cont.).—Systematic list and synoptic information on species of Tettigoniodea (Katydids and allies) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Mecopodidae							
Mecopoda elongata (Linnaeus)	S., S.E. & E. Asia*	Various trees & shrubs	None known	Marianas (Guam)	8-IV-1974	—	Seems well established (records to 28-XI-1984 available).
Meconematidae							
Xiphidiopsis lita Hebard	Polynesia	Miscellaneous herbage, flowers & grases, etc.	Insignifcant.	E. Carolines (Pohnpei) Banaba or Ocean I.	V-1950 XII-1957	pre-1919‡.	Conceivably native to Micronesia, but few scattered records suggest introduction, more probably from Polynesia than Hawaiian Is.
Conocephaiidae							
Conocephalus (Anisoptera) saltator (Saussure)	Tropical America	Grasses & low vegetation	Potential minor pest of miscellaneous herbaceous crops; occasionally damages young cereal grains	? Wake I. only (one record of immature specimen)	8-XII-1958	Well established by 1895; widespread, reaching Midway I‡.	Establishment on Wake. I needs confirmation. Presumably spread from Hawa'ian Is., whence it also reached Line Is. (Palmyra) pre-1948 (Krauss, 1953, confirmed by Pitkin, 1980). Also present in Samoas & Cook Is. (Pitkin, 1980), probably from Hawai'ian Is. via Eastern (American) Samoa.

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* S.E. Asia includes the Philippine Is. whenever referred to.

† Date not previously recorded unless in, or deducable from, literature reference cited.

‡ Based on Zimmerman (1948) unless indicated otherwise; his sources have been checked.

§ Based on information received from Dr. Ilse Schreiner, University of Guam (*in litt.*, 1988).

Table 2.—Systematic list and synoptic information on species of Gryllodea (Crickets) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Gryllotalpoidea Gryllotalpidae							
Gryllotalpa orientallis Burmeister	S., S.E. & E. Asia*	Subterranean root feeder	Localized pest of roots of miscellaneous crops	Marianas (Guam, Saipan, Tinian) Carolines (Yap, Truk, Pohnpei)	1911 (Swezey, 1946) [Guam] 21 & 26-XII-1935 (C. Willemse, 1951) [Truk (Moen & Dublon)]	Common before 1896‡; first found on Oahu, introduced from E. Asia	Long confused with *G. africana* Palisot de B. (see Kevan, 1987); also recorded from Carolines as *G. formosana* Shiraki (Willemse, 1951). Conceivably introduced into Micronesia during early human migrations, but possibly not until much later from Hawai'ian Is. or elsewhere.
Mogoplistoidea Myrmecophilidae							
Myrmecophilus hebardi Mann	Solomon, Santa Cruz, Fiji, Samoan & Society Is. (endemicity uncertain)	Ant inquiline with *Anoplolepis longipes* (Jerdon)	Nil	Carolines (Truk)	Mid-1946. (Townes, 1946)	—	Probably more widespread than indicated. Conceivably long-standing human introduction with host ant which is very widely distributed in Pacific. Other species introduced into Hawai'ian Is.
Grylloidea *s. str.* Gryllidae *s. str.*							
Teleogryllus oceanicus (Le Guillou)	Widespread in Pacific region reaching N. & E. Australia	Ground cover, etc.	Occasional minor pest of miscellaneous herbaceous crops, etc.	Most islands investigated.	? Early 1870's (Schmeltz & Pöhl, 1877, "South-Sea Is" which included Micronesia?)	? Very early (earliest record by Saussure, 1877)	Formerly called *G. innotabilis* Walker. Probably widely transported on early human migrations. Originally described from Pacific.
Modicogryllus sp.	S. & E. Asia - Fiji.	Ground cover, etc.	Slight, if any, on herbaceous crops	Widespread	28-V-1936. Swezey, 1946) [Guam]	*ca.* 1901 (Perkins, 1910) [as "*Gryllus* sp."]	Previously misidentified as *Acheta* or *M. conspersus* (Schaum) from southern Africa. Townes' (1946) Micronesian reference to a "species of *Acheta*, apparently introduced", presumably same.

Table 2 (cont.).—Systematic list and synoptic information on species of Gryllodea (Crickets) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Gryllodes supplicans (Walker) f. *sigillatus* (Walker)	? S., S.E. & E. Asia* (now cosmopolitan, mainly tropical and subtropical)	Synanthropic, usually associated with buildings	Occasionally damaging plant shoots, but mainly a household nuisance	Marianas (Guam) Marshalls	Alredy common 7-VII-1936 (Swezey, 1946) Mid-1946 (Townes, 1946)	Pre-1894‡.	Reached Phoenix Is. (Canton I.), ? from Hawai'ian Is., by early 1940's (Van Zwaluwenbrg, 1943). Macropterous ("typical" form known from Ryu-Kyu. Is. (Ōshiro, 1986), but not yet elsewhere in the Pacific.
Eneopteridae *s. str.*							
Cardiodactylus novaeguineae (Haan)	S.E. Asia* to New Guinea & N. Australia	Bushes	None known	Belaus E. Carolines (?) (Pohnpei, Kosrae)	? Early 1870's (Schmeltz & Pöhl, 1877; Saussure, 1878). Mid-1946 (Townes, 1946)	—	Schmeltz & Pöhl (1877) list species as *Platydactylus* [homonym] *marmoratus* (Haan). Probably native to Belaus, but Holdhaus (1908) suggests introduction; probably introduced in E. Carolines though Townes (1946) queries species. Needs checking.
Podoscirtidae							
Euscyrtus hemelytrus (Haan)	S.E. Asia* to N. Australia	Shrubs & tall herbaceous plants	None known	Marianas (Guam)	24-III-1976.	—	Apparently well established; could conceivably be present naturally though unlikely; not previously recorded for Micronesia, even by Kevan (1987); distribution there not fully investigated.
Oecanthidae							
Oecanthus rufescens Audinet-Serville	S. & S.E. Asia* & apparently to Fiji, New Caledonia & N. Australia	Shrubs & tall herbaceous plants (?).	None known	Marianas (Tinian only)	8-I-1985	—	Identification needs cauttion but seems correct. Distribution not fully investigated; seems to be established.

* S.E. Asia includes the Philippine Is. whenever referred to.

† Dates without literature references given here for first time.

‡ Based on Zimmerman (1948) whose sources have been checked.

Table 3.—Systematic list and synoptic information on species of Acridodea (Grasshoppers, etc.) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Acridoidea Pyrgomorphidae							
Atractomorpha psittacina psittacina (Haan)	S.E. Asia*.	Low vegetation & shrubs	Occasional minor injury to vegetable & other crops	Marianas (Guam)	18-VI-1968	—	Well established on Guam (records to 22-I-1981 available), but so far not known elsewhere in Micronesia. For ambiguous literature references to *A. sinensis sinensis* Bolívar, introduced into Hawai'ian Is. & Line Is., see text.
Acrididae							
Oxya hyla intricata (Stål)	S., S.E. & E. Asia*	Low vegetation in damper situations	Pest of rice & some other crops (The Smaller Rice Grasshopper)	Belaus. W. & C. Carolines. E. Carolines (Pohnpei) (Kosrae) Marshalls (Jaluit)	Early 1860's (Schmeltz & Pöhl, 1869) 6-VII-1905 [Yap] 4-II-1936 (*cf.* C. Willemse, 1951, date omitted) 19-VIII-1946. [23-VIII]1946. (Townes, 1946)	—	Presumably native to Belaus and probably to Carolines, but transported eastwards to Marshalls during World War II.
Oxya japonica japonica (Thunberg)	S., S.E. & E. Asia*	Low vegetation in rather damp situations	Pest of rice, sugar-cane & other crops. (The Lesser Paddy Grasshopper)	Belaus Marianas (Saipan) (Tinian) [not yet known from Guam]	8-IV-1936 (C. Willemse, 1951) 10-XI-1971 22-XII-1984	Pre-1892 (Zimmerman, 1948)	Probably native to Belaus where first record was as *O. gavisa* (Walker). Spread from Hawai'ian Is. to Line Is. (Palmyra) prior to 1948 (Krauss, 1953). Spread to Marianas probably from the Philippines or possibly Hawai'ian Is., rather than from Belaus. Apparent absence from Guam is notable.

Table 3 (cont.).—Systematic list and synoptic information on species of Acridodea (Grasshoppers, etc.) introduced into or spread within Micronesia by Human Agency.

Species	Natural Distribution Outside Micronesia*	Usual Habitat	Actual or Potential Economic Significance	Micronesian Distribution	Earliest Known Micronesian Record†	Approximate Date of Introduction into Hawai'ian Is.‡	Remarks
Gesonula mundata zonocera (Navás)	Philippines — Taiwan	Lush vegetation in wet localities, especially on *Calocasia* spp.	Can cause damage to *Calocasia esculenta* (Linnaeus) (The Taro Grasshopper)	Marianas (Guam)	8-III-1971	—	Was established (records to IV-1979 available) in Guam, where introduced presumably from the Philippines. Record from Ryu-Kyu Is. seems to refer to *G. punctifrons* (Stål).
Stenocatantops splendens (Thunberg)	S.E. Asia*—Kai Is. & ? N. New Guinea. (Introduced in Solomon Is.)	Mesophilic low vegetation	Occasional minor damage to various crops	Marianas (Guam)	15-V-1984	—	Said to be now the commonest acridid on Guam (Dr. I. Schreiner *in litt.*, 8-IX-1986); presumed source the Philipphines.
Locusta migratoria manilensis (Meyen)	S., S.E. & E. Asia*	Mesophilic, mostly graminaceous, vegetation	In swarming phase can be major crop pest, especially of Graminaceae, over much of range; can also be minor pest in solitary phase (The Oriental Migratory Locust)	Bonin or Ogasawara Is. Volcano or Kazan Is. Marianas Belaus W. Carolines C. Carolines Marshalls (Kwajalein & Majuro).	Pre-1905 (Kuwana, 1905) XII-1945 [Iwo Jima] 1911 (Swezey, 1946) [Guam] 7-IV-1936 (C. Willemse, 1951) 12-IX-1939 [Yap] X.1952 [Truk (Moen)] [16 & 27-VIII-1946 (Townes, 1946)	—	Earlier records use name *Pachytilus danicus*. Swarms in Micronesia seem to be rare and restricrted to N.W. (Bonins), ? coming from E. Asia. The Micronesian distribution appears natural except for E. Carolines (not known) and Marshalls, whither carried about time of World War II and now established (records to 8-XII-1972 available).
Trilophidia annulata (Thunberg)	S., S.E. & E. Asia*	Open, drier ground with sparse vegetation	None known	Marianas (Guam)	10-XI-1945	—	Became established on Guam only; may not have persisted as no record available after X-1952.

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* S.E. Asia includes the Philippine Is. whenever referred to.

† Date not previously recorded unless in, or deducible from, literature reference cited.

‡ Not yet found again though sought (Dr. Ilse Schreiner, University of Guam, *in litt.*, 1988).

(1987) has included a short introduction to Micronesia and its insects in his synopsis of the saltatorial orthopteran fauna. He estimates that half of the 90 or so species are endemic to the region. Of the remaining 45 or so more widely distributed species, about a score are introductions or have been spread by human agency within Micronesia. The relevant species are listed in Tables 1-3, though there will doubtless be others to add in future. Identification of certain Micronesian taxa can be difficult because of errors in the literature, but those given here are the best possible at this stage. Many of the Micronesian species, or their close relatives, known from the Ryu-Kyu Islands, are well illlustrated in colour by Ôshiro (1986).

Human activity may cause the dispersal and introduction of animal species, and of insects in particular, from one part of the world to another in a number of different ways. All introductions, however, fall into one or other of two broad classes: deliberate, or accidental.

Deliberate introductions may be made for either utilitarian or aesthetic purposes, but I can think of no instance of an insect introduction into any part of Micronesia for the latter reason. Utilitarian introductions into the region have not been numerous, and, so far as I am aware, have been limited to biological control objectives, *i.e.*, attempts to regulate the size of populations of other invertebrate species (mainly other insects) or of weeds.

Among orthopteroid insects known to have been introduced into Micronesia, and sometimes transported from one island or island group to another within it, are a few species of mantids. Of these, *Orthodera burmeisteri* Wood-Mason (from New Guinea) and *Tenodera aridifolia sinensis* Saussure and *T. australasiae* (Leach) (originally from eastern Asia and other Pacific regions) are most probably deliberate introductions of relatively long standing, as they are recorded by Gressitt (1954) and Beier (1972). Other mantids deliberately introduced quite recently into Guam are the Oriental *Tenodera angustipennis* Saussure and the African *Polyspilota aeruginosa* (Goeze) and *Sibylla pretiosa* Stål. The arrival on Guam of *Statilia pallida* Werner (of Philippine origin), however, is more likely to have been accidental. There is only one, small, apparently endemic Micronesian mantid species, *Acromantis palauana* Beier, restricted to the Belau Islands in the southwestern sector (Beier, 1972).

Accidental introductions into Micronesia may be divided arbitrarily into four categories: (a) those of long standing that have depended upon early, primitive means of transportation (canoes and smaller sailing vessels); (b) those assumed to have taken place by sea with the expansion of foreign (European, American and Japanese) "trade and colonization" (under whatever guise), but prior to World War II; (c) those that occurred just before, during, or within a decade after World War II, mostly by way of Japanese and then American military sea transports, though perhaps also, to some extent, as a result of early, more general use of aircraft; and (d) those of more recent initiation (post 1950's) resulting from a combination of military and commercial transportation, with great increase in the use (and size) of cargo-carrying aircraft, together with intangible factors such as the growth of "economic" and "cultural aid" programs, as well as political and strategic exploitation by the United States of America.

2. Early Introductions

It is very difficult to assess how and when some early dispersals from one part of the world to another may have occurred, but there are certain insect species, widely distributed in the Pacific region, that may well owe their initial presence in Micronesia (or parts of it) to early human migrations. Among orthopteroids other than grasshoppers and crickets, it may be suggested with some confidence that this could apply to certain nearly cosmopolitan earwigs, such as *Chelisoches morio* (F.), originally described from the South Pacific, quite probably *Euborellia annulipes* (Lucas) and *Anisolabis maritima* (Bonelli), and

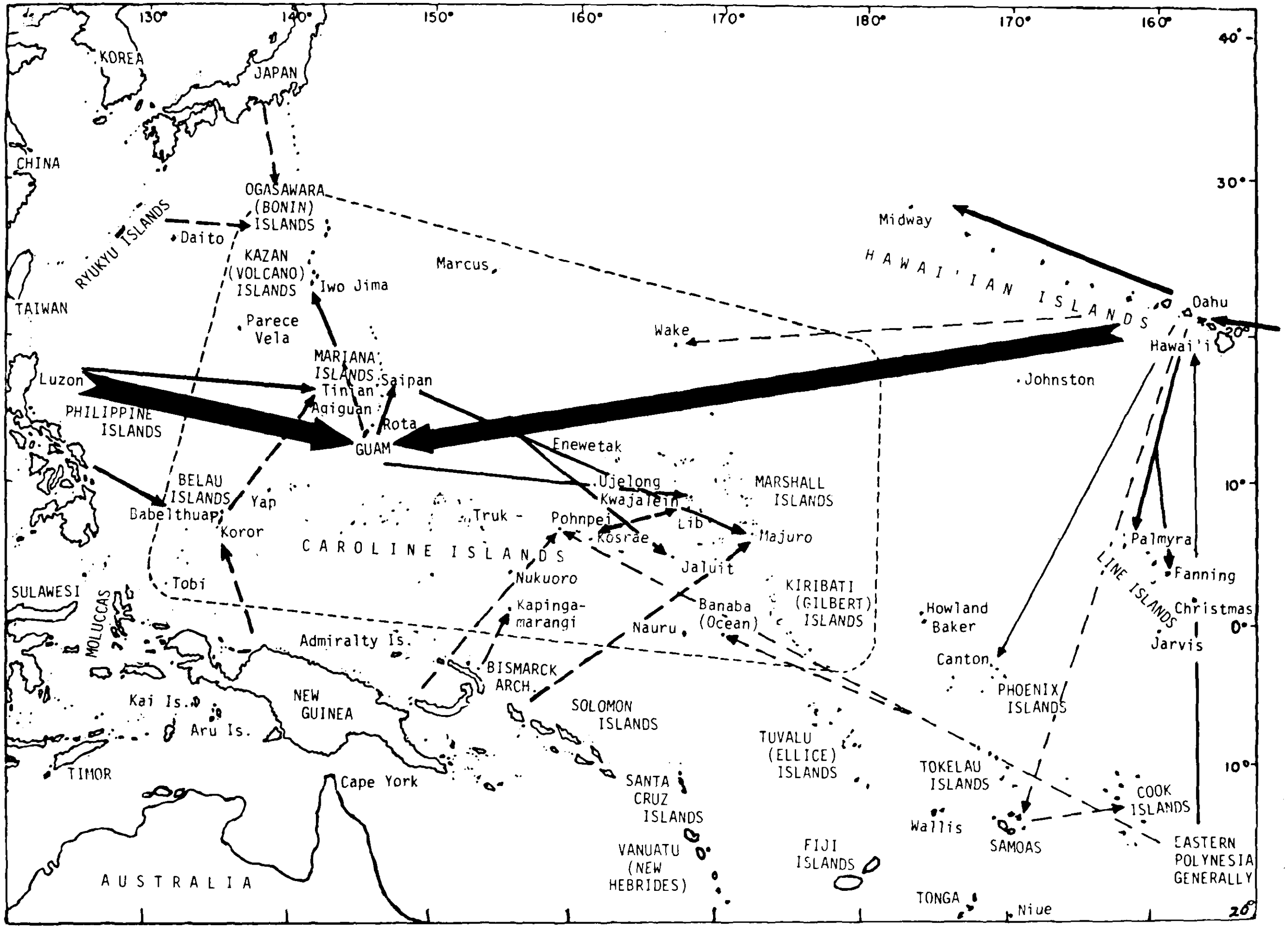

Figure 1.—Micronesia (within broken quadrilateral), showing principal sources of introduced saltatorial orthopteroid fauna. Solid arrows indicate high probability; broken arrows indicate possibilities or alternatives. (Philippines to Guam mostly post-war.)

possibly others (see Brindle, 1972, for candidates). Several species of widely distributed Oceanian cockroaches, such as *Onychostylus* (or *Luppova*) *notulatus* (Stål) and *Melanozostera nitida* (Brunner von Wattenwyl), or termites, such as *Cryptotermes domesticus* (Haviland), surely fall into this category also. It likewise may be suspected that some stick insects, such as *Megacrania batesi* Kirby, were included among early human-assisted travellers. Such insects often have the appearance of being *bona fide* natives of the islands which they inhabit, when they may be really nothing of the kind.

Among crickets, a very likely candidate for inclusion in this category is the very widely distributed grylline, *Teleogryllus oceanicus* (Le Guillou), a species that would easily have been carried about the Pacific at an early date with soil around planting material and with other chattels, both from outside and within Micronesia. Other companions of early human migrants may well have included the Oriental mole cricket, *Gryllotalpa orientalis* Burmeister (presumably the same species as occurs in the Hawaiian Islands and long misidentified as *G. africana* Palisot de Beauvois - see Kevan, 1987), and the ant-guest cricket, *Myrmecophilus hebardi* Mann. The former is known from a rather scattered range of Micronesian islands in the Marianas (Guam, Saipan, Tinian) and the Caroline Islands (Yap, Truk, Pohnpei), to which I do not believe it to be native. It may have been present for a long time and over a wider area without being discovered. *Myrmecophilus hebardi,* known to me otherwise only from Fiji and the Solomon Islands, may also be an early introduction into Micronesia, presuming (as is quite likely) that its very widely distributed host, the long-legged ant, *Anoplolepis longipes* (Jerdon), has been dispersed by human agency. This ant-guest cricket is known in Micronesia, so far, only from Truk in the central Carolines (Townes, 1946). With a more conspicuous insect, this might indicate more recent introduction, but myrmecophilines, being tiny and obscure, could easily have been overlooked by collectors.

3. Introductions During the Period of Foreign "Trade and Colonization"

Among non-saltatorial orthopteroids, there have been some obvious introductions dating from this period. They include truly cosmopolitan (rather than widely dispersed Pacific Island) cockroaches, such as *Periplaneta americana* (L.), *P. australasiae* (F.), *Pycnoscelus surinamensis* (L.) and *Supella longipalpa* (F.). There have also been introductions of less obviously alien species belonging to different groups, not only into Micronesia, but also between its different sectors.

The earliest direct reference in the literature to a presumably introduced species of saltatorial orthopteroid in Micronesia is to one of the latter, though the author (Schnee, 1904) probably thought that the species in question, *Gryllacris appendiculatus* Brunner von Wattenwyl, had come from outside the region. Clearer examples of other species that have been introduced into, and dispersed within, Micronesia by human agency are the leaf-katydid, *Phaneroptera furcifera* Stål, and a species of the cricket genus *Modicogryllus,* previously misidentified as *M. conspersus* (Schaum), as well as the Tropical house cricket, *Gryllodes supplicans* (Walker) f. *sigillatus* (Walker).

A summary of the known and possible Micronesian introductions of the "trade and colonization" period is as follows:

Gryllacris appendiculatus (Gryllacrididae). This is known from the Samoas and Bismarck Archipelago, and, in Micronesia, from the eastern Caroline Islands and the Marshall Islands.

Schnee (1904) reported that the species ("*Gryllacris* n. sp.") had been introduced into the Marshalls "recently" (*i.e.,* about the turn of the century) and that it had not then reached all of the [main] islands of the group, being absent, for example, from Ujelang [or Providence] Island. The author (an observant medical officer) commented that a large proportion of the Marshall Island flora consisted of introduced weeds, which would have alerted him to the probability that some of the fauna had also been introduced. Schnee lived for several years in the Marshall Islands and therefore had time to observe and reflect on such matters. His conclusions thus have credibility, even if they are debatable. Without his observation, it might appear that the Marshall Islands form a natural eastward extension of the species' range from the Caroline Islands. Now it is not certain that extension, as an introduced species, might not have proceeded in the opposite direction! The earliest Micronesian specimens known to me are, indeed, from the Marshalls (Jaluit [Atoll], 7.XI.1900)[1].

Phaneroptera furcifera Stål (Phaneropteridae). This is a native of the Philippine Islands. Ragge (1956), in his revision of the genus *Phaneroptera,* recorded it elsewhere only from Guam in the Marianas, and suggested it may have been introduced by sea (the specimen was not of recent date). Previously, however, several authors had already recorded it from the Marianas. Swezey (1946; *cf.* also Gurney, 1958), followed by Beller (1948), reported it from Guam as another species, *P. brevis* Audinet-Serville. Under its correct name, Townes (1946) recorded it from the Marianas, on grass and tobacco, as did Oakley (1953) on peppers and egg-plant (on Rota, Saipan, and Tinian Islands) and Dumbleton (1954) on egg-plant. Swezey (1946) had indicated that D.T. Fullaway collected *"P. brevis"* on Guam as long ago as 1911, and I have seen a corroborative specimen, though it bears no date, only a reference number, on the label. Otherwise the earliest-collected Micronesian specimen known to me (also from Guam) is dated 1923. From other islands in the Marianas, the earliest dates are: Rota, 1926, and Saipan, 1937 (and 1939). There may have been some extension of the range during World War II, as records from Tinian are no earlier than 1945, and from Aguiguan, not until 1952. Wartime transport is also almost certainly the explanation of the first known occurrence in the Marshall Islands about the same time (Kwajalein, 31.XII.1952; Lib, 23.X.1953), though there is no record in the literature earlier than 1965-1969 (Sugerman, 1972). *Phaneroptera furcifera* seems to have "leapfrogged" over the Caroline Islands, though there is now a recent record from Pohnpei in the eastern part of the archipelago (Dr. Ilsa Schreiner, University of Guam, *in litt.*, 1988), conceivably as a result of "backtracking" from the Marshalls.

Phaneroptera furcifera has also spread northwards, presumably from the Marianas, and has now been reported from the Volcano (or Kazan) Islands (Kevan, 1987), specifically from Iwo Jima, for 10.VI.1958, the initial introduction doubtless having occurred considerably earlier than that. As there were extraordinarily heavy military operations on this island toward the end of World War II, it may be assumed that the species was transported from the Marianas to Iwo Jima either by retreating Japanese or by advancing American vessels at that time or, as the species is not recorded for Iwo Jima by Van Zwaluwenburg (1947), more probably by the latter shortly afterwards. A species of *Phaneroptera* is also known to occur further north still, in the Bonin (or Ogasawara) Islands, but only from a single nymph, probably of *P. gracilis* Burmeister and quite possibly native. It is probable that the initial introduction of *P. furcifera* into Micronesia was directly to Guam from the Philippines, as suggested by Ragge (1956). Subsequent introduction into the Hawaiian Islands (first record from Oahu, 15.IX.1957 [Gurney, 1958]; common by 1966) may have been from Guam (or from some other Micronesian island), though perhaps directly from the Philippines; I have no way of assessing this.

Gryllotalpa orientalis (Gryllotalpidae). There is a distinct possibility that this is an introduction into Micronesia of very long

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[1] In the Humboldt University Zoological Museum, East Berlin: 2 males, 2 females, 2 immatures, collected by a Dr. Bartels; see also Griffini (1908), who recorded 3 males and 4 females, presumably retaining 1 male for the Turin Museum and regarding the immatures as females. In the Natural History Museum, Vienna, there is also 1 female collected by Schnee himself, but without closer locality than Mars(c)hall Islands and without date (see also Griffini, 1914: as *"Gr[yllacris]* spec.").

standing. If it is a more recent arrival, its occurrence certainly dates from before World War I, as Swezey (1946) indicated that D.T. Fullaway collected it on Guam in 1911. The same species, presumably, was already common in the Hawaiian Islands before 1896 (see Zimmerman, 1948). If introduction into Micronesia occurred during the "trade and colonization" period, it would seem probable that this was first to Guam from Oahu (Honolulu) because of the United States connection between them.

Modicogryllus sp. (Gryllidae). What mistakenly has been called *M. conspersus* (Schaum), a species confined to southern Africa (Otte and Cade, 1984), has been recorded widely in southern and eastern Asia. Presumably from the latter, it was introduced into the Hawaiian Islands, where it was first recorded in the late 19th century (Zimmerman, 1948) The *Modicogryllus* species known from both the Hawaiian and Fiji Islands remains undetermined (Otte and Cade, 1984), but it is probably safe to assume that the one found in Micronesia is the same, not *M. conspersus* as in Kevan (1987). Hitherto, the earliest Micronesian record that I have is from Guam, Marianas, 28.V.1936 (see also Swezey, 1946), though I have not undertaken a proper investigation. Townes (1946) refers to a "species of *Acheta,* apparently introduced" as being widespread in Micronesia (no specific island named), and it is likely that he referred to *Modicogryllus.* Species of that genus, like *Teleogryllus,* including *T. oceanicus,* were formerly assigned to *Acheta,* for example, as in Zimmerman (1948). Had Townes meant *oceanicus,* he would doubtless have used that name, for he was familiar with that species, which in any event, does not usually give the impression of being introduced where it occurs.

Gryllodes supplicans f. *sigillatus.* The Tropical or Decorated, house cricket is a cosmopolitan species of unknown (probably S.E. Asian) origin. It is widely distributed throughout the Pacific region, having reached the Hawaiian Islands well before 1895 (Zimmerman, 1948). The species normally occurs only in the brachypterous (or micropterous) form indicated (see Kevan, 1980 and elsewhere in preparation), most authors having used this as the species name. The macropterous ("typical") form is, so far unknown from Micronesia, though Ôshiro (1986) illustrates it as occurring in the Ryu-Kyu Islands. Despite the facility with which it accompanies humans, there seems to be no authenticated Micronesian record of it prior to that for Guam in 1936 (Swezey, 1946), though it was then already widespread and abundant, particularly in buildings. It was not recorded from beyond the Marianas in Micronesia until Townes (1946) noted its occurrence in the Marshall Islands a decade later. It had, however, reached the remote Phoenix Islands (specifically Canton Island), beyond the bounds of Micronesia, by the early 1940's at latest, by which time an air base (in addition to the earlier British Cable and Wireless station) had been established there (Van Zwaluwenburg, 1943).

Cardiodactylus sp.?*C. novaeguineae,* (Haan) (Eneopteridae). *C. novaeguineae* appears to be but one of a complex of species widely distributed from southeastern Asia to New Guinea and Melanesia generally, as well as to northern Australia. That *Cardiodactylus* can be transported by human agency is indicated by its occurrence in the Marquesas. Long ago, Holdhaus (1908) suggested that *C. novaeguineae* had been introduced into the Belau Islands, though, in view of its allegedly wide natural distribution, it could be native there. Otte *et al.* (1987) mentioned the genus (but no species) from the "Western Carolines"; they presumably meant the same group. The status of *Cardiodactylus* in other parts of Micronesia would also bear investigation, as the genus is known also from the eastern Caroline Islands (Pohnpei and Kosrae) - see Townes (1946), who believed that species found there were endemic.

4. Introductions about the Time of World War II

A number of species introduced earlier, and noted already, almost certainly availed themselves of the increased human activity during wartime operations to expand their areas of dispersal in Micronesia. Besides some of the less generally abundant cricket species, *Phaneroptera furcifera, Gryllodes supplicans* f. *sigillatus,* and probably *Modicogryllus* sp., may be cited as examples. Some species native to one or another part of Micronesia, such as the Smaller Rice grasshopper, *Oxya hyla intricata* (Stål), and the Oriental Migratory locust, *Locusta migratoria manilensis* (Meyen), also appear to have extended their ranges with human assistance during this period. "New" aliens to come in included a grasshopper, *Trilophidia annulata* (Thunberg), though whether this survived for more than a year or two is uncertain.

Elimaea punctifera (Walker) (Phaneropteridae). This slender leaf-katydid is native to southeastern Asia. It was introduced into the Hawaiian Islands, perhaps shortly after the middle of the 19th century; its occurrence there was published as early as 1882 (see Zimmerman, 1948). The first known Micronesian record (Kevan, 1987) is from Guam in the 1950's ("28.VII.195-" on label). The introduction may well have been from Hawaii, rather than directly from Asia. It is not known to me from other Micronesian Islands, nor whether it has become established on Guam.

Xiphidiopsis lita Hebard (Meconematidae). *Xiphidiopsis* is badly in need of revision, as it encompasses species that should be transferred into several genera, but the present species is apparently endemic to Polynesia, where it is widely distributed. It is interesting in that it seems to be parthenogenetic (Zimmerman, 1948), which would be advantageous in establishing the species amongst widely scattered islands and would readily make for establishment by human agency. *Xiphidiopsis lita* has been introduced into the Hawaiian Islands, though records go back no further than 1919. As it is known in Micronesia (Kevan, 1987) from only two widely separated islands, introduced status is suggested. The islands are Pohnpei, in the eastern Caroline Islands, and the isolated Banaba (or Ocean) Island, in the southeast. Records date from May to October, 1950, for the former, suggesting a wartime introduction. For the latter, the date of the single specimen is December, 1957. While the species could have reached Micronesia from the Hawaiian Islands, direct Polynesian sources seem more probable in this instance.

Conocephalus (Anisoptera) saltator (Saussure) (Conocephalidae). This small, cone-headed katydid is of tropical American origin. It was carried to the Hawaiian Islands before 1890 and was well established there prior to 1895 (Zimmerman, 1948; Pitkin, 1980). It has been a successful colonizer and occurs throughout these islands, being established even on Midway Island (Zimmerman, 1948). From the Hawaiian Islands, presumably, it has also been transported by man to the Line Islands, and became established on Palmyra Atoll before 1948 (Krauss, 1953; identification confirmed by Pitkin, 1980). It is also present in the Samoas and in the Cook Islands. Pitkin (1980) considered that it arrived there from the Hawaiian Islands. If so, it probably came first to eastern (American) Samoa. It is not certain that *C. saltator* is indeed established as an introduced species in Micronesia (Kevan, 1987), for the only evidence is a nymph (almost certainly of this species) from Wake Island, taken 8.XII.1958. Fairly early post-war naval or air transport from Hawaii would be presumed in the event of verification.

Oxya hyla intricata (Stål) (Acrididae). The Smaller Rice grasshopper is widely distributed in southeastern Asia, including the Philippine Islands, though it has not yet been recorded from the Hawaiian Islands. In Micronesia, it occurs throughout much of the Belau and Caroline Islands proper, where, for want of contrary evidence, it may be deemed to be native. Its presence as far east as the Marshall Islands (Kevan, 1986), however, probably does not date from much, if at all, before World War II. Townes (1946) noted that, when he took the species on Jaluit Atoll (specimens seen by me date from 23.VIII.1946), it was limited to the area around the former Japanese base, indicating that it had probably been introduced there during the war by the

Japanese. It may well be that it did not reach Kosrae in the eastern Caroline Islands until about the same time, as the earliest specimen I have seen from there is dated 19.VIII.1946. This species may be a minor pest, particularly of rice, so that its spread may be of some economic concern.

Locusta migratoria manilensis. The Oriental Migratory locust, or a form close to that subspecies, is widely distributed throughout the whole of western Micronesia from the Bonin (or Ogasawara) Islands to the Belau Islands. It is naturally distributed, and presumably resident, as far east as the central Caroline Islands. Despite its powers of dispersal, however, the species does not seem to have extended its range naturally any further eastwards in Micronesia, for there is a gap in its distribution between Truk (central Carolines) and the Marshall Islands. Townes (1946; see also Gressitt, 1954), maintained that this locust was accidentally introduced into the latter (Kwajalein and Majuro Atolls) during World War II - probably under similar circumstances to those for the previous species. There is certainly no evidence of the presence of locusts in the Marshall Islands at an earlier date. The earliest Marshall Islands specimens known to me were collected 16.VIII.1946 (Kwajalein) and 27.VIII.1946 (Majuro)[2]. It is, of course, possible that the populations from which these specimens came were residual progeny of natural migrants, but the absence of any evidence of the presence of the species in the eastern Carolines at any time, and the proximity of the early Marshall Islands specimens to past human activity (Townes, 1946), are against this. That the species subsequently established itself further afield in the Marshall Islands is evidenced by various later specimens (up to 1972 examined). Although, in its "solitary" phase, the Oriental Migratory locust is not a devastating pest, its potential as an injurious species should not be disregarded.

Trilophidia annulata (Thunberg) (Acrididae). This small, locustine (oedipodine) grasshopper is another species that is widely distributed in southeastern Asia and common in the Philippines as well as elsewhere. Like the two previous species it is unknown in the Hawaiian Islands. In Micronesia, it has been found only on Guam in the southern Marianas (Kevan, 1987), where it must have been a wartime introduction, the earliest known specimen being dated 10.XII.1945. As it cannot have been introduced from the Hawaiian Islands, it probably came to Guam from the Philippines. Although ecologically a rather tolerant species favouring drier situations, it has not spread to other islands, so far as is known. Indeed there is lack of confirmation of its persistence even on Guam (Dr. I. Schreiner, University of Guam, *in litt.*, 1986). The last record available to me dates from as long ago as October, 1952, though specimens collected later may exist.

5. Introductions in Recent Years

It seems that, in spite of plant quarantine measures, numerous species of insects have been introduced accidentally into Micronesia during recent years. Not only has *Oxya japonica* (Thunberg) spread its range within Micronesia in these later times, but a fair number of orthopteroid species have been encountered for the first time in the region only quite recently. Several such species were indicated by Kevan (1987) as being recently introduced, but only the Marianas (mainly Guam) were involved. All of the species, too, occur naturally in the Philippine Islands. Although all but one of the species are known to occur elsewhere also, the implication is that there has been a considerable immigration by air transport into Micronesia from the Philippines. This applies not only to saltatorial orthopteroids, the mantid *Statilia pallida,* already mentio-

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[2] Schnee (1904) reported "Locustina" (not identified further) from the Marshall Islands, but with the usage of the time, this meant Tettigonioidea, almost certainly a native species, as it had a Micronesian name, and probably *Conocephalus (Anisoptera) longipennis* (Haan).

ned, being but one other example. The major staging point for introduction into Micronesia was probably Manila (Luzon) and the main point of entry, though evidence is lacking for certain species, was apparently Guam. An exception is the relatively large, more or less cosmopolitan Cinereous cockroach, *Nauphoeta cinerea* (Olivier), taken first in the Belau Islands ("Palau Airport 9-8 86", presumably meaning near Airai, Babelthuap Island (8.IX.1986). The more spectacular species recently introduced into Micronesia are two large katydids, *Holochlora fuscospinosa* Brunner von Wattenwyl and *Mecopoda elongata* (L.). The small cricket, *Euscyrtus hemelytrus* (Haan), is an undoubted recent introduction into Guam. It has not hitherto been reported from Micronesia. The bush-hopper *Atractomorpha psittacina* (Haan), the large, brown grasshopper *Stenocatantops splendens* (Thunberg) and the Philippine Taro grasshopper, *Gesonula undata zonocera* may have some potential as crop pests. The following species are recent introductions:

Holochlora fuscospinosa (Phaneropteridae). This large leaf-katydid was previously known only from the Philippines until Kevan (1987) noted its occurrence in the Marianas (Guam). On account of its size, it is unlikely that it was overlooked in the past. The earliest Guam specimen known to me is dated 8.XI.1971. I have seen others only up to 10.X.1974, but I have no doubt that it is established on the island. It may also be noted that *H. nawae* Matsumura and Shiraki is also found in Micronesia, occurring, probably naturally, in the Bonin (or Ogasawara) Islands, where it was first recorded in 1915. The Hawaiian Islands also have their (introduced) species of the genus, *H. japonica* Brunner von Wattenwyl, imported from eastern Asia prior to 1896 (Zimmerman, 1948).

Mecopoda elongata (Mecopodidae). This is another large katydid which is not likely to have been overlooked in the past. It is the *kutsuwa mushi*, in Japanese, and famed in the Orient for its song. It is very widely distributed in southern and eastern Asia, but was first recorded for Micronesia (Marianas) only very recently (Kevan, 1987). The Philippine Islands were, again, the most probable source of introduction. So far, there is no evidence to indicate that it has gained a foothold other than on Guam. The earliest known specimen from there is dated 8.IX.1974. The latest that I have seen was collected on 28.XI.1984, so that the species seems to be well established and thriving. It has not yet been reported from the Hawaiian Islands.

Pteronemobius spp. (Trigonidiidae, Nemobiinae). No nemobiine cricket, other than the shore-dwelling "sand-cricket," *Tahitinemobius* (formerly *Speonemobius*) *tigrinus* (Saussure), has been certainly recorded from Micronesia, though Townes (1946) indicated that unnamed species of Nemobiinae (implicitly differing from what was undoubtedly the widespread *T. tigrinus*) had been seen on Yap and Pohnpei. If these were not *T. tigrinus* - and the small, brachypterous *"Pteronemobius"* recorded for the latter by Kevan (1987: 309n) seems to be this-Townes may have referred to small landrevine (pteroplistine) Gryllidae (possibly *Neova bodamensis* Otte) and not to nemobiines. What is tentatively identified as *Pteronemobius taprobanensis* (Walker) and a species closely resembling *P. concolor* (Walker), however, are both known to me from Guam (1.XI.1968 and 5.I.1985, respectively; new records, not given in Kevan, 1987). These species are very widely distributed in southern Asia and parts of the eastern Pacific, if determinations are correct (and *"Pteronemobius"* is much in need of revision). The absence of earlier Micronesian records is at least suggestive of recently introduced status for the two species referred to. They are not listed in Table 2, however, in view of the various uncertainties involved.

Euscyrtus hemelytrus (Podoscirtidae). This small, slender, flightless cricket is widely distributed from southeastern Asia (including the Philippine Islands) to northern Australia. It is so far known in Micronesia only from Guam. The earliest record known to me is for 24.III.1976. It is clearly established on the island, though I have not yet examined material captured later than 15.IV.1979. The species was not noted in

Kevan (1987), who was not at the time aware of its existence on Guam. Otte *et al.* (1987) note that Euscirtinae in general are unknown from the Caroline Islands.

Oecanthus rufescens Audinet-Serville (Oecanthidae). Identification of the pale "tree" crickets of the genus *Oecanthus* requires caution, but my determination is as close as possible at present. *Oecanthus rufescens* is said to have a very wide distribution in southern and southeastern Asia, extending eastwards to Fiji, New Caledonia and northern Australia, though it might be questioned whether the last two, at least, of these harbour the same species. In any event (though I have not fully looked into the matter), it seems that the present species has been introduced into the Marianas quite recently (Kevan, 1987) as the only records I have are for the island of Tinian, 8&12.V.&13.I.1985. The species is not recorded from the Hawaiian Islands. No oecanthid is known from the Caroline Islands, including the Belau Islands (Otte *et al.*, 1987).

Atractomorpha psittacina psittacina (Pyrgomorphidae). This elongate pyrgomorphid bush-hopper is common in southeastern Asia, including the Philippines. Its introduction into Micronesia seems to be of about 20 years' standing, though the first report of its occurrence (in the Marianas) is only very recent (Kevan, 1987). Prior to this there was an ambiguous reference by Owen (1971) to the occurrence of *A. sinensis [sinensis]* Bolívar ["Locustidae" (*sic*)] from the [United States'] "Trust Territory of the Pacific Islands". The species was listed as a pest of sugar-cane. This record is followed (with an incorrect source reference) in C.O.P.R. (1982), which, without justification, gives the distribution as "... introduced in (? Caroline Is.), Line Is., Mariana Is., Marshall Is.". In fact, it seems that both Owen (1971) and C.O.P.R. (1982) refer only to the occurrence of *A. s. sinensis* in the Line Islands, not in Micronesia, the original source being attributable to Krauss (1953) who reported the species on sugar-cane, under the synonym *A. ambigua* Bolívar, for Palmyra Atoll in February, 1948[3]. There is no tangible evidence that *A. s. sinensis* has ever been found in Micronesia, though its potential for human introduction is quite high. All Micronesian specimens of *A. p. psittacina* known to me are from Guam, the earliest and latest dates being 18.VI.1968 and 2.I.1981, respectively. As the species now seems to be relatively common, it could probably spread to other islands, though there is, as yet, no evidence that it has done so. It has the potential of being injurious to various crops, but it is not known to be of much economic importance elsewhere (C.O.P.R., 1982).

Oxya japonica japonica (Thunberg) (Acrididae). The Lesser Paddy grasshopper was long confused with *O. chinensis* (Thunberg) - see Kevan (1986) for a summary of the history of this confusion, etc. It is widely distributed in southeastern Asia, including the Philippine Islands. Prior to 1892, it was introduced into the Hawaiian Islands (Zimmerman, 1948) and, presumably from there, it made its way to the Line Islands, where it had become established on Palmyra Atoll before 1948 (Krauss, 1953). In Mi-

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[3] Although Palmyra Atoll is a United States Pacific island naval station, it was not part of the "Trust Territory of the Pacific Islands". The term, at the time, referred to the Mariana Islands (strictly excluding Guam), the Caroline Islands (including the Palau, now Belau, Islands) and the Marshall Islands, but it could be that Owen's (1971) report covered Pacific islands not indicated in his title. C.O.P.R. (1982), it would seem, merely assumed that Owen meant what he said and then presumed that all of the "trust Territory" archipelagos (as well as the Line Islands) harboured *A. sinensis,* through why the Caroline Islands should be singled out as the only area of possible introduction is inexplicable, except as a result of faulty editing; the source reference number erroneously indicated Swezey (1907) as the author concerned! This author did, in fact, publish notes on *A. sinensis,* misidentified as *A. crenaticeps* (Blanchard), shortly after its introduction into the Hawaiian Islands (Oahu), which occurred shortly before 1900 (Zimmerman, 1948). He also suggested that it had been introduced from Australia (where *A. crenaticeps* does not occur), though he did also mention New Guinea (where it does occur; *A. sinensis* is found in neither).

cronesia, *O. j. japonica* occurs in the Belau Islands, quite probably as a natural extension of its range eastwards from the Philippines, though it could perhaps have been an early introduction. Only fairly recently has it appeared elsewhere in Micronesia, namely, in the Marianas, where it has been introduced (Kevan, 1987). The earliest Mariana record that I have is from Saipan (10.XI.1971); for Tinian I have seen nothing earlier than 22.II.1984. Strangely enough, the species is still unrecorded from Guam, though it has been sought (Dr. Ilsa Schreiner, University of Guam, *in litt.*, 1988). One might have expected it to have been found there first, as an introduction either from the Hawaiin Islands or from the Philippines, rather than from the nearer Belau Islands. As the species can be a crop pest (particularly of rice), there may be some reason for concern at its arrival in the Marianas.

Gesonula mundata zonocera (Acrididae). The Taro grasshopper, *G. mundata* (Walker), which is injurious to *Calocasia esculenta* (L.) in some regions, is discussed by Kevan (1986) with particular reference to the Philippine subspecies, *zonocera.* This subspecies also seems to be the one present in Taiwan. The species of *Gesonula* occurring in the Ryu-Kyu Islands has been identified (and figured) as *G. punctifrons* (Stål) (Ôshiro, 1986). It was not until very recently that *G. mundata* was reported from Micronesia (Kevan, 1987); its occurrence there was not noted earlier by Kevan (1986), where it is still known only from Guam. The earliest record now known to me from Guam is for 8.III.1971 (other specimens that I have seen were collected up to 11.IV.1979). The species was presumably introduced directly on to Guam from the Philippines rather than from elsewhere. It has not been found in the Hawaiian Islands. In view of its pest status (even if not major), its introduction into Micronesia might give cause for concern. Nevertheless, although it has been sought, no specimen has been taken recently (Dr. Ilsa Schreiner, University of Guam, *in litt.* 13.VI.1988).

Stenocatantops splendens (Acrididae). The last species to be considered here, a rather large, brown, catantopine grasshopper, seems also to be the most recent immigrant into Micronesia, whence it was first recorded by Kevan (1987). In view of its size, it is not likely to have been overlooked earlier. It is a native of much of southeastern Asia, including Taiwan and the Philippine Islands, and its natural range extends eastwards to the Kai Islands and quite possibly to northern New Guinea. F. Willemse (1968), who gave the known distribution, also recorded the species from Bougainville Island in the Solomons, where he believed it had been introduced. There would thus seem to be a precedent for its introduction into Micronesia[4]. So far, it has been found in the latter only on Guam. It was apparently not known there prior to 1984 (earliest record 15.V.1984), but it is now said to be the commonest grasshopper on the island, according to Dr. Ilse Schreiner of the University of Guam (*in litt.*, 8.IX.1986), to whom I am most grateful for much of my recent information on the orthopteroid insects of the Marianas. *S. splendens,* in countries where it occurs naturally, can be a minor pest of different crops (F. Willemse, 1968; C.O.P.R., 1982), so that it could give some cause for concern in a new environment, even though it is not considered to be very important elsewhere.

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[4] In C.O.P.R. (1982), it is indicated that the Solomon Islands species, like that in New Guinea, requires checking, but F. Willemse (1968) seemed quite confident of his identification.

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Distribution and incidence of grasshoppers (Acrididae) of Sind

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ABSTRACT

A total of 42 species of grasshoppers was collected from Sind during 1983-85. Of these, nine species are recorded for the first time from this area: namely *Dericorys tibialis* (Pallas.), *Mioscritus wagneri rogenhoferi* Saussure, *Scintharista notabilis* (Walker), *Singoderus carinatus* (Saussure), *Gelastorhinus semipictus* (Walker), *Oxya fuscovittata* (Marschall), *Oxya bidentata* (Willemse), *Choroedocus illustris* (Walker) and *Tropidopola longicornis longicornis* (Fieber). The species' distributions and incidence at the district level are also considered.

Key words: Acrididae, Sind, distribution

INTRODUCTION

Sind Province is located in the southeast region of Pakistan and lies between 23° and 29°N latitude and 67° and 71°E longitude. It is about 360 miles long from north to south and nearly 275 miles in its greatest breadth (175 miles average), covering nearly 52,994 miles^2. Until now a detailed survey of the grasshopper fauna of Sind has not been attempted, although several papers have made casual reference to it (Kirby,1914; Bei-Bienko and Mishchenko, 1951a,b; Moeed, 1966, 1971, 1976; Hollis, 1968, 1971, 1975; Jago, 1967, 1977; Ahmad, 1980; Perwin *et al.*, 1983).

To the west of Sind are the Kirthar Mountains and northwestern areas adjoining the Kalat Division. These are dry and arid, with Palaearctic topography. The eastern region consists of the sand belt stretching from the borders of Bahawalpur (Punjab) to the Runn of Kutch and is part of the Rajistan Desert, called Thar. West of Thar lies the Deltaic area, with rich alluvial soil crossed by numerous river channels.

The following study was carried out on the distribution, incidence, and important host plants in order to bring the knowledge of Acrididae of Sind up to date.

MATERIALS AND METHODS

This survey of Sind was carried out from October, 1983, to April, 1985. During this period six trips were made on different dates in the various districts.

The species incidence was determined by taking about 400 sweeps throughout each area of Sind (an average of 30 sweeps in each district during each trip) with an insect collecting hand net of 8" diameter and 20" depth.

The collected material was preserved by conventional methods and deposited in the Department of Zoology Museum, University of Sind. The system of classification followed is that of Uvarov (1966). The names recently proposed by Vickery and Kevan (1983) for the subfamilies Calliptaminae, Hemiacridinae, and Oedipodinae are used.

Table 1.—Total numbers of Adults collected in a average of 2400 sweeps

	DISTRICTS												
Group and species	Karachi	Thatta	Dadu	Hydera-bad	Badin	Thar-parkar	Sanghar	Nawab-shah	Khair-pur	Sukkur	Shikar-pur	Jacoba-bad	Larkana
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Dericorythinae													
Dericorys tibialis (Pallas)	1	—	9	—	—	—	—	—	—	—	—	—	—
Oxyinae													
Oxya hyla hyla Audinet-Serville	—	14	8	2	7	1	—	1	—	2	18	271	183
O. fuscovittata (Marschall)	—	2	—	—	4	1	—	—	—	1	2	2	2
O. bidentata (Willemse)	—	1	—	1	—	—	—	—	—	—	—	—	4
O. velox (F.)	—	1	—	—	—	—	—	—	—	—	1	—	2
Euthyminae (= Hemiacridinae)													
Spathosternum prasiniferum (Walker)	1	5	10	21	16	14	10	5	9	16	2	2	23
Tropidopolinae													
Tropidopola longicornis longicornis (Fieber)	—	—	—	—	1	—	—	—	—	1	—	—	2
Cyrtacanthacridine													
Schistocerca gregaria (Forskal)	—	—	2	—	—	—	—	—	—	—	—	—	—
Anacridium aegyptium rubrispinum B. Bienko	—	—	4	—	—	—	—	—	—	—	—	—	—
Calopteninae (=Calliptaminae)													
Acoryha glaucopsis (Walker)	—	—	4	—	—	—	—	—	—	—	—	—	—
Eyprepocnemidinae													
Eyprepocnemis alacris alacris (Audinet-Seville)	—	—	1	1	5	—	—	—	—	—	1	—	7
Choroedocus[1] *illustris* (Walker)	—	—	1	—	—	—	—	—	—	—	—	—	1
Ch. robustus[2] (Audinet-Serville)	—	—	5	7	2	—	—	2	—	—	—	—	—
Ch. capensis[3] (Thunberg)	—	—	12	—	—	1	—	2	—	—	—	—	—
Heteracris (s. str.) *adspersa* (Redtenbacher)	—	—	—	—	—	2	—	—	—		1	1	—

Table 1 (Contd.).—Total numbers of Adults collected in a average of 2400 sweeps

Group and species	DISTRICTS Karachi	Thatta	Dadu	Hydera-bad	Badin	Thar-parkar	Sanghar	Nawab-shah	Khair-pur	Sukkur	Shikar-pur	Jacoba-bad	Larkana
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Catantopinae													
Catantops pinguis innotabilis (Walker)	—	—	2	—	—	—	—	—	—	—	—	—	—
Locustinae (= Oedipodinae)													
Hilethera aeolopoides (Uvarov)	—	—	1	1	—	—	—	2	4	—	—	—	—
Aiolopus thalassinus (F.)	34	8	33	20	19	17	30	20	44	21	10	2	108
A. thalassinus tamulus (F.)	21	2	9	5	6	6	8	4	3	3	1	—	4
Trilophidia annulata (Thunberg)	11	12	9	18	12	3	9	1	6	14	2	3	19
Locusta migratoria L.	—	—	4	—	—	—	—	—	—	—	—	—	8
Oedaleus rosescens Uvarov	—	—	1	5	—	—	—	—	—	—	—	—	—
Scintharista notabilis (Walker)	—	—	1	—	—	—	—	—	—	—	—	—	—
Mioscirtus wagneri rogenhoferi (Saussure)	—	—	6	3	—	7	—	—	—	—	—	—	—
Acrotylus humbertianus (Saussure)	—	2	19	—	—	6	5	1	2	2	—	—	1
A. longipes Charpentier	—	2	19	—	—	6	5	1	2	2	—	—	1
A. longipes subfasciatus B. Bienko	—	—	7	—	—	—	—	—	—	—	—	—	—
**Sphingoderus carinatus* (Saussure)	—	—	1	—	—	—	—	—	—	—	—	—	—
Sphingonotus savignyi (Saussure)	8	5	19	—	—	—	—	—	—	—	—	—	—
S. rubescens rubescens (Walker)	—	6	5	—	—	—	—	—	—	—	—	—	—
**Sphingonotus sp.*	—	—	4	—	—	—	—	—	—	1	—	—	—
Truxalinae													
Truxalis eximia eximia Eichwald	—	1	12	1	—	—	—	—	1	—	—	—	1
T. grandis fitzgeraldi Dirsh	—	1	—	—	—	2	2	—	—	—	—	—	1
Acridinae													
**Gelastorhinus semipictus* (Walker)	—	—	—	7	—	—	2	1	—	—	—	—	—

Table 1 (Contd.).—Total numbers of Adults collected in a average of 2400 sweeps

Group and species	DISTRICTS												
	Karachi	Thatta	Dadu	Hyderabad	Badin	Tharparkar	Sanghar	Nawabshah	Khairpur	Sukkur	Shikarpur	Jacobabad	Larkana
1	2	3	4	5	6	7	8	9	10	11	12	13	14
Acrida exaltata (Walker)	4	17	10	32	22	14	20	18	3	7	5	3	27
Oxypterna afghana Ramme	—	—	—	4	—	4	6	3	8	1	—	1	—
O. akbarii Moeed	—	—	—	2	—	4	2	1	6	—	—	—	—
Phlaeoba tenebrosa Walker	—	2	—	15	7	—	—	—	—	1	—	—	—
Duroniella laticornis (Krauss)	4	22	34	37	21	25	35	30	31	30	20	21	64
Gomphocerinae													
Ochrilidia geniculata (Bolivar)	—	—	7	—	—	—	—	—	—	1	—	—	—
O. gracilis gracilis (Krauss)	—	—	2	3	—	—	—	—	—	—	—	—	—
Aulacobothrus luteipes (Walker)	1	6	15	—	—	1	—	1	—	—	—	—	—

(1, 2, 3 earlier named as *Heteracris illustris*).

(*H. robustus* and *H. capensis* respectively, as reported in personal communication by Kevan in 1986).

RESULTS AND DISCUSSION

A total of 42 species of grasshoppers were collected, and their distributions at district level are shown in Table 1. The species *Acrida exaltata* (Walker), *Duroniella laticornis* K., *Aiolopus thalassinus* (F.), *Trilophidia annulata* (Thunberg), and *Spathosternum prasiniferum* (Walker) occur in all the districts, while the majority of the other species is restricted to their respective districts.

Most of the species were collected from grasses, herbs, and shrubs. However, some species, e.g., *Acrida exaltata, Aiolopus thalassinus thalassinus, A. thalassinus tamulus* (F.), *Oxya hyla hyla* Serville, *O. velox* (F.), *O. fuscovittata* (Marsch.), *O. bidentata* Willemse, *Ochrilidia gracilis gracilis* (Krauss), *Eyprepocnemis alacris alacris* (Serville), and *Choroedocus robustus* (Serville) [earlier named *Heteracris robustus,* as reported in a personal communication by Kevan in 1986] were collected from cultivated rice, sugar cane, maize, jowar, and wheat fields, where they are regarded as a minor pest.

Table 1 also shows the incidence of adult grasshopper species in the various districts of Sind during 1983-85. The most abundant species was *Aiolopus thalassinus,* forming more than 20% of the total number of all the grasshopper species collected, followed by *Duroniella laticornis* (19.62%), *Oxya hyla hyla* (13.8%), and *Acrida exaltata* (9.54%), while the single collected individuals of *Scintharista notabilis* (Walker), *Sphingoderus carinatus* (Saussure), and *Sphingonotus* spp. were considered rare.

Moeed (1966, 1971) collected a single femal of *Phlaeoba tenebrosa* (Walker) from Hyderabad District. We have collected a fair number of this species from the other districts of Sind and thus confirm its presence. The distribution of *Oxypterna* earlier reported from Hyderabad only by Moeed (1966, 1976) and Ahmad (1980), has been extended to Tharparkar, Sanghar, Nawab Shah, Khairpur, and Jacobabad District of Sind. In addition, the distributions of many of the previously recorded species have been extended.

Species recorded for the first time from this area are *Dericorys tibialis* (Pall.), *Mioscirtus wagneri rogenhoferi* (Saussure), *Scintharista notabilis* (Walker), *Sphingoderus carinatus* (Saussure), *Sphingonotus* sp., *Gelastorhinus semipictus* (Walker), *Oxya fuscovittata* (Marschall), *O. bidentata* Willemse, *Choroedocus illustris* (Walker), and *Tropidopola longicornis longicornis* (Fieber).

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Aportación al conocimiento de la fauna de ortópteros, mántidos y fásmidos de la zona occidental de la provincia de Guadalajara (España)

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RESUMEN

Los ortopteroides de la provincia de Guadalajara han sido muy poco muestreados, sobre todo en esta zona, que incluye la reserva natural del río Sonsaz y está próxima al gran núcleo de presión urbana de Madrid. Aparecen citas dispersas y escasas en la bibliografía (Navás, 1902; Harz, 1969; Gangwere and Morales 1970; Presa, 1976; Herrera, 1982; y Llorente, 1983). El trabajo recoge los resultados de muestreos en 20 puntos aleatorios realizados desde los meses de Mayo a Octubre de los años 1985 y 1986.

Palabras clave: Orthoptera, Mantodea, Phasmatodea, biogeografía, Guadalajara, España.

ABSTRACT

Despite this area's proximity to Madrid, including the natural reserve of Sonsaz river, there is a poor knowledge of it, due perhaps to difficulties of transport. There are only a few literature records (Navás, 1902; Harz, 1969; Gangwere and Morales, 1970; Presa, 1976; Herrera, 1982; and Llorente, 1983). This paper shows the results of samples taken from over 20 randomly chosen sites from May to October during the years 1985 and 1986.

Key words: Orthoptera, Mantodea, Phasmatodea, biogeography, Guadalajara, Spain.

INTRODUCCION

Durante los años 1985 y 1986 se realizaron campañas de muestreo en el macizo oriental del Sistema Central, entre los meridianos U.T.M. 30TVL5 y 30TWL0 y los paralelos 30TVL2 y 30TVL7, un cuadrado de 50 km de lado (Mapa 1). Se escogieron, mediante un programa de ordenador, 40 puntos aleatorios de muestreo en esa zona, que comprende parte de las provincias de Madrid, Segovia, y Guadalajara. Este trabajo aporta los resultados de los primeros 20 puntos de muestreo estudiados, pertenecientes todos ellos a la última provincia citada (Mapa 2), contabilizando más de 300 ejemplares adultos capturados. Se han identificado 8 especies de Tettigonoidea, 2 de Grylloidea, 12 de Acridoidea, 1 de Mantodea y 2 de Phasmatoptera. Salvo aquellos casos en los que se indique lo contrario, todos los ejemplares han sido recolectados por J. Mateos.

Para la determinación de los ejemplares se han utilizado las claves de Bolívar (1898), Harz (1969, 1975, 1976), Clemente, García y Presa (1973), de la Cuadra (1973), Presa (1977), Soltani (1978), Llorente

(1983), Bermejo, de la Fuente y Peris (1974), Pinedo (1984), Peinado (1984, 1985).

RELACION DE ESPECIES

Mantodea: Mantinae
Ameles spallanzania (Rossi, 1792)
Localidad 17. Mes: 8.

Phasmatoptera: Pachymorphinae
Leptynia (Lyptynia) hispanica (Bolívar, 1878)
Localidades: 11, 17, Meses: 7, 8.
Especie asociada a substratos calizos con vegetación de gramineas y matorral.

Leptynia (Leptyniella) attenuata Pantel, 1890
Localidad 17. Mes: 7.

Tettigoniidae: Decticinae
Decticus albifrons (Fabricius, 1775)
Localidad 17. Mes: 7.
Platycleis (Platycleis) albopunctata hispanica Zeuner, 1941
Localidades 1, 4, 5, 14, 15. Mes: 7.
Especie encontrada entre los 1000 y 1400 m de altitud en praderas y vegetación asociada a las orillas de los ríos.
Platycleis (Platycleis) sabulosa sabulosa (Azam, 1901)
Localidad: 17. Mes: 7.
Platycleis (Platycleis) intermedia intermedia Serville, 1839
Localidad: 6. Mes: 7.
Platycleis (Platycleis) affinis Fieber, 1853
Localidades 6, 11, 12, 17. Meses: 7, 8.
Se encuentra en campos de gramíneas y zonas arbustivas.
Se cita por primera vez para la provincia de Guadalajara.
Platycleis (Montana) carpetana Bolívar, 1857
Localidad: 17. Mes: 7.
Nueva cita para Guadalajara
Platycleis (Tessellana) tessellata (Charpentier, 1825)
Localidades: 6, 10, 11, 12, 15, 17. Meses: 7, 8.
Especie muy abundante localizada principalmente entre gramineas.

Tettigoniidae: Ēphippigerinae
Steropleurus brunneri (Bolívar, 1877)
Localidad: 17. Mes: 7.
Primera cita de esta especie para la provincia de Guadalajara.

Gryllidae: Gryllinae
Sciobia lusitanica (Rambur, 1839)
Localidad: 16. Mes: 7.
Cita nueva para la provincia.

Gryllidae: Oecanthinae
Oecanthus pellucens (Scopoli, 1763)
Localidad: 11. Mes: 8.

Catantopidae: Calliptaminae
Calliptamus italicus (L., 1758)
Localidades: 11, 12. Mes: 8.
Calliptamus wattenwylianus (Pantel, 1896)
Localidad: 17. Mes: 7.
Citada por primera vez para la provincia de Guadalajara.
Calliptamus barbarus barbarus (Costa, 1836)
Localidades: 1, 6, 10, 14, 15, 17, 18. Meses: 7, 8.
Es la especie más abundante dentro del género. Capturada en todo tipo de terrenos, desde praderas húmedas hasta zonas áridas con gramíneas y matorral disperso. Todos los ejemplares han sido capturados por encima de los 700 m (entre 750 y 1400 m) y presentan tres manchas negras perfectamente separadas en la cara interna de los fémures posteriores.
Esto concuerda con la hipótesis planteada por Aguirre y Pascual (1986) en relación con la variación de dichas manchas en función de la altitud. En cuanto a la longitud de los órganos de vuelo estos nunca sobrepasan de forma apreciable las rodillas de los fémures posteriores; solamente en alguna hembras apenas las sobrepasan, pero esto nunca ocurre en los machos capturados.

Acrididae: Locustinae
Oedaleus decorus (Germar, 1826)
Localidad: 17. Meses: 7, 8.
Nueva cita para la provincia de Guadalajara.
Oedipoda coerulescens coerulescens (L., 1758)

Localidades: 6, 12, 14, 17. Meses: 7, 8.
Especie muy abundante. Se encuentra en zonas de caliza con gramineas y vegetación arbustiva y de matorral dispersa. No se ha encontrado por encima de los 1000 m.

Oedipoda fuscocincta coerulea Saussure, 1884
Localidades: 10, 14. Mes: 7.
Contrariamente a lo que ocurre con la especie anterior, únicamente se ha encontrado por encima de los mil metros lo cual podría indicar una segregación de hábitats entre las dos especies en función de la altitud.

Oedipoda charpentieri Fieber, 1853
Localidades: 6, 15. Mes: 7.
Presenta mayor variación altitudinal que las dos especies anteriores, habiéndose capturado desde los 800 hasta los 1400 m.

Acrididae: Gomphocerinae

Dociostaurus hispanicus (Bolívar, 1898)
Localidad: 17. Mes: 7.
Unicamente se ha capturado una hembra en la cual, si bien se presentan el resto de las características propias de la especie (Morales, 1942; Harz, 1976; Soltani, 1978) los élitros no cubren totalmente el abdomen y no llegan hasta las rodillas de los fémures posteriores. Esta característica se da también en varios de los ejemplares de la colección del Museo de Ciencias Naturales de Madrid. Por todo ello, hemos optado por incluir esta hembra dentro de la especie. Se cita por primera vez para la provincia de Guadalajara.

Dociostaurus (Kazakia) jagoi occidentalis Soltani 1978
Localidades: 11, 12, 17. Mes: 8.
Capturado en altitudes entre 850 y 950 m, en campos de gramíneas con matorral.
Nueva cita para Guadalajara.

Dociostaurus (Kazakia) genei genei (Ocksay, 1832)
Localidad: 11. Mes: 8.
Se cita por primera vez para la provincia.

Omocestus (Dirshius) ventralis (Zetterstedt, 1821)
Localidad: 1. Mes: 7.
Nueva cita para Guadalajara.

Omocestus (Omocestus) panteli (Bolívar, 1887)
Localidades: 1, 5, 8. Mes: 7.
Encontrada en altitudes superiores a 1200 m.
Se cita por primera vez para Guadalajara.

Stenobothrus (Stenobothrus) festivus Bolívar, 1877
Localidades: 8, 13, 20. Mes: 7.
Al igual que la especie anterior, capturada sólo por encima de los 1200 m.

Chorthippus (Glyptobothrus) biguttulus yersini Harz, 1975
Localidades: 1, 2, 3, 4, 8, 9, 10, 11, 12, 15, 20. Meses: 7, 8.
Especie muy abundante, encontrada en altitudes que van desde los 900 a los 1500 m, ocupando una gran variedad de hábitats, desde praderas húmedas hasta zonas áridas con gramíneas y matorral disperso.
Se cita por primera vez para esta provincia.

Chorthippus (Glyptobothrus) biguttulus hispanicus Presa, 1977
Localidad: 14. Mes: 7.
Se cita también por primera vez para Guadalajara.

Chorthippus (Glyptobothrus) binotatus dilutus Ebner, 1941
Localidad: 17. Meses: 7, 8.
Cita nueva para la provincia.

Chorthippus (Glyptobothrus) apicalis (Herrich-Schaeffer, 1840)
Localidad: 2. Mes: 7.

Chorthippus (Glyptobothrus) vagans (Eversman, 1848)
Localidades: 8, 10, 19. Mes: 7.
Ejemplares capturados entre los 800 y los 1300 m, en campos de gramíneas con matorrales, arbustos y árboles diseminados.
Cita nueva para Guadalajara.

Chorthippus (Chorthippus) parallelus erythropus Faber, 1958 Localidades: 3, 4. Mes: 7.

Chorthippus (Chorthippus) jucundus (Fischer, 1853)
Localidades: 1, 4, 5, 14, 15. Mes: 7.
Encontrado únicamente por encima de los 1000 m.
Se cita por primera vez para la provincia.

Euchorthippus pulvinatus gallicus Maran 1957
Localidad: 6. Mes: 7.
Cita nueva para Guadalajara.

CONCLUSIONES

Se citan 18 especies por primera vez para la provincia de Guadalajara (3 de Tettigoniidae, 1 de Gryllidae, 1 de Catantopidae y 13 de Acrididae).

Se confirma para esta provincia la hipótesis de Aguirre y Pascual (1986) sobre la variabilidad de las manchas negras en la parte interna del femur posterior de *Calliptamus barbarus barbarus.*

Se ha encontrado una posible segregacion de hábitats entre *Oedipoda coerulescens coerulescens* y *Oedipoda fuscocincta coerulea* en función de la altitud. Este aspecto deberá ser confirmado en posteriores trabajos en esta y otras zonas.

RELACION DE LOS PUNTOS MUESTREADOS

1. 30TVL9763. Albendiego (30TVL9664). 1200 m. Puente sobre el río Manadero, junto a desvío hacia Albendiego. Jarales en las laderas, gramíneas, juncos y chopos junto al río.
2. 30TVL6629. Alpedrete de la Sierra (30TVL6629). 900 m. Gramíneas.
3. 30TVL6551. Bocígano (30TVL6552). 1250 m.
4. 30TVL8669. Campisábalos (30TVL8869). 1350 m. A 2 km en direccion a Grado del Pico. Pradera de montaña entre pinar muy abierto.
5. 30TVL7663. Cantalojas (30TVL7965). 1400 m. Puente sobre el río Lillas, en el km 6 del camino de Cantalojas a Majaelrayo. Gramíneas y juncos.
6. 30TVL9028. Cerezo de Mohernando (30TVL9025). 800 m. 2 km después de salir de Cerezo de Mohernando en dirección a Fuencemillán. Juncos, zarzamora, esparto y gramíneas entre cultivos.
7. 30TVL9436. Cogolludo (30TVL9333). 950 m. Carretera de Cogolludo a Alcorlo, 2 km antes de llegar a la desviación a Veguillas. Herbazal alto entre pinos y jara pringosa sobre tierras rojas.
8. 30TVL8863. Condemios de Arriba (30TVL9063). 1300 m. 1 km antes de llegar desde Galve de Sorbe. Gramíneas y rosales entre pinos.
9. 30TVL8461. Galve de Sorbe (30TVL8564). 1500 m. 3 km por la pista de La Huerce. Pradera húmeda entre pinos.
10. 30TVL8355. La Huerce (30TVL8656). 1200 m. Puente sobre el río Sorbe en el km 3 de la pista forestal que une Umbralejo con Valverde de los Arroyos. Hierba entre carrascas, jara y sauces.
11. 30TVL7623. Matarrubia (30TVL7524). 950 m. Km 24 de la carretera de Cogolludo a Uceda, 1 km al S de Matarrubia. Campo de gramíneas con jara pringosa y esparto.
12. 30TVL8437. Muriel (30TVL8337). 900 m. Campo de gramíneas secas justo frente a Muriel en la orilla opuesta del Sorbe.
13. 30TVL8948. La Nava de Jadraque (30TVL8849). 1250 m. 1 km al E del pueblo, en los prados entre éste y la carretera. Pradera abierta con roble, jara pringosa y cantueso.
14. 30TVL9442. Semillas (30TVL9045). 1000 m. Km 5 de la carretera a La Huerce, en el valle del arroyo Hondo. Vega con jara pringosa, helechos, pinar y chopera.
15. 30TVL9468. Somolinos (30TVL9566). 1400 m. A 2 km en dirección a Campisábalos, en el curso del río Manadero (Bornova). Praderas en desfiladero tallado por el río en las calizas.
16. 30TVL7941. Tamajón (30TVL7939). 1050 m. Ermita de la Sta. Virgen de los Enebrales, Carretera de Tamajón a Majaelrayo, km 2. Afloramientos

calizos mezclados con pizarras. Thymus.

17. 30TVL6524. Uceda (30TVL6421). 850 m. Carretera del embalse de Pontón de la Oliva a Valdepeñas de la Sierra, km 3,6. Substrato calizo con gramíneas, Cytisus, almendros, olivos, higueras y cardos.
18. 30TVL8751. Umbralejo (30TVL8554). 1300 m. A 3 km de Umbralejo en el puerto de la carretera de La Nava de Jadraque. Ladera aterrazada con jaral pringoso.
19. 30TVL7028. Valdepeñas de la Sierra (30TVL6829). 800 m. Robles aislados. Gramíneas.
20. 30TVL6644. La Vihuela (30TVL6643). 1400 m. Km 7.6 de la pista que va desde el km 12.8 de la carretera de Montejo de la Sierra a Colmenar de la Sierra hasta La Vihuela, La Vereda y Matallana.

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Los Orthoptera, Mantodea y Phasmatodea (Insecta) de la Sierra de Alcaraz (Albacete), S. E. España.

I. Estudio faunístico

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RESUMEN

En el presente trabajo se exponen los resultados de los muestreos realizados durante los años 1986, 1987 y 1988 en la Sierra de Alcaraz (Albacete).

Se aportan los primeros datos en conjunto, en cuanto a altitud y relación con el tipo de vegetación de las 57 especies capturadas, pertenecientes a las órdenes *Orthoptera, Mantodea* y *Phasmatodea.*

De entre las especies que se citan, 44 son nuevas para la provincia de Albacete.

Palabras clave: *Orthoptera, Mantodea, Phasmatodea,* Faunística, Sierra de Alcaraz, Albacete, España.

ABSTRACT

In this paper we present the results obtained from sampling in Sierra de Alcaraz (Albacete) during 1986, 1987 and 1988. Results mainly refer to the relationships between both altitude and vegetation and the 57 different species captured that belong to 9 families included in the orders *Orthoptera, Mantodea* and *Phasmatodea.* Up to 44 of the species described here are reported for the first time in the Albacete province.

Key words: Orthoptera, Mantodea, Phasmatodea, faunistie, Sierra de Alcaraz, Albacete, Spain.

INTRODUCCION

La Sierra de Alcaraz, situada al S. O. de la provincia de Albacete, está formada por una serie de alineaciones montañosas orientadas del suroeste al noroeste, y está considerada como una zona de transición entre la Meseta Central y la Cordillera Bética, constituyendo una Cordillera Prebética que enlaza con la Sierra de Cazorla y Segura.

El punto más alto es el pico de Las Almenaras, con una altitud de 1.797 m, situado en la Sierra de Las Almenaras, de la cual surgen ramificaciones para formar la auténtica Sierra de Alcaraz, con suelo de naturaleza caliza, formado durante el Mioceno tardío.

Los estudios entomológicos de esta zona han sido muy escasos, aun cuando se sabe que ocupa un lugar de intersección entre las influencias faunísticas del Mediterráneo, del Norte de Africa, y de Europa.

La vegetación está formada por pastizales, matorrales, pinares de repoblación y autóctonos y bosques de frondosas.

El objetivo que se persigue con la realización de este trabajo es dar a conocer la ortopterofauna de la Sierra de Alcaraz, así como los primeros datos en cuanto a su distribución altitudinal y medios que ocupan.

MATERIALES Y METODOS

Se ha muestreado mensualmente, desde enero de 1986 a septiembre de 1988, así como en el mes de abril de 1989, en 57 localidades repartidas por toda la Sierra, cuya relación aparece a continuación:

Lista de Localidades

1. Alcaraz. 900 m. WH 4583. Prado alto.
2. Alcaraz. 1.060 m. WH 4782. Prado alto.
3. Alcaraz. 1.060 m. WH 4678. Matorral alto denso.
4. Alcaraz. 900 m. WH 4380. Pastizal bajo.
5. Alcaraz. 1.100 m. WH 4981. Matorral disperso.
6. Alcaraz. 1.000 m. WH 4578. Vegetación ruderal.
7. Bienservida. 1.220 m. WH 3764. Matorral bajo y vegetación ruderal.
8. Bienservida. 820 m. WH 3065. Pastizal alto.
9. Bienservida. 880 m. WH 3463. Vegetación ruderal.
10. Bienservida. 840 m. WH 3066. Pastizal bajo.
11. Bienservida. 1.000 m. WH 3463. Pastizal bajo.
12. Bogarra. 1.690 m. WH 4866. Matorral bajo disperso.
13. Bogarra 1.660 m. WH 4866. Matorral bajo disperso.
14. Bogarra. 1.630 m. WH 4966. Matorral bajo disperso.
15. Bogarra. 1.320 m. WH 4866. Matorral bajo disperso.
16. Cotillas. 940 m. WH 4354. Matorral denso.
17. Cotillas. 740 m. WH 3952. Pastizal bajo.
18. Cotillas. 1.010 m. WH 4453. Prado verde.
19. Cotillas. 900 m. WH 4453. Prado y matorral disperso.
20. Cotillas. 1.000 m. WH 4453. Prado y matorral disperso.
21. Cotillas. 1.000 m. WH 4353. Pastizal bajo.
22. Paterna. 990 m. WH 6275. Matorral bajo disperso.
23. Paterna. 1.080 m. WH 5874. Matorral alto disperso.
24. Paterna. 1.270 m. WH 5570. Matorral bajo claro y prado verde.
25. Paterna. 1.370 m. WH 5270. Matorral bajo claro y pastizal.
26. Paterna. 1.410 m. WH 5373. Pastizal y borde de camino.
27. Paterna. 920 m. WH 6175. Prado alto.
28. Paterna. 1.030 m. WH 5873. Prado alto.
29. Paterna. 1.310 m. WH 5369. Prado bajo.
30. Peñascosa. 1.170 m. WH 5081. Vegetación de ribera y prado bajo.
31. Peñascosa. 1.125 m. WH 5280. Prado alto.
32. Riopar. 1.140 m. WH 4956. Matorral disperso.
33. Riopar. 1.500 m. WH 4956. Matorral disperso.
34. Riopar. 1.580 m. WH 5256. Prado verde y matorral disperso.
35. Riopar. 1.460 m. WH 5156. Prado verde.
36. Riopar. 1.400 m. WH 5557. Prado verde.
37. Riopar. 1.080 m. WH 4857. Vegetación ruderal y prado verde.
38. Riopar. 1.000 m. WH 4956. Vegetación de ribera.
39. Riopar. 970 m. WH 5061. Prado alto.
40. Riopar. 980 m. WH 5159. Prado alto.
41. Riopar. 900 m. WH 4454. Prado alto.
42. Salobre. 890 m. WH 3773. Matorral alto denso.
43. Salobre. 930 m. WH 3872. Prado verde.
44. Salobre. 870 m. WH 3773. Vegetación ruderal.
45. Salobre. 900 m. WH 3970. Matorral bajo y pastizal.
46. Salobre. 1.370 m. WH 4652. Matorral alto disperso.
47. Salobre. 1.320 m. WH 4855. Matorral alto disperso.

48. Salobre. 1.110 m. WH 4365. Prado alto.
49. Salobre. 1.138 m. WH 4375. Pastizal.
50. Salobre. 900 m. WH 3978. Pastizal.
51. Salobre. 1.000 m. WH 4377. Matorral bajo y pastizal.
52. Salobre. 1.100 m. WH 4278. Matorral disperso.
53. Villaverde de Guadalimar. 970 m. WH 3955. Matorral bajo.
54. Villaverde de Guadalimar. 920 m. WH 3954. Matorral alto denso.
55. Villaverde de Guadalimar. 1.100 m. WH 3958. Matorral disperso.
56. Villaverde de Guadalimar. 840 m. WH 4255. Vegetación ruderal.
57. Villaverde de Guadalimar. 800 m. WH 3951. Vegetación ruderal.

Las especies se han ordenado de acuerdo con Harz (1969, 1975) y Harz y Kaltenbach (1976).

Los ejemplares se encuentran depositados en la Cátedra de Dasometría, Departamento de Ciencia y Tecnología Agroforestal de la Escuela Universitaria Politécnica de Albacete, Universidad de Castilla-La Mancha.

RESULTADOS

Grylloidea: Oecanthinae

1. **Oecanthus pellucens** (Scopoli, 1763).

Se localiza en pastizales secos y matorrales, también en lugares ruderales y bordes de caminos. En los meses de más calor (julio y agosto) se ha capturado en vegetación de pastizales con cierto grado de humedad. Localidades: 1, 3, 4, 7, 9, 15, 24, 53. Meses: III, IV, VII, VIII, IX.

Grylloidea: Gryllinae.

2. **Gryllus campestris** L., 1758.

Se ha capturado únicamente durante el mes de abril, en pastos y matorrales secos. Localidades: 14, 16. Meses: IV.

3. **Sciobia lusitanica** Rambur, 1839.

Sólo se han capturado dos ejemplares en pastizal seco y matorral bajo disperso. Localidades: 4, 22. Meses: IV, X.

Tettigonioidea: Decticinae.

4. **Decticus albifrons** (Fabricius, 1775).

Se encuentra en formaciones vegetales variadas, desde pastizales y prados altos hasta matorrales; se encontró un gran número de ejemplares en un rastrojo. Localidades: 1, 13, 17, 41. Meses: VI, VII, X.

5. **Platycleis (Platycleis) albopunctata hispanica** Zeuner, 1941.

Esta especie ha sido capturada en matorrales bajos claros y en prados bajos. Localidades: 12, 13, 14, 30. Meses: VII, VIII, IX.

6. **Platycleis (Platycleis) albopunctata sculpta** Zeuner, 1941.

Las localidades de captura son matorrales bajos claros y prados altos, en este último caso es común encontrar los ejemplares sobre juncos, *Scirpus holoschoenus* o alguna gramínea que forme el prado.

Se considera endémica de España Central (Pinedo, 1982). Localidades: 13, 14, 15, 26, 31. Meses: VII, VIII, IX.

7. **Platycleis (Platycleis) sabulosa sabulosa** Azam, 1901.

Se ha capturado en matorrales, pastizales, y en lugares pedregosos e incultos.

Citada anteriormente para la provincia de Albacete (Pinedo, 1982). Localidades: 3, 16, 21, 50. Meses: VI, VII, IX.

8. **Platycleis (Platycleis) intermedia intermedia** (Serville, 1839).

Se han capturado únicamente dos ejemplares, sobre biotopos aparentemente distintos, entre las ramas de las matas que forman el matorral bajo claro y en claros de un matorral muy denso de jara, sobre el suelo. Localidades: 13, 42. Meses: VII, X.

9. **Platycleis (Platycleis) affinis** Fieber, 1853.

Se ha capturado en prados altos. Localidades: 1, 9, 41. Meses: VII, VIII, IX.

10. **Tessellana tessellata** (Charpentier, 1825).

Se presenta en muy diversos tipos de hábitats, prado alto, matorrales así como en pastizales y lugares ruderales. Localidades: 1, 2, 4, 17, 25, 41, 44, 46, 51. Meses: VI, VII, IX.

11. **Ctenodecticus ramburi** Morales Agacino, 1956.

Sólo se ha capturado en prados bajos. Está considerada como endémica del Sureste Español (del Cerro, 1978; Pinedo, 1982). Localidad 36. Mes: VIII.

12. **Thyreonotus bidens** Bolívar, 1887.

Se ha capturado en localidades con matorrales de espesor y altura variables. Los ejemplares se encontraban sobre la vegetación. Localidades: 7, 22, 24. Meses: V, IX, XI.

Tettigonioidea: Tettigoniinae

13. **Tettigonia viridissima** L., 1758.

Capturada en prados verdes y navas con pastizal alto principalmente, también aparece en prados bajos.

Citada anteriormente para la provincia de Albacete (Pinedo, 1985). Localidades: 36, 41, 56. Meses: VI, VII.

Tettigonioidea: Ephippigerinae.

14. **Ephiggigerida zapateri** (Bolívar, 1877).

Sobre matorrales de distinto porte y sobre prados.

Se considera endémica del centro de España (Peinado de Diego y Mateos Martín, 1985). Localidades: 13, 17, 20, 24, 41. Meses: VI, VII.

Tettigonioidea: Pycnogastrinae.

15. **Pycnogaster (Bradygaster) sanchezgomezi constricta** Bolívar, 1926.

Muestran preferencia por la vegetación de matorral bajo claro, es muy común que se encuentren entre las ramas de *Erinacea anthyllis;* también se han capturado en prados bajos y en pocos casos en pastizales secos y áridos.

Se considera especie endémica del sureste de España: Jaén, Granada y Albacete (Pinedo y Llorente, 1986). Localidades: 12, 13, 14, 24, 25, 34, 37. Meses: III, IV, V, VII, IX.

Acridoidea: Calliptaminae.

16. **Calliptamus italicus** (L., 1758).

Se ha capturado en prados verdes y en diversos tipos de matorral así como en lugares áridos y sin vegetación.

Citada para Albacete (Llorente, 1982). Localidades: 7, 16, 24, 25, 26, 29, 31, 36, 41. Meses: IV, VII, VIII, IX, X.

17. **Calliptamus barbarus** (Costa, 1836).

Los hábitats preferidos por esta especie son matorrales, pastizales bajos, y prados bajos.

Especie citada anteriormente para Albacete (Llorente, 1982). Localidades: 1, 3, 5, 7, 9, 12, 13, 14, 15, 16, 17, 22, 23, 24, 25, 26, 27, 29, 31, 34, 36, 37, 39, 41, 42, 45, 47, 52, 53. Meses: III, VI, VII, VIII, IX, X, XI.

18. **Calliptamus wattenwylianus** (Pantel, 1896).

Capturada en matorral alto claro, sobre pastizal escaso que hay entre los matorrales de coscoja, *Quercus coccifera* y enebro, *Juniperus oxycedrus,* y en prados altos.

Citada con anterioridad para la provincia de Albacete (Llorente, 1982). Localidades: 1, 4, 17, 30, 41, 45. Meses: VII, VIII, IX.

19. **Pezotettix giornae** (Rossi, 1974).

Se la puede capturar en casi todos los hábitats posibles, con más abundancia en el prado bajo, en el matorral, preferentemente en el claro y disperso. También se han realizado algunas capturas en pastizal bajo y en prados altos. Localidades: 1, 2, 3, 6, 7, 9, 10, 13, 14, 15, 16, 18, 22, 23, 24, 25, 26, 30, 36, 37, 39, 40, 44, 45, 46, 47, 50, 52, 53. Meses: II, III, IV, V, VIII, IX, X, XI, XII.

Acridoidea; Akicerinae

20. **Prionotropis flexuosa perezii** Bolívar, 1873.

Se ha capturado en matorrales dispersos, prados bajos y pastizales altos.

Está considerada como una especie endémica española (Presa y Llorente, 1982). Localidades: 14, 26, 33, 36. Meses: IV, V, VI, VII.

Acridoidea: Phamphaginae

21. **Eumigus punctatus** (Bolívar, 1902).

Las capturas se hicieron en pastizales bajos, matorrales dispersos y en lugares ruderales sin vegetación, áridos y pedregosos.

Se considera una especie endémica del Sureste de España. Localidades: 13, 14, 25, 26, 32, 34, 36, 37, 53. Meses: III, IV, V, VI, VII, IX, XI.

22. **Ocnerodes brunneri** (Bolívar, 1876).

Se ha capturado en una única localidad,

matorral bajo denso y suelo pedregoso, sobre el cual estaban los ejemplares.

Citada anteriormente para la provincia de Albacete (Llorente y Presa, 1983).

Está considerada como endémica española (Llorente y Presa, 1983). Localidad: 7 meses: IV, VII.

Acridoidea: Locustinae

23. **Oedipoda coerulescens coerulescens,** (L., 1758).

Es la especie más numerosa de todas las inventariadas en la Sierra de Alcaraz.

Muy abundante en matorrales aclarados, en prados verdes, también en lugares con vegetación más densa, así como en bordes de caminos, desprovistos de vegetación.

Esta especie está citada para la provincia de Albacete (Herrera, 1982). Localidades: 1, 2, 3, 7, 12, 13, 14, 15, 16, 17, 22, 23, 24, 25, 26, 27, 29, 30, 31, 35, 36, 37, 39, 42, 44, 45, 46, 47, 53. Meses: VI, VII, VIII, IX, X, XI.

24. **Oedipoda charpentieri** Fieber, 1853.

Se localiza en matorral disperso y en pastizales y prados verdes. Localidades: 1, 2, 3, 5, 7, 11, 12, 13, 14, 15, 16, 20, 22, 23, 24, 25, 26, 30, 34, 37, 39, 45, 46, 53. Meses: VI, VII, VIII, IX, X, XI.

25. **Oedipoda charpentieri** Fieber, 1853.

Se localiza en matorral disperso y en pastizales y prados verdes. Localidades: 5, 12, 14, 15, 22, 27, 28, 30, 34, 50. Meses: VII, VIII, IX.

26. **Oedaleus decorus** (Germar, 1826).

Capturada en pastizales y matorrales dispersos, sobre el pasto existente entre el matorral. Localidades: 16, 47. Meses: VII, VIII.

27. **Locusta migratoria** L., 1758.

Se ha capturado un único ejemplar en un pastizal agostante. Localidad: 11. Mes: IX.

28. **Acrotylus insubricus** (Scopoli, 1786).

Se ha capturado en matorrales de todo tipo, en pastizales bajos agostantes y en prados altos.

Citada para la provincia de Albacete (Presa y Llorente, 1979). Localidades: 2, 4, 7, 16, 25, 27, 30, 47, 49, 50, 53. Meses: III, IV, V, VII, IX, X.

29. **Acrotylus fischeri** (Azam, 1901).

Las capturas se han realizado en matorrales bajos densos y en medios pedregosos, y sin vegetacion, en prados altos y en pastizales. Localidades: 1, 2, 7, 9, 12, 14, 15, 16, 22, 23, 24, 25, 26, 27, 33, 39, 40, 42, 46, 47, 50, 53. Meses: II, III, IV, V, VI, VII, VIII, IX, X, XI, XII.

30. **Sphingonotus coerulans corsicus** Chopard, 1923.

Se ha capturado en los claros de matorrales densos, y en lugares áridos. Localidades: 7, 16, 42. Meses: VI, VII, VIII, IX.

31. **Sphingonotus arenarius** (Lucas, 1849).

Se han capturado dos ejemplares en un pastizal bajo con suelo granuloso. Localidades: 44, 50. Meses: IX.

32. **Aiolopus strepens** (Walker, 1870).

Se ha capturado esta especie en prados, pastizales, matorrales y lugares áridos. Localidades: 1, 2, 4, 7, 9, 10, 11, 16, 17, 18, 22, 23, 27, 28, 29, 30, 37, 39, 40, 44, 48, 50. Meses: II, III, IV, V, VI, IX, X, XII.

Acridoidea: Gomphocerinae

33. **Arcyptera (Pararcyptera) microptera microptera** (Fischer Waldheim, 1883).

Se ha capturado en una única estación un prado verde.

Los ejemplares capturados presentan ciertas diferencias morfológicas con las propias de la especie, en particular respecto a los órganos de vuelo y copulador de los machos. A la espera de disponer de más ejemplares que confirmen estas diferencias y poder estudiar sus manifestaciones sonoras, se ha preferido adjudicarlos a esta forma. Localidad: 36. Meses: VI, VII.

34. **Dociostaurus jagoi occidentalis** Soltani, 1978.

Se ha capturado con abundancia en matorral disperso, prados bajos, pastizales, y con menos abundancia en matorrales densos y lugares ruderales y pedregosos. Localidades: 1, 2, 3, 4, 5, 7, 9, 10, 11, 15, 16, 20, 22, 23, 24, 25, 26, 27, 30, 39, 41, 42, 44, 46, 47, 50, 51, 52, 53, 57. Meses: IV, VII, VIII, IX, X.

35. **Omocestus raymondi** (Yersin, 1863).

Los ejemplares han sido capturados en matorrales diversos y en pastizales y prados bajos.

Citada anteriormente para la Sierra de

Alcaraz (Clemente, 1987). Localidades: 1, 2, 7, 13, 14, 15, 16, 22, 23, 24, 25, 26, 36, 42, 45, 46, 47, 48, 53. Meses: V, VI, IX, X, XI.

36. **Omocestus femoralis** Bolívar, 1908.

Ha sido capturada con preferencia en prados bajos y en matorrales bajos claros.

Es la tercera cita de esta especie para la Península Ibérica, anteriormente había sido citada de Santiago de la Espada (Jaén) (Bolívar, 1908), y Sierra Espuña (Murcia) (García García, 1984), ampliándose con esta nueva cita su distribución peninsular y el tipo fisionómico donde ha sido capturada.

Está considerada como un endemismo peninsular (Clemente, 1987). Localidades: 12, 13, 14, 26, 34, 36. Meses: VII, VIII, IX, X.

37. **Omocestus panteli** (Bolívar, 1887).

Las capturas se hicieron principalmente en prados verdes, en menor número en matorrales más o menos densos y en pastizales bajos.

Ha sido citada con anterioridad para la provincia de Albacete (Clemente, 1987).

Está considerada como una especie endémica de España (Clemente, 1987). Localidades: 1, 2, 24, 27, 28, 29, 31, 40, 41, 42, 44. Meses: VII, VIII, IX, X, XI, XII.

38. **Stenobothrus festivus** Bolívar, 1897.

Esta especie se ha capturado en lugares con vegetación aclarada, en prados y en matorrales dispersos.

Citada para la provincia de Albacete (Clemente *et al.)* (en prensa). Localidades: 25, 34, 36, 46, 47. Meses: V, VI, VII.

39. **Stenobothrus bolivari** (Brunner, 1876).

Se han realizado dos capturas en una misma localidad, con vegetación de matorral bajo claro.

Esta especie está citada para la Sierra de Alcaraz (Clemente, 1987). Está considerada como un endemismo península (Clemente *et al.)* (en prensa). Localidad: 14. Meses: VI, VII.

40. **Stenobthrus grammicus** Cazurro, 1888.

Se ha capturado un único ejemplar, en vegetación de matorral bajo aclarado. Localidad: 14. Mes: VII.

41. **Euchorthippus chopardi** Descamps, 1968.

Ha sido capturada principalmente en biotopos con vegetación de pastizal no agostante. Localidades: 1, 2, 4, 7, 9, 11, 13, 16, 19, 22, 23, 24, 25, 26, 28, 29, 30, 31, 37, 39, 40, 41, 44, 50, 51, 53. Meses: VI, VII, VIII, IX, X, XI.

42. **Euchorthippus pulvinatus gallicus** Maran, 1957.

Esta especie muestra tendencia por el prado alto, también se ha capturado en matorrales dispersos y lugares incultos. Localidades: 1, 2, 4, 9, 10, 11, 12, 13, 15, 23, 24, 28, 29, 30, 31, 39, 40, 41, 44, 50. Meses: VI, VII, VIII, IX, X.

43. **Chorthippus parallelus** (Zetterstedt, 1821).

Ha sido capturada en una estación con prado alto. Localidad: 40. Mes: VII.

44. **Chorthippus jucundus** (Fischer, 1853).

Capturada en prados altos y matorrales aclarados. Localidades: 24, 28, 37, 40, 41. Meses: VII, IX.

45. **Chorthippus apicalis** (Herrich Schaffer, 1840).

Ha sido capturada en pastizales, prados, matorrales, lugares incultos y bordes de caminos. Localidades: 13, 14, 15, 26, 30, 35, 42. Meses: V, VI, VII, VIII.

46. **Chorthippus vagans** (Eversman, 1848).

Es común en todas las estaciones muestreadas, con más abundancia en matorrales claros, en prados, y en lugares ruderales.

Es muy común verles sobre los tallos y ramas de las plantas, en especial sobre las gramíneas que forman los pastizales. Localidades: 1, 2, 3, 7, 12, 13, 14, 15, 16, 22, 23, 24, 25, 26, 30, 34, 36, 37, 46, 47, 53. Meses: II, VI, VII, VIII, IX, X, XI, XII.

47. **Chorthippus binotatus** (Charpentier, 1825).

Se ha capturado en matorrales claros, prados altos, pastizales bajos, matorrales densos y en lugares sin vegetación. Localidades: 2, 3, 12, 14, 26. Meses: V, VI, VII, VIII, XI.

48. **Chorthippus jacobsi** Harz, 1975.

Se ha capturado en prados bajos y en pastizales, así como en matorrales dispersos.

Se considera endémica por el momento de la Península Ibérica y Mallorca (Ragge y Reynolds, 1988). Localidades: 1, 2, 3, 9, 12, 13, 14, 15, 16, 23, 24, 25, 26, 28, 29, 30, 31, 34, 35, 36, 39, 42, 44, 45, 46, 48. Meses: V, VI, VII, VIII, IX, X, XI.

Tetrigoidea: Tetrigidae

49. **Paratettix meridionalis** (Rambur, 1838).

Se ha capturado un único ejemplar sobre vegetación de ribera, prado bajo. Localidad: 30. Mes: IX.

50. **Tetrix (Tetrix) depressa** (Brisout, 1848).

El único ejemplar se capturó en un prado bajo semiencharcado. Localidad: 38. Mes: IV.

51. **Mishtshenkotetrix brachyptera** (Lucas, 1849).

Se ha capturado un único ejemplar en vegetación semiencharcada, prado bajo. Localidad: 30. Mes III.

Mantodea: Mantinae

52. **Mantis religiosa** L., 1758.

Ha sido capturada en matorrales claros, en prados y pastizales. Localidades: 1, 13, 17, 24, 29. Meses: VII, VIII, IX, X.

Mantodea: Amelinae

53. **Ameles spallanzania** (Rossi, 1792).

Las capturas han tenido lugar en pastizales y prados, matorrales dispersos y algún ejemplar se ha capturado en prado alto. Localidades: 10, 13, 15, 16, 20, 29, 39, 51. Meses: III, VII, VIII, IX.

54. **Ameles decolor** (Charpentier, 1825).

Capturas realizadas en matorrales dispersos principalmente.

Citada para Albacete (Pinedo y Llorente, 1988). Localidades: 2, 7, 14. Meses: VI, IX, X.

55. **Ameles picteti** (Saussure, 1869).

Se capturó en prados y en matorrales dispersos. Localidades: 1, 43, 49. Meses: II, V.

Mantodea: Empusinae

56. **Empusa pennata** (Thunberg, 1815).

Ha sido capturada en matorrales dispersos, prados altos y en bordes de caminos. Localidades: 2, 7, 24, 56. Meses: III, VI, VIII, XII.

Phasmoptera: Pachymorphinae

57. **Leptynia hispanica** (Bolívar, 1878).

Capturada principalmente en el prado alto, en matorrales de distinto porte y espesor y en pastizales bajos. Localidades: 1, 12, 21, 23, 24, 41. Meses: V, VI, VII, VIII.

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Investigations on the band-winged grasshoppers (Oedipodinae) of Iran

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ABSTRACT

In an investigation of the oedipodine grasshoppers of Iran, samples were collected for ten years from different habitats in the Tehran Province of Iran. Conditions of topography, soil type, and dominant floral species (over 150 species) were recorded.

Grasshoppers were identified to species, based on characters such as size, color, foviolae, fastigium, size of pronotum, presence and arrangement of median and lateral carinae, wing venation and coloration, size of tympanal lobe, and male genitalic characters, including shape of epiphallus, size and shape of lateral plates and projections, and size and shape of lophi and oval sclerites.

Key words: Oedipodinae, male genitalic characters, ancorae, lophi, anterior and posterior projections, lateral plates, dominant species.

INTRODUCTION

The Oedipodinae of Iran stand out among the grasshoppers because of their species diversity and of their occurrence in a wide range of habitats, from rocky hillsides to desert-like plains. Some species cause damage to agricultural crops, although the magnitude of their destruction is concealed by that of occasional swarms of gregarious locusts, which constitute the major orthopteroid pest of agricultural crops in many parts of Iran.

Bei-Bienko (1963) reported 126 species of this subfamily from the USSR, northern Iran, Afghanistan, northwestern China, Korea and Japan. His classification, as well as that of Uvarov (1966), is based on common morphological characters including the head capsule, antennae, legs, body coloration, wing venation, sound production organs and the external genitalia. Bardan *et al.* (1969) presented extensive information concerning the relative density of different acridoid species in various habitats of Egypt and related grasshopper diversity to the abundance of plant species in each habitat. Mirzayans (1959) noted 45 species of this subfamily occurring in Iran. In the only systematic treatment of the Iranian Oedipodinae, Fard (1975) included an identification key to 15 genera from the vicinity of Karaj. This paper presents a summary table for the identification of the species collected in Tehran Province, Iran.

MATERIALS AND METHODS

Collections were made over the course of several years at five different locations, using three collecting sites per location. These were selected according to elevation, topography, and conditions of moisture, vegetational diversity, and plant density. At all locations the plant species were collected and the dominant ones recorded. Collections were made on a weekly basis at about 10:00 am to 5:00 pm from early May until early December. The collecting time interval at each site was fixed, 40 min. per person and 5 sweeps per min. Each sweep covered approximately one m^2. The population density of each of the three dominant species was recorded.

Besides the use of general morphological characters such as the head capsule, pronotal carina, wing venation, organs of sound production and hearing, the male genitalia were studied. The epiphalli were mounted on slides and drawn under 40x to 70x magnification.

RESULTS AND DISCUSSION

The phallic complex is stout, strongly sclerotized, and apically directed posteriorly. The epiphallus arises from the ectophallic membrane on the dorsal surface of the phallic complex. In the Oedipodinae, it has a bridge-like form. The lateral plates are sometimes connected by a membrane with the bridge. Anteriorly the epiphallic disc bears a pair of projections called ancorae, which vary in shape and size. Posteriorly it bears another pair of projections called lophi, which vary greatly in shape. The lateral plates, whose anterior and posterior ends are extensions of the disc, usually form more or less strongly developed projections. Near the sides of the epiphallus, there are a pair of oval or irregularly shaped sclerites which serve for muscle attachment.

The terminology in Table 1 is that of Roberts (1941), with some modifications:

A = ancorae. A pair of processes from the anterior margin of the epiphallus.
Ap = anterior projections from the lateral plates.
B = bridge. The middle of the epiphallus, connecting the lateral plates.
L = lophi. Processes on or near the posterior end of the epiphallus, sometimes arising from the lateral plates of the bridge.
Lp = lateral plates. A pair of symmetrical plates, sometimes connected to the bridge by membrane.
Os = oval sclerites. A pair of small circular, oval, or irregular sclerites and located laterally on the epiphallus.
pP = posterior projections. The posterior ends of the lateral plates, sometimes strongly projected.

The dominant species in each ecosystem included *Aiolopus thalassinus* (F.), *Acrotylus insubricus* (Scop.) and *Oedipoda miniata* Pall. Dominance was determined by weekly collections from the 15 sites. The specimens were recorded and their respective curves drawn.

Table 1.—Differentiation of the Epiphallus of 35 Iranian Oedipodine species from Tehran Province, Iran

Name of species and subspecies	Width of epiphallus (in mm)	Form of disc	Size and shape of ancorae	External lobe, anterior and posterior projections of lateral plates	Size and shape of lophi	Length of body (♂) Length of body (♀)	Length of tegmina (♂) Length of tegmina (♀)
1. *Aiolopus thalassinus* (F.)	1	nearly curve	weakly oval	uneven, acute angles	weakly conical	20-25 24-30	22-28 26-34
2. *Aiolopus savignyi* (Krauss)	1.2	narrow and flat	nearly triangular	weakly smooth, rounded	conical	18-20 24-27	19-21 25-28
3. *Hilethera maculata* (Karny)	1.25	nearly broad and curved	small and beak shaped	flat, rounded, sharpened apically	nearly cylindrical	17-21 20-24	17-22 21-25
4. *Locust migratoria migratoria* L.	1.23	slightly curved	small, beak shaped	nearly smooth, right angled	two parts	34-40 42-48	40-45 50-55
5. *Oedaleus decorus* (Germ)	1.6	roughened	irregular	roughened	cylindrical with constriction in the middle	22-28 30-38	24-33 33-38
6. *Oedaleus senegalensis* (Krauss)	1.5	nearly straight	irregular	smooth, right angled	cylindrical with weak depression	20-25 25-34	21-24 26-34
7. *Scintharista notabilis brunneri* Sauss.	2	weakly curved	small	smooth, rounded	cylindrical, with constriction in the middle	25-30 34-7	26-31 36-39
8. *Pyrgodera armata* F.-W.	1.6	distinctly convex	enlarged, beak shaped	roughened, acutely angled	narrow and long	24-28 26-30	27-31 30-33
9. *Brunnerella mirabilis mirabilis* Sauss.	1.7	weakly curved	sharp apical	smooth, rounded acute angle	large	21-23 25-28	20-25 24-28
10. *Celes variabilis* (Pall.)	1.2	roughened	very small	roughened, rounded	two parts with distinct constriction	18-21 20-24	13-15 14-16
11. *Mioscirtus wagneri rogenhoferi* (Sauss.)	1.6	straight	small	nearly smooth	two parts with constriction	14-16 24-26	14-17 22-27

Name of species and subspecies	Width of epiphallus (in mm)	Form of disc	Size and shape of ancorae	External lobe, anterior and posterior projections of lateral plates	Size and shape of lophi	Length of body (♂) Length of body (♀)	Length of tegmina (♂) Length of tegmina (♀)
12. *Oedipoda miniata* (Pall.)	1.1	slender and convex	falciform	smooth, rounded	two parts with distinctly constriction	17-24 23-25	18-21 23-26
13. *Oedipoda coerulescens* (L.)	1.3	slightly concave	small	smooth, rounded	bean shaped	18-24 24-27	18-26 23-26
14. *Oedipoda schochi* Sauss.	1.5	wider, convex	small	smooth, right angled	nearly bean shaped	21-24 28-33	22-25 29-34
15. *Acrotylus insubricus insubricus* (Scop)	1.2	roughened	beak shape	rounded	nearly conical	14-18 19-25	14-18 17-21
16. *Acrotylus insubricus inficitus* (Walk.)	1.4	smoothly curve	falciform	roughened	small, bean shaped	15-19 19-25	17-20 19-24
17. *Pseudoceles persa* (Sauss.)	1.1	weakly convex	small	roughened acute angled	bean shaped	15-18 22-25	15-19 20-23
18. *Heliopteryx humeralis* (Kuthy.)	1.3	nearly oval	small	roughened	falciform	22-25 29-35	21-25 28-35
19. *Sphingonotus theodori* Uv.	0.9	thin and curved	small	roughened	nearly Sshaped	18-20 20-24	21-23 22-26
20. *Sphingonotus maculatus maculatus* Uv.	1.9	narrow	beak shaped	roughened	nearly bean shaped	15-18 17-20	17-19 19-21
21. *Sphingonotus rubescens rubescens* (Walk.)	1.6	wide, roughened	beak shaped	smooth, acute angled, right angled	long and narrow	16-18 22-26	20-23 23-25
22. *Sphingonotus pilocus* Sauss.	1	slender	small	weakly smooth	long and narrow	17-18 25-28	17-18 23-26
23. *Sphingonotus fuscus mistshenkoi* Predt.	1.7	wide	small	roughened	bean shaped with constriction	18-20 21-23	19-21 23-25

Name of species and subspecies	Width of epiphallus (in mm)	Form of disc	Size and shape of ancorae	External lobe, anterior and posterior projections of lateral plates	Size and shape of lophi	Length of body (♂)	Length of tegmina (♂)
						Length of body (♀)	Length of tegmina (♀)
24. *Sphingonotus coerulans caspicus* Mistsh.	1.5	nearly curved	small	smooth rounded	cylindrical	18-21	19-21
						25-28	25-29
25. *Sphingonotus coerulipes* Uv.	1	curved	slender	smooth	long and narrow	15-17	15-18
						18-23	18-24
26. *Sphingonotus eurasius eurasius* mistsh.	0.9	slender	long and slender	weakly smooth	nearly enlarged	14-18	15-19
						16-22	18-22
27. *Sphingonotus savignyi Sauss.*	2	enlarged	beak shaped	roughened, rounded	two parts, bean shaped	22-23	23-31
						29-38	29-37
28. *Sphingonotus nebulosus persa* Sauss.	1.35	weakly curved	sharp apically	roughened, acute angles	slender and long	18.5-22	20-25
						27.5-35	29-35
29. *Sphingonotus octofasciatus* (Serv.)	2.3	enlarged	sharp apically	weakly roughened	slender and convex	17-22	18-25
						26-29.5	26-32
30. *Sphingonotus obscuratus brunneri* Sauss.	2	not smooth	beak shaped	rounded	two parts	28-32	30-34
						30-35	33-37
31. *Sphingonotus satrapes* Sauss.	2.2	weakly curved	large	roughened, curved	long and thin	28-35	29-36
						38-42	33-40
32. *Sphingoderus carinatus* (Sauss.)	1.2	slender and convex	beak shaped	roughened	two parts	15-20	16-21
						20-26	22-28
33. *Helioscirtus moseri moseri* Sauss.	2	slender and concave	triangular	smooth, acute angle	nearly bean shaped	24-30	25-32
						29-33	30-34
34. *Hyalorrhipis shestoperovi* Uv. & Mor.	1.5	enlarged	falciform	weakly roughened rounded	large and Sshaped	13-14.5	14-16
						18.5-21	19.5-21
35. *Leptopternis gracilis* (Ev.)	0.8	weakly curved	beak shaped	smooth	narrow and convex	15-18	16-19
						22-25	23-27

SIGNIFICANT LITERATURE

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Estudio preliminar de los mántidos de la Comunidad de Madrid (Insecta: Mantodea)

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RESUMEN

Con el presente trabajo se incrementa el conocimiento sobre este orden de insectos en Madrid. De 473 ejemplares estudiados, se citan las especies *Perlamantis alliberti* Guérin-Méneville, 1843, *Ameles spallanzania* (Rossi, 1792), Ameles assoi (Bolivar, 1873), *Ameles decolor* (Charpentier, 1825), *Mantis religiosa* Linneo, 1758, *Iris oratoria* (L., 1758), *Apteromantis aptera* (Fuente, 1894), *Geomantis larvoides* Pantel, 1896, y *Empusa pennata* (Thunberg, 1815).

Se aportan datos bibliográficos y se añaden citas de los autores hasta 1988.

Palabras clave: Mantodea, biogcografía, Madrid, España.

ABSTRACT

This paper increases our knowledge of Mantodea of Madrid. It includes 473 records of the species *Perlamantis alliberti* Guérin-Méneville, 1843, *Ameles spallanzania* (Rossi, 1792),*Ameles assoi* (Bolivar, 1873), *Ameles decolor*(Charpentier, 1825), *Mantis religiosa* Linné, 1758, *Iris oratoria* (L., 1758), *Apteromantis aptera* (Fuente, 1894), *Geomantis larvoides* Pantel, 1896, and *Empusa pennata* (Thunberg, 1815).

Bibliographic references and records of other authors in addition to records of the present authors up to 1988 are included.

Key words: Mantodea, biogeography, Madrid, España.

INTRODUCCION

La comunidad de Madrid es una de las provincias españolas con mayores diferencias altitudinales (480 m.s.n.m. en la salida del río Tajo a 2.430 m.s.n.m. en Peñalara). Aunque es una de las provincias españolas más muestreadas, de su fauna de mántidos no existen datos concretos, sólo hay refencias a través de diversas recopilaciones bibliográficas que les reunían con otros ortopteroides (Gangwere y Morales, 1970) o revisiones como la de Morales, 1947; o Kaltenbach, 1969; Bolívar, 1877, 1898 y 1900; Burr, 1898 y Chopard, 1943.

Esta comunidad está sufriendo un gran deterioro por la gran presión urbana a la que se ve sometida, padeciendo esta situación también sus poblaciones de insectos, sobre todo especies menos abundantes como son los mántidos. El desequilibrio ecológico que se produce sólo es detectable a través de inventarios de poblaciones, con registros actuales y de tiempos anteriores.

El orden Mantodea en Madrid comprende siete géneros: *Perlamantis* Guérin-Méneville, *Ameles* Burm., *Mantis* L., *Iris* Sauss., *Apteromantis* Wern., *Geomantis* Pant., y *Empusa* Ill.

De las especies estudiadas las más afectadas parecen ser *Ameles spallanzania, Apteromantis aptera* y *Geomantis larvoides*. La más abundante actualmente es *Iris oratoria,* mientras *Mantis religiosa* mantiene el numero de citas.

MATERIALES Y METODOS

Se han estudiado 473 ejemplares procedentes de 47 puntos de muestreo, que constituyen la totalidad del material de mántidos de Madrid depositados en la colección del Museo de Ciencias de Madrid (ejemplares datados antiguos) y en la Universidad Complutense de Madrid. Se han conservado todos los datos concretos de captura, incluyendo los incompletos de ejemplares antiguos.

Para la localizacion de las especies se han utilizado mapas generados por computador que detallan las cuadrículas de 2.5 km de lado que configuran la Comunidad de Madfrid. En las cuadrículas limítrofes se han considerado incluidas en la comunidad aquellas en las cuales al menos el 50% pertenece a la provincia en consideración. Se han relizado mediante digitalizacion de los mapas de las series 2C y L del Servicio Geográfico de Ejército.

Se han utilizado para identificar las especies los trabajos de Kaltenbach, 1969; Morales, 1947; Bolívar, 1876-78; Chopard, 1943; y Pantel, 1886.

ESTUDIO DE LAS ESPECIES

Perlamantis alliberti Guérin-Méneville, 1843

Adulta entre los meses de Junio y Septiembre sobre el suelo de terrenos secos o en la base de las plantas. De hábitos crepusculares, suele acudir a la luz.

Localidades (Mapa 1): (6) 3 machos, 7-1935, Pujol. (7) 1 macho, 7-1938, Morales. (10) 2 machos, 9-1929, Bonet. (13) 1 macho, 8-1962, Abajo. (17) 1 macho, 9-1917, 1 macho, Lauffer. (19) 1 macho, 6-1917, pangolín. (28) una ooteca, 8-1913. (35) 2 machos, Arias. (45) 1 macho, 9-1974, Miguel. (46) 1 macho, Lauffer. (47) 3 machos, 8-1925, Escalera.

Distribución en la Península Ibérica: se extiende desde el centro hacia el sur de la Península.

Ameles spallanzania (Rossi, 1792)

Adulto de Junio a Agosto. Vive preferentemente en colinas incultas sobre la tierra, en la hierba o en los arbustos (*Echium, Retama, Rosmarinus, Quercus, Genista*) de lugares cálidos y secos.

Localidades (Mapa 2): (1) 1 hembra, 8-1950, Agenjo. (1) 3 hembras, 7-1910, Agenjo (2) 1 macho, 6-1908, Arias. (3) 1 macho, 6-1897, I. Bolívar. (6) 1 macho, 7-1936, Pujol. (7) 1 hembra, 7-1938, Morales; (Cienvallejos), 6 machos, 11 hembras, 6-1927, C. Bolívar. (10) 4 hembras, 1 ninfa, C. Bolívar; 1 macho, 1 hembra, Bonet; 2 machos, 1 hembra, sin datos. (11) 12 machos, 13 hembras, 7-1952, 1 hembra, 8-1957, 1 hembra, 8-1959, Abajo; 1 hembra, 7-1945, Esteban; 1 hembra, 7-1933, Morales. (13) 3 machos, 2 hembras, 8-1959, 1 hembra, 8-1960, 3 hembras, 8-1961, 1 macho, 8-1963, Abajo. (17) 1 hembra, 7-1942, Alvarez; 1 hembra, I. Bolívar; 1 macho, 3 hembras, Meléndez; 1 hembra, 12-1885; 1 macho, 8-1905, Mercet; 1 hembra, 7, Morales; 1 hembra, sin datos. (23) 1 ninfa, Abajo. (31) 1 macho, 1 hembra, 7-1911, Collado. (35) 1 macho, 6-1934, C. Bolívar; 1 macho, 1 hembra, 7-1932, Morales.

Distribución en la Península Ibérica: presente en casi toda la Península.

Ameles assoi (Bolívar, 1873)

Adulto desde Junio, vive en lugares cálidos y secos sobre la hierba, arbustos y tierra.

Localidades (Mapa 3): (1) 1 hembra, 7 1950, Agenjo (2) 1 macho. 6-1906, Arias. (6) 1 macho, 1 macho, 7-1936, Pujol. (7)

2 machos, 1 hembra, I. Bolívar; (Cienvallejos), 7 machos, 2 hembras, 6-1927, C.Bolívar. (8) 1 macho, Jiménez. (15) 1 macho, 6-1985, Dorado. (17) 1 macho, C. Bolívar; 1 macho, Meléndez; 4 hembras, 4 ninfas, Abajo; 1 macho, Martín. (19) 2 hembras. 6-1917, Arias. (22) 1 macho, 1 hembra, sin datos. (23) 2 ninfas, Abajo. (24) 1 macho, Bolívar; 1 macho, Dusmet; 1 macho, 2 hembras, sin datos. (26) 1 hembra, 6-1981. (31) 1 macho, 1 hembra, 6-1934, C.Bolívar; 1 ninfa, 11-1934, Peláez; 1 hembra, Quirós. (35) 6 machos, Abajo; 3 machos, 6-1908, 1 hembra, Arias; 20 machos, 4 hembras, C. Bolívar; 5 machos, 3 hembras, 6-1908, 2 hembras, 6-1934, I. Bolívar; 1 hembra, Ceballos; 5 machos, Lauffer; 1 h sin datos. (45) 5 machos, 6-1942, Abajo

Distribución en la Península Ibérica: especie propia del centro de la Península (Madrid, Toledo, Cuenca).

Ameles decolor (Charpentier, 1825)

Adulta desde Junio a Agosto sobre los arbustos y en las hierbas altas de colinas u hondonadas abiertas.

Localidades (Mapa 4): (10) 1 macho, Morales. (11) 1 macho, Abajo; 3 machos, Hernández. (11) 1 macho, 10-1959, Peris. (17) 1 hembra, 10-1974, Berenguer; 1 hembra, 8-1903, Sanz. (33) 1 macho, 5-1980, Canalda. (35) 2 machos, 10-1925; 1 macho, 6-1916. (37) 1 macho, 1 hembra, 10-1977, Marcos.

Distribución en la Península Ibérica: desde el centro de España se extiende hasta el litoral mediterráneo.

Mantis religiosa Linneo, 1758

Habita las praderas, campos secos, arbustos, terrenos cultivados en donde exista una mediana vegetación y estén bien soleados. Adulta de Junio a Noviembre.

Localidades (Mapa 5): (7) 4 hembras, 7-1938, Morales. (9) 1 macho, 1 hembra, 8-1932, Izquierdo. (10) 1 hembra, C. Bolívar; 1 h. (11) 1 macho, 1 hembra, 8-1944, 3 machos, 9-1951, 1 macho, 7-1952, 1 hembra, 8-1959, 4 machos, 2 hembras, Abajo. (13) 1 macho, 3 hembras, 8-1959, 2 machos, 1 hembra, 8-1960, 3 machos, 1 hembra, 8-1961. 5 machos, 3 hembras, 8-1962, 2 machos, 1 hembra, 8-1964, Abajo; 1 ooteca, Dorado; 1 hembra, 5-1960. (17) 1 macho, 1 hembra, 8; 1 hembra, Meléndez. (18) 1 macho, 8-1987, Mateos. (22) 2 hembra, 9-1963, Alvarez; 1 macho, 9-1963, Llorente. (23) 1 macho, 9-1977, Compte. (24) 2 machos, 2 hembras, Abajo; 1 macho, P. Ceballos; 1 macho, 2 hembras, 10-1982, Dorado; 1 macho, 9-1961, Montanya; 3 hembras, Morales; 1 hembra, Garcia Velazquez. (26) 1 macho, 10-1956, G-Rave. (29) 1 macho, 2 hembras, Abajo. (31) 1 hembra, 11-1932, Pelaez. (35) 2 machos, 2 hembras, 1 ninfa, Abajo; 1 hembra, Agenjo; 1 macho, 6-1908, Arias; 2 machos, 1 hembra. I. Bolívar: 1 hembra, C. Bolívar, 1 hembra, 9, Escalera; 3 ootecas, 4-1932, 1 ninfa, 4-1966, Morales; 2 hembras, Sanz. (38) 1 hembra, 9-1938, Morales. (39) 1 macho, Abajo. (40) 1 hembra, 1961, Ruano. (42) 1 macho, 9-1974, Perez-Iñigo. (44) 1 macho, 5-1981, Cano. (45) 1 macho, 1 hembra, 6-1942, Abajo. (46) 6 machos, 9-1964, Fernandez Rubio.

Distribución en la Península Ibérica: Es la especie más común en Europa. Existe en toda la península.

Iris oratoria (L., 1758)

Lugares húmedos y soleados donde haya arbustos y plantas elevadas o entre los campos cultivados, hallándose adulto desde Junio a Septiembre.

Localidades (Mapa 6): (5) 1 macho, 8-1983, Dorado. (7) 11 ninfas, 7-1938, Morales. (9) 1 macho, 8-1932, Izquierdo. (14) 1 hembra, 10-1934, Rubio. (18) 2 machos, 8-1987, 2 machos, 8-1988, Mateos. (23) 1 hembra, Diaz. (24) 2 hembras con ooteca, 9-1962, Abajo; 1 hembra, Alvarez; 1 macho, 9-1985, Arillo; 7 ninfas, 4-1933, Morales; 1 hembra, 10-1935, Peláez; 1 macho, 8-1940, Pujol; 1 macho, 9-1954, Templado; 1 hembra, sin datos. (26) 1 macho, 9-1956, G-Rave. (27) 1 hembra, 10-1983, Dorado. (28) 1 hembra, C. Bolívar; 2 macho, 9- 1935, Morales. (30) 2 machos, Peris. (32) 1 hembra, Abajo. (35) 4 machos, 16 hembras, Abajo; 1 hembra, Arias; 1 macho, 11 hembras, I. Bolívar; 3 hembras, 9, Escalera. (40) 1 hembra, 9-1958, Ruano. (42) 1 macho, 8-1985, Atero. (43) 1 hembra, 10-1988, Dorado. (45) 1 macho, 6-1942, Abajo.

Distribución en la Península Ibérica: centro y sur de la peninsula, siendo escaso en el norte.

Cita bibliografica: Aranjuez (Lopez Seoane) citado en Bolívar, 1877.

Apteromantis aptera (Fuente, 1894)

Adulto durante los meses de Junio y Julio, vive sobre las matas y arbustos bajos de las colinas secas y soleadas.

Localidades (Mapa 7): (7) 1 hembra, I. Bolívar; 2 hembras, 7-1938, Morales; (Cienvallejos), 6 machos, 9 hembras, 6-1927; 1 hembra, C. Bolívar.

Distribución en la Península Ibérica: se extiende por la mitad sur de la Península.

Geomantis larvoides Pantel, 1896

Se la encuentra en la tierra desnuda de lugares secos y muy soleados, así como en los márgenes de los bosques y en las tierras cultivadas. Adulto en Junio.

Localidades (Mapa 8): (31) 1 hembra, 6-1934, C. Bolívar.

Distribución en la Península Ibérica: desde el centro hacia el sur de la Península.

Empusa pennata (Thunberg, 1815)

Adulto en los meses de primavera y primeros del verano. En forma de ninfa durante todo el año. Sobre arbustos de lugares secos y calidos. Habitos crepusculares. Vuela con relativa facilidad.

Localidades (Mapa 9): (1) 1 ninfa, Escalera. (2) 1 ninfa, 5-1972, Buencuerpo. (4) 1 hembra, 7-1982, Dorado. (7) (Cienvallejos), 1 macho, 6-1927, Escalera. (12) 1 macho, 6-1962, Agenjo. (16) 1 hembra, 6-1989, Dorado. (20) 1 macho, 7-1946, Peris. (21) 1 ninfa, 5-1972, Buencuerpo. (22) 1 macho, sin datos. (24) 1 macho, 1 ninfa, Abajo; 1 ninfa, 4-1975, Blázquez; 1 ninfa, 10-1983, Dorado; 5 ninfas, 9-1988, Izquierdo; 2 ninfas, 10-1931, 1 macho, 5-1965, Morales; 1 macho, 5-1963, Peris; 1 ninfa, Rioja; 1 ooteca, Selgas; 1 ninfa, 12-1955, 1 macho, 1 hembra, sin datos. (25) 1 ninfa, 6-1982, López. (26) 1 ninfa, 4-1972, Toimil. (27) 1 ninfa, 5-1970, Gurrea; 1 ninfa, 4-1974, Salvador; 1 ninfa, 5-1975, Toribio. (29) 1 hembra, Abajo. (31) 1 ninfa, 9-1934, Peláez. (32) 1 macho, 6-1986, Ruano. (34) 1 hembra, sin datos. (35) 3 ninfas, 1 ooteca, Abajo; 1 ninfa, 10-1962, Agenjo; 1 macho, 1 ninfa, 6-1908, I. Bolívar; 1 ninfa, C. Bolívar; 1 ninfa, 4-1932, Morales; 1 ninfa, 5-1964, Viedma; 1 macho, 6-1905, 2 ootecas, sin datos. (36) 1 ninfa, 9-1983, Costa, (38) 1 ninfa, 11-1938, Morales. (40) 1 ninfa, 6-1958, Ruano. (42) 1 macho, 7-1985, Atero. (45) 1 macho, 1 ooteca, 4-1942, 1 ninfa, 6-1942, Abajo.

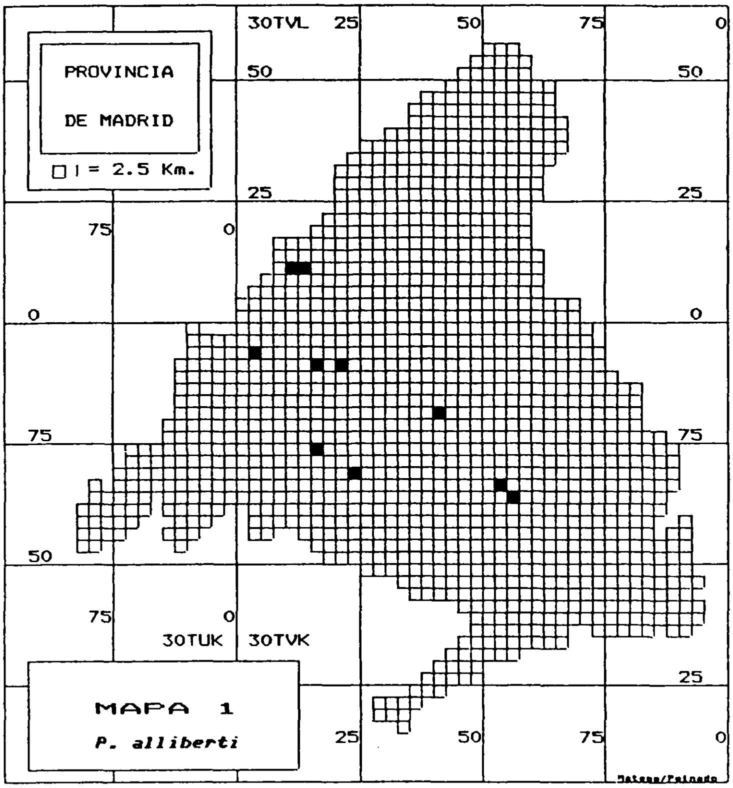
Distribución en la Península Ibérica: presente en toda la Península, es mas común en la región meridional.

APENDICE TOPONIMICO

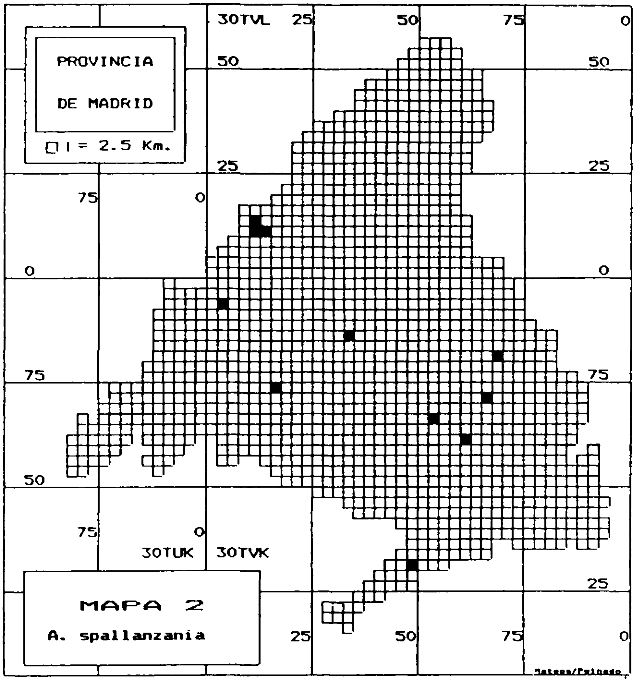
Coordenadas y altitudes de los topónomos en los que existen citas de las distintas especies.

(1)	Alcalá de Henares	30TVK6982, 587 m.
(2)	Aranjuez	30TVK4932, 489 m.
(3)	Arganda	30TVK6262, 618 m.
(4)	Barajas	30TVK5181, 620 m.
(5)	Barajas (La Muñoza)	30TVK5579, 575 m.
(6)	Beacos	?
(7)	Brunete	30TVK1673, 656 m.
(8)	Campo Real	30TVK6865, 777 m.
(9)	Cenicientos	30TUK7558, 775 m.
(10)	Cercedilla	30TVL1010, 1214 m.
(11)	Cercedilla (Estación Alpina)	30TVL1014, 1500 m.
(12)	Cercedilla (Puerto de la Fuenfria)	30TVL1116, 1793 m.
(13)	Cercedilla (El Ventorrillo)	30TVL1412, 1480 m.
(14)	Collado Mediano	30TVL1405, 1030 m.
(15)	Colmenar Viejo	30TVL3501, 883 m.
(16)	Coslada	30TVK5275, 620 m.
(17)	El Escorial	30TVK0494, 909 m.
(18)	Encinar del Alberche	30TUK8560, 520 m.

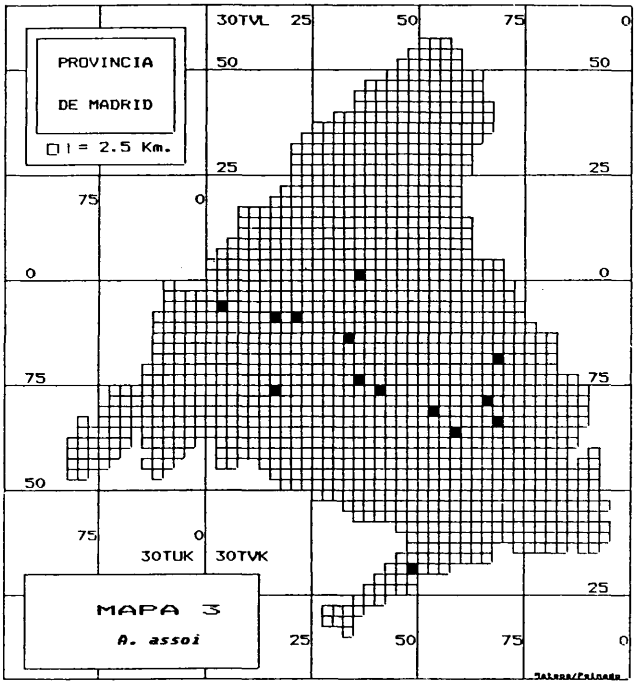
(19) Galapagar..........30TVK1592, 881 m.
(20) Getafe ....30TVK3862, 623 m.
(21) Hoyo de Manzanares.....30TVK3862, 1001 m.
(22) La Poveda ....30TVK5963, 618 m.
(23) Loeches.............30TVK6570, 647 m.
(24) Madrid..............30TVK4074, 655 m.
(25) Madrid (Alameda de Osuna) ....30TVK4979, 645 m.
(26) Madrid (Casa de Campo)30TVK3775, 635 m.
(27) Madrid (Ciudad Universitaria)........................30TVK3878, 640 m.
(28) Madrid (Chamartín).30TVK4280, 700 m.
(29) Madrid (Hortaleza)..30TVK4582, 700 m.
(30) Madrid (Moncloa)30TVK3977, 660 m.
(31) Madrid (El Pardo)30TVK3486, 610 m.
(32) Madrid (Villaverde) .30TVK4065, 600 m.
(33) Manzanares el Real..30TVL2709, 908 m.
(34) Miraflores de la Sierra....30TVL3619, 1150 m.
(35) Montarco...........30TVK5467, 600 m.
(36) Móstoles............30TVK2765, 661 m.
(37) Navacerrada......30TVL1409, 1203 m.
(38) Navalespino......30TUK9394, 1405 m.
(39) Peñalara...........30TVL1923, 2430 m.
(40) Pozuelo de Alarcón..30TVK3176, 690 m.
(41) Rivas-Vaciamadrid...30TVK5664, 590 m.
(42) Robledo de Chavela.30TUK9584, 903 m.
(43) Somosaguas ....30TVK3375, 690 m.
(44) Soto de Viñuelas.30TVK4295, 700 m.
(45) Torrelodones......30TVK2292, 845 m.
(46) Vaciamadrid (hoy Rivas-Vaciamadrid) ....30TVK5671, 560 m.
(47) Villaviciosa de Odón 30TVK2468, 672 m.



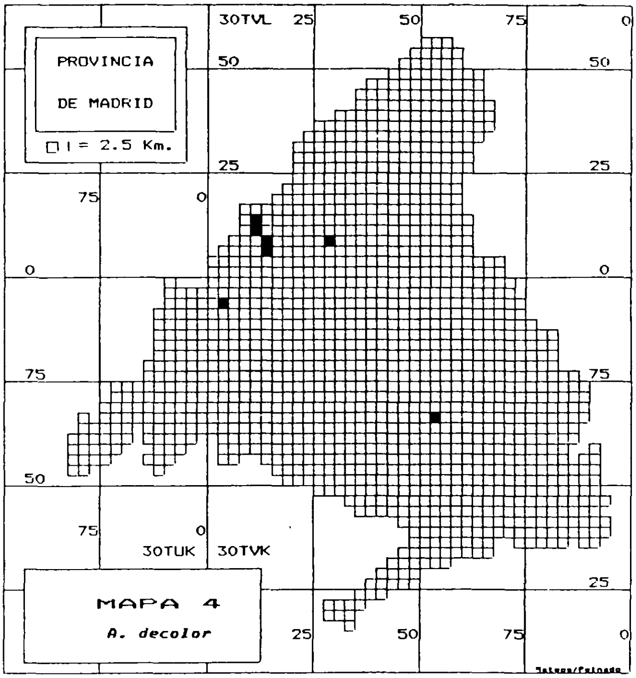
Mapa 1.— Citas en Madrid de *Perlamantis alliberti* Guérin-Méneville, 1843.



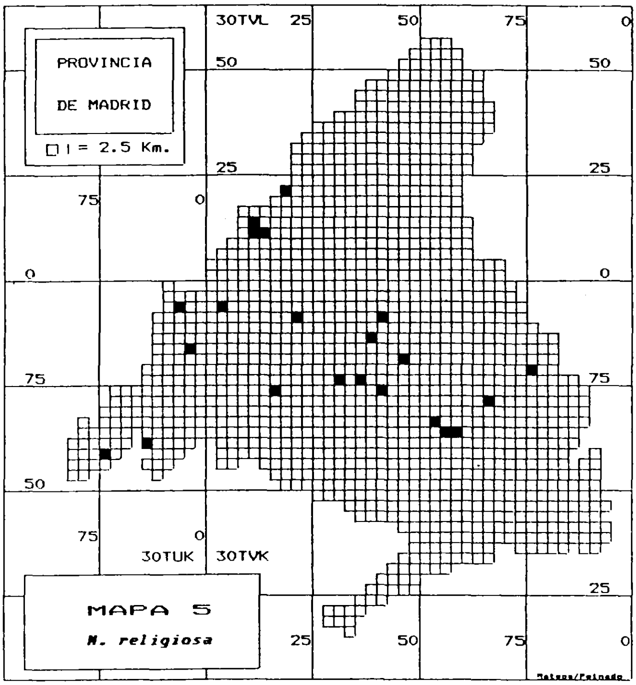
Mapa 2.—Citas en Madrid de *Ameles spallanzania* (Rossi, 1792).



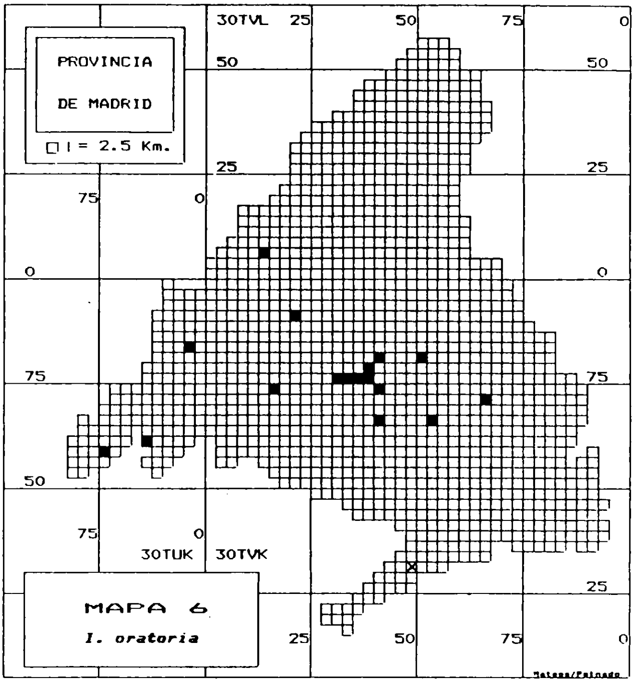
Mapa 3.— Citas en Madrid de *Ameles assoi* (Bolívar, 1873).



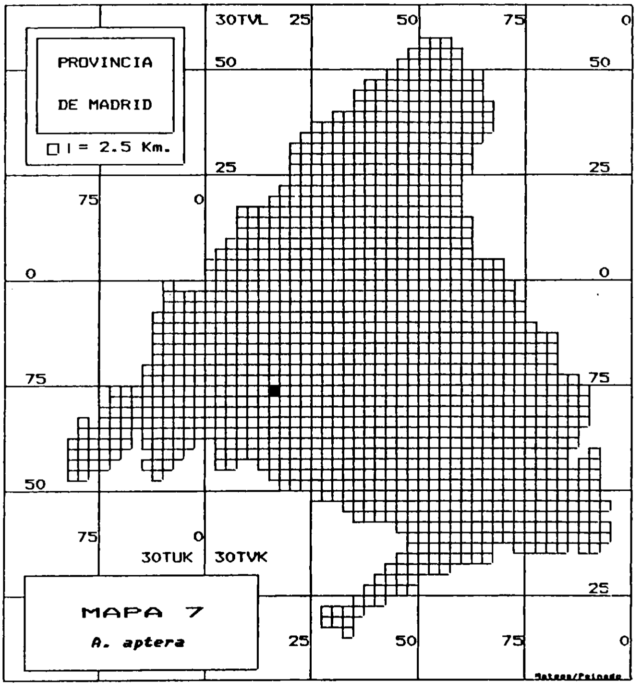
Mapa 4.—Citas en Madrid de *Ameles decolor* (Charpentier, 1825).



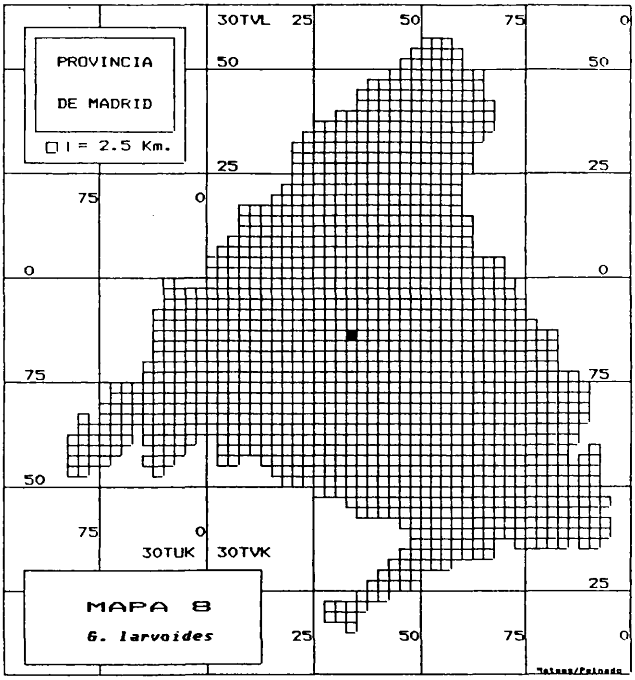
Mapa 5.—Citas en Madrid de *Mantis religiosa* Linneo, 1758.



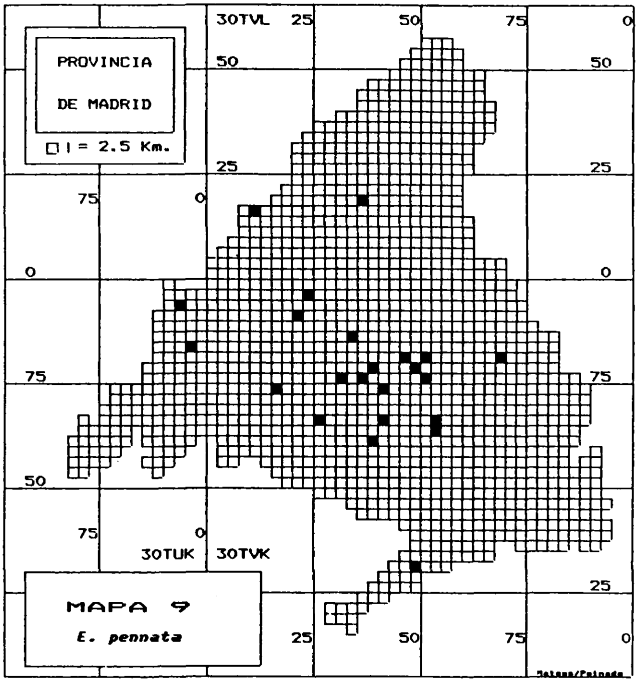
Mapa 6.— Citas en Madrid de *Iris oratoria* (L., 1758). (X¸ Cita bibliografica).



Mapa 7.— Citas en Madrid de *Apteromantis* aptera (Fuente, 1894).



Mapa 8.— Citas en Madrid de *Geomantis larvoides* Pantel, 1896.



Mapa 9.— Citas en Madrid de *Empusa pennata* (Thunberg, 1815).

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Sobre la bionomía de los celíferos (Orthoptera, Caelifera) de Cantabria (N. España)

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RESUMEN

Se presenta un estudio bionómico sobre el muestreo de Ortópteros Celíferos realizado en la Comunidad Autónoma de Cantabria desde el año 1985 hasta el actual. La Comunidad de Cantabria, situada en el norte de la Península Ibérica, tiene una extensión aproximada de 5.300 km^2 y una gradación altitudinal desde 0 hasta los 2.600 m. Presenta igualmente grandes variaciones climáticas con la consiguiente diversidad botánica.

El citado muestreo se efectuó en un total de 119 localidades, de las que se han obtenido 162 muestras con las que se ha procurado recolectar ejemplares en todas las cuadrículas con coordenadas U.T.M. de 10 km de lado, así como todos los biotopos existentes.

Esta prospección ha proporcionado un total de 6.496 ejemplares de Ortópteros Celíferos pertenecientes a 41 especies de 20 géneros agrupados en 3 familias (Tetrigidae, Catantopidae y Acrididae), de las cuales 12 especies y dos subespecies constituyen nuevas citas para Cantabria. Se describen las comunidades vegetales muestreadas y se relacionan las especies de Celíferos encontradas.

Palabras clave: biogeografía de Orthoptera, Zoogeografía, bionomía.

ABSTRACT

This is a bionomical study based on a sampling of Orthoptera Caelifera carried out in the Comunidad Autónoma of Cantabria from 1985 to 1988. Cantabria, in the North of the Península Ibérica, has an area of about 5.300 km^2 and a elevation from 0 to 2.600 m. It also presents great climatic variations with the consequent botanic diversity.

The sampling was made in 119 localities, from which were obtained 162 samples with which we have attempted to get exemplars from all the squares with U.T.M. coordinates of 10 km of side, and from all the biotopes.

As a result, we have obtained a total of 6,496 exemplars from 41 species of 20 genera grouped in 3 families (Tetrigidae, Catantopidae and Acrididae) of which 26 species and a subspecies are new for Cantabria. The sampled vegetal communities and the species of Orthoptera are reviewed.

Key words: biogeography of Orthoptera, Zoogeography, bionomy.

INTRODUCCION

La Comunidad Autónoma de Cantabria está situada en el Norte de la Península Ibérica, entre la Cordillera Cantábrica y la costa, con una extensión de unos 5.300 km^2 distribuidos en las cuadrículas U.T.M. de 100 km de lado 30TUP, VP, UN y VN. (Fig. 1). Presenta una gran variación altitudinal, desde 0 hasta casi 2.600 m sobre el nivel del mar. Igualmente son importantes las variaciones climáticas, desde zonas con clima atlántico hasta otras de clima continental, pasando por zonas de clima de alta montaña e incluso otras de tendencias mediterránea.

Estas variaciones van acompañadas de la correspondiente diversidad florística, pudiéndose encontrar gran número de comunidades vegetales como las propias de playas, marismas, pastizales mesófilos y de alta montaña, ruderales, landas, brezales y piornales, comunidades de bordes de caminos o cultivos y comunidades forestales (robledal, hayedo, pinar, encinar, etc.) (Fig. 2).

El conocimiento de la fauna de Ortópteros de dicha Comunidad es bastante escaso, reduciéndose casi exclusivamente a los trabajos de Bolívar (1898b), Llorente y Presa (1981), todos ellos referidos a un reducido número de localidades y de especies. Por ello se planteó el interés de un estudio lo más amplio posible de los Ortópteros de Cantabria.

Se establecieron diversos itinerarios que, a lo largo de cuatro años, han permitido tomar 162 muestras en 119 localidades, con un total de 6.496 ejemplares de Ortópteros Celíferos pertenecientes a 41 especies de 20 géneros incluidos en 3 familias (Tetrigidae, Catantopidae y Acrididae). De estas 41 especies se han citado para Cantabria 28, según el Cátalogo de Ortópteros de España (Herrera, 1982), los Tetrigidae de la Península Ibérica (Llorente y Presa, 1981), y la primera contribución al conocimiento de los Ortópteros de Cantabria (Larumbe y Herrera, 1987), por lo que el presente trabajo incrementa en un 32% aproximadamente el número de especies y subespecies para esta Comunidad.

MATERIAL Y METODOS

La recolección de ejemplares se realizó mediante la manga entomológica y fueron fijados en acetato de etilo. En cada punto de muestreo se recogieron las especies vegetales que permitiesen la identificación de la comunidad.

Los Ortópteros se extendieron para su identificación y clasificación. En ciertos casos fue necesario realizar preparaciones de genitalias. Los ejemplares están depositados en el Museo de Zoología de la Universidad de Navarra.

DESCRIPCION DE CANTABRIA

Esta Comunidad está situada en la Cornisa Cantábrica, entre la Cordillera y el Mar del mismo nombre. A pesar de su reducida extensión presenta grandes contrastes en el medio natural, y si bien en ella predominan las bajas altitudes (0 a 300 m), con clima templado y húmedo, podemos encontrar también zonas de clima continental (seco y extremado), zonas de alta montaña e incluso una zona de transición entre el clima mediterráneo y el atlántico, variando estas características simplemente en función de la orientación (Guinea, 1953).

Es tradicional distinguir en Cantabria dos comarcas o áreas naturales: "La Marina" y "La Montaña" (Fig. 1), con grandes diferencias en cuanto a topografía, clima, fauna y flora. "La Marina" es la franja costera, al norte de la Comunidad, con escasa altitud, topografía suave, clima atlántico y una fuerte ocupación humana; comprende alrededor de un tercio de la superficie total.

"La Montaña" representa los dos tercios restantes y se caracteriza por su elevación, la presencia de numerosas cadenas montañosas surcadas por valles orientados de Norte a Sur, clima más duro y escasa ocupación humana. A estas dos zonas podemos añadir una tercera de transición a la Meseta, con una altitud generalmente superior a 800 m, con amplias zonas llanas y bien iluminadas, presentando un clima de transición.

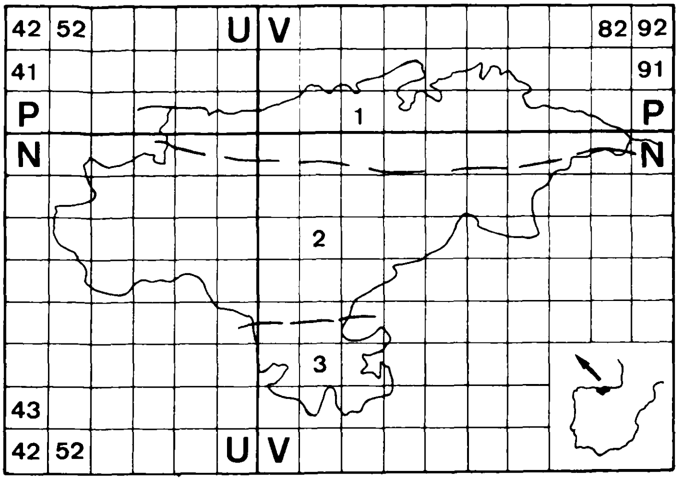

Figura 1. Mapa en coordenadas U.T.M. con cuadrículas de 10 km de lado, en la que se ha representado la Comunidad Autónoma de Cantabria y los límites aproximados de sus comarcas naturales (1, La Marina; 2, La Montaña; 3, Transición a la Meseta).

LAS COMUNIDADES VEGETALES

La caracterización de las comunidades vegetales presenta dificultades derivadas tanto de la diferente nomenclatura y taxonomía utilizada por los distintos autores como, sobre todo, por la existencia de numerosas formaciones vegetales de transición o intermedias entre dos o más clases taxonómicas, y por la complejidad de la toma de datos y del procesamiento necesarios para su caracterización.

Por todo ello, para el presente trabajo nos hemos basado en las descripciones y catálogos de comunidades vegetales realizados por distintos autores (Bellot, 1978; Guinea, 1953; Loriente, 1974; Mayor López, 1988 y Nava, 1988), aplicables a la zona objeto de nuestro estudio. La identificación de los ejemplares vegetales recolectados en cada muestra nos ha permitido adscribirlas a 18 comunidades.

Tanto por alcanzar una mayor claridad como por evitar los problemas expuestos al comienzo de este apartado, se enumeran las comunidades vegetales muestreadas con los nombres que a continuación describimos señalando las especies vegetales más características:

1. Comunidades costeras. Aparecen en el borde de las aguas marinas o de estuarios y rías, caracterizándose por un ambiente rico en sales. Están sometidas a gran presión por el hombre, por lo que su superficie disminuye rápidamente. (Tabla 1).

1.1. Arenas de playas antrópicas. Clase *Cakiletea maritimae: Agropyrum junceum, Cakile marítima, Salsola kali, Euphorbia peplus*, etc. Zonas muy abundantes en el litoral cántabro, en la parte posterior de las dunas, con una comunidad muy influenciada por la acción humana (pisadas, basuras, etc.). La cobertura vegetal es escasa y herbácea, adaptada a un medio rico en sales.

1.2. Carrizal: *Phragmites communis, Juncus maritimus, Limonium vulgare, Agrostis stolonifera, Plantago maritima, Halimione portulacoides*, etc. Comunidad propia de estuarios y bordes de lagos.

1.3. Dunas costeras. Clase *Ammophiletea: Ammophila arenaria, Eryngium maritimum, Convolvulus soldanella, Medicago marítima, Euphorbia paralias, Ononis ramossisima*, etc. Comunidad propia de las arenas de playa, cada vez más restringida y alterada por la ocupación humana.

2. Comunidades pratenses. Caracterizadas por la presencia dominante de plantas herbáceas, anuales generalmente, que permanecen verdes la mayor parte del año. Una buena parte de estas comunidades proceden de la quema de zonas cubiertas por bosque. Este grupo de comunidades es el que mayor superficie ocupa en Cantabria.

2.1. Bordes de senderos y cultivos. Diversas formaciones vegetales, caracterizadas por la presencia de: *Plantago major, Lolium perenne, Poa annua, Cynodon dactylon, Urtica dioica, Malva sylvestris,* etc. Con frecuencia presentan ejemplares de *Rubus, Rosa,* etc. Aparecen entre 0 y 1.500 m.

2.2. Cervunal. Comunidad caracterizada por: *Nardus stricta, Carex pyrenaica, Trifolium alpinum, Jasione perennis,* etc. Son pastizales densos procedentes a menudo de la quema de brezales. Superan los 1.900 m de altitud.

2.3. Pastizal mesófilo. Clase *Festuco - Brometea: Bromus erectus, Carex brevicollis, Potentilla erecta, Festuca rubra, Lotus corniculatus,* etc. La formación más frecuente en Cantabria, incluye prados de siega y otros sometidos al pastoreo, distribuidos desde el nivel del mar hasta casi las mayores cotas. En general están modificados por la acción humana o el ganado.

2.4. Pradera juncal: *Juncus effusus, Scirpus lacustris, Lythrum salicaria, Galium elongata, Oenanthe fistulosa, Carex nigra, Poa annua,* etc. Ocupa los bordes de zonas higroturbosas y de lagunas, en transición continua hacia el pastizal, generalmente.

2.5. Ruderal: *Stellaria media, Polygonum convolvulus, Raphanus raphanistrum, Myosotis arvensis, Senecio vulgaris, Centaurea cyanus, etc.* Comunidades nitrófilas de difícil catalogación, situadas junto a asentamientos humanos y de ganado, así como en zonas cultivadas hasta época reciente.

3. Comunidades de matorral. Predominan en ellas los vegetales sufruticosos y plurianuales; ocupan a menudo zonas deforestadas que fueron empleadas en el pastoreo y actualmente están en desuso.

3.1. Brezales. Formaciones vegetales de composición florística muy variada, predominando las ericáceas y el género *Ulex: Erica vagans, Erica cinerea, Calluna vulgaris, Daboecia cantábrica, Avena sulcata, Ulex gallii,* etc. Son comunidades muy abundantes en Cantabria, constituidas por matorrales subarbustivos heliófilos, asentados sobre suelos ácidos. Se originan generalmente por desaparición de comunidades forestales. Ocupan grandes superficies desde 0 hasta 1.800 m de altitud.

3.2. Helechal: *Pteridium aquilinum, Ulex europaeus.* Etapa aparentemente intermedia entre el pastizal y el brezal, ocupa superficies extensas en algunas laderas montañosas. Se ha incluido en este grupo por estar frecuentemente interpenetrada con landas y brezales.

3.3. Landa con *Ulex: Ulex gallii, Ulex europaeus, Arrenatherum thorei, Pteridium aquilinum, Juniperus communis, Carex caryophyllea,* etc. Comunidad típicamente cantábrica, muy próxima al brezal, si bien en ella predominan las papilionáceas frente a las ericáceas. Ocupa muy amplias zonas entre 0 y 1.800 m, con composiciones florísticas variadas.

3.4. Landa altitudinal. Clase *Vaccinio - Piceetea: Vaccinium myrtillus, Juniperus nana, Arctostaphyllos uva-ursi,* etc. Corresponde a los pisos de coníferas que no existen en Cantabria. Entre 2.000 y 2.400 m.

3.5. Piornal: *Genista florida, Genista hispánica, Genista legionensis, Sarothamnus scoparius, Globularia nudicaulis, Helianthemum numularium,* etc. Formación de matorral mesófilo con abundancia de papilionáceas. Alcanza los 2.400 m.

4. Comunidades forestales. Muy reducidas en Cantabria en cuanto a su extensión original, forman en general pequeñas manchas entre comunidades de los otros grupos.

4.1. Encinar. Clase *Quercetea ilicis: Quercus ilex, Ilex aquifolium, Laurus nobilis, Ligustrum vulgare, Ulex europaeus, Primula vulgaris, Aquilegia vulgaris, Teucrium scorodonia,* etc. Se encuentra en Cantabria en suelos básicos, entre el nivel del mar y los 800 m.

4.2. Eucaliptal: *Eucaliptus globulus, Rubus, Ulex europaeus, Daboecia cantábrica,* etc. Repoblaciones que permanecen alrededor de 20 años; debido a la ausencia de celíferos en los muestreos realizados en el interior de eucaliptales maduros, los incluidos en esta categoría corresponden en realidad a zonas próximas al borde o al interior de eucaliptales jóvenes con predominio de ejemplares que no superan los 4 m. Se encuentran por debajo de los 400 m.

4.3. Hayedo. Clase *Querco - Fagetea: Fagus sylvatica, Crataegus monogyna, Ilex aquifolium, Galium rotundifolium, Helleborus viridis, Anemone nemorosa,* etc. Bosque caducifolio sobre suelos ricos en nutrientes. Su límite altitudinal alcanza los 1.800 m.

4.4. Pinar: *Pinus sylvestris, Pinus insignis, Calluna vulgaris, Polygala vulgaris,* etc. Repoblaciones con especies de crecimiento rápido que permanecen hasta 30 años. Distribuidas por toda Cantabria.

4.5. Robledal. Clase *Quercetea roboripetraeae: Quercus robur, Quercus petraea, Q. pyrenaica, Cornus sanguinea, Erica vagans, Ulex europaeus, Daphne laureola, Fragaria vesca, Helleborus viridis,* etc. Comunidades de caducifolias sobre suelos ácidos. En el norte hay algunas pequeñas manchas con *Q. robur* y *Q. petraea,* mientras que en el sur se encuentran algunas formaciones mayores con *Q. pyrenaica.*

DISTRIBUCION DE LOS ORTOPTEROS CELIFEROS

La necesaria brevedad que debe caracterizar una publicación de este tipo impide hacer una relación completa de las características de cada una de las localidades muestreadas, así como de las citas de las especies de celíferos que en ellas se han recolectado. Por ello a continuación nos limitaremos a indicar para cada una de las cuarenta y dos especies y subespecies de Ortópteros celíferos identificadas, las comunidades vegetales en que aparecen (Tabla 1).

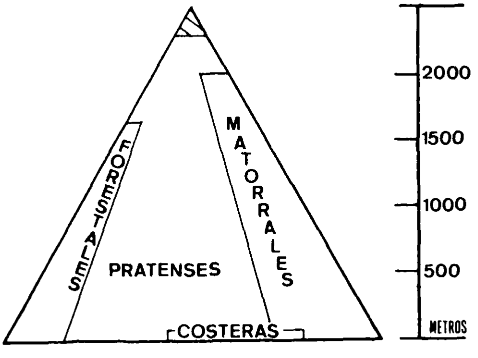

Figura 2. El diagrama muestra la proporción de superficie ocupada por cada grupo de comunidades vegetales en relación con la altitud.

Se han señalado con el símbolo (*) las especies o subespecies que constituyen nueva cita para la fauna de Cantabria.

1. *Tetrix (Tetrix) subulata* (Linneo) 1761: Arenas antrópicas, Landa, Robledal.

2. *Tetrix (Tetrix) ceperoi* (Bolívar) 1887: Arenas antrópicas, Landa, Pradera juncal.

3. *Tetrix (Tetratetrix) undulata* (Sowerby) 1806: Borde de sendero, Brezal, Carrizal, Encinar, Hayedo, Helechal, Landa, Landa altitudinal, Pastizal mesófilo, Pinar, Pradera juncal, Ruderal.

4. *Tetrix (Tetratetrix) nutans* Hegenbach, 1892: Brezal, Landa, Robledal, Ruderal.

5. *Mishtshenkotetrix brachyptera* (Lucas) 1849: Arenas antrópicas, Borde de sendero, Brezal, Carrizal, Dunas, Hayedo, Helechal, Landa, Pastizal mesófilo, Piornal, Pradera juncal, Ruderal.

6. *Podisma pedestris* (Linneo) 1758: Cervunal, Pastizal mesófilo.

7. *Calliptamus barbarus barbarus* (Costa) 1836: Arenas antrópicas, Borde de sendero, Brezal, Carrizal, Encinar, Eucaliptal, Helechal, Landa, Pastizal mesófilo, Pinar, Piornal, Pradera juncal, Ruderal.

* **8.** *Psophus stridulus* (Linneo) 1758: Brezal.

9. *Locusta migratoria cinerascens* (Fabricius) 1781: Carrizal, Landa, Pastizal mesófilo, Ruderal.

10. *Oedipoda caerulescens* (Linneo) 1758: Borde de sendero, Brezal, Eucaliptal, Helechal, Landa, Pastizal mesófilo, Pinar, Piornal, Pradera juncal, Robledal, Ruderal.

* **11.** *Oedipoda fuscocincta fucocincta* (Lucas) 1849: Pastizal mesófilo.

12. *Oedipoda fuscocincta caerulea* Saussure, 1884: Brezal, Helechal, Landa, Pastizal mesófilo, Piornal, Robledal, Ruderal.

13. *Oedipoda charpentieri* Fieber, 1853: Brezal, Pradera juncal.

* **14.** *Sphingonotus caerulans caerulans* (Linneo) 1767: Piornal, Ruderal.

15. *Aiolopus thalassinus* (Fabricius) 1781: Carrizal.

16. *Aiolopus strepens* (Latreille) 1804: Arenas antrópicas, Borde de sendero, Dunas, Brezal, Carrizal, Eucaliptal, Helechal, Landa, Pastizal mesófilo, Pinar, Piornal, Pradera juncal, Ruderal.

17. *Mecosthetus grossus* (Linneo) 1758: Pradera juncal.

18. *Paracinema tricolor bisignata* (Charpentier) 1825: Carrizal.

19. *Calephorus compressicornis* (Latreille) 1804: Arenas antrópicas, Borde de sendero, Dunas, Pastizal mesófilo.

* **20.** *Parapleurus alliaceus* (Germar) 1817: Carrizal, Landa, Ruderal.

21. *Euthystira brachyptera* (Orskay) 1826: Landa altitudinal.

* **22.** *Stauroderus scalaris* (Fischer-Waldheim) 1846: Brezal, Pastizal mesófilo, Piornal.

23. *Chorthippus (Glyptobothrus) apricarius* Linneo, 1758: Brezal, Ruderal.

24. *Chorthippus (Glyptobothrus) brunneus-biguttulus-mollis* gr.: Arenas antrópicas, Borde de sendero, Brezal, Carrizal, Cervunal, Dunas, Encinar, Eucaliptal, Helechal, Landa, Landa altitudinal, Pastizal mesófilo, Pinar, Piornal, Pradera juncal, Ruderal.

25. *Chorthippus (Glyptobothrus) binotatus* (Charpentier) 1825: Brezal, Encinar, Helechal, Landa, Landa altitudinal, Pastizal mesófilo, Piornal, Pradera juncal, Ruderal.

26. *Chorthippus (Glyptobothrus) vagans* (Eversman) 1848: Borde de sendero, Dunas, Brezal, Encinar, Landa, Pastizal mesófilo, Piornal, Robledal, Ruderal.

* **27.** *Chorthippus (Glyptobothrus) cazurroi* (Bolívar) 1898: Cervunal, Pastizal mesófilo.

28. *Chorthippus (Chorthippus) dorsatus* (Zetterstedt) 1821: Brezal, Landa.

* **29.** *Chorthippus (Chorthippus) parallelus erythropus* Faber, 1958: Borde de sendero, Brezal, Carrizal, Hayedo, Helechal, Landa, Landa altitudinal, Pastizal mesófilo, Piornal, Pradera juncal, Robledal, Ruderal.

30. *Chorthippus (Chorthippus) jucundus* (Fischer) 1853: Pastizal mesófilo, Ruderal (higrófilo).

* **31.** *Euchorthippus pulvinatus gallicus* Maran, 1846: Pastizal mesófilo, Ruderal.

* **32.** *Euchorthippus declivus* (Brisout-Barnville) 1848: Landa, Pastizal mesófilo, Piornal, Ruderal.

* **33.** *Stenobothrus (Stenobothrus) lineatus* (Panzer) 1796: Brezal.

34. *Stenobothrus (Stenobothrus) stigmaticus* Rambur, 1838: Brezal, Carrizal, Helechal, Landa, Landa altitudinal, Pastizal mesófilo, Pinar, Piornal, Pradera juncal, Ruderal.

* **35.** *Stenobothrus (Stenobothrus) nigromaculatus* (Herrich-Schaffer) 1840: Brezal, Cervunal.

* **36.** *Omocestus (Dirshius) raymondi* (Yersin) 1863: Brezal, Ruderal.

37. *Omocestus (Omocestus) ventralis* (Zetterstedt) 1821: Borde de sendero, Dunas, Brezal, Encinar, Eucaliptal, Hayedo, Helechal, Landa, Pastizal mesófilo, Piornal, Ruderal.

38. *Omocestus (Omocestus) panteli* (Bolívar) 1887: Borde de sendero, Dunas, Brezal, Eucaliptal, Helechal, Landa, Pastizal mesófilo, Pinar, Pradera juncal, Ruderal.

39. *Omocestus (Omocestus) kaestneri* (Harz) 1972: Brezal, Landa altitudinal, Pastizal mesófilo, Pradera juncal.

* **40.** *Aeropus sibiricus* (Linne) 1767: Brezal, Landa altitudinal, Piornal.

41. *Myrmeleotettix maculatus hispanicus* Harz, 1975: Brezal, Cervunal, Landa, Landa altitudinal, Pastizal mesófilo, Piornal, Pradera juncal.

42. *Dociostaurus genei* (Ocskay) 1832: Pastizal mesófilo, Ruderal.

Tabla 1. Distribución de los Celíferos en las distintas comunidades vegetales.

Tetrix subulata	X										X							X
Tetrix ceperoi	X					X					X							
Tetrix undulata		X			X	X	X		X	X	X	X				X	X	
Tetrix nutans							X	X	X		X			X				X
Mishtshenko. brach.	X	X	X		X	X	X	X	X	X	X		X			X		
Podisma pedestris				X	X													
Calliptamus barba.	X	X			X	X	X	X	X	X	X		X	X	X		X	
Psophus stridulus									X									
Locusta migratoria		X			X		X				X							
Oedipoda caerues.					X	X	X	X	X	X	X		X		X		X	X
Cedipoda fus. fus.					X													
Oedipoda fus. cae.					X		X		X	X	X		X					X
Oedipoda charpent.						X			X									
Sphingonotus caer.							X						X					
Aiolopus thalassi.		X																
Aiolopus strepens.	X	X	X		X	X	X	X		X	X		X		X		X	
Mecosthetus gross.						X												
Paracinema tricol.		X																
Calephorus compre.	X		X		X			X										
Parapleurus allia.		X					X				X							
Euthystira brachy.												X						
Stauroderus scala.					X				X				X					
Chorthippus apric.									X									
Chorth. bru-bi-mol	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	
Chorthippus binot.					X	X	X		X	X	X	X	X	X				
Chrothippus vagans			X		X		X	X	X		X		X	X				X
Chorthippus cazur.				X	X													
Chorthippus dorsa.									X		X							
	1.1	1.2	1.3	2.1	2.2	2.3	2.4	3.1	3.2	3.3	3.4	3.5	3.6	4.1	4.2	4.3	4.4	4.5
	COSTERAS			PRATENSES				MATORRALES						FORESTALES				

Tabla 1. (Continuación).

Chorth. par. eyrt.		X			X	X	X	X	X	X	X	X	X		·	X		X
Chorthippus jucun.					X		X											
Euchort. pulvinat.					X		X											
Euchort. declivus					X		X				X		X					
Stenobothrus line.									X									
Stenobothrus stig.		X	X		X	X	X		X	X	X	X	X				X	
Stenobothrus nigr.				X					X									
Omocestus raymondi							X		X									
Omocestus ventral.			X		X		X	X	X	X	X		X	X	X	X		
Omocestus panteli			X		X	X	X	X	X	X	X				X		X	
Omocestus kaestne.					X	X			X			X						
Aeropus sibiricus									X			X	X					
Myrmeleott. macul.				X	X	X			X		X	X	X					
Dociostaurus genei					X		X											
	1.1	1.2	1.3	2.1	2.2	2.3	2.4	3.1	3.2	3.3	3.4	3.5	3.6	4.1	4.2	4.3	4.4	4.5
	COSTERAS			PRATENSES				MATORRALES						FORESTALES				

CONCLUSIONES

De los datos anteriormente expuestos se pueden inferir los siguientes resultados:

De las 42 especies y subespecies citadas, un total de 11 están representadas en un 50% o más de las 18 comunidades muestreadas; destacan *Chorthippus (G.) brunneus-biguttulus-mollis* gr. que como tal grupo de especies está presente en 16 comunidades y *Calliptamus barbarus barbarus*, con una gran valencia ecológica, que está presente en 13 de ellas.

En cambio 23 especies y subespecies aparecen en menos del 20% de las comunidades, incluso 7 de ellas aparecen únicamente en una comunidad: *Psophus stridulus*, especie relativamente termófila que se ha recolectado en el brezal; *Oedipoda fuscocincta fuscocincta* en el pastizal mesófilo; *Aiolopus thalassinus*, especie higrófila mucho menos frecuente que *A. strepens*, se ha recolectado en carrizal; *Mecosthetus grossus* es también una especie higrófila de la pradera juncal; *Paracinema tricolor bisignata* en el carrizal; *Euthystira brachyptera*, especie mesófila sobre los 2.000 m en landa altitudinal y *Stenobothrus (St.) lineatus*, xerófila colectada en brezal.

Los tetrigidos, con 5 especies, están representados en 15 comunidades, no habiendo sido recolectados en cervunal, eucaliptal ni landa altitudinal; los catantopidos, con sólo 2 especies, aparecen en 14 comunidades, no encontrándose en dunas de playa, hayedo, landa altitudinal o robledal; finalmente, la familia de los acrididos con un total de 34 especies y subespecies, está representada en todas las comunidades muestreadas por su elevado número de especies de diferente valencia ecológica.

Atendiendo al número de especies de celíferos presentes en los distintos grupos de comunidades (Tabla 1), se muestra la siguiente distribución:

- Comunidades costeras o lacustres (arenas antrópicas, dunas, carrizal), con 17 especies, de las cuales 2 aparecen únicamente en estas comunidades: *Aiolopus thalassinus y Paracinema tricolor bisignata*. La comunidad de dunas presenta la mayor diversidad del grupo, con 11 especies.
- Comunidades herbáceas, con predominio de gramíneas, compuestas o papilionáceas (cervunal, pastizal mesófilo, pradera juncal y ruderal), en las que se encuentran presentes 34 especies de celíferos, resultando ser el grupo con mayor número de especies. Por comunidad, oscilan entre las 5 especies del cervunal y las 25 del pastizal mesófilo. Hay 6 especies exclusivas de este grupo de comunidades herbáceas: *Podisma pedestris, Oedipoda fuscocincta fuscocincta, Mecosthetus grossus, Chorthippus (G.) cazurroi, Chorthippus (Ch.) jucundus y Dociostaurus genei.*
- Comunidades de matorral y helechal, con predominio de sufruticosas (borde de sendero, brezal, helechal, landa, landa altitudinal, piornal), en las que aparece un total de 33 especies o subespecies de celíferos, de las cuales 3 son exclusivas de las comunidades de este grupo: *Psophus stridulus, Euthystira brachyptera* y *Stenobothrus (St.) lineatus*. El número de especies representadas en cada comunidad oscila entre 9 para landa altitudinal y 24 para el brezal.
- Comunidades forestales (encinar, eucaliptal, hayedo, pinar y robledal) con 15 especies de celíferos representadas, ninguna de las cuales aparece en las cinco comunidades. Este grupo de comunidades no presenta ninguna especie de celífero exclusiva, apareciendo en cada comunidad un número reducido de especies (entre 4 para el hayedo y 7 para el pinar).

Las comunidades que presentan mayor variedad de celíferos son los brezales y los pastizales mesófilos, con 25 especies, mientras que el menor número de especies se da en las comunidades leñosas mesotérmicas y microtérmicas, sobre todo en el hayedo con 2 especies de tetrígidos y una de acrídidos. Se puede inferir por tanto que las comunidades herbáceas y xerófilas son más ricas en especies de celíferos que las comunidades forestales microtérmicas y mesotérmicas.

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Consideraciones sobre la morfología, biología y relaciones filogenéticas de los Gomphocerinae de la península Ibérica: *Stenobothrus* Fischer, 1853; *Omocestus* Bolívar, 1878 y *Myrmeleotettix* Bolívar, 1914. (ORTH., Caelifera)

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RESUMEN

A partir de la revisión efectuada a los géneros *Stenobothrus* Fischer, 1853, *Omocestus* Bolívar, 1878 y *Myrmeleotettix* Bolívar, 1914 en la península Ibérica y, en base a múltiples caracteres morfológicos y biológicos en sentido amplio se establecen grupos de taxones afines y se hacen consideraciones sobre la filogenia y evolución de dichos taxones.

Palabras clave: *Omocestus, Stenobothrus, Myrmeleotettix,* península Ibérica, morfología, biología, filogenia.

ABSTRACT

Starting from the revision made on *Stenobothrus* Fischer, 1853, *Omocestus* Bolívar, 1878 and *Myrmeleotettix* Bolívar, 1914 species living in the Iberian peninsula and on the basis of some morphological and biological "sensu lato" characters, some related taxa groups are stablished and some considerations about these taxa evolution and phylogeny are given.

Key words: *Omocestus, Stenobothrus, Myrmeleotettix,* Iberien Peninsula, morphology, biology, philogeny.

INTRODUCCION Y OBJETIVOS

Los estudios sobre los distintos grupos de insectos tienen su fundamento en los trabajos faunísticos. Este tipo de trabajos sirve para el posterior desarrollo del conocimiento de los grupos animales considerados. Con el paso del tiempo todos estos conocimientos deben ser sometidos a revisión con objeto de ser puestos al día con la ayuda de las nuevas metodologías desarrolladas.

En la actualidad se tiende al estudio de los animales de un modo integral, teniendo en cuenta todos los aspectos posibles y haciendo especial hincapié en los relacionados con la biología, en sentido amplio, como complemento indispensable de las revisiones morfológicas.

En base a estos planteamientos nos propusimos la realización de la revisión de las especies de los géneros *Stenobothrus* Fischer, 1853; *Omocestus* Bolívar, 1878 y *Myrmeleotettix* Bolívar, 1914 que pueblan la península Ibérica, debido a que estas especies reúnen una serie de condiciones que las hace susceptibles de revisar, de entre las que destaca el que muchas de ellas resulten problemáticas en cuanto a su validez taxonómica, adscripción genérica, estatus poblacional, distribución, etc.

El estudio individual y pormenorizado de estas especies aparece en Clemente, 1987 y Clemente *et al.*, 1989b.

En este trabajo nos proponemos presentar los resultados globlales del estudio de todas las especies, consideradas en conjunto, con objeto de tratar de establecer si las opiniones, vertidas por algunos autores en el sentido de que no pertenecen a géneros distintos sino a subgéneros (Jago, 1971) o de que algunos de los endemismos ibéricos pudieran constituir un grupo independiente (Uvarov, 1928), son acertadas.

MATERIAL Y METODOS

Para realizar el trabajo se han utilizado aproximadamente, 12.500 ejemplares procedentes de diversas colecciones y de recolecciones propias y se ha procedido a una profunda revisión bibliografica.

El estudio se ha realizado desde diversos aspectos morfológicos y biológicos (biología, comportamiento acústico, fenología, distribuciones horizontal y altitudinal, preferencias bióticas, etc.) para todas y cada una de las especies y, también, para el conjunto de las mismas. En su caso, los datos obtenidos del estudio de los ejemplares se han discutido con los existentes en la bibliografía. La metodología empleada para estos estudios es la que aparece en Clemente, 1987 y Clemente *et al.*, 1989a y 1989b.

Para el análisis de los datos y el cálculo de los índices se tuvieron en cuenta los aspectos morfológicos de 21 taxones (Tabla 1).

Los datos morfológicos se codificaron en forma binaria de modo que cada aspecto morfológico se dividió en tantas unidades como posibilidades de manifestación de ese carácter existen en el total de especies consideradas. El carácter era codificado con valor 0 cuando no se presentaba y, con valor 1 en caso contrario. De este modo, al finalizar la codificación de los datos, todas las especies tenían el mismo peso efectivo pues, en cada uno de los datos morfológicos aparecía una y sólo una de las posibilidades del carácter, con valor 1.

Los datos, codificados del modo descrito, se estructuraron en una matriz de 21 especies (columnas) por 17 aspectos morfológicos que hacen un total de 44 posibilidades (44 filas). Esta matriz aparece en la Tabla 1.

El análisis de los datos se efectuó con una serie de programas de análisis estadísticos diversos que integran un paquete denominado BIOMECO, realizado por el GROUPE DE BIOMETRIE, CEPE-CNRS, Route de Mende, B. P. 5051, 34033 Montpellier CEDEX (Francia).

El análisis se realizó calculando el índice de Jaccard entre los elementos de la matriz de datos (ficheros de distancias XXX.JAC). Posteriormente se ordenaron según jerarquías elementales con agregación en torno a la distancia media (ficheros XXX.HIE). El índice de Jaccard es idóneo al estar considerando variables de tipo cualitativo. Respecto al método de agregación, respecto a la distancia media, se puede decir que es interesante, frente a otras alternativas, por permitir separar grupos netamente distintos, mientras que otros provocan la agregación de grupos no bien definidos en el sentido que interesa para la clasificación a obtener. En la práctica, la agrupación respecto a la distancia media es recomendable con datos binarios con el índice de Jaccard como índice de similaridad entre los elementos a clasificar (Nakache, 1987).

Table 1

	ANT	BOL	BUR	FEM	HAE	KAE	MIN	NAV	PAN	RAY	UHA	RUF	VIR	SBO	FES	FIS	GRA	LIN	NIG	STI	MMA
1	0	0	0	1	1	1	1	1	1	0	0	1	1	0	0	1	0	1	0	0	0
2	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0
3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
4	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
5	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1
6	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1
7	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0
8	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0
9	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
10	0	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0	1	0
11	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1
12	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1
13	1	0	0	1	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	0	0
14	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
15	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0
17	1	1	1	1	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	1
18	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
19	1	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0
20	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1
21	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1
22	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
24	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1
25	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0
26	0	1	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1
27	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0
28	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
29	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
30	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
31	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1
32	1	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0
33	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1
34	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
35	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	1	0	0	0
36	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1
37	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1
38	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0
39	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0
40	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	1
41	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
42	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0	1	1
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Fila superior

ANT: O. antigai; BOL: O. bolivari; BUR: O. burri; FEM: O. femoralis; HAE: O. haemorrhoidalis; KAE: O. kaestneri; MIN: O. minutissimus; NAV: O. navasi; PAN: O. panteli; RAY: O. raymondi; UHA: O. uhagoni; RUF: O. rufipes; VIR: O. viridilus; SBO: St. bolivari; FES: St. festivus; FIS: St. fischeri glaucescens; GRA: St. grammicus; LIN: St. lineatus; TNIG: St. nigromaculatus; STI: St. stigmaticus; MMA: M. maculatus.

Columna izquierda

1: antenas filiforme; *2:* antenas algo ensanchadas; *3:* antenas muy ensanchadas; *4:* cabeza robusta; *5:* cabeza esbelta; *6:* vertex sin quilla; *7:* vértex con quilla confusa; *8:* vértex con quilla marcada; *9:* sin pilosidad corporal; *10:* pilosidad escasa; *11:* abundante pilosidad; *12:* prozona menor que la metazona; *13:* prozona igual a metazona; *14:* prozona mayor que metazona; *15:* quillas laterales rectal; *16:* quillas flexuosas; *17:* quillas angulosas; *18:* estigma ausente; *19:* estigma confuso; *20:* estigma presente; *21:* sin faja estigmática en el área subcostal; *22:* con faja estigmática; *23:* sin área cubital; *24:* con área cubital; *25:* escotadura del X terguito estrecha; *26:* escotadura amplia o trapezoidal; *27:* escotadura semicircular; *28:* valvas del evopositor dentadas; *29:* valvas del ovopositor sin diente; *30:* valvas del ovopositor largas; *31:* valvas del ovopositor cortas; *32:* valvas basales con porción basal mayor que la apical; *33:* valvas del ovopositor cortas; *32:* valvas basales con porción basal mayor que la apical; *33:* valvas basales con porción basal igual a la apical; *34:* valvas basales con porción basal menor que la apical; *35:* cercos del macho cónicos; *36:* cercos del macho redondeados; *37:* epifalo de puente recto/epíphallus withh right bridge; *38:* epifalo de puente curvado; *39:* valvas ventrales del pene sin diente; *40:* valvas ventrales del pene con diente; *41:* 0-100 púas estriduladoras; *42:* 100-150 púas; *43:* 150-200 púas; *44:* más de 200 púas.

RESULTADOS

Resultados generales

El estudio llevado a cabo ha permitido conocer lo siguiente:

De las 37 especies, subespecies o formas, consideradas o citadas de la península Ibérica hasta la realización de la revisión quedan, con toda seguridad, 21 taxones, pertenecientes: 7 al género *Stenobothrus* Fischer, 1853 *(St. bolivari* (Brunner, 1876), *St. festivus* Bolívar, 1887, *St. fischeri glaucescens* Bolívar, 1897, *St. grammicus* Cazurro, 1888, *St. lineatus* (Panzer, 1796), *St. nigromaculatus* (Herrich-Schaeffer, 1840), *St. stigmaticus* (Rambur, 1838); 13 al género *Omocestus* Bolívar, 1878(*O. antigai* (Bolívar, 1897), *O. bolivari* Chopard, 1939, *O. burri* Uvarov, 1936, *O. femoralis* Bolívar, 1908, *O. haemorrhoidalis* (Charpentier, 1825), *O. kaestneri* (Harz, 1972), *O. minutissimus* (Bolívar, 1878), *O. nasavi* Bolívar, 1908, *O. panteli* (Bolívar, 1887), *O. raymondi* (Yersin, 1863), *O. rufipes* (Zettersted, 1821), *O. uhagoni* (Bolívar, 1876), *O. viridulus* (Linneo, 1758) y 1 al género *Myrmeleotettix* Bolívar, 1914 *(M. maculatus* (Thunberg, 1815)).

Las 21 especies estudiadas presentan una serie de caracteres de tipo morfológico, cariológico, acústico y biológicos, en general, que hacen pensar, sin lugar a dudas, que se trata de taxones independientes y claramente diferenciados.

No obstante, estos mismos caracteres permiten, a su vez, establecer una serie de grupos que, en nuestra opinión, se encuentran relacionados en mayor o menor medida.

Morfología

Estudiando el conjunto de las especies desde el punto de vista morfológico, se pueden establecer los siguientes grupos (Fig. 1): los "stenobothrus", los "omocestus" y las especies de transición entre ambos. Dentro de los primeros se pueden diferenciar, claramente, dos unidades: la primera, formada por *St. lineatus*, *St. fischeri glaucescens* y *St. nigromaculatus*, se caracteriza, principalmente, por la peculiar venación de las tegminas y la similitud de la armadura genital de los machos; la segunda, formada por las restantes especies, puede separarse, a su vez, en dos: la unidad formada por *St. bolivari* y *St. grammicus*, con los palpos coloreados y más parecidos al grupo anterior, y la unidad formada por *St. festivus* y *St. stigmaticus*, que presentan la armadura genital, el epiprocto de los machos y el tamaño general semejante a los de algunas especies de *Omocestus*.

Dentro de los "omocestus" se pueden diferenciar, en principio, dos grupos. El primero de ellos es bastante homogéneo; está formado por *O. bolivari*, *O. burri*, *O. femoralis*, *O. minutissimus*, *O. rufipes*, *O. haemorrhoidalis*, *O. raymondi* y *O. panteli*, caracterizados por presentar, en general, el mismo tipo de armadura genital en los machos y, en las hembras, las valvas del ovopositor cortas. Aquí *O. raymondi* resulta independiente por la extremada longitud de sus tegminas y sus particulares valvas apicales del pene. El segundo grupo estaría formado por las restantes especies, que presentan las valvas del ovopositor largas *(O. viridulus*, *O. kaestneri*, *O. navasi* y *O. antigai)*. Las dos últimas presentan unos caracteres que las asemejan entre sí y con el grupo precedente. *O. viridulus* se separa, claramente, de ellas y de todas las demás especies de *Omocestus* por su armadura genital, en particular por el epifalo. En cuanto a *O. kaestneri*, resulta semejante a la anterior por los caracteres morfológicos.

Dentro del grupo denominado como de transición, se encuentran *O. uhagoni* y *M. maculatus*. Estas aparecen con un mosaico de caracteres. Así, las hembras muestran las valvas del ovopositor cortas y muy sinuosas, sin casi formar escalón, caracteres éstos propios de las hembras del género *Omocestus* y, en el caso de los machos, los cercos aplanados, con el ápice redondeado, la escotadura del último terguito abdominal engrosada y triangular o cuadrangular, las valvas apicales del pene con una proyección basal de aspecto dentiforme, caracteres éstos que aparecen en los machos del género

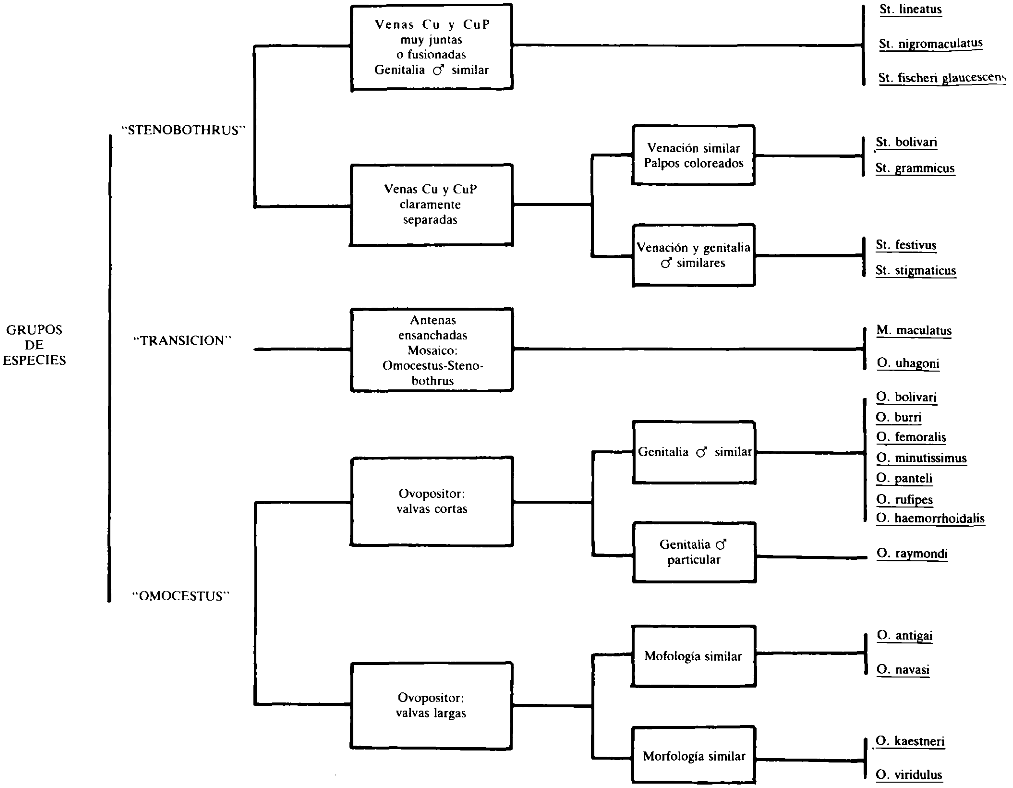

Figura 1. —Grupos de especies de los géneros considerados establecidos por afinidad morfológica.

Stenobothrus. Además, estas dos especies muestran, como carácter propio y exclusivo suyo, las antenas con el extremo ensanchado y aplanado.

Considerando lo antes expuesto y a fin de poner de manifiesto, de modo objetivo, las tendencias de agrupación entre los distintos taxones, se procedió a realizar el análisis estadístico de todos los caracteres morfológicos posibles mediante el análisis de grupos (Cluster analysis). Los resultados de este análisis aparecen representados en el dendrograma de la figura 2. En él, como se presumía, aparecen los mismos grupos de especies que han sido mencionados con anterioridad, así como el mismo nivel de relación entre ellas. Así, es posible distinguir un grupo, homogéneo, que incluye todas las especies del género *Stenobothrus*, y otro grupo, muy numeroso, con el resto de los taxones considerados.

En el grupo de los "stenobothrus", muy tempranamente se diferencian dos grupos, uno formado por *St. fischeri glaucescens, St. lineatus* y *St. nigromaculatus*, de características uniformes y otro, formado por *St. stigmaticus, St. festivus, St. bolivari* y *St. grammicus*, si bien estas dos últimas se separan más tardíamente apareciendo, por tanto, estrechamente relacionadas.

En el otro grupo de taxones, muy numeroso, es de destacar que las especies antes denominadas "de transición" *(O. uhagoni* y *M. maculatus)* se desgajan muy tempranamente del grupo quedando, pues, en posición intermedia entre los "stenobothrus" y los "omocestus". De este último grupo la especie *O. panteli* se aísla muy pronto debido, sin duda, al carácter de sus quillas laterales del pronto, paralelas, caso único dentro de este grupo. En el resto se pueden distinguir tres grupos de especies de

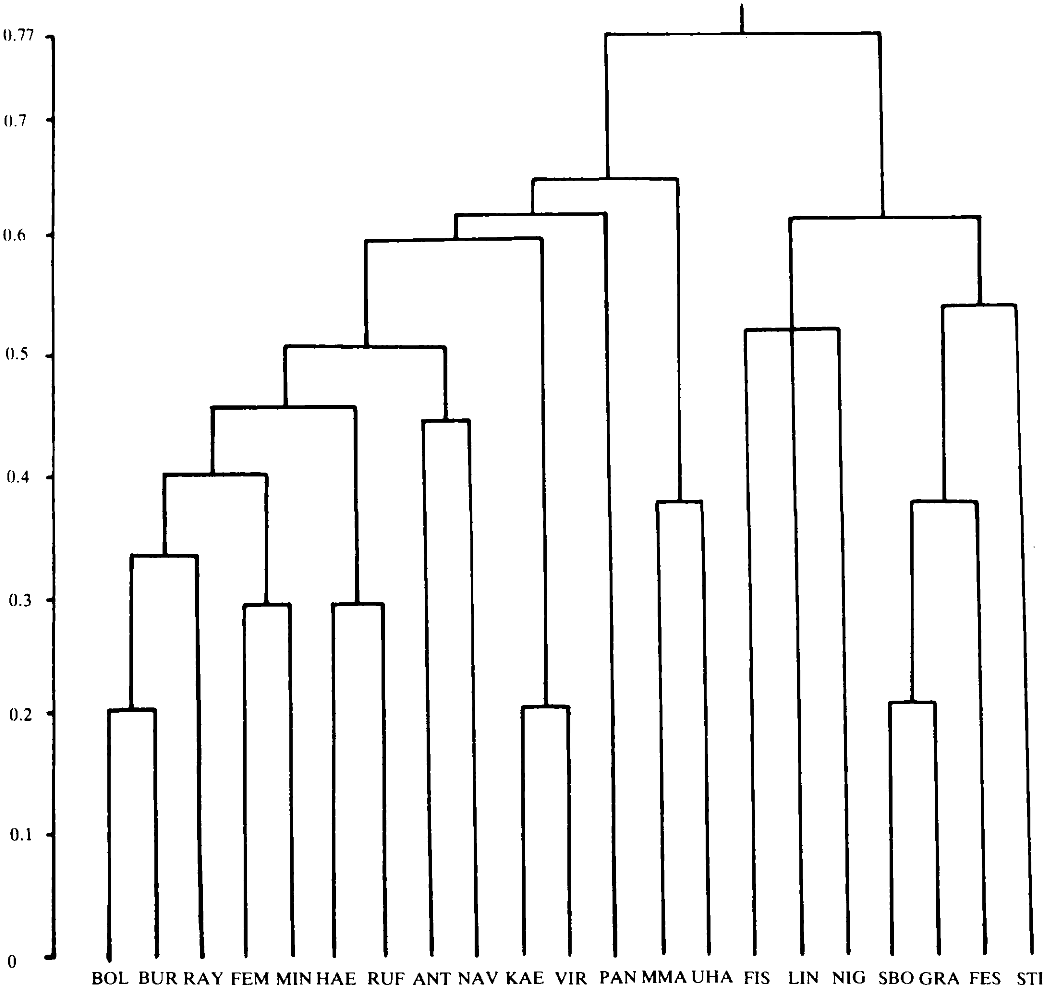

Figura 2.—Dendrograma elaborado a partir de los resultados del análisis de grupos de la matriz 21 × 44.

"omocestus" que se ajustan a los indicados con anterioridad.

Biología

Teniendo en cuenta los diferentes aspectos de la biología de cada especie, se puede observar que, en general, las especies estudiadas presentan una sola generación al año, de mayo a septiembre, con un máximo probable en agosto. La calidad de probable se debe a que los muestreos están sesgados hacia ese mes por múltiples causas. Es destacable el caso de *O. raymondi* quien, aparentemente, presenta un ciclo bivoltino.

Respecto al rango altitudinal, las especies aparecen desde el nivel del mar hasta las más altas cumbres. No obstante, parecen preferir las zonas montanas y montanas-altas, entre los 1.000 y 1.800 m de altitud si bien todo ello depende de la climatología particular de la zona, igual que acontece con la fenología.

En general se puede considerar, al conjunto de las especies, como pratícola, prefiriendo la mayoría los prados húmedos.

Sin embargo, *O. burri*, *O. femoralis* y *O. navasi* muestran unas preferencias bióticas bastante diferentes pues se inclinan hacia las vegetaciones xerófilas, con matorrales almohadillados y espinosos. También hay que separar a *O. raymondi*, que ocupa medios, en general, secos.

Distribución

En lo que respecta a su distribución geográfica en la Península, teniendo en cuenta su carácter preferentemente montano, aparecen especies con una distribución restringida, siendo sólo conocidas de un sistema montañoso. Esto es manifiesto en algunas especies del género *Omocestus (O. navasi, O. femoralis, O. antigai)* y no se da en ninguna del género *Stenobothrus*. Salvando éstas, la mayoría de las especies presentan una distribución amplia que, si bien en algunas no se manifiesta en la Península, sí lo hace en otras zonas europeas *(O. viridulus* y *O. haemorrhoidalis)*.

En cuanto a la distribución general de las especies hay 11 endémicas de la Península Ibérica; 2 ibero-francesas, a las que se considera un origen ibérico (*St. grammicus* y *St. festivus*); 2 mediterráneas occidentales *(St. stigmaticus* y *O. raymondi)*, con un posible origen paleotirrénico, y 6 eurosiberianas, de probable origen angariano (La Greca, 1964).

Cariología

Considerando ahora el estudio cariológico de las distintas especies, en todas las analizadas la constitución cromosómica es de 17 cromosomas en los machos y 18 en las hembras (determinismo sexual XO-XX), excepto en *St. nigromaculatus* cuya dotación cromosómica es de 16 cromosomas en los machos y 17 en las hembras (determinismo sexual neo XY).

De acuerdo con el tamaño de los cromosomas, se pueden distinguir tres grupos: L (largos), M (medianos) y S (pequeños). El cromosoma sexual es de tamaño intermedio entre los autosomas L y M. El bivalente M6 se comporta durante la espermatogénesis de todas las especies analizadas como megamérico, presentando un ciclo heteropicnótico similar al del cromosoma X.

La morfología de los cromosomas es bastante uniforme, puesto que las tres parejas de mayor tamaño (L1-L3) son metacéntricas o submetacéntricas y los demás cromosomas parecen ser, en la mayoría de los casos, telocéntricos.

Los patrones de bandeo C de las especies de los géneros *Omocestus* y *Stenobothrus* estudiadas en el presente trabajo, muestran poca variación, ya que la heterocromatina constitutiva aparece fundamentalmente en las regiones centroméricas (Tabla 2).

Excepcionalmente, algunas especies presentan bloques paracentroméricos de tamaño diferente en cromosomas no homólogos (M6 de *O. panteli* , S8 de *O. burri* y *O. navasi*, X de *St. lineatus)*.

Aparte del caso concreto de *O. burri*, cuyo patrón de bandeo C se caracteriza por la presencia de una banda intersticial en el cromosoma X, la uniformidad de los patrones de bandeo C en las especies analizadas, es casi absoluta con sólo dos excepciones: *O. raymondi*, con bandas teloméricas en los brazos cortos de L2 y L3 muy características, y el patrón de los cromosomas M7 y S8 de *St. festivus*. Curiosamente (Cabrero, 1985) describe un patrón de bandeo C para esa última especie en el que los cromosomas M7 y S8 sólo tienen heterocromatina centromérica. Estas diferencias, quizá se puedan encuadrar en la extremada variabilidad que presenta en muchas ocasiones la heterocromatina C, tanto a nivel inter como intrapoblacional, aunque es obvio que un estudio posterior entre especímenes procedentes de distintas poblaciones naturales, puede ayudar a clarificar esta situación.

Con la técnica de detección de las regiones NORs se ponen de manifiesto las que habían sido activas en la interfase anterior; esto significa que no en todas las células se observa el mismo número de nucleolos, especialmente si el número de NORs es elevado.

Se han considerado cromosomas portadores de NORs a los que organizaban el nucleolo al menos en el 50% de las células.

Tabla 2.—Patrón de bandeo de las especies analizadas de *Omocestus*, *Stenobothrus* y *Myrmeleotettix*.

		R. paracentr. (bloques)				
Especies	2n	pequeños	normales	grandes	R. interst.	R. telos.
O. antigai	17	—	Todos	—	—	—
O. bolivari	17	—	Todos	—	—	X
O. burri	17	—	Todos excepto	S8	X	—
O. femolaris	17	—	Todos	—	—	—
O. haemorroidalis	17	—	Todos	—	L3	—
O. minutissimus	17	—	Todos excepto	X	—	—
O. navasi	17	—	Todos excepto	S8	—	M6
O. panteli	17	—	Todos excepto	M6	—	—
O. raymondi	17	—	Todos	—	X	L2-L3
O. viridulus	17	—	Todos excepto	M6	L3	—
St. bolivari	17	—	—	Todos	—	
St. festivus	17	—	Todos	—	M7-S8	M4, M5, M6, S8
St. fischeri glaucenses	17	—	Todos	—	—	—
St. grammicus	17	—	Todos	—	—	—
St. lineatus	17	—	Todos excepto	X	M6	M7
St. nigromaculatus	16	L1-L3	M, S	—	—	—
St. stigmaticus	17	L1-L3	M, S	—	—	—
M. maculatus	17	—	—	Todos	—	—

Tabla 3.—NORs en las especies analizadas de *Omocestus*, *Stenobothrus* y *Myrmeleotettix*.

		NORs		
	2n	Reg. paracent.	Reg. interst.	Reg. terminal
O. antigai	17	X	—	—
O. bolivari	17	M4, X	—	X
O. burri	17	—	X	—
O. femoralis	17	X, M4, M7	M6	—
O. haemorrhoidalis	17	—	Brazo largo L3	—
O. navasi	17	X	—	—
O. panteli	17	—	Brazo corto L3	—
O. raymondi	17	—	X	—
O. rufipes	17	—	Brazo largo L3	—
O. viridulus	17	—	Brazo largo L3	—
St. bolivari	17	X	—	—
St. festivus	17	X	—	—
St. fischeri glaucescens	17	X	—	—
St. grammicus	17	X	—	—
St. lineatus	17	X	X	—
St. nigromaculatus	16	X	—	—
St. stigmaticus	17	X	—	—
M. maculatus	17	—	Brazo corto L3, X	—

El número y localización de los NORs aparecen en la Tabla 3. Todos los resultados son bastante uniformes en el sentido de que, dichas regiones, se encuentran restringidas, mayoritariamente, a los cromosomas L3 y X.

Hay que hacer notar la relación que existe entre las regiones NORs y la presencia de heterocromatina C en dichas regiones. Rufas *et al.*, 1983 aplicando, simultáneamente, la técnica de bandeo C y de impregnación argéntica, observaron una completa dependencia bandas C-NORs en especies de saltamontes.

En las especies aquí analizadas, esta relación parece evidente y es especialmente patente cuando la región organizadora del nucleolo está localizada, intersticialmente, en el brazo largo del cromosoma L3 de *O. viridulus* y *O. haemorrhoidalis*. El tamaño de estas bandas C relacionadas con NORs puede variar, desde muy finas, como en *St. nigromaculatus*, hasta bastante gruesas, como en *O. haemorrhoidalis* y *O. viridulus*.

En los *Gomphocerinae*, como en otros grupos de saltamontes, puede observarse variabilidad intraespecífica e intraindividual para la actividad de las NORs. Sin embargo, a nivel de localización de las NORs, las mayores diferencias se observan a nivel interespecífico.

En el cromosoma X, los cistrones ribosomales están situados cerca de la región centromérica, excepto en *O. burri*, donde ocupan una posición intersticial. En el cromosoma L3 pueden estar, en el brazo corto, como sucede en *O. panteli*, o en el largo, caso de *O. haemorrhoidalis*, *O. rufipes* y *O. viridulus*. Esta situación es bastante distinta a la encontrada en otros géneros con 17 cromosomas de las misma subfamilia, ya que las especies del género *Chorthippus* tienen, al menos, dos NORs localizados en el brazo corto de los cromosomas L2 y L3 y, los del género *Euchorthippus* tienen, al menos, dos NORs, una de ellas siempre en el brazo corto del cromosoma L3.

Las especies del género *Stenobothrus* aparecen, con respecto a este carácter, como un grupo muy homogéneo mientras que, en el género *Omocestus*, se pueden hacer dos grupos de especies en función de si es el cromosoma X o el L3 el que organiza el nucleolo. El primer grupo se encontraría más próximo al género *Stenobothrus* pues, en él, es también el cromosoma X el organizador nucleolar aunque puede haber otros cromosomas de complemento que manifiesten esta actividad. Las especies que formarían parte de este grupo son: *O. burri*, *O. femoralis*, *O. bolivari*, *O. antigay*, *O. navasi* y *O. raymondi*. El segundo grupo, con entidad propia, es aquel en que el cromosoma L3 es el organizador nucleolar. Este grupo se encuentra formado por: *O. panteli*, *O. rufipes*, *O. viridulus* y *O. haemorrhoidalis*. En cuanto a *M. maculatus*, el organizador nucleolar se encuentra en los cromosomas X y L3.

Manifestaciones acústicas

En cuanto a las manifestaciones acústicas del grupo, ya Ragge, 1986, indica la existencia de dos grupos claros en el seno del género *Omocestus*. Según él, el canto de proclamación puede estar constituido por un único equema, de gran longitud o varios, no tan largos y muy separados, o, por el contrario, por una secuencia de equemas de corta duración y elevada tasa de emisión de sílabas. Estos dos patrones de canto se repiten para el género *Stenobothrus*, como se desprende de los resultados obtenidos por Ragge, 1987. Respecto al género *Myrmeleotettix*, la especie aquí considerada muestra un canto de proclamación compuesto por secuencias de equemas relativamente cortos.

Según esto las especies cuyo canto de proclamación es un único equema, de gran longitud son: *O. viridulus*, *O. rufipes*, *O. haemorrhoidalis*, *O. raymondi*, *O. panteli*, *O. antigai*, *O. bolivari*, *O. uhagoni*, *St. lineatus*, *St. nigromaculatus*, *St. festivus y St. stigmaticus*.

Las especies cuyo canto de proclamación está compuesto por secuencias de equemas de menor longitud que los anteriores son: *O. minutissimus*, *O. burri*, *O. femoralis*, *St. grammicus*, *St. bolivari* y *M. maculatus*.

Los grupos derivados de esta separación son heterogéneos. Por ello, este carácter no parece ser definitorio de grupos jerárquicos. Más bien podría entenderse el diferente tipo de canto en función del medio de vida del animal. De este modo, los habitantes de prados, en sentido amplio, poseerían un canto de proclamación prolongado, que facilitaría la localización del individuo en un medio homogéneo y uniforme. Sin embargo, las especies que habitan matorrales espinosos, muy venteados, o matorrales sin vegetación intermedia o con ella muy escasa o, como *M. maculatus* resulta indiferente respecto a medio, poseen un canto de proclamación caracterizado por llamadas breves, sonoras, rítmicas, a modo de "semáforo biológico".

CONCLUSIONES

Como resumen de lo expuesto hasta aquí, puede decirse que las 21 especies, de *Stenobothrus*, *Omocestus* y *Myrmeleotettix*, presentan una heterogeneidad que hace, prácticamente, imposible situar concretamente todas y cada una de las especies dentro de los géneros considerados. Resumiendo:

Morfológica y cariológicamente se ha observado la existencia de especies que aparecen en situación transicional entre las, puede decirse, "modelos típicos" de *Omocestus* y *Stenobothrus*. Estas especies son *M. maculatus* y *O. uhagoni*. Aunque en el caso de *O. uhagoni* no existen datos sobre su cariología, sus semejanzas morfológicas con *M. maculatus* son tan intensas que no existen motivos para no incluir dicho taxón en este grupo transicional.

Existen especies de enlace *(St. festivus, St. stigmaticus, O. bolivari, O. burri)* que permiten establecer, por medio de las especies de transición, una continuidad entre las que podrían denominarse típicas de uno y otro género.

Las características del canto parecen diferenciar dos grupos de especies, que no se ajustan de un modo exacto a los géneros considerados.

Sin embargo, hay que tener en cuenta la presencia de especies que presentan uno o más caracteres, tan particulares, que les separan de las restantes. Entre ellas se encuentra, muy particularmente, *O. raymondi,* que no sólo discrepa en cuanto a morfología (hay que recordar la forma tan particular de las valvas apicables del pene) sino, también, en cuanto a su fenología y distribución.

Todas estas consideraciones, y otras expuestas ya a lo largo de la revisión, llevan a presuponer que, realmente, no nos encontraríamos ante tres géneros diferentes sino uno solo, *Stenobothrus*, con tres subgéneros, el nominado, *Omocestus*, y *Myrmeleotettix*. Esto se encontraría en concordancia, al menos en parte, con la opinión de Jago, 1971. No obstante nuestro convencimiento del aserto anterior, hemos preferido dejar la revisión estructurada en los tres géneros pues, todavía, quedaría pendiente, para poseer la más absoluta seguridad, la revisión de las restantes especies de estos géneros que no pueblan la península Ibérica, máxime si se considera la opinión de Uvarov, 1928, en el sentido de que, en España, los elementos mediterráneos, en especial del género *Omocestus*, alcanzan grandes altitudes y producen formas locales muy restringidas que forman un grupo muy especial dentro del género o, incluso otro género. Todo ello, a la vista de los resultados obtenidos en este trabajo, podría proporcionar algunas sorpresas.

Por último, a partir de los mismos datos, en algunos aspectos parciales o fragmentarios, nos permitimos hacer algunas consideraciones de carácter general, productos de una mera especulación, sobre las relaciones filogenéticas y el origen de los distintos taxones tratados, teniendo en cuenta, en lo referente al origen, las opiniones de La Greca, 1951, 1977, 1984 y 1985.

En primer lugar, la fauna considerada está caracterizada por un elevado número de endemismos que, en nuestra opinión, tiene un doble origen: por un lado a partir de elementos de origen angariano y, por otro, a partir de elementos paleotirrénicos o paleomediterráneos o autóctonos. El origen dataría de épocas cuaternarias o precuaternarias.

La fauna se completa con especies eurosiberianas (de origen angariano) que han

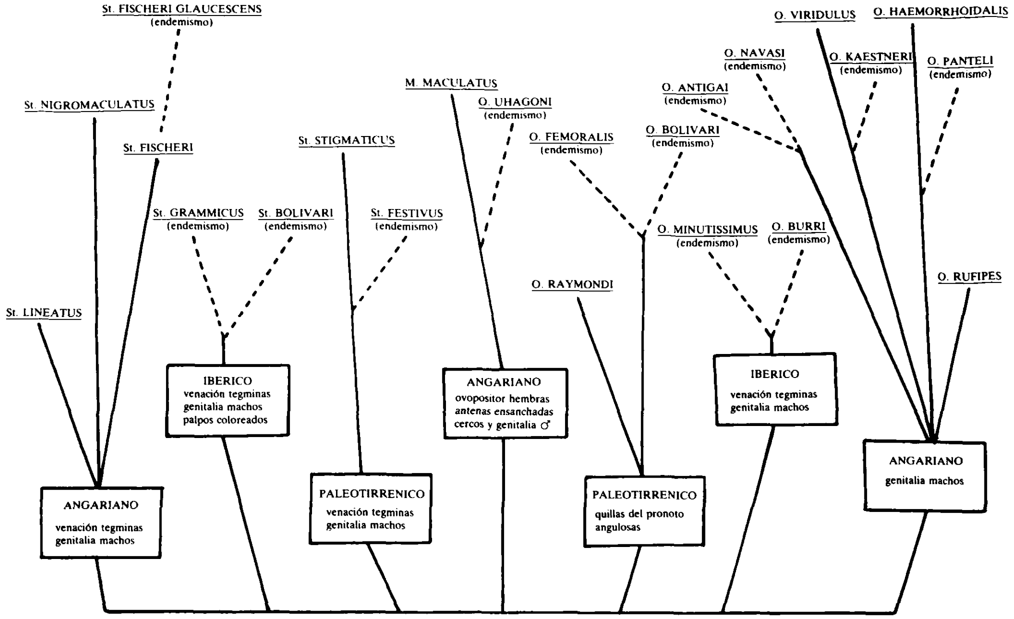

Figura 3.—Diagrama filético que ilustra las relaciones entre los 21 taxones estudiados.

poblado la Península en el Pleistoceno y otro grupo, de especies pertenecientes al viejo grupo paleotirrénico.

A continuación, se señalan los grupos de especies que, en nuestra opinión, presentan un posible parentesco (Fig 3.):

— Un primer grupo, compuesto por formas hermanas, con un origen común antiguo, y por formas derivadas de ellas, dentro del cual se distinguen tres unidades. La primera está formada por las especies de "stenobothrus" de origen angariano *"(St, lineatus, St. nigromaculatus)* y *St. fischeri glaucescens,* esta última endémica de la península Ibérica y derivada de *St. fischeri fischeri.* La segunda está integrada por *M. maculatus,* de origen angariano y *O. uhagoni,* endemismo ibérico derivado de la especie anterior. Esto se encuentra en contraposición a la opinión de La Greca, 1965 en el sentido de que *M. maculatus* ha migrado durante el Cuaternario sin dar lugar a poblaciones diferenciadas. La tercera incluye las especies de "omocestus" de origen angariano *(O. viridulus, O. rufipes* y *O. haemorrhoidalis)* y *O. kaestneri* y *O. panteli,* endemismos ibéricos derivados de *O. viridulus* y *O. haemorrhoidalis,* respectivamente.

Todas las especies incluidas en cada una de las unidades muestran semejanzas en cuanto a morfología, cariología y manifestaciones acústicas, por lo que constituyen bloques homogéneos.

— Un segundo grupo está constituido por formas hermanas de origen común reciente, siendo este origen diverso. Así, originadas posiblemente de formas pobladoras ancestrales de la península Ibérica, se encuentran *St. bolivari* y *St. grammicus* y *O. burri* y *O. minutissimus.* Ambas parejas manifiestan semejanzas muy fuertes y todas son endemismos ibéricos. Por otro lado, a partir de antiguos elementos paleotirrénicos o paleomediterráneos *(O. raymondi* y *St. stigmaticus)* se han originado endemismos ibéricos *(O. bolivari* y *O. femoralis* y *St. festivus* respectivamente). En el caso de *O. bolivari* y *O. femoralis* hay que señalar las semejanzas que muestran entre ellas. Así, son de morfología similar, pueblan medios vegetales coincidentes, son los únicos endemismos de los sistemas montañosos meridionales de la península Ibérica y, sobre todo, presentan la peculiaridad de que su organizador nucleolar se encuentra localizado en varios cromosomas, hecho único en el conjunto de especies estudiadas. Por último, se encuentra una pareja de especies muy similares, la formada por *O. antigai* y *O. navasi*. Ambas son endemismos ibéricos de posible origen angariano habida cuenta de su distribución y localización en la península Ibérica.

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Notes on Japanese Dermaptera including some interesting problems

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ABSTRACT

I would like to present some synonymic notes and the species complexes of Japanese Dermaptera. For years I have carried out Dermapteran integrated taxonomy emphasizing numerical, chemo-, physico-, and cyto-taxonomic information and published taxonomic and biogeographic records. Based on my survey in the *Dermapterorum Catalogus* I-XXI (1970-88), the world fauna to date includes 4 suborders, 6 superfamilies, 11 families, 55 subfamilies, 206 genera, 32 subgenera, 1,880 species, 34 subspecies, 37 varieties, and 9 forms (including 50 fossil species).

In all of Japan may be found 1 suborder, 2 infraorders, 3 superfamilies, 6 families, 9 subfamilies, 15 genera, 4 subgenera, 23 species, 1 subspecies, and 7 forms.

Key words: Dermaptera, Japanese fauna, Species Complex.

Check List of Dermaptera of Japan

Japanese Dermaptera are recorded as follows: Subordo Forficulina Burr (1911), Infraordo Catadermaptera Steinmann (1985), Superfamilia Pygidicranoidea Popham (1965), Pygidicranidae Verhoeff (1902), Challinae Steinmann (1974), *Challia* Burr (1904), *Challia fletcheri* Burr (1904); Superfamilia Anisolabioidea Sakai (1982), Familia Anisolabididae Verhoeff (1902) et Kevan (1980), Subfamilia Anisolabidinae Zacher (1911), Genus *Anisolabis* Fieber (1853), Subgenus *Paralabis* Burr (1915), *Anisolabis (Paralabis) ryukyuensis* (Nishikawa) (1969); *Anisolabis (Anisolabis) maritima* (Bonelli) (1832); Genus *Gonolabis* Burr (1900), *Gonolabis marginalis* (Dohrn) (1864); *Gonolabis distincta* (Nishikawa) (1969); Genus *Euborellia* Burr (1910), *Euborellia (Euborellia) annulata* (Fabricius) (1793); *Euborellia (Euborellia) annulipes* (Lucas) (1784); *Euborellia (Euborellia) plebeja* (Dohrn) (1863); Familia Labiduridae Verhoeff (1902), Subfamilia Nalinae Steinmann (1975), Genus *Nala* Zacher (1910), *Nala lividipes* (Dufour) (1829); Genus *Labidura* Leach (1815), *Labidura riparia japonica* (de Hann) (1842), Infraordo Eudermaptera Verhoeff (1902), Superfamilia Forficuloidea Tillyard (1926), Familia Spongiphoridae Verhoeff (1902) et Kevan (1980), Subfamilia Labiinae Burr (1911), Genus *Labia* Leach (1815), *Labia minor* (Linnaeus) (1758); Genus *Paralabella* Steinmann (1989): *Paralabella curvicauda Motschulsky (1863); Subfamilia Nesogasterinae Verhoeff (1902), Genus Nesogaster* Verhoeff (1902), *Nesogaster lewisi* (Bormans) (1903), [*Nesogaster nigrita* (Shiraki) is a synonymy: syn.nov.]; Familia Chelisochidae Burr (1904), Subfamilia Chelisochinae Burr (1907), Genus *Proreus* Burr (1907), *Proreus simulans* (Stal) (1860); Familia Forficulidae Stephens (1831), Subfamilia Opisthocosmiinae Verhoeff (1902), Genus *Timomenus* Burr (1907), *Timomenus Komarovi* (Semenov) (1901); Genus *Paratimomenus Steinmann (1974), Paratimomenus flavocapitatus* (Shiraki) (1906); Genus *Eparchus* Burr (1907), *Eparchus yezoensis* (Matsumura et Shiraki) (1905); Subfamilia Anechurinae Burr (1907), Genus *Anechura* Scudder (1876), Subgenus *Odontopsalis* Burr (1904), *Anechura (Odontopsalis) japonica* (Bormans) (1880); *Anechura (Odontopsalis) harmandi* forma *harmandi* Burr (1904); *Anechura (Odontopsalis) harmandi* forma *lewisi* (Burr) (1904); *Anechura (Odontopsalis) harmandi* forma *soedaensis* Terata et Sakai (1989): forma nov.; Subfamilia Foriculinae Burr (1907); Genus *Forficula* Linnaeus (1758), *Forficula mikado* Burr (1904); *Forficula tomis* ssp. *scudderi* Bormans (1880) [senddebase: a subspecies of *Forficula tomis* (Kolenati) (1845)]; *Forficula hiromasai* Nishikawa (1970).

The lesser form of *Anisolabis maritima* (Bonelli) is often recognized, but the genitalia are similar to those of the normal form adult male.

Euborellia pallipes (Shiraki) was sunk as a synonym of *Euborellia plebeja* (Dohrn) by Hincks (1947), but the scientific name has continued in use until recently in Japan.

Labidura riparia japonica (de Haan) has recognized color variations, but the White race has not been collected in Japan though it has been in Palm Beach, Florida, USA, and other localities. As pointed out by Hebard (1923), Caussanel and Albouy (1986), and others, variation in coloration, flight organs, forceps, and size have been found in *Labidura riparia* (Pallas) and *Labidura truncata* Kirby (1903).

The pygidial variation of *Nesogasteria lewisi* (Spongiphoridae) intergrades continuously with the pygidium of Nesogaster nigrita (Shiraki) (1905), and the genitalia of both type species are similar.

Nesogaster nigrita (wrong spelling: *nigritus*) is sunk as a synonym of *Nesogaster lewisi* (syn.nov.). I am also changing the trivial name of Spongiphoridae in Japanese from "Chibi-Hasami-Mushi-Ka" to "Kuro-Hashami-Mushi-Ka" because "chibi" means very small, and the species of the family are not commonly smaller.

The Forficulidae, including *Anechura (Anechura) quelparta* Okamoto (1924), in Quelparta Island, Korea, and *Anechura (Anechura) nigrescens* Shiraki (1936), in Manchuria, compose the *Anechura (Odontopsalis) japonica* Complex with *Anechura (Odontopsalis japonica* (Bormans) (1980). Both species may be synonymized with the latter.

The genitalia of *Eparchus yezoensis* (Opisthocosmiinae) were observed for the first time.

The Forficulinae may be composed of the *Forficula tomis* Complex including *Forficula tomis* (Kolenati) (1845), *Forficula scudderi* Bormans 1880, and *Forficula robusta* Semenov (1908). Several authors [Bormans 1900, Kirby (1904), Burr (1914), Shiraki (1928), Bey-Bienko (1934), Hebard (1924), and Giles (1963)] have treated them as synonyms. *Forficula scudderi* and *Forficula robusta* are recognized as synonyms of *Forficula tomis* based on comparison of characters and biogeographical distribution.

Based on the external and genital characters of the Japanese species of Dermaptera, 1 suborder, 2 infraorders, 3 superfamilies, 6 families, 9 subfamilies, 15 genera, 4 subgenera, 23 species, 1 subspecies, and 7 forms are recorded from Japan. *Nesogaster nigrita* (Shiraki) (1905) was synonymized with *Nesogaster lewisi* (Bormans) (1903) *(syn.nov.)*. All the described species are indicated on the check list.

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Anomalías morfológicas en el pronoto de *Steropleurus asturiensis* (Bolívar) (Orthoptera: Tettigoniidae)

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RESUMEN

En este trabajo se describen dos anomalías del pronoto de *Steropleurus asturiensis* (Bolívar, 1898). El estudio se realiza sobre un ejemplar hembra de Asturias [Norte de España] y un macho de Salamanca [España Central]. Se analizan estas anomalías y se contrastan con la descrita para *Ephippiger terrestris terrestris* (Yersin, 1856) por Grandcolas, 1986.

Palabras claves: Tettigoniidae, *Steropleurus asturiensis, teratología.*

ABSTRACT

In this paper two pronotal anomalies of *Steropleurus asturiensis* (Bolivar, 1898) (one in a female collected in Asturias [Northern Spain] and one in a male from Salamanca [Central Spain]) are studied and compared with the normal species and with a similar anomaly that, according to Grandcolas (1986), occurs in *Ephippiger terrestris terrestris (Yersin, 1856).*

Key words: Tettigoniidae, *Steropleurus asturiensis, teratology.*

MATERIAL Y METODOS

Aunque en poblaciones de insectos no es raro encontrar anomalías morfológicas o teratologías, en ortópteros no son demasiado frecuentes (Cappe de Baillon, 1927, 1931; Chopard, 1938; Grandcolas, 1986), y son menos frecuentes aún en especies cuyas poblaciones constan con escasos efectivos. En este trabajo se presenta un caso más raro si cabe, dos anomalías muy similares en individuos de la misma especie, *Steropleurus asturiensis,* una hembra procedente de Asturias y un macho procedente de Salamanca.

Steropleurus asturiensis es una especie típica de Asturias (Cangas de Tineo) que se encuentra también en el Valle de la Ceana (León), Portugal (Mata do Fundao, Ramalhais) (Morales, 1945), Orense (Peinado, 1984), pero no se había observado su presencia en Salamanca.

DESCRIPCION DE LOS EJEMPLARES NORMALES

Los caracteres que poseen los machos y hembras normales de esta especie, según Harz (1969) y Peinado (1984) son:

Aspecto general: tamaño pequeño; color

verde amarillento. Longitud del cuerpo: macho 19-26 mm, hembra 20-22 mm.

Cabeza: pequeña, con el fastigio del vertex triangular comprimido, con surco.

Pronoto (Figs. 1 y 2): amarillento, con una longitud de 6-6.5 mm en el macho y de 6.5-7 mm en la hembra. Metazona rugosa y punteada con quilla media y laterales marcadas. Borde inferior de los lóbulos paranotales sinuado en el centro.

Tégmenes: ocre amarillentos. En la hembra, casi siempre ocultos bajo el pronoto. Venas radiales engrosadas (Nadig, 1980), con el aparato estridulador característico (Ragge, 1955). Campo marginal doblado y no areolado.

Fémures posteriores poco espinosos en su cara inferior, con una longitud de 13-15 mm en el macho y de 15 mm en la hembra. Tibias anteriores inermes.

Abdomen: décimo terguito masculino de borde posterior semicircular. Epiprocto afilado, rematado por un diente agudo. Cercos cilindricos. Apice del diente terminal de los cercos diferenciado y con la misma coloración que el resto del cerco. Diente interno muy puntiagudo e intensamente negro, situado a 1/3 del extremo final del cerco. Longitud del asa interna del titilador rebasando las 2/3 partes del asa interna, que se presenta adelgazada por igual desde su base hasta la zona distal, en la que presenta 8 dientecillos puntiagudos negros.

La hembra tiene la lámina subgenital grande, transversa, rugosa, membranosa, con el borde posterior engrosado y sinuado. Ovipositor corto y curvado ligeramente en toda su longitud, que alcanza los 13 mm.

DESCRIPCION DE LOS EJEMPLARES ANOMALOS

1. Macho recogido en el Puerto de Béjar (Salamanca), U.T.M. 30TTK5968, el dia 4 de Agosto de 1988, por J. Mateos.

Aspecto general: color similar a los individuos normales, un poco más pajizo. Longitud del cuerpo: 26 mm.

Pronoto (Figs. 3. 4 y 7): Longitud desigual en ambos lados, 5.5 mm en el lateral derecho y 6.5 mm en el izquierdo. Sulcus ligeramente adelantado. Metazona de aspecto más abombado y ensanchado que en los ejemplares normales, con puntuación menos patente en el lado derecho, más afectado por la deformación. Las quillas central y laterales menos patentes que en individuos normales. El borde posterior derecho presenta, además, un surco de apariencia cicatricial.

Tégmenes: bastante abultados y de color ocre amarillento, algo más claros que en ejemplares normales. Venación normal, pero más señalada que en otros individuos.

El resto de los caracteres no presenta diferencias con los de otros individuos de su misma especie.

2. Hembra recogida en el Desfiladero de Fresnedo (Asturias). U.T.M. 30TQH3979, el día 31 de Octubre de 1987 por P. Pascual.

Aspecto general: coloración más obscura que en los ejemplares normales. Longitud del cuerpo: 26 mm (montado por insuflación de aire seco calentado) (macho normal de la misma localidad: 26 mm de longitud, hembra de la misma localidad, montada sin insuflar, 22 mm).

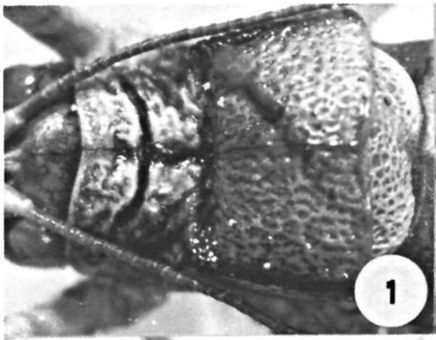
Pronoto (Figs 5. 6 y 8): presenta una longitud de 6.5 mm en el lado derecho y de 6 mm en el lado izquierdo. (macho normal: 6.5 mm: hembra normal: 6 mm). Sulcus ligeramente retrasado. Metazona rugosa y punteada, con la quilla media y la quilla derecha marcadas, mientras la quilla izquierda es apenas patente. El borde inferior del lóbulo paranotal izquierdo es también anómalo, carece de sinuación.

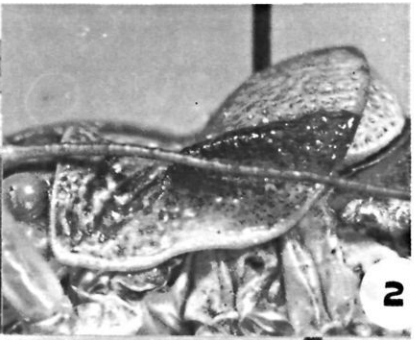
Tégmenes: Más visibles que en los ejemplares normales, debido al acortamiento de la metazona, pero no parecen afectados. Su venación es igual a la de los especímenes normales.

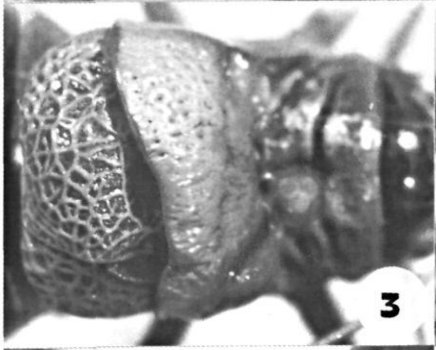
El resto de los caracteres no presenta variaciones con los de otros ejemplares de su misma especie.

CONCLUSIONES

Las anomalías observadas presentan similitud con la observada por Grandcolas (1986) en *Ephippiger terrestris terrestris*







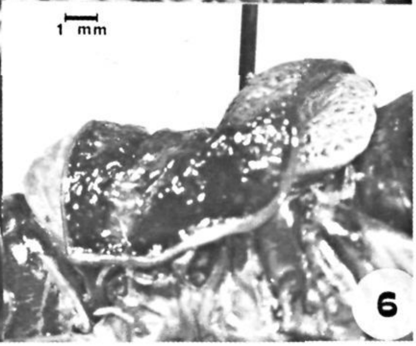


Figura 1.- Aspecto dorsal del pronoto de un ejemplar normal de *Steropleurus asturiensis* (Bolívar).

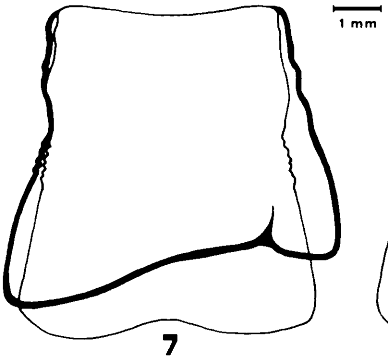
Figura 2.- Aspecto lateral del pronoto de un ejemplar normal de *S. asturiensis*.

Figura 3.- Aspecto dorsal del pronoto del ejemplar macho anormal de *S. asturiensis* procedente del Puerto de Béjar (Salamanca).

Figura 4.- Aspecto lateral del pronoto del ejemplar macho anormal de *S. asturiensis* procedente del Puerto de Béjar (Salamanca).

Figura 5.- Aspecto dorsal del pronoto de un ejemplar hembra anormal de *S. asturiensis* procedente del Desfiladero del Fresnedo (Asturias).

Figura 6.- Aspecto lateral del pronoto del ejemplar hembra anormal de *S. asturiensis* procedente del Desfiladero del Fresnedo (Asturias).



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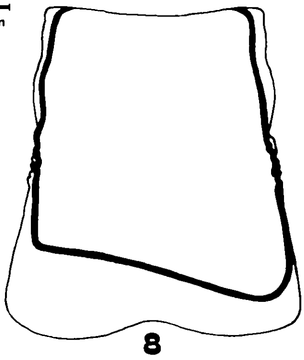

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Figura 7.- Comparación del perfil del pronoto del ejemplar macho anomalo de *S. asturiensis* procedente del Puerto de Béjar (Salamanca) (línea gruesa), con el perfil normal de la especie (línea fina).

Figura 8.- Comparación del perfil del pronoto del ejemplar hembra anómalo de *S. asturiensis* procedente del Desfiladero del Fresnedo (Asturias) (línea gruesa), con el perfil normal de la especie (línea fina).

(Yersin), si bien en los ejemplares de *Steropleurus asturiensis* (Bolívar) no parece haber grandes diferencias en la venación alar.

Sobre las causas de estas anomalías solo podemos aventurar hipótesis de escaso valor. A la vista de los ejemplares. se puede conjeturar que la causa probable es traumática, suposición reforzada por la propia estructura en voladizo de la metazona y por las señales cicatriciales que presenta el borde de la metazona del macho de Salamanca, aunque juega en contra de la hipotesis la extensión de las lesiones al borde paranotal en el ejemplar femenino de Asturias. En cualquier caso, un trauma no queda excluido, ya que lesiones serias en el borde posterior de la metazona en una ninfa pueden provocar esas malformaciones en el estadío siguiente. En todo caso, se precisarían muchos más casos para llegar a conclusiones fiables.

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Estudio del comportamiento y desarrollo postembrionario de *Acinipe hesperica hesperica* Rambur, 1838, en cautividad (Orthoptera: Pamphagidae)

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RESUMEN

En este trabajo se recogen los resultados obtenidos en una experiencia de cría y reproducción en cautividad de la especie *Acinipe hesperica hesperica* Rambur, 1838. Las observaciones fueron llevadas a cabo durante los años 1984 a 1987.

Se describen los caracteres morfológicos de la ooteca, el huevo y los estadios postembrionarios, prestando especial atención al estudio del desarrollo de los rudimentos alares, primero que se efectúa para una especie microptera. Se incluye una tabla para la diferenciación de los dos sexos en cada uno de los estadios basada en la genitalia externa y sus correspondientes figuras.

Esta especie tiene siete estadios ninfales (después de la larva vermiforme).

Se realiza un estudio morfométrico de distintas partes del cuerpo a lo largo del desarrollo y del adulto reflejado en varios gráficos.

Se aportan datos sobre la duración de los estadios ninfales así como sobre distintos aspectos del comportamiento del adulto y su longevidad.

Palabras clave: *Acinipe hesperica,* comportamiento y desarrollo postembrionario, Orthoptera: Pamphaginae.

ABSTRACT

This research presents the results obtained through rearing and reproduction in captivity of *Acinipe hesperica hesperica* Rambur, 1838. The observations were made during the 1984 years through 1987.

The morphological characters of the egg-pod or ootheca, egg and postembryonic stages are described, paying especial attention to the development of wing rudiments, which is the first study carried out for a micropterous species. A table to determine both sexes of each stage based on external genitalia with corresponding figures is included.

This species has seven nymphal instars (after the vermiform larva).

A morphometric study was carried out of the various parts of the body during nymphal development and in the adult, and the results are shown in diagrams.

Data are also given on the duration of stages as well as various aspects of the the behaviour of adult and its longevity.

Key words: *Acinipe hesperica,* behaviour and postembrianic development, Orthoptera: Pamphaginae.

INTRODUCCION

El estudio de la familia *Pamphagidae* resulta de gran interés debido al carácter primitivo del grupo y la escasez de datos existentes respecto a su biología, ciclos y comportamiento. Cabría citar los trabajos de Korsakoff (1941), Dirsh (1968) y Aiouaz (1975) en relación con el ciclo biológico y en lo relativo a distintos aspectos del comportamiento, los de Dumortier (1965), Johnsen (1972) y García y Presa (1985); no refiriéndose ninguno de ellos al género *Acinipe* Rambur.

Los objetivos de este trabajo son el estudio y descripción del desarrollo postembrionario y del comportamiento de *Acinipe hesperica hesperica* Rambur en cautividad.

MATERIAL Y METODOS

El estudio se ha realizado desde abril de 1984 hasta octubre de 1987.

El material inicial estaba compuesto por: 2 machos y 1 hembra en el VI estadio, capturados por C. Orozco el 7 de abril de 1984 en Torremolinos, Málaga, sobre *Erigeron canadensis* L. en un pinar; 2 machos y 4 hembras adultos, capturados por J. L. Santos el 11 de septiembre de 1984 también en Torremolinos en un pinar.

Los ejemplares fueron mantenidos en cautividad en una jaula de cría de dimensiones 36 × 40 × 35 cm de metacrilato transparente, con todas las paredes con pequeños agujeros de 2 mm de diámetro. Una de las paredes tiene una abertura redonda de 13 cm de diámetro que se cierra con tela de nylon por la que se realizaron todas las manipulaciones necesarias.

En principio se colocó una bombilla de 40 W para proporcionar calor y luz, pero más adelante se comprobó que la luz y el calor ambiente del laboratorio eran suficientes, por lo que se retiró la bombilla. La temperatura diurna osciló entre los 22-24 grados C en invierno y los 28-30 en verano, la nocturna lo hizo entre 12-15 en invierno y 20-22 en verano.

En el interior de la jaula se colocaron dos recipientes con tierra, donde se colocaban las plantas nutricias.

En un primer momento las ninfas fueron alimentadas con lechuga; posteriormente se probaron otros tipos de alimento a los que nos referiremos en el apartado de alimentación.

Para la puesta se dispuso otro recipiente de 13 × 8 × 7 cm con tierra, que se mantuvo en todo momento libre de plantas. Estos recipientes eran convenientemente regados cada dos días, para mantener la humedad ambiental.

Para el estudio biométrico de los distintos estadios se realizaron las siguientes medidas en milímetros: longitud del cuerpo, pronoto y fémur posterior, según Harz (1969); longitud de la antena: desde la base al ápice del último artejo; anchura del fémur posterior, tegmina y ojo en su parte más ancha.

Todas las medidas están realizadas a los 3-5 primeros días después de cada muda y habitualmente sobre individuos vivos, excepto cuando esto no ha sido posible.

COMPORTAMIENTO:

Locomoción

Los individuos, aún siendo ninfas, se desplazan con movimientos muy lentos por el suelo, paredes e incluso techo de la jaula. En el caso de las hembras adultas es todavía más lento, ya que para desplazarse llevan su enorme abdomen (casi 5 cm de longitud) arrastrándolo por el suelo, ayudándose principalmente de las patas posteriores que son muy fuertes.

Casi todo el tiempo lo pasan suspendidos de ramas o sobre el suelo; cuando existe una fuente de calor (bombillas o rayos de sol) se aproximan a ella y se disponen en una postura muy "relajada", completamente inmóviles, con las antenas hacia delante y abajo.

Alimentación

Se ha podido observar que es una especie más bien polífaga. De las plantas probadas: *Diplotaxus virgata* (Cav.) DC, *Lipedium draba* (L.) Desv., *Malus communis* Lam., *Medicago sativa* L., *Plantago major* L., *P. lanceolata* L., *Rosmarinus officinalis* L., *Taraxacum* gr. *officinale, Trifolium repens* L. y *Ulmus pumilla* L. las mejor aceptadas fueron el romero *(Rosmarinus officinalis)*, olmo *(Ulmus pumilla)*, llantén *(Plantago major* y *P. lanceolata)* y de estas dos últimas tanto las hojas como las semillas.

En los primeros estadios comían preferentemente hojas de olmo. Se les suministró también pan, salvado y diferentes frutas: manzana, melocotón, higos, etc., que asimismo comían con agrado.

Si bien en los recipientes crecían diversas gramíneas no se observó que las comieran, lo que concuerda con los datos de Gangwere y Morales (1973), aunque es posible que no lo hicieran al no tenerlas como único alimento, ya que en experiencias anteriores, tanto nuestras como de otros autores (Johnsen, 1972; García y Presa, 1985) no las rechazaron. Tampoco se han observado casos de canibalismo.

Eliminación de heces

El comportamiento observado coincide con el descrito por Johnsen (1972) y García y Presa (1985) para otras especies de *Pamphagidae* como *Glauia durieui* (Bolívar, 1878) y *Eumigus cucullatus* (Bolívar, 1878). Curvan el abdomen hacia arriba y a la vez que expulsan el excremento lo golpean con la pata posterior con lo cual éste sale lanzado a gran velocidad produciendo un fuerte ruido contra la jaula; en varias ocasiones, al dejar la puerta abierta, la distancia alcanzada era de 100-120 cm.

Cortejo y cópula

No se ha observado ningún comportamiento que pueda ser considerado como cortejo por parte de los machos, ni de reclamo por parte de las hembras. Durante la cópula la hembra tiene sus antenas dirigidas hacia arriba y divergentes, dando la impresión de estar en alerta. Las del macho, también divergentes, se dirigen sin embargo hacia abajo, casi rozando el pronoto de la hembra, con un aspecto mucho más relajado. El macho se sujeta a la hembra con sus patas anteriores agarrando las anteriores de ésta; con las intermedias sobre la mitad de los fémures posteriores; al menos una pata posterior de los machos, plegada, reposa sobre el abdomen de la hembra. El cuerpo del macho se encuentra desplazado a un lado y hacia abajo del abdomen de la hembra, doblándose hacia arriba en su extremo para contactar con el orificio genital de la hembra. En esta posición la hembra sigue desplazándose con relativa facilidad, salta, se cuelga de las ramas y se alimenta, lo que, sin embargo, no hace el macho (Fig. 2).

La duración de la cópula es muy variable, desde 4 horas a un máximo de 30. En el caso de haber más de un macho para una sola hembra se observó que éstos se turnaban con una periodicidad casi constante. Es frecuente ver a las hembras soportando a uno o varios machos sobre su dorso, situación que puede durar varias horas e incluso días (Fig. 1).

Las cópulas empiezan a producirse a partir del 2.° o 3^er^ día después de que la hembra haya mudado a adulto, es decir desde últimos de junio, en adelante, hasta últimos de diciembre, siendo más abundantes en julio. En los individuos que pasan el invierno en estado adulto las cópulas en su 2.° año empiezan antes, reanudándose a primeros de marzo hasta un poco antes de morir, hecho que se produce, por regla general, desde mediados de junio a últimos de agosto e incluso hasta octubre.

Puesta

En este apartado incluimos tres comportamientos diferentes: las «pruebas», la puesta y las "puestas ficticias".

En el primero de ellos, la hembra, con

su abdomen, intenta hacer orificios en la tierra, pero pasado un breve período de tiempo abandona su labor; se han observado en algunas hembras de 15 a 20 "pruebas". Este comportamiento no es nuevo y es conocido tanto en la naturaleza como en cautividad, donde se han observado hasta 25 "pruebas" antes de realizar la puesta (Uvarov, 1977).

En la puesta la hembra va introduciendo poco a poco su abdomen en la tierra, enterrándolo hasta la base de los fémures posteriores. No parece realizar esfuerzos bruscos, a excepción de unos movimientos laterales. A las 2-3 horas de permanecer en esta posición, empieza a sacar lentamente el abdomen haciendo contracciones verticales; a los 15 minutos ya se ven los primeros terguitos abdominales y a los 30 ya ha sacado totalmente el abdomen, colocando su extremo hacia arriba, evitando tocar el suelo.

Apoyada en todas las patas, se dispone a tapar el agujero de la puesta; para ello utiliza los tarsos del tercer par, los cuales alternativamente y a modo de palas empujan la tierra hasta formar un pequeño montículo sobre el agujero donde se hizo la puesta; todo ello dura aproximadamente 15 minutos. Resulta interesante señalar que este mismo proceso de "enterramiento" se observó también en una hembra que realizó la puesta en el suelo sin tierra de la jaula.

Las "puestas ficticias" se diferencian de las anteriores en su menor duración y sobre todo en que nunca finalizan con el «ritual» de tapar con tierra el agujero hecho.

El inicio de las puestas tiene lugar aproximadamente un mes después de la cópula, en este caso a últimos de julio de 1984 hasta primeros de octubre, aunque se observaron puestas ficticias hasta mediados de noviembre. En 1985 —2.° año de vida de los individuos— se reanudaron a partir de finales de marzo hasta últimos de julio o mediados de agosto. El número de ootecas que pone una hembra varía entre 4 y 5 por temporada.

Por lo general, las hembras realizan la puesta sin ser molestadas por los machos, en caso contrario tratan de liberarse de ellos, pateándolos con las extremidades posteriores.

Otros aspectos del comportamiento

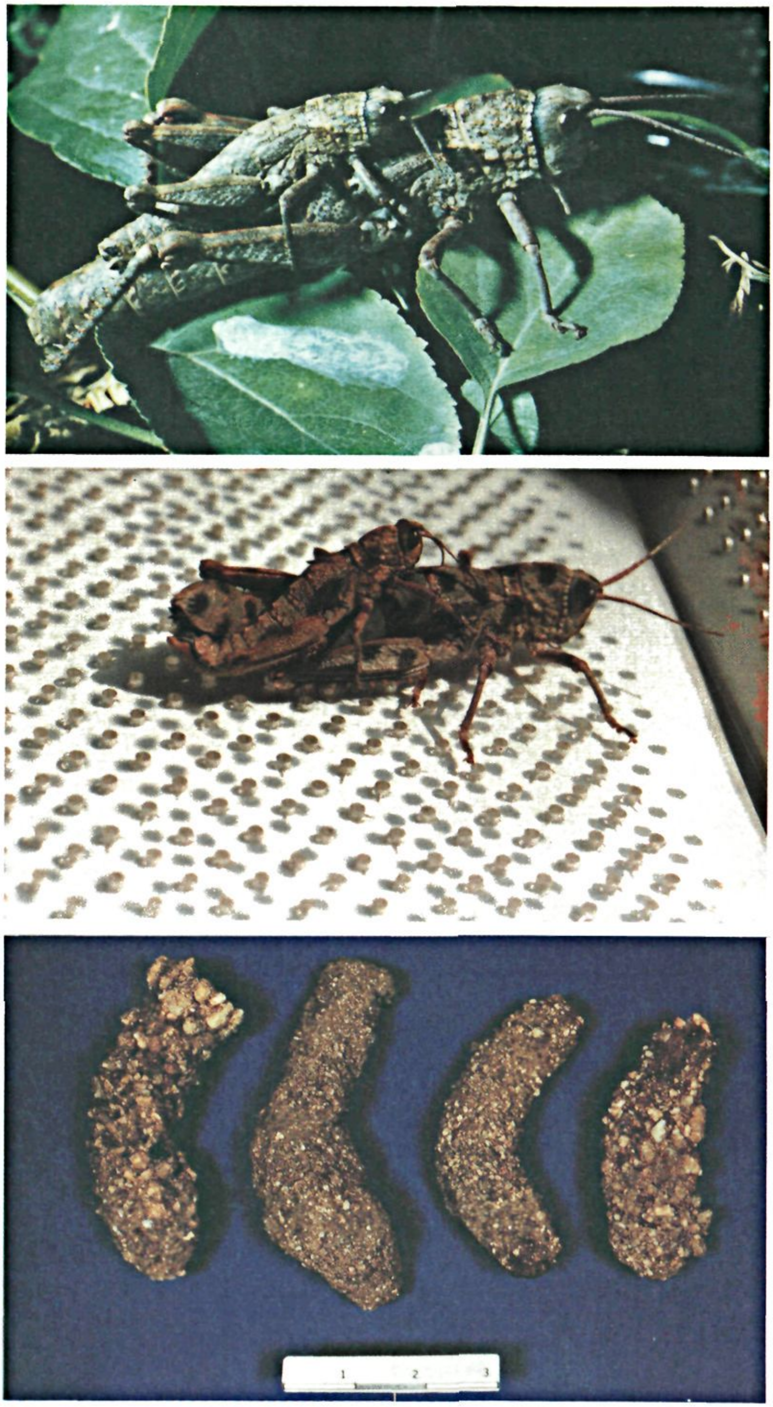
A diferencia de otras especies (García y Presa, 1985), no se han observado el comportamiento de "defensa-ofensa" ni canibalismo a pesar de que en las jaulas han convivido con otros insectos —ortópteros, dípteros, hemípteros—. Tampoco se ha observado la producción de manifestaciones acústicas.

OOTECA Y HUEVO

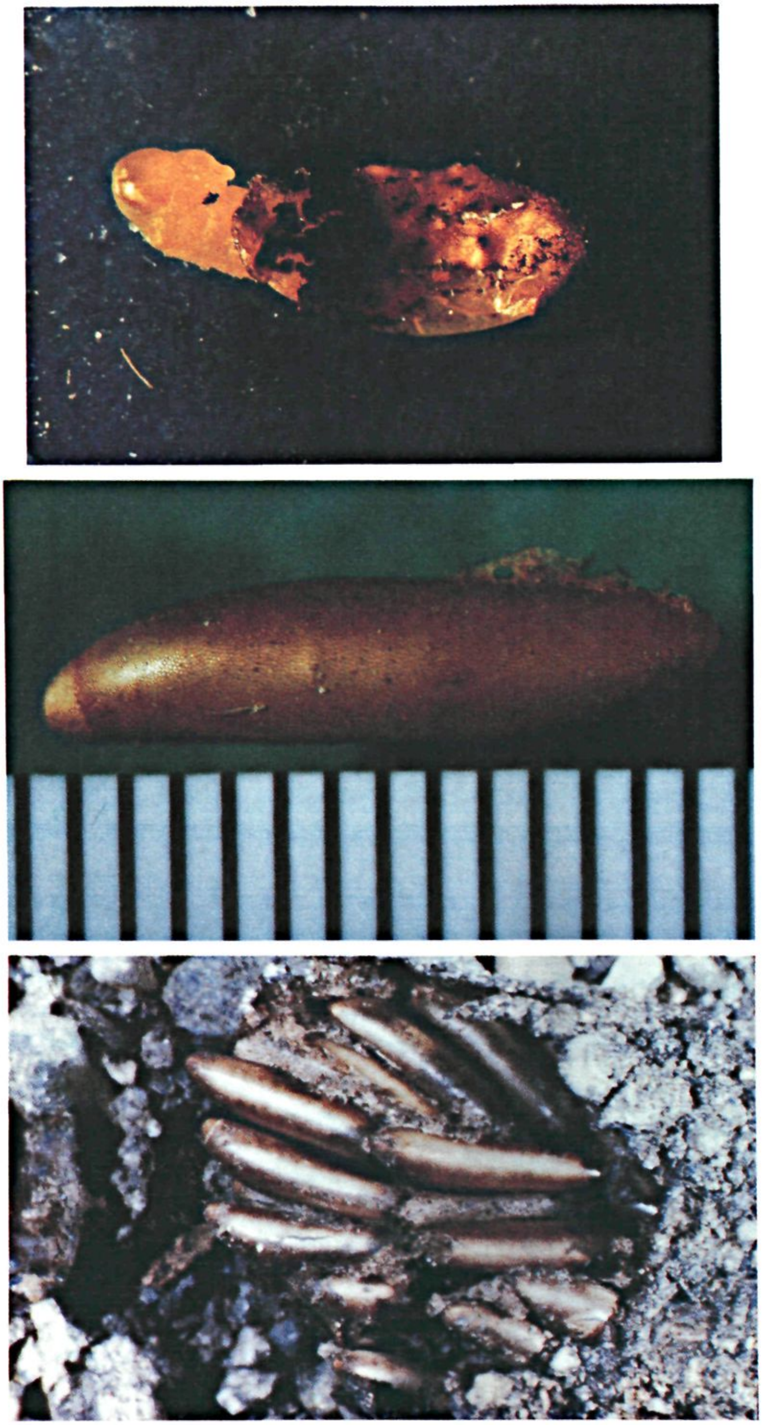
La ooteca tiene la forma de un tubo, claramente curvado cerca del medio. El extremo superior es casi plano, un poco hundido en el centro y el inferior está suavemente redondeado. El primero sirve de tapadera y es por donde emergen las larvas vermiformes. Está formado por una capa esponjosa que, recién fabricada por la hembra, es de color caramelo para más tarde oscurecerse, tornándose pardo oscuro. Esta capa ocupa el tercio superior de la ooteca, así como las paredes; sobre toda su superficie externa se adhieren partículas del sustrato donde se ha realizado la puesta. En sus dos tercios inferiores se disponen los huevos, orientados en una misma dirección, con una cierta inclinación y casi paralelos entre sí. Las dimensiones de la ooteca son: longitud 35-45 mm; anchura máxima 13-15 mm, anchura mínima 10 mm (Figs. 3 y 4).

Los huevos recién puestos son amarillos o de color caramelo, pero en ambos casos, con el paso del tiempo, se van oscureciendo hasta llegar a ser pardo oscuro. Su forma es subcilíndrica, ligeramente curvados en el medio y con los extremos más o menos agudos. El corión presenta una esculturación en celdas, en su mayoría hexagonales, si bien aparecen algunas penta y heptagonales. Las esculturas cubren todo el huevo, haciéndose más patentes y gruesas hacia el extremo posterior y más suaves en el anterior (Fig. 5).

En cada ooteca el número de huevos varía entre 100 y 143, con unas dimensiones de: 7,5-8 mm de longitud y una anchura de 1,7 mm.



Figuras 1-3.—*Acinipe hesperica* Rambur. 1, Macho sobre el dorso de la hembra, posición muy habitual. 2, Cópula. 3, Ootecas.



Figuras 4-6.—*A. hesperica*. 4, Huevos y parte de la ooteca. 5, Un huevo, 6, Larva vermiforme, saliendo del huevo (vista lateral).

Figuras 7-9.—*A. hesperica.* 7, Mudando al I estadio (vista ventral). 8, Final de la muda al I estadio (vista dorsal). 9, Ninfa, en el I estadio.

DESARROLLO POSTEMBRIONARIO

Eclosión

Esta se produce aproximadamente un mes después de haberse realizado la puesta, desde primeros de julio hasta mediados de septiembre y en cada ocasión los jóvenes saltamontes eclosionan durante dos días sucesivos. Además, según se ha podido observar, la proporción de hembras y machos fue parecida: en la 1.ª eclosión de 51 individuos, 26 eran hembras y 25 machos, en la 2.ª, de 29 nacidos, 12 eran hembras y 9 machos, diferencia ésta que en tan bajo número no consideramos significativa.

Larva vermiforme

El corión de un huevo preparado para la eclosión se raja y la larva sólo tiene que romper la delgada cutícula amarilla. La eclosión comienza con unos movimientos activos y serpenteantes de la larva. La fina membrana comienza a inflarse entre la cabeza y el pronoto, formando un par de ampollas cervicales, las pulsaciones de las cuales fuerzan la presión sobre la cutícula y causan su ruptura transversal.

La larva que acaba de emerger del huevo se diferencia muy poco del embrión completamente desarrollado que está todavía dentro del huevo. La cabeza está dirigida hacia abajo, sus antenas y patas están colocadas muy cerca, casi pegando al cuerpo y el insecto entero está envuelto en una membrana transparente y muy fina, a modo de saco pero con unas "fundas" separadas para las patas, la parte distal de las antenas, así como los cercos (Fig. 6).

Muda intermedia

La muda de la larva vermiforme se inicia cuando ésta está todavía dentro del huevo y la pérdida de la cutícula provisional comienza tan pronto como la cabeza de la larva ha salido a la superficie del suelo. Mientras la larva yace en el suelo, la cutícula estalla bruscamente a causa de las fuertes pulsaciones de las empollas cervicales y los movimientos serpenteantes del cuerpo, asistidos también por las patas ya liberadas, ayudan a la larva a salir de su primera piel (Fig. 7).

Desde el momento que rompe la cutícula hasta que se desprende de ella sólo pasan 15 a 20 minutos. Los movimientos que realiza el joven saltamontes, recién mudado, son rápidos y dirigidos hacia delante, así como para los lados, hasta que se libra de la exuvia que queda como una pelotita blanca muy cerca del extremo del abdomen. Ya desde ahora el aspecto general del insecto es muy parecido al del adulto (Fig. 8).

Mudas de los restantes estadios

Las mudas del I al VII incluido, son parecidas a la intermedia, excepto en que la posición del insecto es vertical, con la cabeza siempre hacia abajo y las antenas colocadas ventralmente. Previamente el saltamontes deja de alimentarse, perdiendo además el color, ya que la cutícula empieza a separarse del cuerpo estallando por la quilla media del pronoto en dirección hacia la cabeza y el abdomen. Poco a poco va saliendo la cabeza, el pronoto, las patas, siendo las posteriores las últimas, aunque todavía queda el extremo del abdomen. Esto último lo logra cambiando de posición: es decir, gira la cabeza hacia arriba, balancea el abdomen y al fin éste se libera de toda la cutícula vieja, que queda prendida en una rama.

La duración de las mudas van aumentando desde 15 a 20 min hasta 1 h 15 min en la muda final. La diferencia también está en que en las primeras mudas el insecto se recupera en seguida, mientras que en las últimas, en especial en la muda final, tarda más tiempo en emprender sus desplazamientos y en alimentarse.

Seguidamente pasamos a la descripción de los siete estadios ninfales y del adulto, omitiendo las medidas de las distintas partes del cuerpo, ya que al estar reflejadas en la tabla 1 se aprecian mejor las diferencias

Tabla 1.—Datos biométricos de los estadios ninfales y de los adultos. Medidas extremas y (*) valores medios.

Estadio	I		II		III		IV		V		VI		VII		ADULTO	
Sexo	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Longitud cuerpo	11,0-11,8 * 11,4	10,2-10,3 * 10,26	12,0-13,9 * 12,82	12,3-14,3 * 13,3	15,3-18,0 * 16,4	14,4-16 * 15,4	19,0-24,0 * 21,82	17,2-17,8 * 17,5	26,5-32 * 29,2	21 * 21	32,5-36,5 * 34,5	23,5-31,0 * 27,5	44-50 * 48	31,5-39 * 34,9	60-65 * 63,3	40-46 * 43,4
Longitud pronoto	1,0-1,2 * 1,1	1,0-1,2 * 1,1	1,6-1,7 * 1,66	1,3-1,8 * 1,53	2,3-2,5 * 2,38	2,1-2,4 * 2,25	2,7-3,0 * 2,82	2,5-2,7 * 2,6	4,0-4,6 * 4,4	3,5-3,7 * 3,63	6,5-6,7 * 6,6	5,0-5,5 * 5,15	8,4-9,8 * 9,2	6,7-7,3 * 6,88	11,3-12,0 * 11,7	7,5-8,1 * 7,8
Fémur posterior long./anch.	3,5:0,9- 3,7:1,0 * 3,6:0,95	3,5:0,9- 3,7:1,0 * 3,56:0,95	4,5:1,2- 4,8:1,4 * 4,6:1,3	4,3:1,1- 4,7:1,4 * 4,46:1,25	5,8:1,4- 6,2:1,7 * 6,05:1,6	5,5:1,3- 5,9:1,5 * 5,67:1,42	6,8:1,9- 7,3:2,0 * 7,0:1,95	6,7:1,8- 7,0:1,9 * 6,85:1,85	8,3:2,3- 10:2,6 * 9,3:2,4	8,0:2,1- 8,2:2,3 * 8,06:2,2	12,3:3,1- 12,6:3,4 * 12,4:3,25	10,5:2,7- 11,0:3,0 * 10,7:2,8	16,5:4,0- 19,0:4,8 * 17,6:4,4	13,0:3,4- 14:3,9 * 13,5:3,6	23:5,2- 24,5:5,5 * 23,8:5,3	17,0:4,2- 19,0:4,8 * 17,9:4,4
Longitud antenas	1,9-2,3 * 2,05	2,0-2,3 * 2,1	2,5-2,9 * 2,78	2,4-2,8 * 2,63	3,4-3,8 * 3,55	3,3-3,6 * 3,42	3,6-4,8 * 4,15	3,9-4,2 * 4,05	5,5-6,3 * 6,0	5,0-5,2 * 5,13	8-8,6 * 8,3	6,5-6,8 * 6,65	11,5-14,5 * 12,2	9 * 9	17 * 17	11-14 * 12,7
Ojo long./anch.	1,2:0,5- 1,3:0,7 * 1,25:0,6	1,1:0,5- 1,3:0,6 * 1,2:0,6	1,4:0,6- 1,6:0,7 * 1,48:0,6	1,4:0,5- 1,5:0,7 * 1,43:0,63	1,7:0,9- 1,8:1,0 * 1,74:0,95	1,6:0,8- 1,7:0,9 * 1,63:0,83	1,6:1,0- 1,9:1,2 * 1,77:1,03	1,7:0,9- 1,8:1,0 * 1,75:0,95	1,9-1,3- 2,2:1,6 * 2,0:1,4	1,9-1,2- 2,0:1,3 * 1,9:1,26	2,4:1,8- 2,5:1,8 * 2,45:1,8	2,2:1,5- 2,3:1,6 * 2,23:1,53	2,8:2,1- 3,0:2,3 * 2,9:2,2	2,4:1,8- 2,8:2,2 * 2,65:1,95	3,3:2,6- 3,5:2,7 * 3,43:2,65	2,7:2,2- 3,0:2,5 * 2,8:2,3

en cada estadio, así como entre ambos sexos.

I estadio

Color general gris pálido, con puntos oscuros diseminados por todo el cuerpo, especialmente en la quilla dorsal de los fémures posteriores, así como en los dientecillos de la quilla media abdominal. Cara interna de los fémures posteriores con la mitad basal oscurecida; tibias del mismo par con una pilosidad blanquecina muy densa y con 10 espinas externas y 10 internas, incluidas las apicales; número que se conserva durante todo el desarrollo ninfal, así como en el adulto (Fig. 9).

Ojos saltones, fuertemente ovalados, con una única banda vertical, relativamente ancha, situada en la parte anterior del ojo y alcanzando algo menos del tercio inferior; el resto con muchas y pequeñas manchas pardas irregulares, distribuidas más bien transversalmente.

Antenas muy ensiformes y aplastadas, compuestas de 8 artejos, bien divididos en 3 partes: 1.ª, escapo y pedicelo; 2.ª, parte basal del flagelo, con 5 artejos muy ensiformes y 3.ª, parte apical del flagelo, con un solo artejo alargado (Fig. 10).

Pronoto con el borde posterior ligeramente escotado. Rudimentos alares del meso y metatorax apenas insinuados, presentando los bordes inferiores redondeados (Fig. 11, I).

La longitud del cuerpo de los saltamontes inmediatamente después de la muda al I estadio es de 8 a 9 mm, casi igual o un poco más que la del huevo. En la tabla 1 es mayor, ya que las medidas están tomadas a los 3 días de mudar.

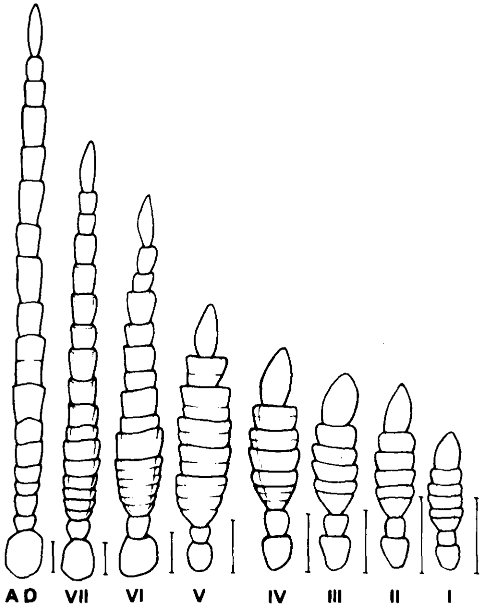


Figura 10.—Crecimiento de la antena de la hembra en los siete estadios ninfales y en el adulto. La línea representa 1 mm.

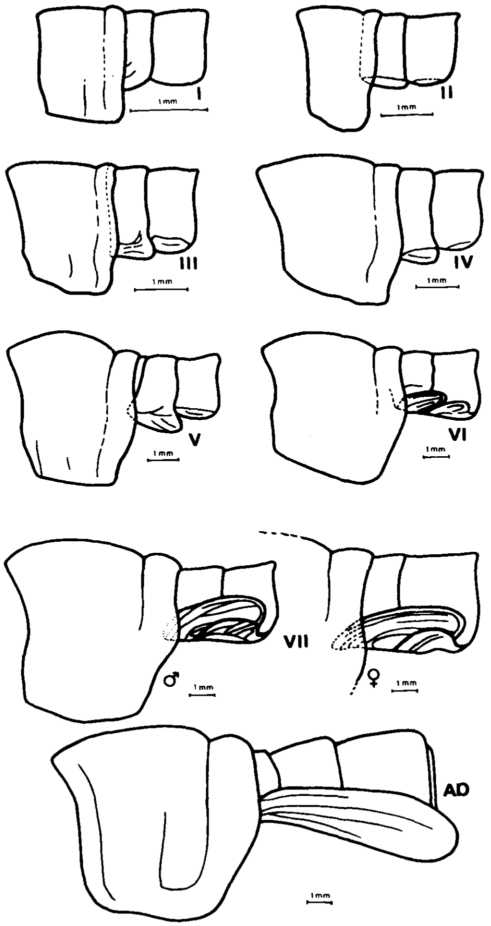


Figura 11.—Desarrollo del pronoto y los rudimentos alares del macho en los siete estadios ninfales y en el adulto, así como en el VII de la hembra (vista lateral).

II estadio

Color general parecido al I estadio.

Ojos con 2 bandas que ocupan la parte anterior del ojo; la 2.ª, completa, alcanzando el borde superior; la 1.ª, más posterior y sólo perceptible en el tercio inferior, longitud que mantendrá durante todo el desarrollo; el resto también con pequeñas manchas transversales.

Las antenas siguen fuertemente ensiformes y parecidas a las del I estadio, aunque un poco más largas (Fig. 10).

Pronoto un poco más convexo y los rudimentos alares muy débiles: lóbulo mesotorácico ligeramente dirigido hacia abajo y hacia atrás y el metatorácico sigue redondeado (Fig. 11, II).

III estadio

Color parecido a los estadios anteriores, pero ya un poco más oscuro, con tonos pardos.

Los ojos tienen ya 3 bandas que ocupan aproximadamente un tercio de la anchura total.

Antenas más largas y un poco menos ensiformes con idéntica distribución de los artejos: 2-5-1; en los de la parte basal del flagelo se observan ya líneas de su futura división (Fig. 10).

Paranotos con el borde posterior más convexo en el medio. Límites de los rudimentos alares mejor visibles: el lóbulo mesotorácico dirigido hacia atrás y redondeado y el metatorácico mejor delimitado por un engrosamiento, con los bordes ventral y posterior redondeados. Ambos lóbulos presentan ya abultamientos longitudinales que más tarde serán las venas (Fig. 11, III).

Tibias posteriores, en su cara interna color entre crema y gris pálido, sin apreciarse todavía tonos rojizos.

IV estadio

Color general más oscuro combinando el gris con el pardo; los puntos diseminados por todo el cuerpo y patas también más oscuros.

Ojos con 4 bandas; las manchitas transversales son ya menos apreciables.

Antenas más largas y menos ensiformes con la división todavía bien neta en 2-5-1; el 3.º con dos finos surcos y sólo uno en el 6.º y el 7.º (Fig. 10).

Lóbulo mesotorácico parecido al anterior estadio, aunque dirigido un poco más hacia atrás, el metatorácico redondeado (Fig. 11, IV).

Tibias posteriores con la cara interna en su tercio apical rosa pálido, al principio del estadio, y más rojiza al final; la pilosidad sigue siendo densa y blanquecina. También se aprecia un color rojizo en las mandíbulas.

En este estadio todavía no hay diferencias notables de tamaño entre los dos sexos.

V estadio

Al ser más oscuro el tono general del cuerpo los puntos se hacen menos evidentes.

Ojos con 5 bandas.

Antenas con los artejos 2-5-1, todavía bien diferenciados, aunque el 3.° ya tiene tres finos surcos y los cuatro siguientes sólo uno en su línea media; en la antena ya se aprecian, por tanto, 15 artejos, aunque no bien definidos (Fig. 10).

Paranotos con el borde posterior más sinuoso; quilla media del pronoto más arqueada. Rudimentos alares mejor delimitados: tegminas (alas anteriores) bien lobuladas hacia abajo y hacia atrás, sin alcanzar el medio del metatorax y las alas posteriores más pronunciadas hacia abajo (Fig. 11, V).

Fémures posteriores con puntos blancos en el tercio basal de la cara interna; tibias del mismo par con el tercio apical rojizo.

Ya se empiezan a apreciar pequeñas diferencias en la longitud del cuerpo, antenas, pronotos y fémures posteriores, siendo más largos en la hembra.

VI estadio

El color general más oscuro, ya se parece mucho al del adulto, siendo un poco más oscuros los machos.

Ojos con 6 bandas, mucho menos ovalados que en los primeros estadios; siendo la diferencia entre longitud y anchura, también menor. Las bandas se ven siempre mejor en los machos que en las hembras; en los individuos que están próximos a la muda se hacen muy borrosas.

Antenas menos ensiformes, la división en 2-5-1 todavía es patente; el 3.° ya tiene de 5 a 6 surcos y del 4.° al 7.° uno cada uno, es decir, que ya se aprecian débilmente 17 artejos, incluyendo el apical (Fig. 10).

Pronoto con la quilla media menos curvada. Lóbulos alares bien delimitados con la futura venación mejor visible: tegminas ya invertidas hacia arriba, más cortas que el ala y sin alcanzar el medio del metatorax; alas posteriores muy pequeñas, pero bien delimitadas con su borde superior curvado y colocado por delante de las tegminas (Fig. 11, VI).

VII estadio

Color general como en el adulto.

Ojos con 7 bandas, ya han perdido la forma ovalada de los primeros estadios.

Antenas más largas y todavía algo ensiformes en especial en los artejos basales del flagelo; el 3.°, ya tiene 7-8 surcos más o menos definidos, en particular los distales; los cuatro siguientes (4 al 7) ya están bien divididos cada uno en dos, siendo ya 8; en total ya se ven claramente los 18-19 artejos en la hembra y 16-17 en el macho (Fig. 10).

Tegminas invertidas sobrepasando el medio del metatorax y la longitud del ala, con 3-4 futuras venas longitudinales y el borde superior bien patente. Alas posteriores más pequeñas y con la venación más débil. En el macho las tegminas son un poco más cortas que en la hembra (Fig. 11, VII ♂ y ♀).

Fémures posteriores con los puntos blancos ocupando ya las dos terceras partes de la cara interna; tibias del mismo par con la cara interna enteramente roja y la pilosidad también muy abundante.

Estadios intermedios

A veces se encuentran individuos que combinan caracteres de dos estadios; este fenómeno ocurre a partir del III estadio. Así, individuos que ya han alcanzado un determinado estadio conservan el final del abdomen, los rudimentos alares o las bandas de los ojos, correspondientes al estadio anterior. Se da también el caso contrario, por ejemplo, una hembra del VII estadio tenía ya 8 bandas en los ojos, propias del adulto.

Tabla para la determinación de los sexos (Figs. 12 y 13)

Estadios	Macho	Hembra
I	Placa subgenital escotada en el ápice en semicírculo, lóbulos cortos y algo obtusos, cubriendo sólo la base de los paraproctos; éstos y el epiprocto largos y agudos.	Valvas superiores del oviscapto cortas y obtusas, separadas entre sí por una incisión en ángulo recto o ligeramente semicircular. Valvas inferiores representadas por dos pequeños semicírculos que ya se ven desde principio del estadio.
II	Placa subgenital estrechándose hacia el ápice, con la escotadura más estrecha y sin llegar al tercio de los paraproctos.	Valvas superiores del oviscapto más largas y agudas en el ápice, separadas entre sí por un espacio paralelo. Valvas inferiores ampliamente triangulares, ocupando el tercio del esternito.
III	Placa subgenital parecida a la del II, pero con la escotadura más cerrada y en forma de V.	Valvas superiores del oviscapto más agudas y más largas, entre éstas están las internas, pequeñas y bien manifiestas. Las inferiores ocupan menos de la mitad del esternito.
IV	Placa subgenital estrechándose más en el ápice, con la escotadura más pequeña y más cerrada y de forma semicircular.	Valvas superiores más largas y menos agudas, ocupando más de la mitad del esternito y separadas entre sí por un espacio paralelo en cuya base están las valvas internas. Valvas inferiores más desarrolladas y alcanzando la base de las superiores.
V	Placa subgenital sin escotadura en el ápice, de forma estrechamente parabólica y llegando casi a la mitad de los paraproctos.	Valvas superiores más largas, alcanzando el tercio basal de los paraproctos; los ápices casi se tocan mientras que el resto está ocupado por las inferiores, por encima de cuyos ápices asoman los de las internas.
VI	Placa subgenital con el ápice anchamente parabólico, sobrepasando la mitad de los paraproctos y alcanzando el ápice de los cercos. Por los lados se ve el palio.	Valvas superiores alcanzando la mitad de los paraproctos y casi al mismo nivel del ápice de los cercos. Las inferiores sobrepasan la mitad de las superiores, estando todavía por debajo del ápice de los cercos.
VII	Placa subgenital más alargada y sobrepasando más de 2 veces la longitud de los cercos, sólo dejando al descubierto los ápices de los paraproctos y epiprocto. Palio más ancho.	Valvas superiores sobrepasando el ápice de los cercos, al final del estadio con los ápices algo ennegrecidos. Las inferiores casi al nivel de los cercos y con la quilla transversal bien patente. Borde posterior de la placa subgenital parecida a la del adulto.
AD.	Placa subgenital con el ápice anchamente parabólico y cubriendo por completo los paraproctos y epiprocto. El palio ya no se ve.	Valvas superiores con los ápices robustos y completamente ennegrecidos, casi cubriendo los paraproctos. Las inferiores al mismo nivel que los cercos, con los ápices ennegrecidos; parte basal muy ancha; quilla ventral transversal bien patente.

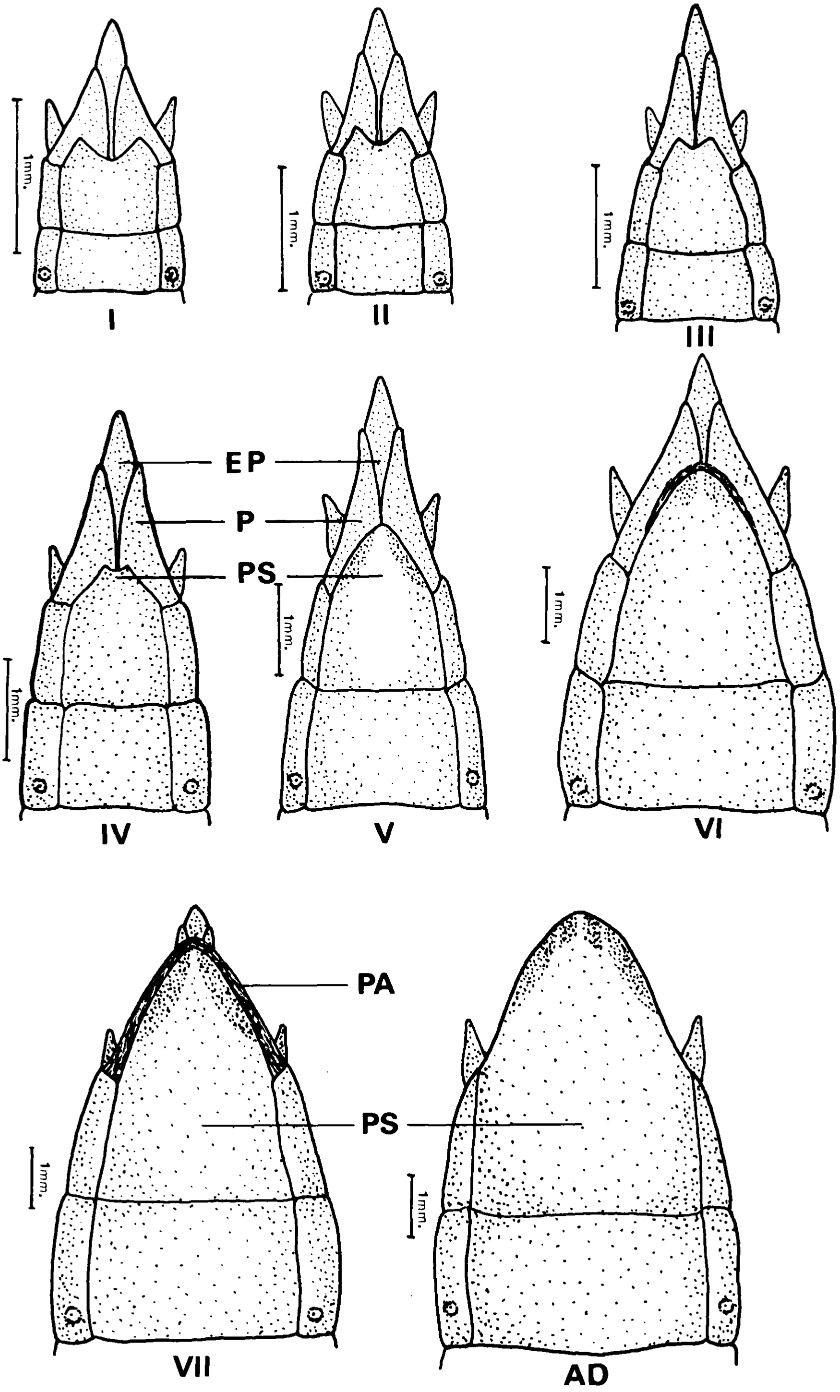


Figura 12.—Desarrollo de la genitalia externa del macho en los siete estadios ninfales y en el adulto (vista ventral). P, paraproctos; EP, epiprocto; PS, placa subgenital; PA, palio.

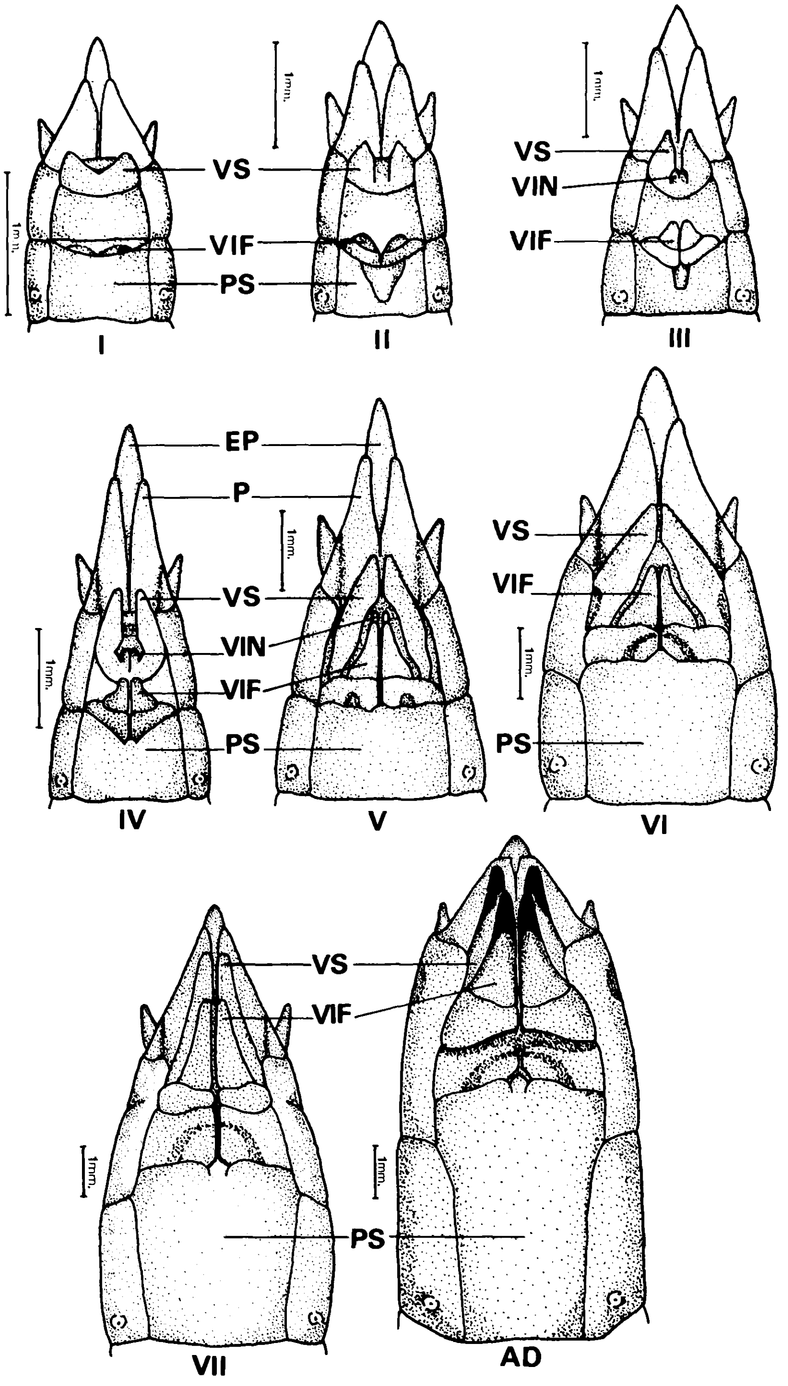


Figura 13.—Desarrollo de la genitalia externa de la hembra en los siete estadios ninfales y en el adulto (vista ventral). P, paraproctos; EP, epiprocto; PS, placa subgenital; VS, valvas superiores; VIN, Valvas internas; VIF, valvas inferiores.

Adulto

Color pardo oscuro, alternándose con blanco o crema, con aristas y verrugas. Ojos con 8 bandas la 1.ª también mal definida. En este estado, como en las ninfas, el número de bandas coincide, generalmente, con el del estadio (Burnet, 1951; Uvarov, 1966). Y, según hemos podido observar las bandas se conservan mientras los insectos están vivos, una vez muertos desaparecen, aunque a veces se pueden ver algunas de ellas, pero siempre borrosas.

Antenas gruesamente filiformes con 16-17 artejos en el macho y 18-19 en la hembra (Fig. 10, AD).

Tegminas lobiformes, laterales y estrechas, casi alcanzando o sobrepasando un poco el borde posterior del primer terguito abdominal, de coloración uniforme y con los bordes casi rectos, en especial el superior. Alas posteriores vestigiales, completamente cubiertas por las tegminas (Fig. 11, AD).

Fémures posteriores con la cara interna blanquecina y con puntos oscuros dispersos; tibias del mismo par con pilosidad blanca abundante y la cara interna roja.

La longitud del cuerpo de los adultos es aún mayor, en especial en las hembras, llegando a medir 70-80 mm, cuando están preparadas para realizar la puesta.

Más detalles sobre caracteres morfológicos del adulto, en especial la estructura de la genitalia interna del macho, así como sobre otros datos de biología, ecología y su distribución en España figuran en Presa y Llorente (1983).

Inversión de los rudimentos alares

En los Acridoidea en general, la inversión de los rudimentos alares puede tener lugar en diferentes mudas, del II al V estadio; pero al parecer siempre precede en dos estadios a la muda final. Lo que también se cumple cuando los dos sexos de una misma especie no coinciden en el número de estadios, produciéndose entonces la inversión en mudas distintas (Uvarov, 1966).

Esto se confirma en el caso de *A. hesperica hesperica*, ocurriendo la inversión, en ambos sexos, en la muda del V al VI estadio, al ser siete el número total de ellos.

El desarrollo de la genitalia externa de ambos sexos, así como el de los rudimentos alares (Figs. 11-13) coinciden bastante con las observaciones realizadas por Burnett (1951) sobre *Nomadacris septemfasciata* (Serville, 1838), ya que se trata de especies con el mismo número de estadios ninfales. Pero al pertenecer a distintas familias de Acridoidea se diferencian, además, de otros caracteres morfológicos, por presentar *A. hesperica hesperica* las tegminas laterales y lobiformes. Es esta característica la que, a nuestro parecer, aporta un nuevo interés al estudio realizado, ya que, hasta ahora no se había descrito el desarrollo de las tegminas en una especie micróptera.

ESTUDIOS BIOMETRICOS

Damos en primer lugar la tabla 1 con las medidas de diversas partes del cuerpo, tomadas a lo largo del desarrollo y en el adulto, según se indica en la introducción. Se expresan los valores extremos y la media correspondiente.

Los valores medios consignados en la Tabla 1 se representan gráficamente en la Figura 14. En esta última se observa que la diferencia de tamaño entre machos y hembras no sólo afecta a la longitud total del cuerpo —debido al mayor desarrollo del abdomen de las hembras—, sino que para cada una de las partes del cuerpo consideradas en este estudio, los machos presentan medidas menores en proporciones relativamente parecidas.

La diferencia entre ambos sexos se evidencia a partir de la 4.ª muda, excepto en el caso de la longitud del cuerpo (L.c.) en el que se hace notable antes, a partir de la 3.ª muda, debido lógicamente al abdomen, ya que en el pronoto se conservan todavía longitudes muy similares.

Respecto al ojo, hemos representado los valores medios, correspondientes, en cada estadio, a su longitud y anchura así como la razón entre ambas. Se observa que dicha razón (long./anch.) tras aumentar en la 1.ª

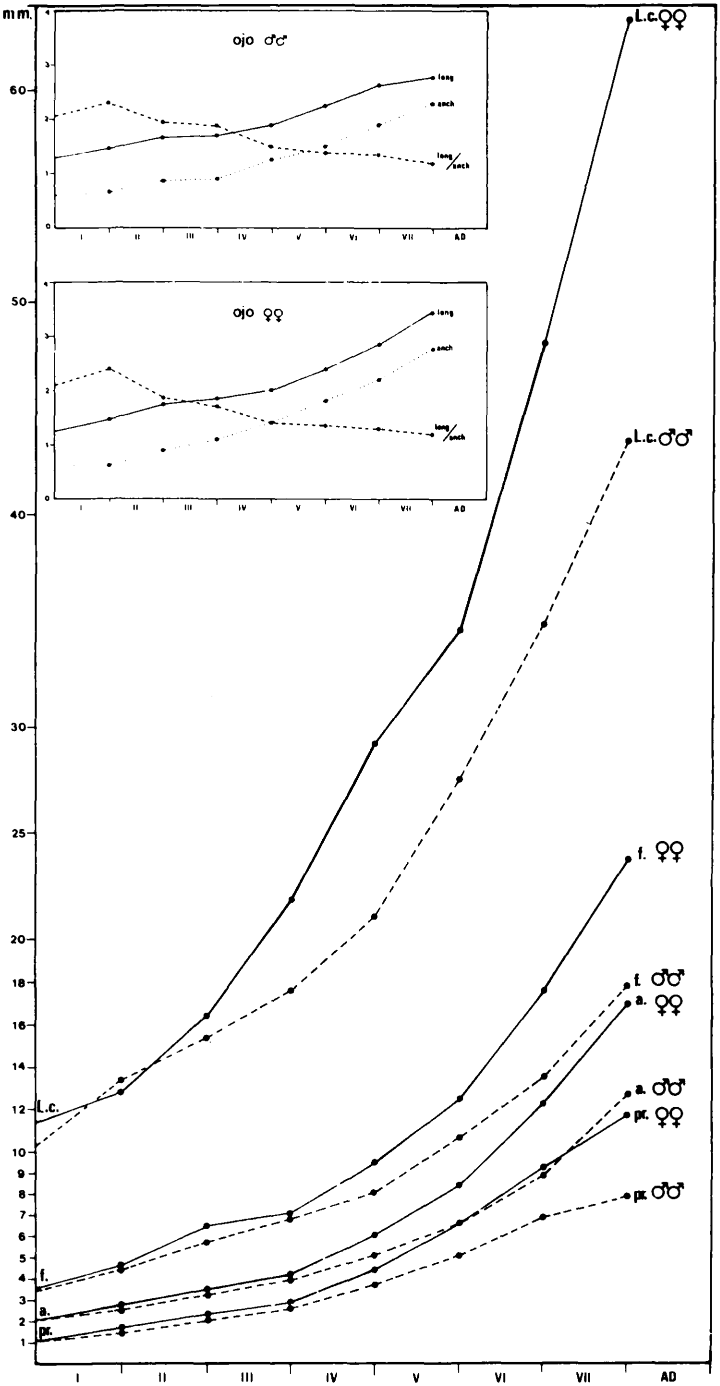


Figura 14.—Gráficas de crecimiento de distintas partes del cuerpo. En el ángulo superior, longitud y anchura del ojo y razón entre ambas. En el inferior longitud: del cuerpo (L.c.), fémur posterior (f), antena (a) y pronoto (pr). I-VII, estadios ninfales, AD, adulto.

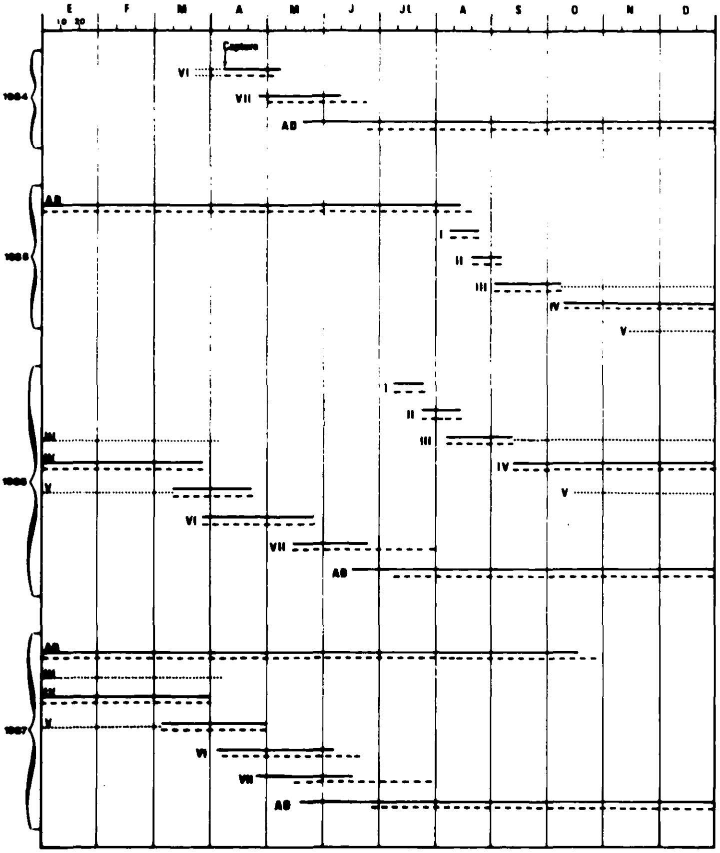


Figura 15.—Duración de los estadios ninfales y del adulto; (—) machos; (--) hembras y (...) ejemplares aislados que adelantan o atrasan notoriamente su desarrollo.

muda, disminuye a lo largo de los estadios ninfales, y muy especialmente en los cuatro primeros.

Los ojos, efectivamente, muy ovalados en las ninfas jóvenes de *A. hesperica* se hacen progresivamente más redondeados hasta alcanzar el estado adulto. Es decir, que el diámetro horizontal crece más rápido que el vertical. Hecho que también fue observado por Burnett (1951) en *Nomadacris septemfasciata* y que Uvarov (1966), basándose en las figuras del autor anterior, lo matiza aún más. Los gráficos, realizados separadamente para cada sexo, muestran que el proceso es similar en machos y hembras.

DURACION DE LOS ESTADIOS Y LONGEVIDAD

En la Figura 15 se representan las sucesivas etapas del desarrollo de *A. hesperica* y la duración relativa de cada una de ellas, según datos obtenidos a lo largo de esta experiencia de casi 4 años.

Creemos importante indicar que las fechas de las mudas y por tanto la duración de cada estadio, representada en la gráfica, se ha obtenido, promediando las de los individuos con un desarrollo "normal" y teniendo en consideración las correspondientes desviaciones que se evidencian en los solapamientos de la gráfica —pero prescindiendo de los datos de aquellos que, de forma muy notable, adelantaron o retrasaron su desarrollo, respecto a los restantes.

Los ejemplares con que iniciamos este estudio, capturados en abril de 1984, eran ninfas del VI estadio que llegaron a adultos entre mayo y junio de ese mismo año. A partir de los individuos de la segunda generación, nacidos entre el 8 y 10 de agosto de 1985, observamos, para cada estadio la siguiente duración: I: 12-15 días; II: 14-17; III: 31-35; el IV estadio, que se alcanza entre septiembre y octubre, es el más largo, 150 a 160 días, correspondiendo por tanto a los meses de invierno, que estos insectos pasan prácticamente aletargados con movimientos muy escasos y casi sin alimentarse. Korsakoff (1941) hace una observación similar respecto a *Euryparyphes sitifensis* (Brisout, 1854), aunque en este caso el IV estadio sólo dura unos 80 días. Hay que señalar no obstante, que algunos individuos invernan en los estadios III o V. Todo esto debe ocurrir también en la naturaleza, ya que se registró en el laboratorio durante los años 85 a 87.

A últimos de febrero empiezan de nuevo a moverse y alimentarse, reanudándose las mudas a primeros de marzo. El V y VI estadios duran aproximadamente 22-26 días, observándose que la muda al VII se retrasa unos días en las hembras respecto a los machos, fenómeno que volverá a repetirse, de modo mucho más evidente en la muda final; debido a ello los machos permanecen en el VII estadio entre 20 y 25 días, mientras que este intervalo es casi el doble —40 a 48 días— en las hembras. Así los primeros machos llegan a adultos a mediados de mayo o junio, casi un mes antes que las primeras hembras. Este hecho no parece haberse observado en ninguno de los casos consultados ni tampoco en la lista de 40 especies estudiadas por distintos autores que da Dirsh (1968); podría ser comparable al estadio/s extra que tienen las hembras de algunas especies y que está relacionado con el tamaño mucho más grande de éstas, frente al de los machos.

Para concluir, en nuestra experiencia, la especie *A. hesperica*, desde la eclosión el 8 de agosto de 1985, hasta la muerte de los últimos individuos de esta generación ocurrida el 26 de octubre de 1987 alcanzó una longevidad total de 812 días ¡todo un récord! Hasta ahora parece que lo detentaba una hembra de *Anacridium aegyptium* (L., 1764) que vivió 600 días desde su eclosión (Colombo y Mocellin, 1956; Uvarov, 1966).

Refiriéndonos al estado de ninfa y considerando un desarrollo «normal», los machos llegaron a permanecer como tales hasta 366 días, alcanzando tras ello la fase adulta, y las hembras hasta un total de 384 días. En algunos ejemplares, sin embargo, se produjo un notable retraso durante los estadios VI y VII, hasta de uno o dos meses, mudando finalmente a adultos; otros, con un desarrollo aún más lento (cinco meses en un mismo estadio e incluso más de 2 años como ninfa), nunca alcanzaron la fase de imago.

Y respecto a la duración del estado adulto, aunque algunos sólo sobrevivieron de 4 a 6 meses, la mayoría de ellos sobrepasaron el año y unos pocos llegaron a vivir hasta 440 días como imago.

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Significance of seasonal adaptations in Tettigoniidae

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ABSTRACT

In Europe, major climatic characteristics to which orthopteroid insects must adapt are (1) a moderately long vegetation period with temperate summers in the center and the north and (2) hot and dry or even rainless summers in the south. Tettigonioidea are subject to unfavorable environmental conditions in the egg stage. The eggs have to take up water and are thus susceptible to desiccation in certain stages of development. Seasonal synchronization of development is usually achieved by diapause.

In the European Tettigoniidae *s.str.*, a diapause can occur in several embryonic stages. The most important dormancies are an "initial diapause" after blastoderm formation, which might extend for up to seven years, and a "final diapause" in the fully grown embryo. Evolutionary changes in response to environmental stimuli (photoperiod, temperature, moisture) make this dormancy sequence adaptive for:

(1) a univoltine life cycle with estivation and hibernation under the Mediterranean climate;

(2) a plurivoltine life cycle with two hibernations in central European species depositing eggs in the soil (cool egg habitat);

(3) a uni- to plurivoltine life cycle in central European species depositing eggs in plant tissues (warmer egg habitat); and

(4) a univoltine life cycle by largely suppressing initial diapause in a few south and central European species.

The water balance of the eggs is, therefore, adaptive, *e.g.*, in the three *Tettigonia* species *T. cantans* (Fuessly, 1775), *T. viridissima* Linne, 1758, and *T. caudata* (Charpentier, 1845) the water content of freshly laid eggs is 34.0%, 41.6%, and 49.5% respectively; water uptake until hatching 73%, 54%, and 31%; and the mean transpiration rate of developing eggs at 30% RH 7.2, 4.7, and 2.2 μg/mg/d. Whereas eggs of *T. viridissima* and *T. cantans* absorb water mainly during embryonic development in summer, water uptake in *T. caudata* eggs is restricted almost completely to the final diapause and winter. *Tettigonia viridissima* has the greatest distribution. It occurs everywhere in not-too-cool and not-too-dry regions; *T. cantans* is adapted to cool and humid and *T. caudata* to warm and dry climates. Adaptations to the climatic situation thus comprise (1) parental investment in the water content of the eggs and (2) synchronization of periods of water uptake and drought resistance with periods of rainfall and drought, independently of the progress of embryonic development.

Key words: climatic speciation, diapause, embryonic development, life cycles, maternal photoperiod, seasonal synchronization, Tettigoniidae, water absorption of eggs, transpiration of eggs.

INTRODUCTION

For insects as ectothermous organisms the primary challenge to survival in a given environment are the adaptations to the local climatic conditions. Suitable periods have to be used for development and reproduction, while deteriorations of the environment must be survived in resistant stages. Food, predators, or competitors may additionally influence distribution.

Climatic factors that restrict the distribution of orthopteroid insects in Europe are (1) a short growing season with moderate temperatures in the center and the north and (2) lack of moisture during a hot summer in the south.

European Tettigoniidae do not have more than one generation per year. Hatching of larvae takes place in spring, mating and oviposition in summer and autumn. Survival of the egg can be affected by predators, energy reserves, temperature, precipitation, unfavorable periods of cold, heat, or drought, and catastrophes (Fig. 1). Those factors require adaptations that concern the female in advance of oviposition or the embryo itself.

The aim of the present paper is to show how characters of dormancy, life cycle, and water uptake are modified as a result of adaptations to local climatic conditions. In Tettigoniidae, timing of seasonal events and survival of unfavorable conditions always involve the egg stage. Thus the paper concentrates on egg development and diapause.

LIFE CYCLE STRATEGIES

Adaptations of the individuals of a species to the mean long-term conditions of a local environment are basic characteristics of life cycles. Limitation of resources (food availability and quality, warmth, precipitation) restricts the number of successive generations and thus voltinism. Sensitive stages of development must be synchronized with favorable conditions. This necessitates the occurrence of dormancies in resistant, preceding stages.

In Tettigoniidae, the embryonic stages in which the diapause can occur depend on taxonomic affinity: In Conocephalinae and Meconematinae there is only one diapause stage in the half-grown embryo shortly before or after katatrepsis, while in the Tettigoniinae, Decticinae, Saginae, Ephippigerinae, and European Phaneropterinae, there are basically two diapause stages during embryonic development: after blastoderm formation (*initial diapause*) and in the fully grown embryo (*final diapause*) (Hartley and Warne, 1972; Ingrisch, 1984, 1986). The induction of the initial diapause depends on the conditions before oviposition and during early embryonic development. The final diapause occurs independently of experimental conditions and synchronizes hatching.

Due to different responses of the embryos to the proximate factors photoperiod, temperature, and moisture, the following four principal types of life cycles occur in the Tettigoniidae with a dormancy sequence during embryonic development (for details see Ingrisch, 1986):

1. a univoltine life cycle with estivation in initial and hibernation in final diapause and embryonic development in autumn under the Mediterranean climate and oviposition in the soil (*e.g., Eupholidoptera smyrnensis* (Brunner, 1882); Rhodes/Greece 36°10'N 28°00'E) [inner circle in Fig. 1];
2. a plurivoltine life cycle with hibernations in both initial and final diapause and embryonic development during the summer between both hibernations under moderate, Central European climate and oviposition in the soil (*e.g., Decticus verrucivorus* (L., 1758), Aachen, F.R.G. 50°45'N 6°10'E; *Pholidoptera griseoaptera* (De Geer, 1773), Eifel, F.R.G. 49°50'N 6°15'E; *Tettigonia* sp.); (this type of life cycle can become more complicated by a prolongation of initial diapause for up to seven years) [outer circle in Fig. 1];
3. a uni- to plurivoltine life cycle with a facultative initial diapause and embryonic development either in late summer after oviposition or in the summer of the next year under moderate climate and oviposition in plant tissues (*e.g., Metrioptera roe-*

seli (Hagenbach, 1822); Aachen, F.R.G. 50°47'N 6°05'E) [combination of outer and central circle in Fig. 1]; and

4. a univoltine life cycle by largely suppressing initial diapause and embryos developing in late summer (eventually continuing into the next spring) in species depositing eggs in plant tissues and living in localities with warm local climate (*e.g.*, *Platycleis albopunctata* (Goeze, 1778); Eifel, F.R.G. 50°20'N 7°15'E) [central circle in Fig. 1].

The different life cycles of the European Tettigoniidae are thus based on the variation of a common scheme. Seasonal synchronisation can be more precisely timed by the occurrence of additional, facultative dormancies (Ingrisch, 1986). The precise seasonal timing of embryonic development keeps the energy demand low by preventing late embryonic stages from appearing during the heat of summer (Ingrisch, 1987). In this way the investment of a female in the production of yolk for a single egg can be low and the number of eggs and thus the relative fitness higher than without precise seasonal synchronization. As an example for the mechanisms of seasonal synchronization of embryonic development, the effect of maternal photoperiod on the induction of diapause is shown below.

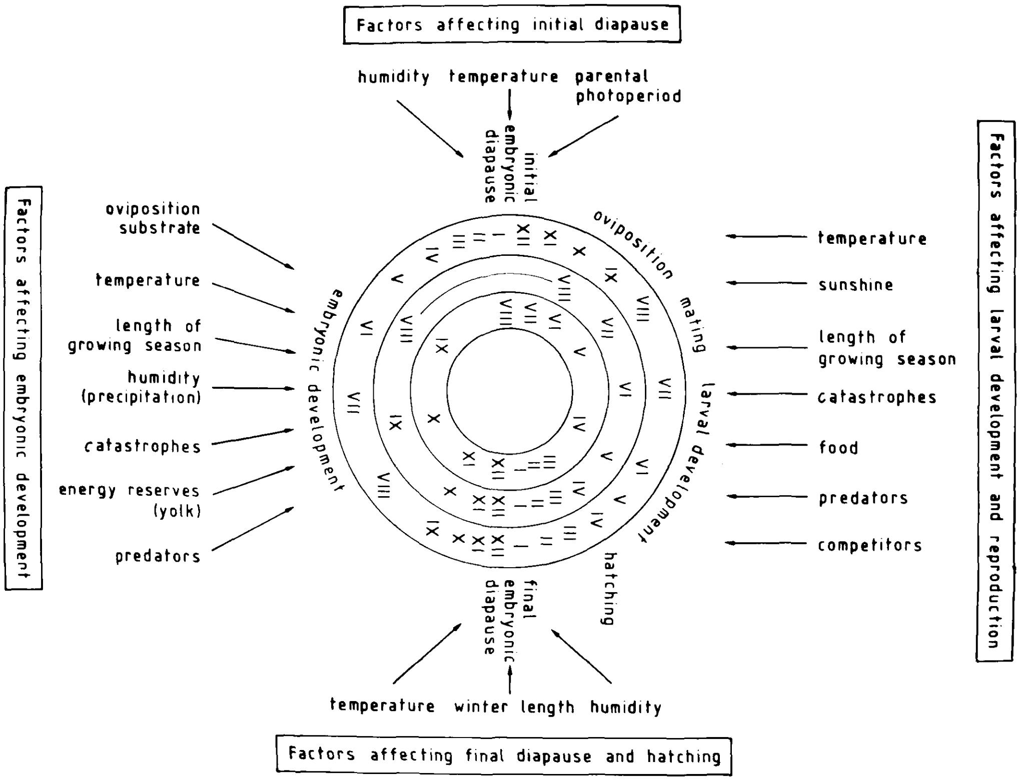

Figure 1. The influence of environmental factors on the succeeding stages of the life history of the Tettigoniidae. The circles in the center give examples of different life-cycles (to be read counter-clockwise). Roman numerals refer to the months of a year. *Outer circle:* Two-year life cycle with hibernations in both initial and final diapause (right first year, left second year). *Central circle:* One-year life cycle with hibernation in final diapause only. *Outer and central circle* together: One-to-two-year life cycle. *Inner circle:* One-year life cycle with estivation in initial and hibernation in final diapause.

INDUCTION OF INITIAL DIAPAUSE BY MATERNAL PHOTOPERIOD

An important cue for the induction of the initial diapause is the photoperiod experienced maternally. The responses differ greatly between species (Fig. 2). In (1) *P. albopunctata,* embryos always develop until the final diapause, independently of photoperiodic conditions. Embryos need 7 weeks at 24°C to reach that stage. In (2) *M. roeseli* and (3) *E. smyrnensis,* after oviposition at long day lengths (LD 16/8), embryos develop until final diapause (in *E. smyrnensis* half of the embryos develop to a prefinal diapause in embryonic stage 20), while after oviposition at moderate long day lengths (LD 14/10 or shorter) an initial diapause is induced. In *M. roeseli* development proceeds as quickly as in *P. albopunctata,* while embryos of *E. smyrnensis* need 10 weeks at 24°C to reach the final diapause stage. Embryos of (4) *P. griseoaptera* react in a contrasting manner, and an initial diapause is induced in 17% or 32% of the eggs after oviposition at LD 16/8 or LD 17/7, while there is no initial diapause after oviposition at LD 14/10 or shorter day lengths (for the percentage of embryos in diapause after incubation for 12 weeks at 24°C, see Ingrisch, 1986). Development proceeds as in *E. smyrnensis.* Finally in embryos of (5) *D. verrucivorus* an initial diapause is induced after oviposition at long or short day lengths. Development does not proceded until after hibernation, and embryos need 12 weeks at 24°C (in a second warm treatment) to reach the final diapause. *Tettigonia* species (from the German middle mountains) behave in the same way as *D. verrucivorus.* After hibernation, embryos of all species in initial diapause continue to grow to final diapause, and embryos in final diapause hatch.

It has been shown that for the slowly developing species such as *P. griseoaptera,* the temperature sums in Western and Central Europe are not high enough to allow completion of the life cycle in one year (Hartley and Warne 1973, Ingrisch 1986). Initiation of development in late summer is suppressed by initial diapause which can be obligatory as in *D. verruciverus* or be induced by long day length as in *P. griseoaptera.* In contrast, quickly developing species as *M. roeseli* in which initial diapause is induced by short day lengths can have a univoltine life cycle if the eggs are laid in early summer. In the Rhodian population of *E. smyrnensis* oviposition starts in spring at LD 14/10 or shorter day lengths. Initial diapause is terminated by a four weeks exposure to heat (30°C) and this fact obviously favors estivation (Ingrisch, 1986).

WATER BALANCE OF EGGS

The amount of water required by the embryo during development can either be provided by the female prior to oviposition as in Phasmida, or it has to be absorbed in part from the environment as in Orthoptera *s.str.* and Grylloptera. Thus adaptations are necessary allowing eggs to absorb water in wet seasons but also protecting them from desiccation in dry periods.

Seasonal adaptations concerning water balance of the eggs are shown for three species with plurivoltine life cycles: *Tettigonia cantans* (Fuessly, 1775; Vogelsberg, F.R.G. 50°30'N 9°14'E), *T. viridissima* Linne, 1758 (Eifel, F.R.G. 50°40'N 6°30'E), and *T. caudata* (Charpentier, 1845; Northern Greece 40°40'N 23°30'E) (for additional species see Ingrisch, 1988). Water absorption and transpiration were determined by weighing eggs individually.

In a first experimental series water was always provided in abundance, a condition prevailing in Central Europe in years with high precipitation. Eggs of European species absorb water during (1) development mainly from late anatrepsis until after katatrepsis, (2) the second half of hibernation in final diapause, and (3) before hatching (Fig. 3). In initial and early in final diapause the egg weight remains constant. Eggs of the southeastern European species *T. caudata* do not show a clear period of water uptake except prior to hatching, and egg weight increases very slowly during the whole development. For this species, the experimental conditions deviate from the conditions in the field.

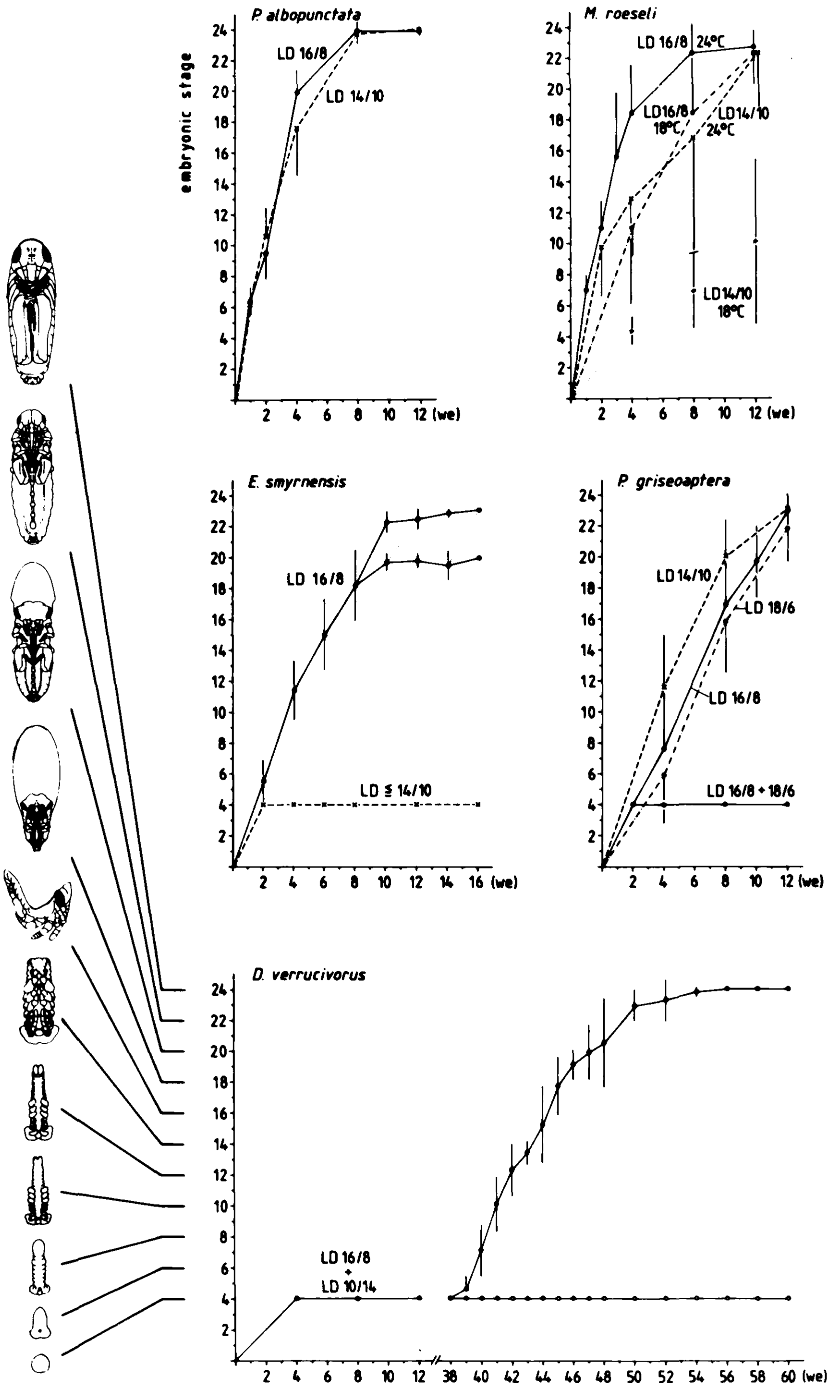

Figure 2. Progress of embryonic development (means and standard deviations) at 24° C (or as stated) after oviposition at different light-dark periods (LD). Examples of five species with different response to photoperiod are given. Embryonic development of *D. verrucivorus* is interrupted by hibernation at 5° C (stippled line).

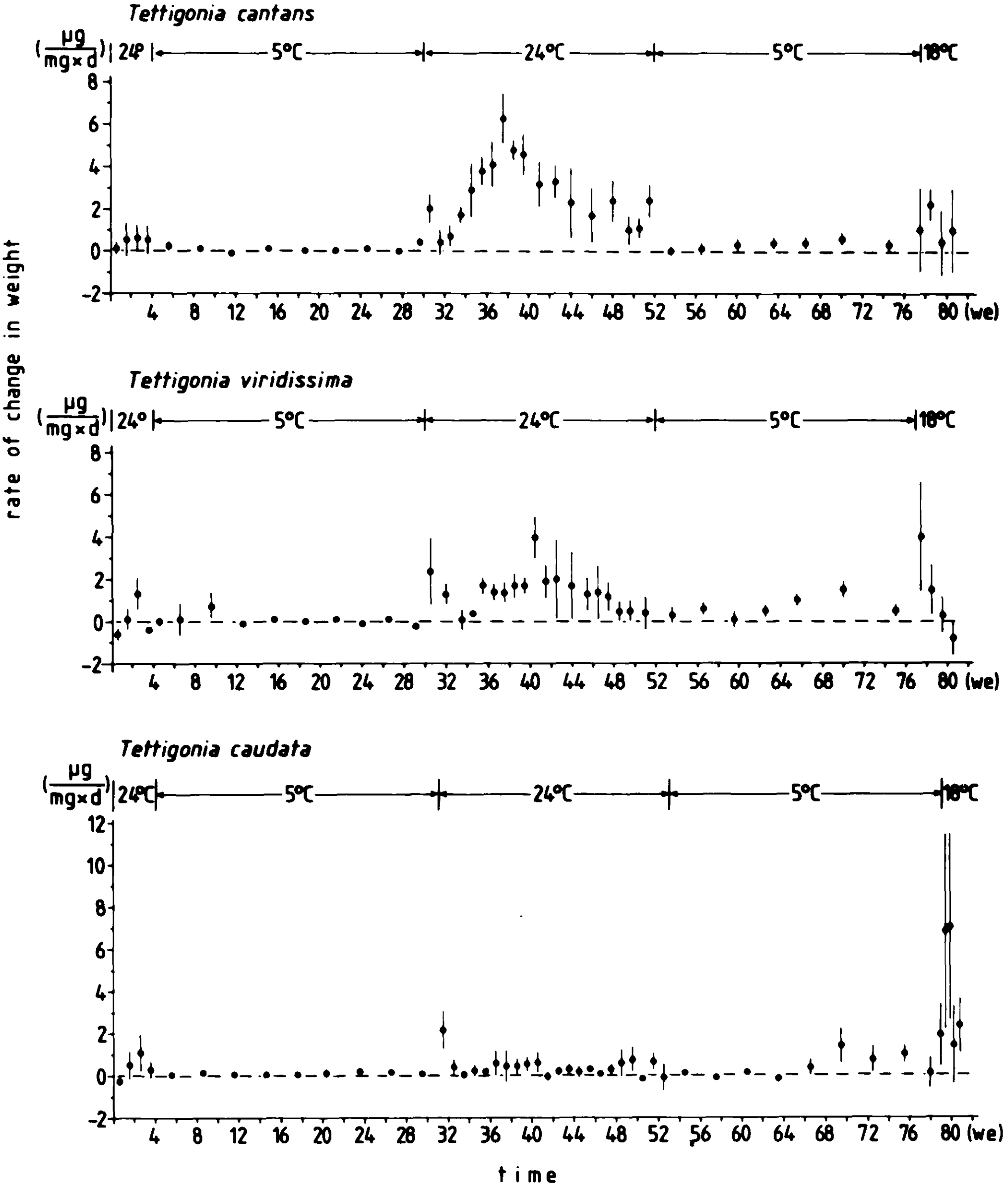

Figure 3. Rates of water uptake of eggs of three *Tettigonia* species from oviposition to hatching. The eggs had access to free water during the whole development.

In the second experimental series the eggs had to develop on dry filter paper at almost saturated humidity. Free water was only provided during hibernations (Fig. 4). Those conditions are typical for the Mediterranean climate. Less severe 6-8 week periods of drought may also occur in Central Europe in dry years. Under those conditions water uptake is restricted to final diapause (Fig. 4). In embryos of Central European species water uptake was fastest at the beginning of hibernation. Obviously, water uptake that should have taken place earlier in embryonic development, is made up as soon as free water becomes available. Embryos of *T. viridissima* can fully compensate for previous insufficient water uptake during hibernation in final diapause. Thus the egg weight at the end of final diapause was about the same as when free water was already available during embryonic development in the preceding warm treatment (mean egg weight 10.6 mg or 152% of the weight at oviposition against 10.1 mg or 162%). Embryos of *T. cantans* could not fully compensate for the water uptake that should have taken place during warm treatment. Thus its egg weight at the end of final diapause was lower (mean egg weight 10.8 mg or 157% of the weight at oviposition against 11.6 mg or 171%). The species occurs in regions with high summer precipitation or on soils with high water capacity (Ingrisch, 1981).

In embryos of *T. caudata* from southeastern Europe water uptake during final diapause shows a short peak at the beginning of hibernation, but otherwise it is highest in the second half of final diapause, *i.e.*, closer to the hatching date.

The egg weight at the end of final diapause was even higher when the eggs had access to free water only during hibernation than when water was also available during the warm treatments (mean egg weight 12.1 mg or 136% of the weight at oviposition against 11.0 mg or 125%). That means this species is well adapted to the climatic conditions under the mediterranean climate with dry summers and precipitation mainly restricted to winter. This adaptation is obviously achieved by uncoupling the mechanisms that control the progress of embryonic development from those that control water uptake.

Similar differences between species are found if transpiration of developing eggs (from initial to final diapause in a second warm treatment) is compared (Fig. 5). The loss of weight of eggs kept at 30% RH and 24°C increased with time. Eggs of *T. cantans* were fully desiccated after 12 weeks, as the weight remained constant after that time. Eggs of *T. caudata* dried up less than half as quickly, those of *T. viridissima* were intermediate. Eggs of *T. cantans* and *T. viridissima* died after 20 weeks of desiccation, while those of *T. caudata* survived.

CLIMATIC SPECIATION OF THE *TETTIGONIA* SPECIES

Species can use or tolerate a factor within a wide range (euryoecious) or they are specialized to a narrow range (stenoecious). Since adaptations to one factor (*e.g.*, temperature) may also require adaptations to another (e.g., humidity), the potency for adaptations is probably also limited in euryoecious species, as far as the identity of the species is not changed.

Climatic adaptability and niche diversification will be discussed at the hand of three allied species *Tettigonia viridissima, T. cantans.* and *T. caudata.*

Tettigonia viridissima has the greatest distribution and is adapted to a wide range of temperature and moisture. The mean water content of the eggs at the time of oviposition is 41.6%, the eggs take up 54% water (referring to the weight at oviposition), and the mean transpiration rate of developing eggs at 30% RH and 24°C is 4.7 μg/mg/d and thus intermediate between the other two species. In Central Europe, *T. viridissima* occurs in not-too-cold habitats at lower elevations (*e.g.*, Ingrisch, 1981). In western Germany, it vicariates with *T. cantans e.g.*, in Hesse east of the Rhine, but occurs alone in the Eifel west of the Rhine. A comparison of the occurrence of *T. viridissima* in both areas does not give a hint that its distribution is restricted by competition with *T. cantans*, but suggests that it

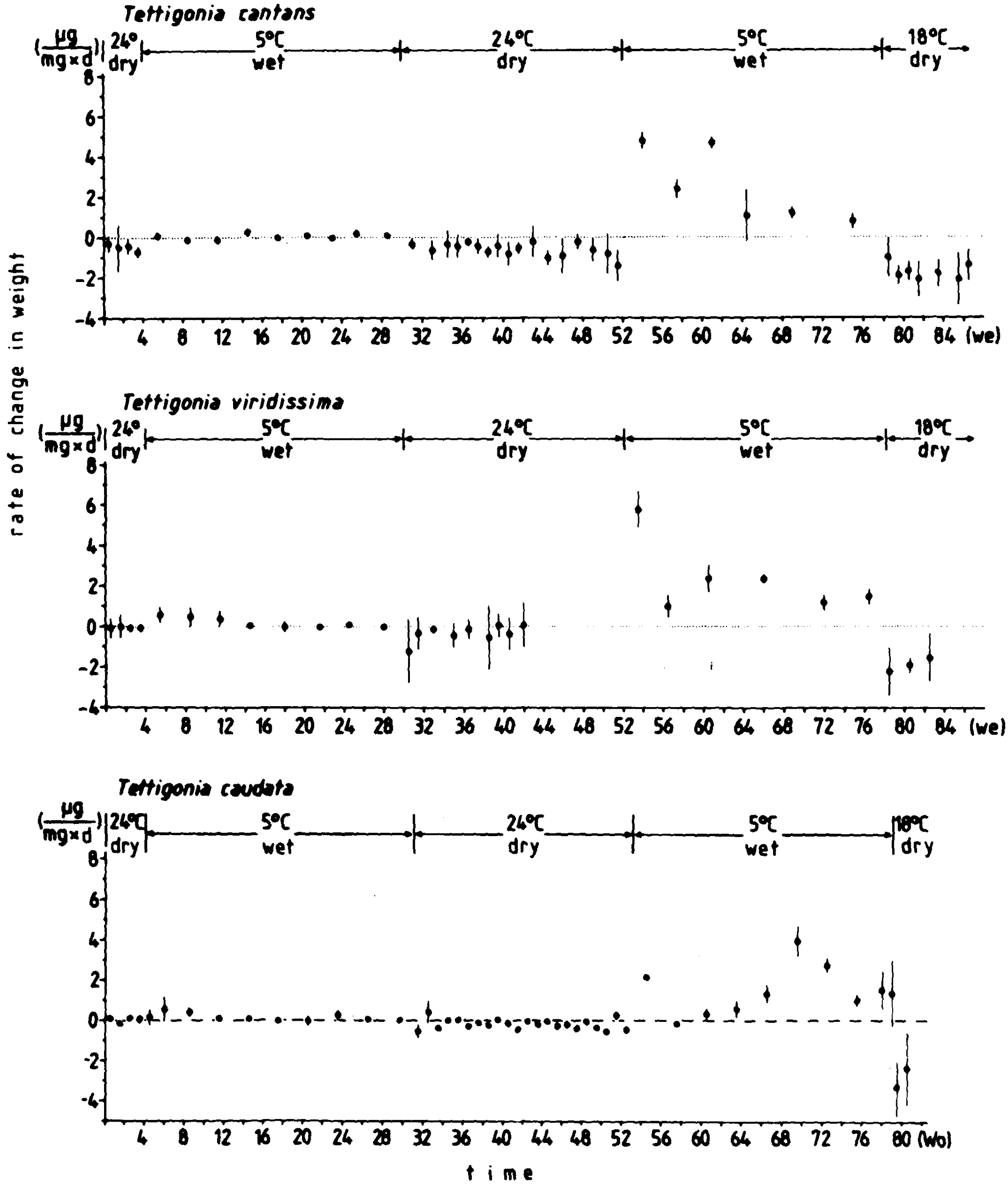

Figure 4. Rates of change in weight due to uptake and loss of water in eggs of three *Tettigonia* species from oviposition to hatching. The eggs were placed on dry filter paper in an almost saturated atmosphere (dry) during the warm treatments in which development and hatching took place and had access to free water (wet) during hibernations.

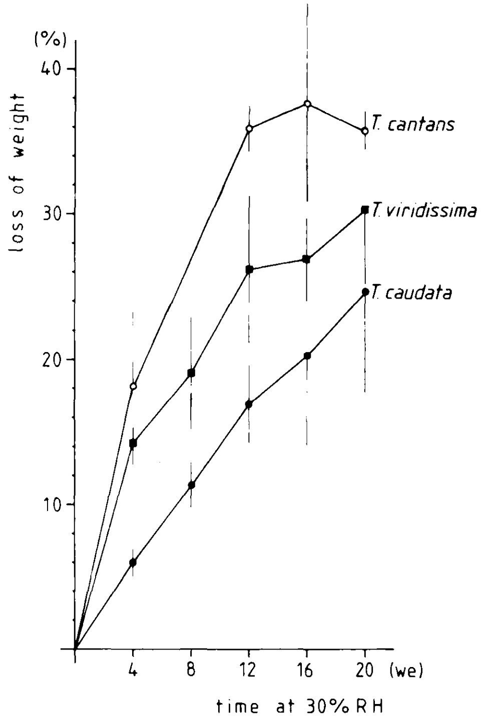

Figure 5. Transpiration of eggs of *Tettigonia cantans*, *T. viridissima*, and *T. caudata* during development from initial to final diapause in second warm treatment: 20 weeks at 24° C and 30% RH.

is merely limited by a deficient adaptability to climatic factors (Ingrisch, 1988). In areas where there are extremes of temperature and humidity, *T. viridissima* is replaced by one of the following, specifically adapted species.

T. cantans is adapted to areas with cool and humid climate. The ultimate factor of adaptation is temperature, *i.e.*, the low temperature sums of one year. The adaptations concern larval and embryonic development. Compared with the other two species, one larval instar is omitted (6 instead of 7 larval instars). Thus postembryonic growth is 1-2 weeks shorter than in *T. viridissima* under similar conditions (Ingrisch, 1978). The investment of the females in the production of a single egg is lower than in the former: the mean water content at the time of oviposition is only 34%. The low investment allows the female to produce enough eggs in spite of a short growing season. However, the eggs have to absorb more water from the environment (73%) to meet the requirements of the growing embryo, which results in a low resistance against desiccation (mean transpiration rate at 30% RH and 24°C 7.2 μg/mg/d, Ingrisch, 1988). Since in a cool and humid climate water is available in abundance, the probability of survival is not lowered by need of water during summer and low resistance against drought. The ability to spread into regions with lower precipitation, however, is strictly limited.

On the other hand, *T. caudata* is adapted to hot and dry climate with warmth in abundance, but prolonged periods of drought that require special adaptations. Larval development is synchronized with the growth period of the plants. Larvae and imagines can cover their water requirements with food. Adaptations to drought thus concern mainly the egg. The investment of females in egg production is large. They lay heavier eggs with a higher water content than either of the other species (49.5%). As a morphological adaptation the ovipositor is prolonged (33-38 mm against 23-32 mm in *T. viridissima*). Thus the eggs are inserted deeper into the soil where desiccation is less likely (see Masaki, 1986). Due to the high water content at the time of oviposition, water absorption from the environment is low (31%). In contrast to the other species, water uptake does not occur while the embryo is developing but during final diapause, and is thus synchronized with the rainy season in winter. It follows that developing eggs are very resistant against desiccation (transpiration rate at 30% RH and 24°C 2.2 μg/mg/d). The sum of adaptations which permit survival under semiarid climatic conditions also restrict the potential of the individuals to spread into cooler and more humid areas.

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Tetrigid phylogeny - biochemical approach (Orthoptera: Tetrigoidea: Tetrigidae)

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ABSTRACT

Phylogenetically, the tetrigids are one of the most primitive groups of *Orthoptera.* These insects are related to tridactylids, on the one hand, and to acridids, on the other. To understand the phylogenetic relationships of orthopteroid groups including the tetrigids, various structural and non-structural parameters have been studied. In this study an attempt was made to establish relationships among tetrigids at the subfamily level, through a biochemical analysis of hemolymph proteins.

Potua sabulosa Hancock, *Euscelimena harpago* Serville, and *Euparatettix personatus* Bolivar were studied, as representative species of three subfamilies, Cladonotinae, Scelimeninae and Tetriginae, respectively. Hemolymph proteins from these species were characterized, using polyacrylamide gel electrophoresis under native, denaturing, and dissociating conditions. The results indicate that there are many proteins present in the hemolymph and that the pattern varies from species to species. The electrophoretic pattern and phylogenetic position of these insects are correlated.

Key words: hemolymph proteins, polyacrylamide gel electrophoresis, phylogeny, tetrigids (grouse locusts).

Although insects are a far more numerous and diverse group of animals than the vertebrates, biochemical knowledge of the former is rudimentary by comparison. Although phylogenetic studies have used information from such disciplines as morphology, anatomy, and ethoecology, biochemical information can also be useful. To be useful, there is a need for an unequivocal classification of proteins based on physiochemical properties. Hemolymph proteins show some promise in investigations on phylogenetic relationships among insects. Although present in relatively small numbers, they are synthesized in the fat body and are diffused into the hemolymph. These proteins are restricted to specific stages of insect life history and may vary from species to species (Levenbook, 1985; Wyatt and Pan, 1978). Tetrigid (grouse locust) hemolymph proteins were characterized in part by Paranjape *et al.* (1987). Isolation, purification, and characterization of proteins and assignment of a biological function are difficult tasks. To determine the types of proteins present in a given material, a methodology should be based on a wide variety of techniques utilizing different principles. We have attempted to characterize hemolymph proteins of three tetrigids, using polyacrylamide gel electrophoresis under native, dissociating, and denaturing conditions.

MATERIALS AND METHODS

Predominantly female adults of three species of tetrigids were used: *Potua sabulosa* Hancock (Cladonotinae), *Euscelimena harpago* Serville (Scelimeninae), and *Euparatettix personatus* Bolivar (Tetriginae). These species were chosen to represent the three subfamilies occuring in Pune-Satara region of Maharashtra, a southwestern State of India. The grouse locusts were collected locally, except for *P. sabulosa,* which were collected from Mahabaleshwar and Panchgani (located in Satara region about 75 km from Pune). Specimens were collected on several field trips during April to June 1989. The insects were maintained in laboratory cages in conditions simulating their natural habitat, for 4-5 days.

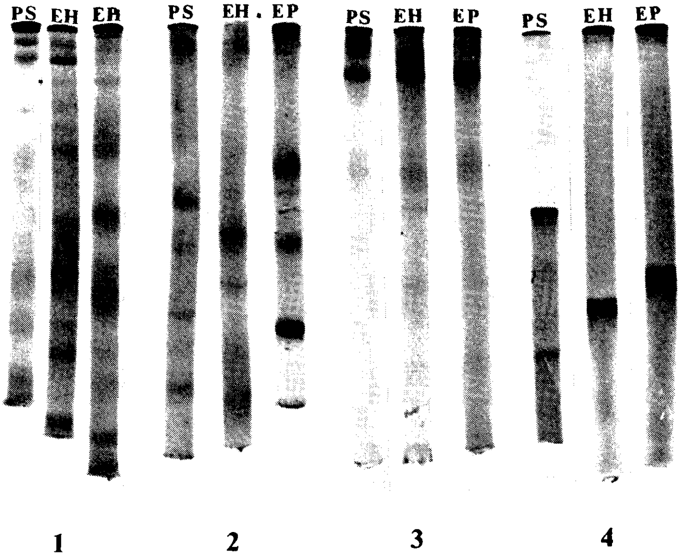
Hemolymph was collected by centrifuging (at 12000 rpm) the whole insect, after the hindleg was cut at the coxa. The hemolymph was collected in an Eppendorf tube (1.5 ml) in phosphate buffered saline (PBS) containing phenylmethysulphonylfluoride. The sample was used immediately for electrophoresis.

Polyacrylamide gel (PAGE) was employed for the electrophoretic separation of hemolymph proteins. A 7.5% PAGE was carried out as described by Work and Work (1972). Hemolymph proteins were also analysed under dissociating conditions at acid pH (Paniym and Chalkey, 1969) and at alkaline pH. The hemolymph proteins were also analysed by SDS PAGE (Laemmli, 1970).

RESULTS AND DISCUSSION

Figures 1-4.— show the electrophoretic pattern under native (Fig. 1), acid pH (Fig. 2), alkaline pH (Fig. 3) and SDS conditions (Fig. 4), respectively. In all species the maximum number of bands are seen under native conditions at pH 8.3 and 30-50% of the bands are located in the upper part of the gel while the remaining proteins are found in the lower part of the gel. The separation patterns of *P. sabulosa* and *E. harpago* are similar. Kinnear (1973) and Kinnear and Thompson (1975) showed that hemolymph proteins migrated as a single band at pH 7.3; at pH 8.6 six bands were noted. These results can be explained in terms of a pH dependent association-dissociation phenomenon. Proteins have a tendency for aggregation, which is maximum under alkaline pH. The bands appearing near the point of application can be regarded as aggregates. In the three species analyzed there is one common band, while *P. sabulosa* and *E. harpago* have two electrophoretically similar proteins.

With PAGE in the presence of 6.25 M urea under alkaline pH a smaller number of bands are noted as compared to native gel. It is worth noting that hemolymph contains basic proteins. Observations of the pattern of basic proteins in the three species shows that the basic protein patterns are more similar in *E. personatus* and *P. sabulosa* in terms of their electrophoretic mobilities in comparison to *P. sabulosa* and *E. harpago*. The similarity in the basic protein profile needs to be examined in further detail in order to clarify whether this similarity is due to similar proteins or different proteins having similar net charges. It is necessary to resolve this issue before any weight can be assigned to this because in all other respects *P. sabulosa* and *E. harpago* show a closer relationship. SDS PAGE profiles (Fig. 4) are indicative of the presence of low molecular weight proteins. It is clear that the electrophoretic patterns for *E. harpago* and *P. sabulosa* are very similar, although in *P. sabulosa* relatively high molecular proteins are seen. Similar low MW proteins were reported for *Drosophila melanogaster* (Brock and Roberts, 1980). Tojo *et al.* (1978) also found similar proteins in different developmental stages and concluded that there are only three or four types of low molecular weight proteins, but that aggregation results in multiple bands. Our observations clearly suggest that there are more than three or four types of proteins,



Figures 1-4.—Hemolymph protein profile by PAGE. 1. Native (pH 8.3, 7.5% gel), 2. Acid Urea (pH 2.7, 7.5% gel). 3. Basic Urea (pH 8.3, 7.5% gel). 4. SDS (pH 8.6, 12.5% gel). PS: *Potua sabulosa, EH: Euscelimena harpago, EP: Euparatettix personatus.*

and these are predominantly low molecular weight proteins. SDS PAGE and urea electrophoresis patterns support these observations.

CONCLUSIONS

Phylogenetically the tetrigids represent one of the most primitive groups of Orthoptera. Studies involving the ethoecology, biogeography, and biosystematics of tetrigids support this view and indicate that the grouse locusts are related to tridactylids, on the one hand, and acridids, on the other. Furthermore, of the three subfamilies under study, the Cladonotinae seem to be most primitive and are closely related to the Scelimeninae, which have an intermediate position, while the Tetriginae are more closely related to the Acrididae (Paranjape *et al.*, 1987).

The present biochemical study on hemolymph proteins also supports this interrelationship at the subfamily level. Additionally, the study reveals that the hemolymph of all the three species contains basic proteins. The hemolymph proteins have a tendency for aggregation which results in a multiple-band profile.

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The preserved fauna of grasshopper glacier (Crazy Mountains, Montana): Unique insights to Acridid biology

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ABSTRACT

In August, 1988, we conducted the first biological survey of Grasshopper Glacier, in the Crazy Mountains of Montana. This glacier lies at an elevation of 2,950 m and covers an area of ca. 45,000 m^2. We also studied a second, unnamed glacier 1 km southeast of Grasshopper Glacier occupying an area of ca. 90,000 m^2. A total of 22 insect families were found on the glaciers. From Grasshopper Glacier we collected 134 whole bodies of acridids (89 females and 45 males) and a number of body parts. From the unnamed glacier we collected only two grasshoppers. Grasshoppers were also intensively collected from the alpine meadows below the glaciers. Eighteen species of grasshoppers were found at or near the surface of the glaciers; 1 m deep ice pits provided no evidence of insects within the ice. Ten acridid species were found on the glaciers but not in the meadows; eight species were found both on the glaciers and in the meadows, and two species were found only in the meadows. Four specimens from Grasshopper Glacier were carbon dated and found to be < 40 years old. The grasshoppers preserved on the glaciers provide valuable information regarding the potential for phase variation and long distance movements of rangeland species.

Key words: grasshopper, accidentals, migration, phase variation, movement.

The migratory tendencies of most species of rangeland grasshoppers are poorly known. Long-distance movements of insects are difficult to track without expensive equipment. Although some migratory insects can be trapped during flight (*e.g.*, aphids [Tatlor, 1972]), this approach is not feasible with grasshoppers. Mark-recapture approaches are also inappropriate (Southwood, 1978). However, there is one other approach to determining the long-distance movements of grasshopper species. Large, aerial traps capable of sampling occasional migrants and large swarms exist in the form of glaciers, but the value of these natural collection sites has not been exploited. Alexander (1951, 1964) surveyed high altitude sites for accidental occurrences of grasshoppers, but this approach only allowed sampling at discrete points in time, rather than over a potentially long period, as is possible with collections from glaciers (700 years

[Lockwood *et al.*, 1989]).

There have been several studies of arthropod fallout on snow and ice (Caudell, 1902; Edwards and Banks, 1976; Spalding, 1979; Liston and Leslie, 1982; Ashmole, 1983; Price, 1985). Insects not consumed by the scavengers on icefields become frozen, and become embedded in the ice by virtue of differential heating (Hayden, 1873; Macauley, 1940; Uvarov, 1977). Thus, preservation in ice is not associated with gross organic changes, and frozen specimens may be of taxonomic value for centuries (Gurney, 1953; Lockwood *et al.*, 1989). Among the insects which become preserved in ice, grasshoppers are often reported in seemingly disproportionate numbers (Caudell, 1902; Liston and Leslie, 1982; Price, 1985). The prevalence of grasshoppers may be due to their propensity to migrate long distances, often in large numbers at high altitudes (Uvarov, 1977). Since glacially preserved grasshoppers cannot be analyzed with regard to physiological and ecological criteria of migration (Rabb and Kennedy, 1979), we simply considered migration to be any long distance movement.

Deposits of grasshoppers have been found in icefields on Mount Kenya (Shipton, 1934), Mount Kilamanjaro (Michelmore, 1934) and the Atlas Mountains (Rungs, 1933) in Africa. In the U.S., frozen grasshopper deposits have been found from 2,900 to 3,700 m (all altitudes are reported above-sea-level) in California, Colorado, Montana, Oregon, and Wyoming (Hayden, 1873; Kimball, 1899; Caudell, 1902; Bevan and Dorf, 1932; Henderson, 1933; Macauley, 1940; Meier, 1951; Dyson, 1952; Gurney, 1953; Spalding, 1979; Price, 1985). Although there are reports of grasshoppers preserved in ice at 15 locations in the U.S., probably no more than 12 of these deposits still exist, based on evidence from United States Geological Survey maps, first-hand descriptions and known rates of glacial recession (Marston *et al.*, 1989). In 1988, we travelled to Grasshopper Glacier and an unnamed glacier in the Crazy Mountains of central Montana. We documented the physical characteristics of these glaciers, determined the species, condition and distribution of grasshoppers in and on the glaciers, and examined the fauna in context of understanding grasshopper migration.

METHODS

Grasshopper Glacier and the associated unnamed glacier are located at 2,950 m, in Park Co., Montana, in the Crazy Mountains of the Gallatin National Forest (USGS map N4600-WI1015/7.5, Crazy Peak Quadrangle). Dyson (1952) noted that during warmer summers, grasshoppers were exposed in large quantities on the glacier. Dyson (1952) also mentioned that grasshoppers were found in a glacier that drained into Pear Lake, near Grasshopper Glacier. The unnamed glacier that we investigated drained into Twin Lakes, so our study included a different body of ice than that described by Dyson (1952). Descriptions of the glaciers and grasshopper deposits are based on observations made in August of 1988.

The sizes of the glaciers were determined with a RangingR Model 1200 rangefinder, and these measurements were photographically corroborated.

Grasshoppers were collected from the glaciers and from alpine meadows below the glaciers (Fig. 1). In the laboratory, specimens were cleaned, labelled and pinned; very poorly preserved specimens and body parts from the glaciers were stored in Riker mounts. The developmental stage, sex and species of each intact grasshopper were determined. A binomial test (Siegel, 1956) was used to determine if the sex ratio within each species differed significantly from 1:1. Other insects collected from the glaciers were identified to family.

A species was considered an accidental if it was found only on the glacier and at an altitude above its normal distribution. Possible accidentals included species that were found only on the glacier but at an altitude within their normal distribution, or were found both on the glacier and in the meadows (only as adults) but at an altitude above their normal distribution. A species was considered as a nonaccidental or resident if it was found in the meadows and at an altitude within its normal distribution, or it was found above its normal distribution in a nymphal stage.

The distributions of specimens on the glaciers were recorded. To determine the depth of grasshoppers within Grasshopper Glacier, an ice pit was dug to a depth of 1 m. In addition, a crevasse across the top of this glacier (10 m deep bergschrund) and ice caves into the back of the glacier (>15 m deep) were investigated for signs of embedded specimens.

Four samples from Grasshopper Glacier were sent to Beta Analytic (Coral Gables, Florida) for conversion of the target material for radiocarbon dating. The grasshoppers were given no pretreatment. They were combusted in an enclosed system and the carbon dioxides were purified and reacted with hydrogen on cobalt catalysts to produce graphite. The graphite was applied to copper targets and the accelerator mass spectrometry (AMS) technique was used for the radiocarbon dating. The AMS measurements were made in triplicate at the Eidgenossische Technische Hochshule University (Zurich, Switzerland). Carbon dates were corrected for the C_{13}/C_{12} ratio.

To determine if grasshoppers found only on the glaciers represented migratory phases, we compared the morphometric values of these specimens to the values of solitary forms of the same species (10 specimens of each sex) in collections at the University of Wyoming, Montana State University, and the Academy of Natural Sciences of Philadelphia. The museum specimens were all collected in Wyoming or Montana between 1909 and 1946. Our assumption was that a cross section of the available museum specimens represented the solitary phase of each species. The diagnostic measurements included length of the femur and tegmen, height of the head, height of the eye, and length, width and height of the pronotum (International, 1937; Dirsh, 1953; Uvarov, 1966). Measurements were made to 0.001 mm, using an ocular micrometer mounted on a binocular microscope. In addition, the dry weights of glacial and museum specimens were determined to the nearest 0.1 mg, using a digital balance. Differences in the glacial and museum specimens were analyzed using Student's t-test (Snedecor and Cochran, 1980). If only a single representative of a species was found on the glacier, the measurements of this specimen were considered as the true mean in the statistical analysis.

RESULTS AND DISCUSSION

Grasshopper Glacier covered an area of 30,000 to 60,000 m^2, with a length of 300 m and a width of 100 to 200 m (Figs. 2 and 3). Precise measurements of the glacier's width were not possible because a large amount of the ice was covered by the moraine (Fig. 2). The entire central portion of the glacier, an area of about 7,500 m^2 was covered by rubble (Fig. 3). From one-half to two-thirds of the ice was covered by rock. These observations suggest glacial recession has occurred, as might be expected from studies of other Rocky Mountain glaciers (Lockwood *et al.*, 1988; Marston *et al.*, 1989). Based on topographic maps (U.S. Geological Survey, 1972), the glacier is about one-tenth of its size just 16 years ago. Because Grasshopper Glacier is at a relatively low altitude, its rate of recession may be somewhat greater than other glaciers in the Rocky Mountains. On the other hand, this glacier lies in a bowl with a northwestern exposure which allows only about 6 hr of direct sunlight each day.

The unnamed glacier had a northern exposure and covered an area of ca. 60,000 to 120,000 m^2, with a width of 400 to 600 m and a length of 150 to 200 m (Fig. 4). As with Grasshopper Glacier, measurements of the glacier were confounded by rocks that covered the ice. One-fourth to one-third of this glacier appeared to be covered by rock. This glacier is about 8% of its size in 1972 (U.S. Geological Survey, 1972).

Insects were most frequently found on

the flat and lower portions of the glaciers, presumably concentrated in these areas by meltwater runoff. There was no evidence of deposits more than 1 cm below the surface. We found seven insect orders represented by 22 families: Coleoptera (Carabidae, Cerambycidae, Chrysomelidae, Coccinellidae, Elateridae, Hydrophilidae, Pedilidae, Scarabaeidae, and Staphylinidae), Diptera (Cecidomyiidae and Syrphidae), Hemiptera (Lygaeidae, Miridae, Reduviidae, and Scutelleridae), Homoptera (Aphidae), Hymenoptera (Formicidae, Ichneumonidae, and Vespidae), Lepidoptera (Noctuidae and Nymphalidae) and Orthoptera (Acrididae).

A total of 20 acridid species were collected (Table 1). Ten species were found only on the glaciers: *Melanoplus fasciatus* (F. Walker), *M. infantilis* Scudder, *M. occidentalis* (Thomas), *Arphia pseudonietana* (Thomas), *Trimerotropis campestris* McNeill, *Xanthippus montanus* (Thomas), *Amphitornus coloradus* (Thomas), *Aulocara elliotti* (Thomas), *Chloealtis conspersa* (Harris), and *Stenobothrus brunneus* (Thomas). Body measurements of seven of these ten species showed significant ($P<0.10$) differences between glacial and museum specimens (Table 2). Eight species were found both on the glaciers and in the meadows below the glaciers: *M. bivittatus* (Say), *M. borealis* (Fieber), *M. bruneri* Scudder, *M. packardii* Scudder, *M. sanguinipes* (F.), *Camnula pellucida* (Scudder), *Chorthippus curtipennis* (Harris), and *Stenophyma gracile* (Scudder). Two species were found only in the meadows: *M. oregonensis* (Thomas) and *Trimerotropis suffusa* Scudder.

Resident Species

Melanoplus borealis is montane (Alexander, 1969), as would be suggested by the species' name. This grasshopper has macropterous and brachypterous forms (Alexander, 1951, 1964); in our collections both sexes possessed wings that extended beyond the tip of the abdomen.

Melanoplus bruneri is a montane species found at moderate elevations (Hebard, 1929; Alexander, 1951; Capinera and Sechrist, 1982). Females were found significantly ($P<0.05$) more often than males on the ice but not in the meadows. Thus, it appears that females may take flight more frequently or engage in longer distance flights than males. Females are more dispersive than males in many insect species (Matthews and Matthews, 1978).

Melanoplus oregonensis is a montane species found at high elevations (Alexander, 1951; Capinera and Sechrist, 1982). Because males and females of this species are brachypterous this species was found only in the meadows.

Melanoplus packardii was considered a "true prairie species" by Capinera and Sechrist (1982). However, Alexander (1964, 1969) suggested that populations might become established up to 3,050 m, although there was direct evidence for completion of a life cycle only up to 2,600 m. Our finding fifth instars in the meadows and adults on the glacier extends the known resident altitude of this species to 2,950 m.

Melanoplus sanguinipes has one of the broadest geographic ranges in its genus (Alexander, 1964; Capinera and Sechrist, 1982). Alexander (1951, 1964) and Price (1985) have found *M. sanguinipes* as high altitude accidentals. The vertical distribution of this species appears to be a function of seasonal weather conditions (Alexander, 1964), and finding a population at 2,950 m suggests that the climate in 1988 was favorable at this site.

Camnula pellucida is common at high altitudes (Caudell, 1903) and may occur above timberline (Hebard, 1929). Alexander (1951, 1969) pointed out that, although specimens have been collected up to 3,050 m, there was no evidence that this grasshopper could complete its life cycle above timberline. Our finding a population which included nymphs and adults above timberline establishes an alpine distribution for *C. pellucida*. Although this species may swarm for short distances (Criddle, 1933; Ball *et al.*, 1942; Helfer, 1953), only a single

Table 1.—Grasshoppers recovered from Grasshopper Glacier (Crazy Mountains, Montana) in 1988.

Species	Location[a]	Males/Females[b]	Stage	Accidental[c] (upper altitude limit)
MELANOPLINAE				
M. bivittatus	glacier[1]	4/3	adult	possible (2,700 m)
	meadow	2/1	adult	
M. borealis	glacier[1]	1/0	adult	no (3,350 m)
	meadow	1/4	adult	
M. bruneri	glacier[1]	5/18*	adult	no (3,400 m)
	meadow	6/8	adult	
M. fasciatus	glacier[1]	2/1	adult	possible (3,350 m)
M. infantilis	glacier[1]	8/4	adult	possible (2,700 m)
M. occidentalis	glacier[1]	1/1	adult	possible (2,100 m)
M. oregonensis	meadow	8/8	adult	no (3,400 m)
M. packardii	glacier[1]	5/8	adult	no (2,600 m)
	meadow	0/2	instar V	
M. sanguinipes	glacier[1]	9/15	adult	no (3,050 m)
	meadow	4/2	adult	
	meadow	0/1	instar V	
OEDIPODINAE				
A. pseudonietana	glacier[2]	1/0	adult	yes (2,100 m)
C. pellucida	glacier[1]	1/0	adult	no (3,300 m)
	meadow	14/16	adult	
	meadow	0/1	instar IV	
T. campestris	glacier[1]	1/0	adult	yes (2,750 m)
T. suffusa	meadow	3/1	adult	no (2,600 m)
X. montanus	glacier[1]	1/0	adult	yes (unknown)
GOMPHOCERINAE				
A. coloradus	glacier[1]	1/0	adult	yes (1,800 m)
A. elliotti	glacier[1]	8/32*	adult	yes (1,750 m)
C. conspersa	glacier[1]	0/1	adult	yes (2,050 m)
C. curtipennis	glacier[1]	1/1	adult	no (3,400 m)
	meadow	4/11*	adult	
	meadow	0/2	instar V	
S. brunneus	glacier[1]	1/0	adult	possible (unknown)
S. gracile	glacier[1]	2/0	adult	no (unknown)
	glacier[2]	1/0	adult	
	meadow	3/0	adult	

[a] glacier[1] = Grasshopper Glacier, glacier[2] = unnamed glacier

[b] An asterisk indicates that the male: female ratio differs significantly ($P<0.10$) from 1: 1.

[c] Upper altitudinal ranges are taken from Alexander (1951, 1964) and Alexander and Hilliard (1969).

yes = the species was found only on the glacier and at an altitude above its normal distribution.

possible = the species was found only on the glacier but was at an altitude within its normal distribution, or it was found on the glacier and in the meadows (only as adults) but at an altitude above its normal distribution.

no = the species was found in the meadows and at an altitude within its normal distribution, or it was found above its normal distribution in a nymphal stage.

Table 2.—Morphometeric (millimetres) and dry weight (mg) comparisons of potentially migratory (glacier deposits) and solitary (museum collections) specimens of grasshopper species ocurring as possible high altitude accidentals.

Species	Sex	N	Location	Measurements*							
				DW	FL	TL	HW	EH	PH	PL	PW
MELANOPLINAE											
M. fasciatus	male	2	glacier	130.2	13.822**	18.174**	4.258**	2.108	3.718	4.676	4.175
	male	10	museum	107.3	9.994**	11.312**	3.537**	2.114	3.762	4.261	3.886
	female	1	glacier	64.4**	15.148**	18.155**	3.908	2.049	4.083	4.762	4.633
	female	10	museum	141.9**	10.890**	11.650**	3.808	2.160	4.256	5.068	4.740
M. infantilis	male	2	glacier	39.6**	8.577	13.702	3.147	1.619	2.556	3.188	2.909
	male	10	museum	66.3**	9.070	12.803	3.153	1.760	2.852	3.406	3.078
	female	7	glacier	42.2**	8.661	13.458	3.359	1.667*	3.124	3.424**	3.421
	female	10	museum	83.8**	9.967	13.050	3.410	1.837*	3.314	3.678**	3.541
M. occidentalis	male	1	glacier	104.6	8.874	14.400	3.205	1.954	2.993	4.407	3.306
	male	10	museum	102.5	9.846	13.660	3.332	1.937	3.276	4.105	3.532
	female	1	glacier	73.3	10.604	17.414	3.662	2.030	4.122	4.376	4.104
	female	10	museum	128.5	10.750	15.835	3.762	2.006	3.706	4.352	4.189
OEDIPODINAE											
A. pseudonietana	male	1	glacier	108.8	13.061	22.875	4.178	1.766	5.169	4.914	5.327
	male	10	museum	129.1	13.240	24.299	4.109	1.749	4.821	4.817	4.629
T. campestris	male	1	glacier	—	—	23.903	4.159	1.669	4.589	4.406	5.230
	male	10	musuem	—	—	25.153	4.128	1.924	4.428	4.610	5.176
X. montanus	male	1	glacier	—	12.011	22.277**	4.067**	1.801**	4.788**	5.076**	5.758**
	male	10	museum	—	13.182	27.571**	4.749**	2.064**	5.770**	6.564**	6.741**
GOMPHOCERINAE											
A. coloradus	female	1	glacier	85.9*	11.771	18.231	4.018	1.827	4.388	3.833	4.421*
	female	10	museum	111.7*	12.222	17.283	3.903	2.060	3.973	3.952	3.911*
A. elliotti	male	8	glacier	56.8**	10.710**	16.461**	3.813**	1.755**	3.333**	3.439**	3.824**
	male	10	museum	80.9**	9.423**	11.214**	3.279**	1.627**	2.900**	2.933**	3.256**
	female	10	glacier	81.0**	11.892	17.882**	4.712**	1.853	4.048*	4.029**	4.710**
	female	10	museum	128.0**	11.388	14.925**	4.333**	1.846	3.727*	3.600**	4.227**
C. conspersa	female	1	glacier	133.9	12.699**	16.656**	3.931	1.166	3.254**	4.361	5.033
	female	10	museum	114.3	10.661**	8.147**	3.835	1.802	4.018**	4.148	4.420
S. brunneus	male	1	glacier	77.2	12.350	17.017*	4.730*	1.791	4.762*	4.224	5.300*
	male	10	museum	88.2	11.053	13.704*	3.882*	1.666	3.558*	3.536	3.958*

* Means of body measurements followed by * (P<0.10) or ** (P<0.05) differ significantly between glacial and museum specimens. DW = dry weight, FL = femur length, TL = tegmen length, HH = head height, EH = eye height, PH = pronotum height, PL = pronotum length, and PW = pronotum width. Body measurements with no indicated values could not be accurately determined for the glacial specimens, due to the state of preservation.

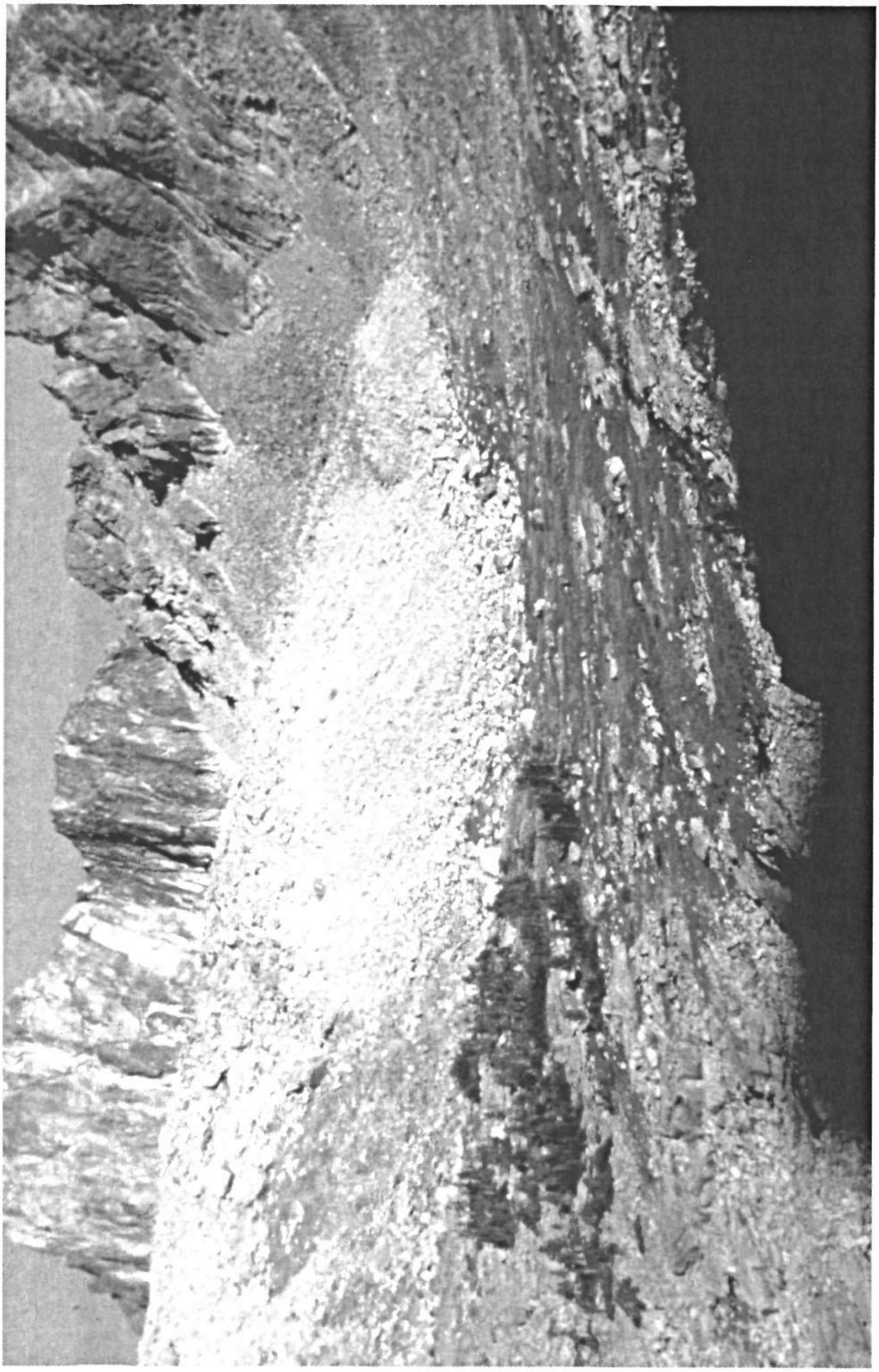

Figure 1. Alpine meadows (lower center) below Grasshopper Glacier. The glacier lies between the ridge (extending from the upper left) and the vertical peaks (in the background).

adult was found on the glacier, suggesting that flights were either uncommon or short distance in the resident population.

Trimerotropis suffusa has a wide altitudinal distribution (Helfer, 1953; Otte, 1984). Although this species may be considered a strong flier, no *T. suffusa* were found on the glacier. As suggested by Alexander (1964), both the possession of well developed wings and a behavioral predisposition are necessary for extended flights.

Chorthippus curtipennis can be found from mountain foothills to timberline (Hebard, 1929; Alexander and Hilliard, 1969). It is interesting to note that there were significantly ($P<0.05$) more females than males in the meadow, and this species is capable of parthenogenesis (Creighton and Robertson, 1941).

Stenophyma gracile is a mountain meadow species (Morse, 1896; Helfer, 1953). Only males were found; because females are brachypterous (Otte, 1981), they would have been unable to reach the glaciers.

Accidental Species

Melanoplus bivittatus is a widely distributed species; it is generally considered an urban pest but can be found on mountain slopes (Capinera and Sechrist, 1982). Although it is generally considered a clumsy and weak flyer (Alexander, 1964), *M. bivittatus* may exhibit migratory tendencies (Scudder, 1897; Corkins, 1923; Criddle, 1933). Alexander (1964) listed this species as a relatively common high altitude accidental in Colorado.

Melanoplus fasciatus has been considered an accidental above timberline (Alexander, 1951). This species is generally considered brachypterous, although individuals may rarely have long tegmina (Alexander, 1964; Capinera and Sechrist, 1982). The three specimens that we collected all had tegmina extending to or beyond the tip of the abdomen. Although macropterous individuals are considered quite reluctant to take flight (Helfer, 1953), the possibility of a migratory phase was suggested by the significantly ($P<0.05$) larger femora, tegmina and tegmen:femur ratios found in the glacial specimens, as compared to the museum specimens.

Melanoplus infantilis was found only on the glacier but may complete its life cycle near the elevation of our study site (Alexander, 1969). Since this species is not known to be migratory (Alexander, 1964; Capinera and Sechrist, 1982), the collected specimens are the first preliminary evidence of long distance flights in *M. infantilis*. As further support for this interpretation, the glacial specimens weighed significantly ($P<0.05$) less than the museum specimens. Cheu (1952) found that in *Locusta*, the dry weight of solitary females was 14 to 38% greater than gregarious females, depending on their age, and in males the dry weights of gregarious males were slightly (5 to 14%) greater than solitary males, depending on their age. Two *M. infantilis* specimens were carbon dated (Beta-29297, ETH-5017 and Beta-29298, ETH-5018); the samples were determined to be less than 40 years old.

Melanoplus occidentalis has been found as a high altitude accidental and is known to be migratory (LaRivers, 1948; Alexander, 1951, 1964). Although early reports suggested that this species may occur above timberline (Hebard, 1928, 1929), Alexander (1964, 1969) considered specimens from above 2,000 m to be accidentals.

Arphia pseudonietana has been documented as a rare high altitude accidental (Alexander, 1964). Although adults of this species fly frequently, their flights are generally less than a meter from the ground and they are not known to engage in long distance movements (Capinera and Sechrist, 1982; Otte, 1984).

Trimerotropis campestris has not been previously documented as a high altitude accidental and is not known to engage in migratory flights. This species may be found up to 2,750 m, although it is not clear that it can complete its life cycle at this elevation (Alexander, 1969). Alexander (1964) found *T. pallidipennis* as a rare accidental between 2,400 and 2,850 m.

Xanthippus montanus is normally associated with flat, dry areas or sandy rolling grasslands (Otte, 1984). Based on Otte's (1984) distribution map, this specimen appears to be a new record for Montana. Oddly, the specimen recovered from the glacier was significantly ($P<0.05$) smaller than the museum specimens in almost every body measurement. In every other species in which there was a significant ($P<0.10$) difference between the glacial and museum specimens, the presumed migrants were larger than the solitary individuals.

Amphitornus coloradus has been previously documented as a rare high altitude accidental (Alexander, 1951, 1964). Since adult females are inactive most of the time and generally stay on a single plant (Anderson and Wright, 1952), it is unusual to have found a female on the glacier. The specimen from the glacier differed slightly ($P<0.10$) from the museum specimens, with regard to dry weight and pronotal width.

Aulocara elliotti has been previously documented as a high altitude accidental (Alexander, 1951, 1964). However, from our collection, it appears that this species may migrate in swarms. Nymphs have been observed to swarm, and there is circumstantial evidence of migration in adults (Pfadt, 1981). Interestingly, significantly ($P<0.05$) more females than males were recovered from the glacier. This is somewhat unusual in that females may suffer higher mortality than males (particularly during oviposition), and other grasshopper swarms have been found to be composed largely of males (Popov, 1954). Morphometric evidence also suggested that the glacial specimens were a migratory phase. To our knowledge, this is the first evidence of phase variation in *A. elliotti.* Although males recovered from the glacier weighed significantly ($P<0.05$) less than museum (solitary) specimens, every body measurement taken on males from the glacier was significantly ($P<0.05$) larger than the measurements of museum specimens: a similar trend was observed in females. Even the tegmen:femur ratio was significantly ($P<0.05$) greater in glacial males and females (1.54:1 and 1.50:1, respectively) than in museum males and females (1.19:1 and 1.31:1, respectively). Given the morphometric differences previously found between solitary and migratory phases of acridids (Faure, 1933; Dirsh, 1953; Uvarov, 1966, 1977), it appears that *A. elliotti* possesses a previously unknown migratory phase. Two *A. elliotti* specimens were carbon dated (Beta-29299, ETH-5019 and Beta-29300, ETH-5019); the samples were determined to be less than 40 years old.

Chloealtis conspersa females have been considered brachypterous (Rehn, 1904; Helfer, 1953; Otte, 1981; Capinera and Sechrist, 1982). Although a number of normally brachypterous species are known to have occasional macropterous forms (Capinera and Sechrist, 1982), this phenomenon has not been previously reported in *C. conspersa.* However, since there are at least two macropterous specimens in the Academy of Natural Sciences of Philadelphia, the macropterous specimen collected from the glacier was apparently rare but not unprecedented. Given the location and morphology of the recovered specimen, it may be taken as the first real evidence that *C. conspersa* has migratory abilities. The significantly ($P<0.05$) larger femora of the glacial specimen support the possibility of a migratory phase.

Stenobothrus brunneus is a montane species (Otte, 1981; Capinera and Sechrist, 1982). The wings of the recovered specimen were very long, extending to the ends of the femora. Some significant ($P<0.10$) differences between the glacial specimen and the museum specimens suggest the possibility of a migratory phase, but a single specimen is not definitive.

CONCLUSIONS

As noted by Uvarov (1977) and others, migratory flight in acridids is not restricted to swarms, but may also occur in solitarious adults and in nonswarming grasshoppers. The deposition of migratory grasshoppers

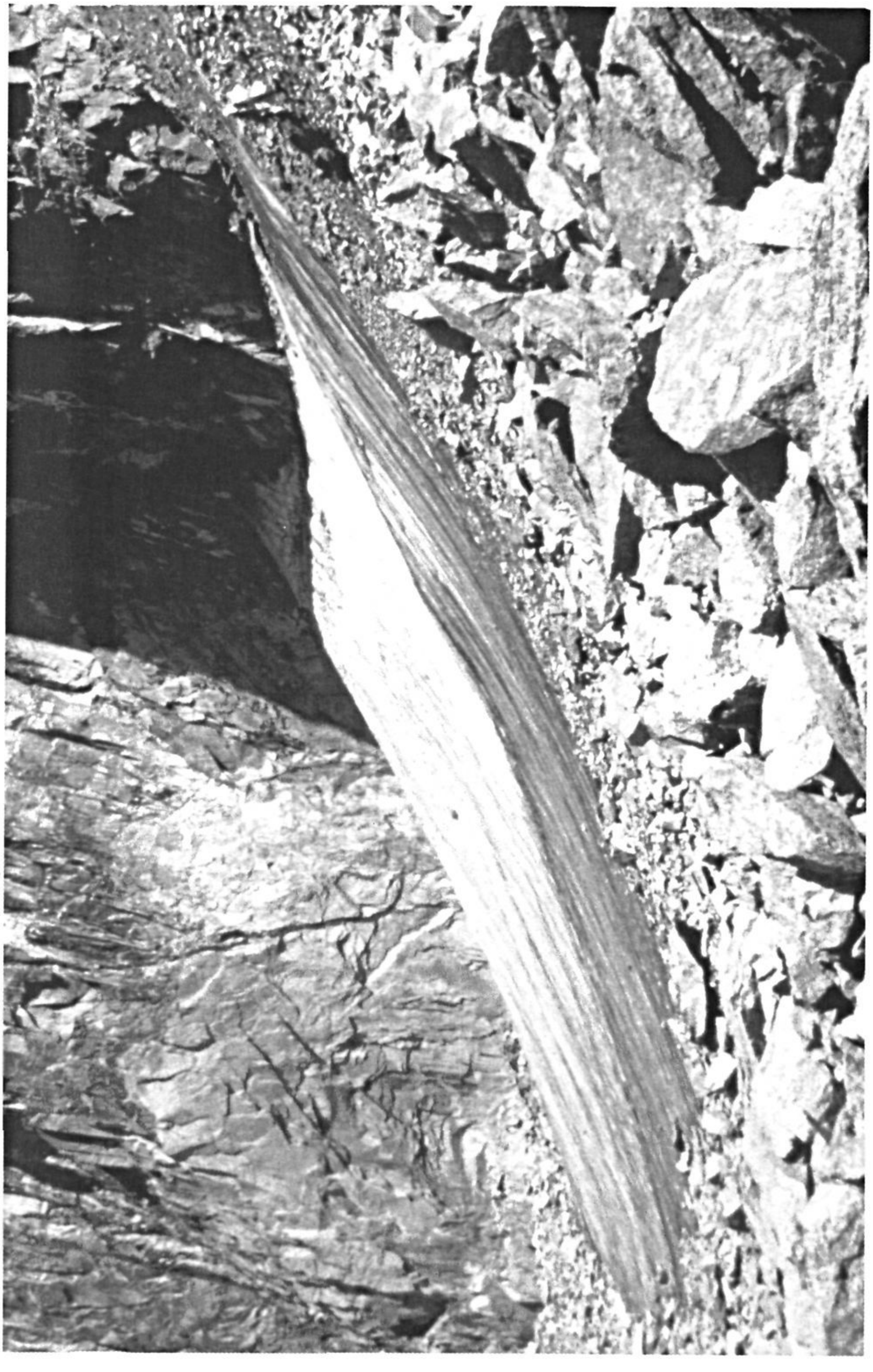

Figure 2. View across the upper portion of Grasshopper Glacier. Note the surrounding cliffs that protect the ice from wind and extended sunlight. The glacier extends beyond and beneath the rocks in the foreground and in the lower left of the photograph.

on glaciers is likely a result of the qualities of migratory movement; migrating grasshoppers are dependent for horizontal transportation on the flow of air at high altitudes. This process of planktonic movement in the prevailing winds accounts for the radically different densities of grasshoppers preserved on glaciers located only 1 km apart. The acridids found on Grasshopper Glacier were well preserved and were of relatively recent origin. There was no evidence of older deposits within the ice, although such layers may have been lost during the extensive glacial recession in the last 25 years. Of the 20 species of grasshoppers found on the glaciers, six species which were considered as accidentals, five were considered as possible accidentals and nine were considered as residents or non-accidentals.

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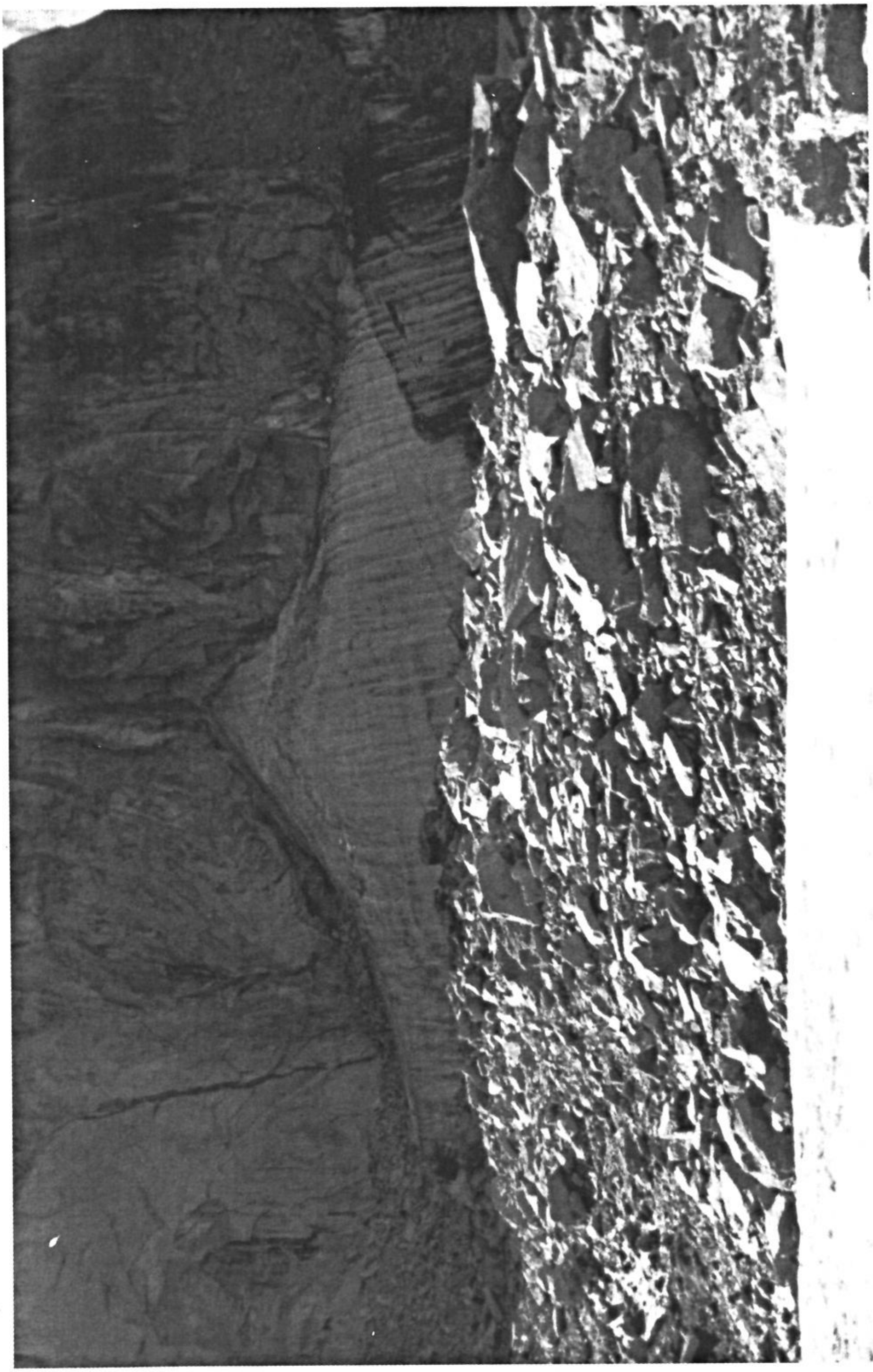

Figure 3. View up the length of Grasshopper Glacier. The ice in the foreground is immediately above the toe of the glacier. The glacier passes under the rocks in the center of the photograph and extends into the background.

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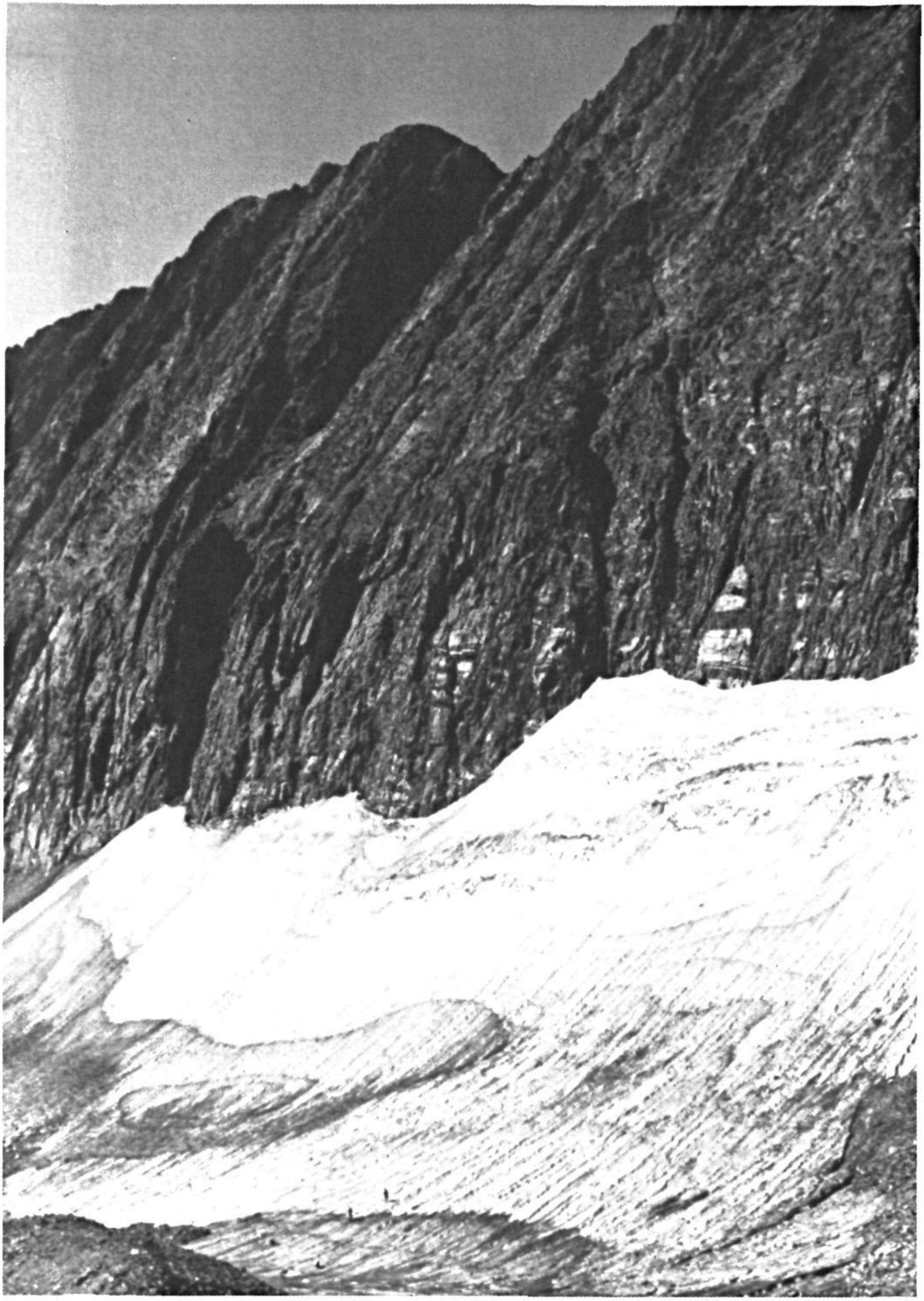

Figure 4. View across the unnamed glacier. Note the people in the lower center of the photograph.

Ecología y comportamiento

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The songs of the European grasshoppers of the *Chorthippus biguttulus* group in relation to their taxonomy, speciation and biogeography (Orthoptera: Acrididae)

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ABSTRACT

Until recently the *Chorthippus biguttulus* group was thought to consist of three widespread species: *biguttulus, brunneus,* and *mollis*. Studies on the songs have now shown that these species are largely replaced in the southern European peninsulas by other species that are morphologically similar but have quite different songs. These southern species are reviewed, their songs described and their status and distribution discussed. For the Balkan Peninsula no more than a tentative, preliminary account is given, much further work being needed before final conclusions can be drawn about this group in south east Europe. The problem of defining species in the biguttulus group is briefly discussed.

Key words: acoustics, Acrididae, biogeography, *Chorthippus biguttulus,* Europe, Orthoptera, song, taxonomy.

INTRODUCTION

Chorthippus biguttulus (L.) is one of the commonest European grasshoppers, occurring in open habitats throughout a large part of northern and central Europe. It was the first-named member of a complex of closely similar species referred to for convenience as the *biguttulus* group and characterized by their slit-like tympana, angled pronotal lateral carinae, fully developed wings and lack of any striking features of colour pattern. We do not pretend that the group can be clearly defined on these characters - some of the Greek members, for example, have more open tympana than is typical - but we think few people would doubt the close relationship of the species we include in this account. Until recently this group was thought to consist of only three species, *C. biguttulus, C. brunneus* (Thunberg) and *C. mollis* (Charpentier), difficult to distinguish morphologically but easily recognized in the field from the highly distinctive calling songs of the males. However, it has become clear, mainly through studies on the songs, that the group contains at least twice this number of species in western Europe alone (Ragge, 1987; Ragge and Reynolds, 1988) and several more in eastern Europe and Asia. Our aim in this paper is to give a brief review of our present knowledge of the composition of the group in western Europe, especially in the southern European peninsulas where most of the interest lies. Our conclusions are strongly influenced by the male calling songs which, in providing the basis for a mate recognition system, we regard as the most reliable indication of species limits.

The bioacoustic terms used in this paper are defined as follows:

Syllable. The sound produced by one complete down and up movement of the hind legs.

Echeme. A first-order assemblage of syllables.

Echeme-sequence. A first-order assemblage of echemes.

Our account is limited to Europe west of Russia, but including North Africa, and for convenience we have divided this area into four zones.

NORTHERN AND CENTRAL EUROPE

As far as we know at present, only the three original members of the group occur in the whole of northern and central Europe, *i.e.*, north of the Pyrenees and Alps (Fig. 14). Oscillograms of the male calling songs of these species are shown in Figs. 1-3. In the extreme north there is a Finnish form of *brunneus* that has a rather different song and small differences in morphology, but Perdeck (1957) found experimentally that the song difference did not form a reproductive barrier of any significance and this form is at present treated as a subspecies of *brunneus* (*C. brunneus brevis* Klingstedt).

In the Alps there are two further variants showing small differences in song and mor-

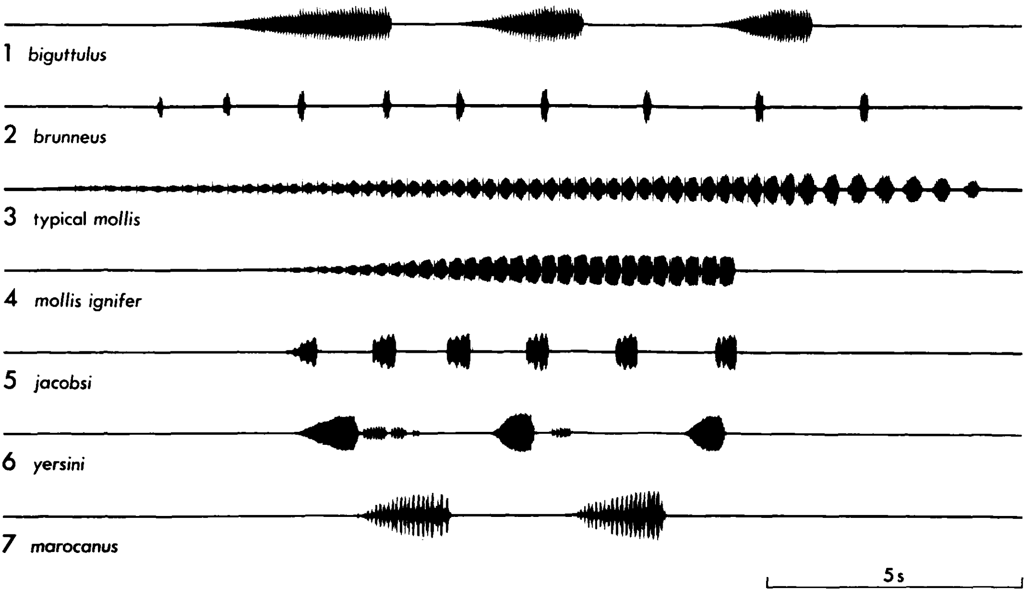

Figure 1-7. Oscillograms of the male calling songs of members of the *Chorthippus biguttulus* group. The song recordings used for Figure 1-3, 5 and 6 were made in the field using a Uher 4200 or 4200IC tape recorder and AKG D202 microphone; those used for Figure 4 and 7 were made in the British Museum (Natural History) Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH 405 microphone. Further data are given in Table 1.

phology, *C. biguttulus eisentrauti* (Ramme) and *C. mollis ignifer* Ramme. The first of these has a calling song very similar to that of typical *biguttulus* and is probably just a local form of it, although sometimes treated as a distinct species. The calling song of *C. mollis ignifer* is about half as long as the typical *mollis* calling song and has a more abrupt ending (Fig. 4). It is likely that the population in the French Alpes-Maritimes, forming the subject of two recent papers by one of us (Ragge, 1981, 1984), represents a southern outlier of *C. m. ignifer* and that this alpine form originated by hybridization between *mollis* and *biguttulus:* the evidence for this, based on morphology and both calling and courtship songs, is given in these two papers.

IBERIAN PENINSULA AND NORTH AFRICA

Two of us recently have been able to demonstrate (Ragge and Reynolds, 1988) that the three original members of the group are absent from most of the Iberian Peninsula, occurring only in the vicinity of the Pyrenees and, in the case of *brunneus,* along a northern strip of the peninsula from Galicia to the Basque Country (Fig. 14). Further south these species are replaced by two others, *C. jacobsi* Harz and *C. yersini* Harz, which are difficult to identify morphologically but can be recognized easily by the calling songs of the males (Figs. 5 and 6).

The only member of the *biguttulus* group that is so far known for certain from North Africa is *C. marocanus* Nadig, which is

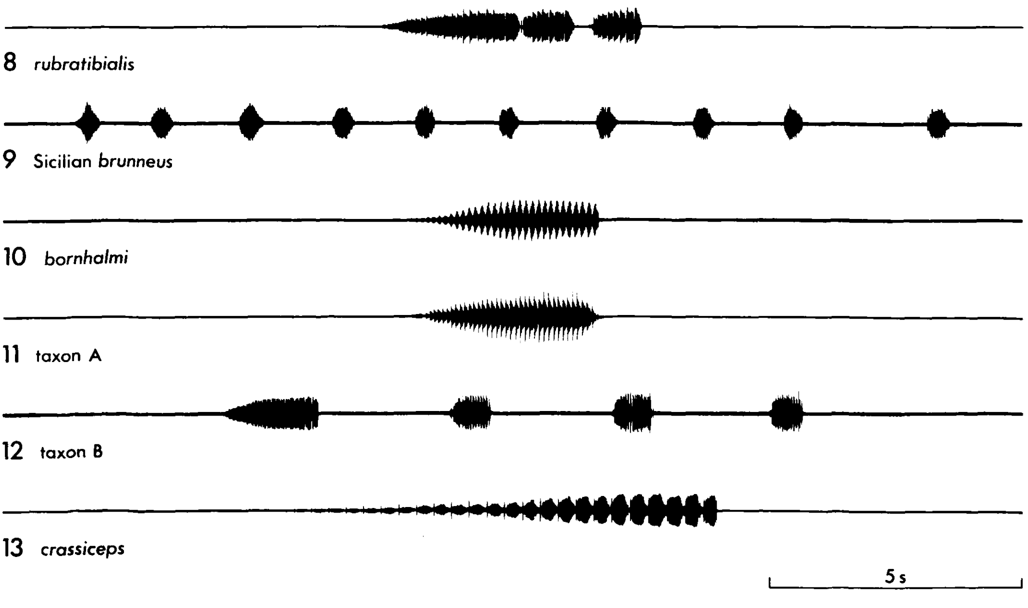

Figure 8-13. Oscillograms of the male calling songs of members of the *Chorthippus biguttulus* group. The song recordings used for these figures were made with a Uher 4200IC or 4200 Monitor tape recorder and AKG D202 or (Figure 12 and 13 only) Sennheiser K30AV/ME88 microphone. Figure 11 is taken from an indoor recording; the remaining oscillograms are all taken from field recordings. Further data are given in Table 1.

again recognized most easily by its calling song (Fig. 7), and especially the highly characteristic rivalry song (Ragge and Reynolds, 1988, Fig. 69).

ITALIAN PENINSULA AND SICILY

Recent fieldwork by one of us (DRR) has established that *biguttulus* and *mollis* are absent from the Italian Peninsula, occurring in Italy only in the vicinity of the Alps (Fig. 14). In the peninsula proper there are only two members of the group: *brunneus* and *C. rubratibialis* Schmidt. Until recently *rubratibialis* has been regarded as a subspecies of *biguttulus* because of its rather similar song (Fig. 8), but Schmidt (1978, 1987) has demonstrated experimentally that, although hybrid eggs and nymphs can be obtained by crossing *rubratibialis* with typical *biguttulus*, most of them die before reaching the adult stage and the few reaching adulthood die within a few days of the final moult. In view of this we agree with Schmidt (in press) that *rubratibialis* is better treated as a distinct species.

In Sicily the situation is different and rather surprising: two members of the group are again present, but they are different from the two on the Italian mainland. One of them is *yersini*, previously known only from Spain; the Sicilian populations agree closely in both morphology and song with Spanish *yersini*. The other is a form of *brunneus* in which the echemes of the male calling song (Fig. 9) have a much slower tempo than that of typical brunneus, and the

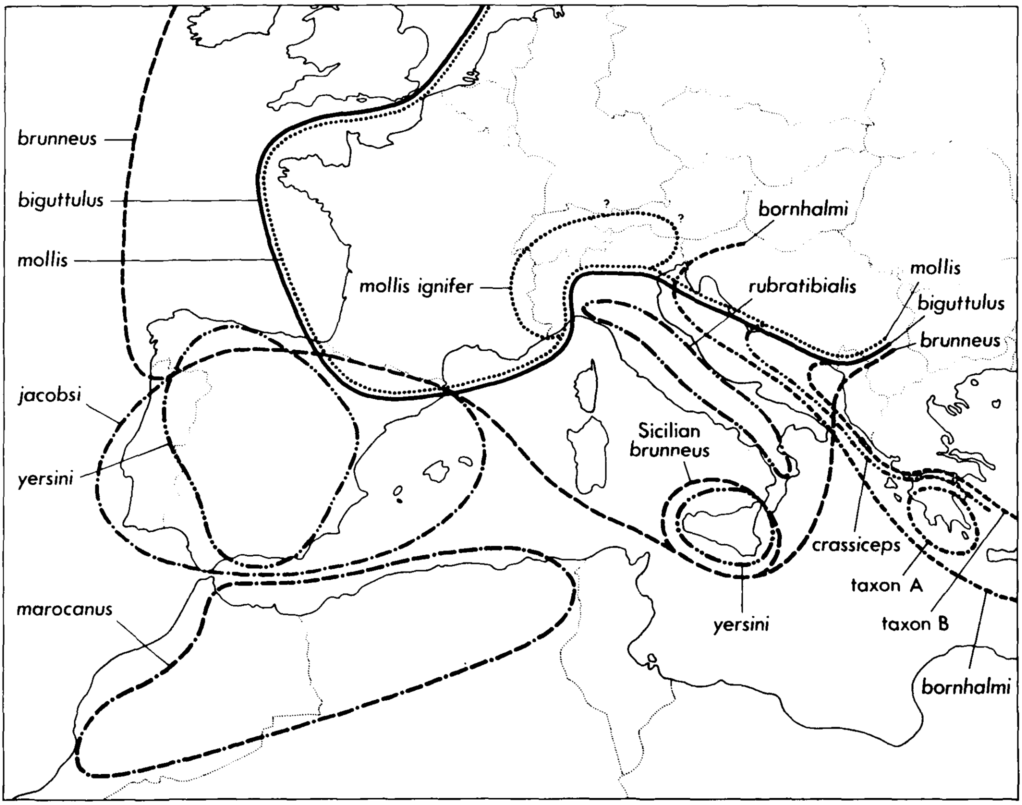

Figure 14. Map showing the very approximate distribution of members of the *Chorthippus biguttulus* group in western Europe and North Africa. The lines drawn in the Balkan region, and the northern and eastern limits of *C. mollis ignifer*, are still very uncertain.

Table 1.—Data for the song recordings used in Figs. 1-13. The recordist was either DRR or WJR for Figs. 1-9 and FW for Figs. 10-13.

Figure	Locality	Date recorded	Air temperature
1	Spain: Lérida, 7 km SE of Seo de Urgel.	12-IX-1978	26° C
2	Spain: Huesca, Valle de Pineta.	23-VII-1983	27° C
3	Spain: Lérida, 7 km SE of Seo de Urgel.	12-IX-1978	27° C
4	Italy: Piedmont, near Cuorgne, S. Elisabetta, 1300 m.	30-IX-1987	28° C
5	Spain: Huesca, near Lanave.	28-VI-1984	28° C
6	Spain, León, 40 km N of León, near Villamanín.	28-VIII-1984	28° C
7	Morocco: Haut Atlas, Oukaimeden, 2650 m.	5-VIII-1986	27° C
8	Italy: Emilia-Romagna, Foresta di Campigna, Passo La Calla, 1300 m.	6-IX-1988	23° C
9	Italy: Sicily, near Messina, 2 km N of Colle San Rizzo.	10-IX-1988	22° C
10	Greece: Peloponnese, Arcadia, Mt. Mainalon, above Kardhara, 1500 m.	20-VI-1986	22° C
11	Greece: Peloponnesse, Messenia, S. of Kalamata, Kardhamili.	27-XI-1987	
12	Greece: Epirus, Ioannina, plateau N of Metsovon, 1300 m.	21-VIII-1988	25° C
13	Greece: Central, Voiotia, Mt. Parnassus, 1300 m.	9-VIII-1988	25° C

number of stridulatory pegs is much higher (110-130). The difference in song is of a similar order to that between typical *brunneus* and Finnish *brunneus* (subspecies *brevis)*, and we think it unlikely that it would constitute a reproductive barrier; we therefore think it best to treat the Sicilian populations as a local form of *brunneus* rather than a distinct species.

BALKAN PENINSULA

All three of the original members of the group occur in the northern part of the peninsula, where they are joined by a fourth member, *C. bornhalmi* Harz, which occurs throughout the peninsula and is again most easily recognized by its song (Fig. 10). In the southern part of the peninsula the situation is different, rather complicated and far from being completely resolved (Fig. 14). *Chorthippus brunneus* is completely absent; as noted by Willemse (1985), the records cited by Willemse (1984) were actually based on *bornhalmi*, which is morphologically very similar. There is a variety of songs of the *biguttulus* type, but they are usually noticeably different from the typical *biguttulus* song and always produced by insects morphologically different from *biguttulus*. One of these songs is shown in Fig. 11; it is produced by a taxon occurring only in the Peloponnese and referred to by Willemse (1984) as *C. crassiceps* (Ramme), but we now believe it is an undescribed taxon which we refer to for convenience as "A". Although the oscillograms shown in Figs. 10 and 11 look superficially similar, these two songs are in fact fundamentally different: in *bornhalmi* the subdivisions of the song visible in the oscillogram are simple syllables, whereas in taxon A they are echemes (*i.e.*, groups of syllables), as in *biguttulus*.

Another song (Fig. 12) consists of an

echeme-sequence of the *biguttulus* type followed by one or more loud and highly characteristic "aftersongs". The grasshoppers producing this song were included by Willemse (1984) in *C. b. hedickei* Ramme, but we now believe they belong to another undescribed taxon which we are calling for the time being "B"; it is known so far only from north of the Peloponnese.

Typical *mollis* seems to be replaced in Greece by a taxon producing a song rather similar to that of *mollis ignifer* in the Alps; it is again much shorter than the typical *mollis* song and has a more abrupt ending (Fig. 13). The insects producing it, however, are quite different in appearance from both typical *mollis* and *mollis ignifer*. This taxon can be confidently named *crassiceps*, at least on the island of Poros, as this island is the type locality of *crassiceps* and the population on it produces this kind of song. The song is also produced by populations in mainland Greece (though it has not yet been heard, surprisingly, in the Peloponnese), but usually from males that are morphologically rather different from those on Poros, and so the application of the name *crassiceps* on the Greek mainland is less certain. It is possible, as noted by Willemse (1985), that *C. lesinensis* (Krauss), described from the Dalmatian island of Hvar, will prove to be a senior synonym of *crassiceps*.

Finally, there is a grasshopper in Greece that looks like a member of the *biguttulus* group but produces a song closely resembling that of *C. vagans* (Eversmann). *C. vagans* typically has wide open tympana and is thus excluded from the *biguttulus* group, but the "sing-alikes" that occur in Greece have much less open tympana and are generally more like the *biguttulus* group in appearance. This is yet another problem that cannot be resolved without further study.

It is clear from this very preliminary account of the Balkan members of the *biguttulus* group that we are still a long way from a complete understanding of the group in this part of Europe. The situation in the southern part of the peninsula seems to be very complex and may well be further complicated by hybridization. Dr. O. von Helversen of the Friedrich-Alexander-Universitat, Erlangen-Nurnberg, is making a comprehensive study of this group in this part of Europe and Turkey, and his conclusions will be eagerly awaited.

THE CRITERIA FOR SPECIES DEFINITION IN THE *BIGUTTULUS* GROUP

The biological species definition, developed in particular by Mayr (*e.g.*, 1969, p. 412), refers to species as "groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups". Recognizing that every gradation exists between, on the one hand, local populations showing slight differences (biological or morphological) but freely interbreeding with each other and, on the other hand, populations that are completely different and quite incapable of interbreeding, we nevertheless accept that the biological species definition is the most reasonable one available. However, applying it to species-complexes like the *biguttulus* group is difficult. We know that several pairs of species within the group will interbreed freely under suitable conditions and will produce fertile hybrids with little or no loss in viability (*e.g.*, Perdeck. 1957; Helversen and Helversen, 1975; Sychev, 1979). These pairs are largely sympatric but are prevented from interbreeding in nature by their acoustic mate recognition system, although we believe that some widespread populations (*e.g.*, *mollis ignifer*) may have had a hybrid origin. Nowadays there seems to be universal agreement that the three largely sympatric original members of the group, *biguttulus*, *brunneus* and *mollis*, are distinct species in spite of the ease with which fertile hybrids can be produced from them. But how should we treat *allopatric* members of the group showing differences in both song and morphology?

In the case of *rubratibialis* we have Schmidt's (1987) valuable experiments establishing that few hybrid adults could be obtained by crossing *rubratibialis* with typical *biguttulus*, and that all these adults died within a few days of the last moult, not even surviving long enough for a test of hybrid fertility. Since *rubratibialis* is thus even less interfertile with *biguttulus* than *biguttulus* is with either *brunneus* or *mollis*, it seems to us reasonable to treat it as a distinct species. Experimental tests of interfertility are still lacking for other allopatric pairs or trios, *e.g.*, *brunneus/jacobsi, biguttulus/yersini/marocanus, mollis/crassiceps*. In our recent study of the Iberian and North African members of the group, two of us (Ragge and Reynolds, 1988), partly influenced by Schmidt's work on *rubratibialis*, considered it best to treat *yersini* and *marocanus* as distinct species. It seemed to us that, if *rubratibialis* has diverged from *biguttulus* to the point where they are no longer interfertile (although the songs are quite similar), it is likely that *yersini* and *marocanus* (in which the songs show a greater contrast with *biguttulus*) have also done so.

Finally, we should like to encourage anyone with the time and facilities to carry out experimental tests of interfertility between appropriate pairs in this group. Where such tests show a significant reduction in hybrid viability (or even complete hybrid sterility), we should feel confident in treating allopatric taxa as distinct species, irrespective of close resemblance in song or morphology. On the other hand, a demonstration of complete interfertility is not in itself a proof of conspecificity, as shown by the three original members of the group; however, the combination of complete interfertility, allopatry, and close similarity in song would be a powerful argument in favour of treating two populations showing small morphological differences as conspecific.

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Notes on the *Chorthippus (Glyptobothrus)* species (Orthoptera: Acrididae) in Greece and the calling songs of their males

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ABSTRACT

In a five-year study of the orthopteran fauna of Greece, six species of *Chorthippus* (subgenus Glyptobothrus) were collected and studied: *biguttulus, willemsei, bornhalmi, mollis, pulloides,* and *vagans*. The male calling songs [pulloides was not recorded] were recorded and compared with oscillograms of male calling songs from other countries. The calling songs of *Chorthippus biguttulus biguttulus* were compared with those from Hungary *(C. biguttulus hedickei)* and *C. bornhalmi* with those from Yugoslavia. The calling song of *C. bornhalmi* is somewhat similar to that of *C. jacobsi* from Spain. A new subspecies is suggested for central Greek populations of *C. biguttulus*.

Key words: *Chorthippus, Glyptobothrus* species of Greece, calling songs.

INTRODUCTION

In the Orthoptera catalogue of Greece, Willemse (1984) cited ten species of *Chorthippus* belonging to the subgenus *Glytobothrus* Chopard, 1951: *brunneus* (Thunberg, 1815); *biguttulus hedickei* Ramme, 1942; *mollis mollis* (Charpentier, 1825); *lesinensis* (Krauss, 1888); *crassiceps* (Ramme, 1926); *sangiorgii* (Finot, 1902); *pulloides* (Ramme, 1926); *willemsei* Harz, 1971; *apricarius apricarius* (L., 1758) and *biroi* (Kuthy, 1907); the latter was recorded only from Crete.

In his supplementary notes, Willemse (1985) mentioned that *brunneus* probably did not occur in Greece but was replaced by another species with a different song and a larger number of stridulatory pegs. The species was determined to be *cypriotus* Uvarov, 1936, which may be synonymous with *miramae* Ramme, 1951, *bornhalmi* Harz, 1971, and lagrecai Harz, 1975, but the synonymy and the distribution are not yet settled. *Chorthippus lesinensis* from Dalmatia and crassiceps from the island Poros may be the same and allied to *mollis*. But the Greek crassiceps recorded by Willemse (1984) at the Peleponnes has a song different from *mollis*. *Chorthippus sangiorgii* may be considered synonymous with *pulloides*.

In this paper six Glyptobothrus species recorded from Greece were examined: *biguttulus, willemsei, bornhalmi, mollis, pulloides* and *vagans*. Of these species, only the songs from *biguttulus, mollis, willemsei, vagans* and *bornhalmi* were recorded.

MATERIAL AND METHODS

The material examined was collected in Central Greece (Mt. Oiti, Olimbos Oros, Ossa Oros, Perivolion, Kastoria), Chalkidiki, Kassandra, along the eastern coast, near Delphi, and at various locations on the Peloponnes. All the species investigated were collected in the mountains of central Greece at an elevation exceeding 1000 m; only some *bornhalmi* specimens were found in lower regions and in coastal areas. *Chorthippus pulloides* was found only in the mountain region of the Peloponnes.

Male specimens were placed inside a nylon-gauze net with a diameter of 30 cm, and song recordings were made under laboratory or indoor conditions. Temperature was measured, and recordings were made using an Uher 4000 or Uher 4200 report Monitor tape recorder and Uher M 53 microphone. Tape speed was always 19cm/sec. In addition some successful recordings were made in a car using gauze nets and sunshine temperatures of about 35°C. The subjects were approached cautiously to avoid disturbance, and the microphone was rested on the ground about 10-20 cm from them.

The songs were analysed on a Type 502A Dualbeam oscillograph together with a special photocamera. The film velocity in most cases was 20 cm/sec. A filter of 600 or 1000 Hz was used to attenuate ambient noise. Song description of each species were based on the oscillograms.

The terminology of Elsner (1974) was followed: a *calling song* is a pair-forming song produced by an isolated male. A *courtship song* is a special song produced by a male in contact with a female. *First-order sequences* are discriminated from *second-order sequences.* A *chirp* is a part of a sequence separated by an interval and consists of a variable number of syllables. A *syllable* is a sound produced by one complete down and up movement of the hindlegs.

RESULTS AND DISCUSSION

1. *bornhalmi* Harz, 1971

This species is widely distributed in Central Greece. The male calling song was recorded from specimens collected at Olimbos Oros, 1000 m above sea level. Figure 1 shows songs of two males compared with *bornhalmi* from Roviny (Yugoslavia) recorded by O. v. Helversen, Erlangen. *Chorthippus bornhalmi* shows signals produced by movements of one hindleg. One sequence lasts about 5/4 sec. The chirp sequence is irregular; two parts can be distinguished: one sequence consists normally of 11-14 chirps. The structure of a chirp is similar to that of *jacobsi* from Spain (Ragge and Reynolds, 1988), but the latter species may have a shorter sequence (about half as long as *bornhalmi).* But Ragge and Reynolds (1988) stated that a sequence of *jacobsi* lasts less than 1.5 sec and was composed of about 4-11 chirps with a chirp repetition rate of 8-13 per sec. The chirp repetition rate of *bornhalmi* is 9-10 per sec at 35°C and the structure of the song appears to be similar to that of *jacobsi.*

2. *willemsei* Harz, 1971

This species does not belong to the *biguttulus* group. The calling song of the males from Mt. Oiti, 1800 m, is much different from that of *biguttulus.* One sequence lasts 3-4 sec or longer. It consists of chirps composed of 4 or 6 syllables. The chirps are separated by a very short interval (Fig. 1). The song is unlike that of other species of the subgenus *Glyptobothrus.* Morphologically, it is most closely related to *pulloides,* but the song of the latter was unavailable for comparison.

3. *mollis* (Charpentier, 1825)

Samples of this species were collected at Perivolion, elev. 1700 m, in the central Greece mountains and compared with spe-

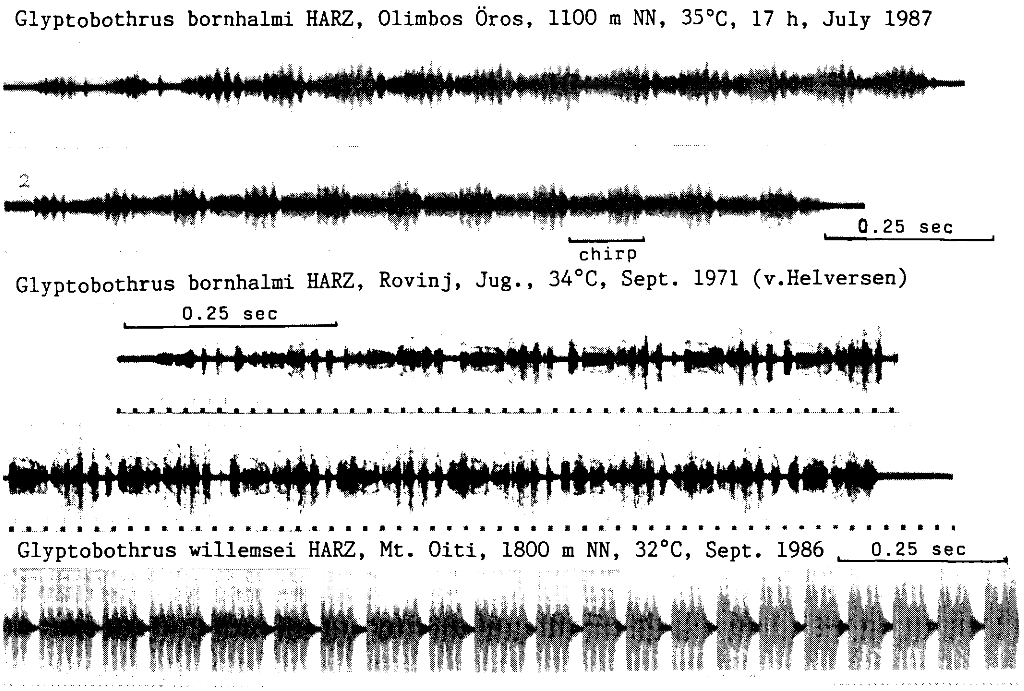


Figure 1.—Oscillograms of the calling songs of two males of *Chorthippus (G.) bornhalmi* (1,2; speed 20 cm/sec) from Greece, compared with that of a male from Yugoslavia, recorded by Prof. O. von Helversen, Erlangen (speed 25 cm/sec) and of the male calling song of *willemsei* (speed 20 cm/sec) from central Greece.

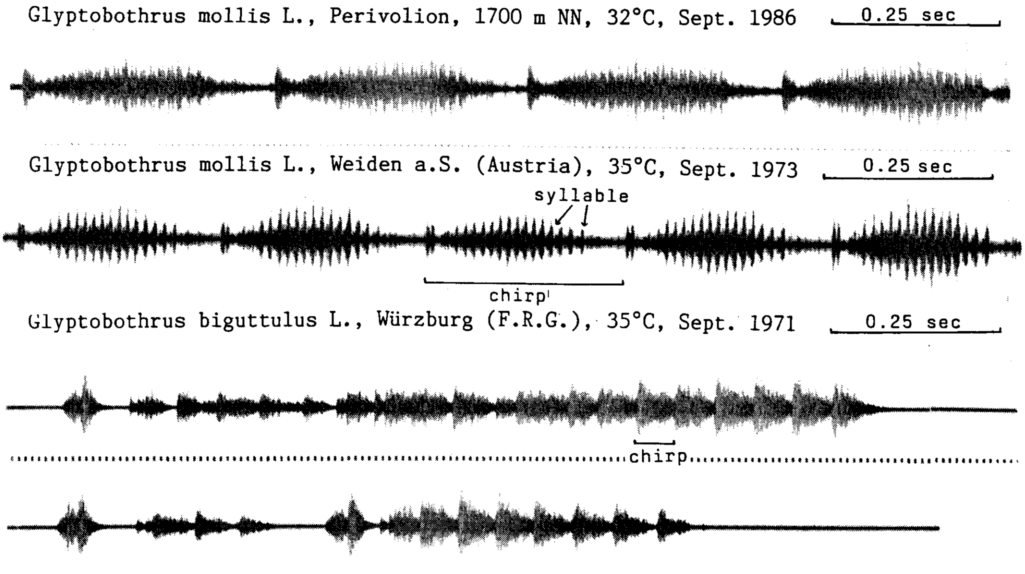
cimens from Austria, near Neusiedl Lake. The calling songs are similar, consisting of a long sequence of chirps, beginning quietly and gradually increasing in intensity until near the end. Nearly all chirps began with a characteristic "tick", produced by the down stroke of one hindleg only (Ragge and Reynolds, 1988). The number of audible chirps in the sequences is widely variable. The duration of the individual chirps (measured between successive "ticks") is temperature dependent; the duration is shorter at 35°C than at 32°C (Fig. 2). The number of the syllables of one chirp was 18-20 and remained nearly constant during the entire sequence.

After the initial "tick", each chirp begins and ends quietly, reaching maximum intensity in the middle and consists of syllables repeated at similar rates. No significant difference was found in the songs of males from central Europe and central Greece.

4. *biguttulus* form X, a possible new subspecies

The calling song of the nominate form of *biguttulus* consists of sequences, each beginning quietly and ending abruptly. The number of sequences in the series ranges from 1 to 3 and is often 3. The first chirp sequence, usually lasting 1.5-3.0 sec, is longer than the others. The interval between sequences differs greatly. There are usually 20-37 chirps in the first sequence, fewer in the following ones (Schmidt, 1978) (Fig. 2). In many cases the sequences begin with a loud chirp, similar to a "tick".

The song of eastern European *b. hedickei* differs from that of the nominate form of central and western Europe. The structure of the chirps is different for males from the Hungarian Puszta (Fig. 3). The first chirp sequence, composed of chirps of 5-8 syllables, starts quietly and ends with a loud

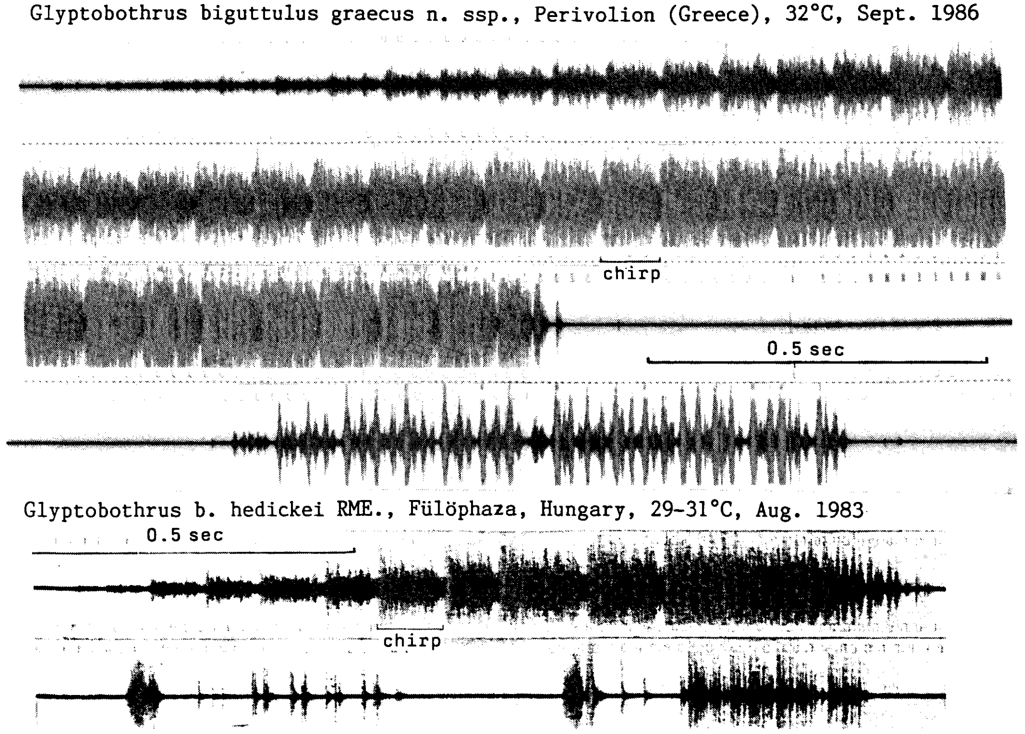


Glyptobothrus mollis L., Perivolion, 1700 m NN, 32°C, Sept. 1986

Glyptobothrus mollis L., Weiden a.S. (Austria), 35°C, Sept. 1973

Glyptobothrus biguttulus L., Würzburg (F.R.G.), 35°C, Sept. 1971

Figure 2.—Oscillograms of the calling songs of a male of *Chorthippus (G.) mollis* from central Greece and Austria for comparison and of a male of *biguttulus biguttulus* from central Europe (speed 20 cm/sec). The latter consists of three parts, each beginning with a «tick».



Glyptobothrus biguttulus graecus n. ssp., Perivolion (Greece), 32°C, Sept. 1986

Glyptobothrus b. hedickei RME., Fülöphaza, Hungary, 29-31°C, Aug. 1983

Figure 3.—Oscillogram of the calling song of a male of *Chorthippus (G.) biguttulus* subspecies X from central Greece (speed 20 cm/sec), consisting of two parts with different structure, compared with one of *biguttulus hedickei* from the Hungarian puszta (see Schmidt, 1987a), consisting of three parts; the second and third parts begin with a «tick» similar to those of the nominate form, but the structure is much different.

and long chirp composed of more than 20 syllables. The first part of the whole sequence is relatively short, lasting about 5/4 sec. Normally, the first part of the sequence is followed by two parts with drastical changes in the chirp pattern with intervals of 1/5 sec. But as in *biguttulus biguttulus*, both the second and third parts of the sequence begin with a loud "tick".

Compared with songs of *biguttulus* from the central Greek mountains, there are some calling song differences; this suggests the presence of a new form, which the author feels may be a new subspecies. The first part of the chirp sequence of this form is much longer than that of *biguttulus hedickei;* it lasts more than 3 sec, beginning very quietly and ending abruptly. After an interval of about 1 sec, the second part of the sequence begins loudly but without a "tick", lasting somewhat less than 1 sec. The structure of the two parts of the sequence differ significantly in this new form, as they do in *b. hedickei.* Sometimes a third part of the sequence was produced with a structure similar to the second one. In the second part of the sequence of this form the syllables are well separated and there are no typical chirps in comparison to the first part. The structure of the chirps of the first part of the sequence is very regular; up to 40 chirps were counted. Each chirp usually is composed of six syllables, which is the main difference with that of *b. hedickei* and *b. biguttulus.* The Greek populations of this form may belong as a separate subspecies within the Rassenkreis (Rensch, 1929) of *biguttulus* (Fig. 4).

5. *vagans* (Eversmann, 1848)

Figure 5 shows a song of a Greek specimen tentatively identified as *vagans*. Comparing its song with that of *vagans* from Mt. Gargano, Italy, the chirp sequence of the Greek specimen is 26, while that of the Italian specimen is only 16. Since the number of chirps in a sequence from *vagans songs* in other parts of Italy (Sabaudia, Latina) can be as few as 5-8, it seems that the chirp number of a sequence can vary greatly. The structure of the chirps is very similar in both cases.

Willemse (1984) pointed out that the occurrence of *vagans* in Greece is doubtful;

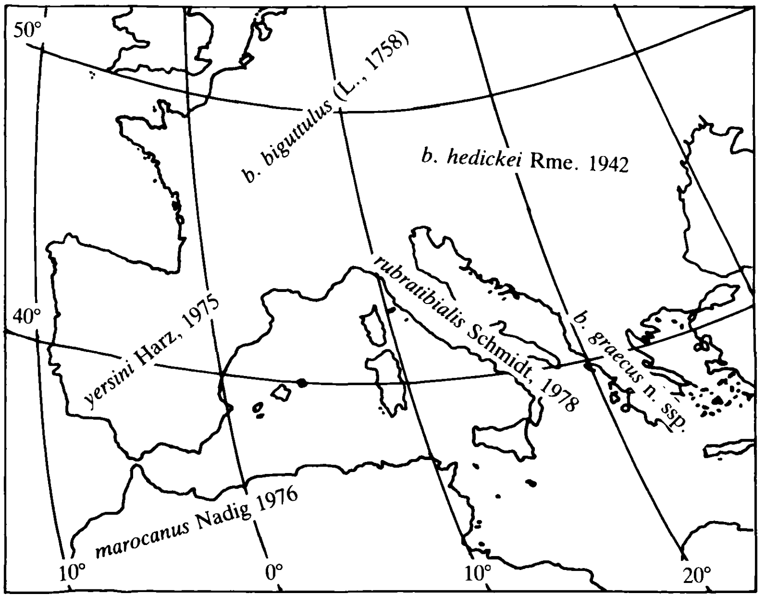


Figure 4.—Distribution of the species and subspecies in Europe and North Africa belonging to the *biguttulus* group (Rassenkreis; Rensch, 1929); detailed information is given by Ragge and Reynolds (1988) and Schmidt (1978, 1987a,b, 1989).

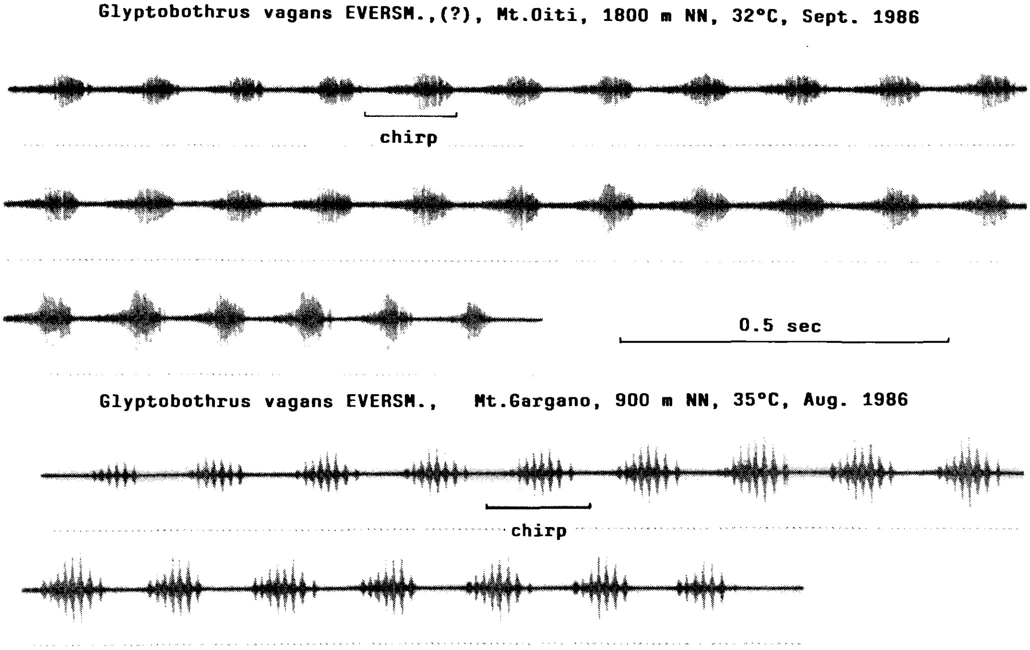


Figure 5.—Oscillograms of the calling songs of males: a comparison of a song of *vagans* from Italy (speed 20 cm/sec) with a song of a specimen from central Greece (speed 20 cm/sec).

no other specimens of this species were available for study. The recording of the song in Fig. 5 was from a single male that was not collected. It was recorded on Mt. Oiti, elev.1800 m. The oscillogram indicates at least that it is a species previously unknown in Greece.

ACKNOWLEDGEMENTS

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Is there heritable variation in female selectivity for male calling song in the grasshopper *Chorthippus brunneus* (Thunberg)?

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ABSTRACT

Calling songs of many acridid grasshopper species are major components of the mate recongnition system. Many authors have suggested that different components of the calling song are important in eliciting a female response. A number of different synthesized calling songs were played back to females of *Chorthippus brunneus* (Thunberg). A female was deemed to have responded if she stridulated in alternation with the synthesized song. Iso-female lines were set up and tested in the parental (GP), G1 and G2 generations. Although no song model was preferred outright, echemes (or chirps) were more important in eliciting responses than syllables in GP. A within-echeme structure was important in the later generations. Iso-female lines varied significantly in both G1 and G2 for number of responses to some song models. In the GP-G1 comparison the heritabilities of principal components 1 (responsiveness) and 2 (selectivity) were non-significant ($h^2 = 0.57 \pm 0.095$ and 0.07 ± 0.029, respectively). However, additive genetic variation is present in the total number of responses made and in the number of song models eliciting a response. Possible factors maintaining response stridulations in the absence of female selectivity are discussed.

Key words: *Chorthippus brunneus,* synthesized songs, female response, female selectivity, additive genetic variation, iso-female lines.

INTRODUCTION

Since song is a major component of the specific mate recognition system (SMRS) (Paterson 1985) in many acoustic species, it is important to ascertain which song components are used in eliciting female response and there by influence female mating decisions.

With the increasing use of synthesized song, females of many orthopteran species have been shown to prefer particular components of the male song. For example, amplitude and temporal components can elicit differential female cricket phonotaxis *e.g.*, pulse rate and within-echeme amplitude variation are important in *Melanogryllus desertus* (Pally) (Popov and Shulavov 1977), and calling bout duration in *Gryllus integer* (Scudder) (Hedrick 1986). Stout *et al.* (1983) demonstrated that altering spectral or temporal parameters varied the attractiveness of the male *Acheta domesticus* (Linnaeus) song to females. In tettigoniids song frequency is often related to male size and is discriminated by females of the bush crickets *Tettigonia cantans* (Feussly) (Latimer and Sippel 1987) and *Requena verticalis* (Walker) (Bailey and Yeoh 1988).

A number of authors have posited that different aspects of the gomphocerine calling song are important in eliciting a response. The ten song models described in this paper were synthesized in order to test a number of these hypotheses in *Chorthippus brunneus* (Thunberg) (Orthoptera: Acrididae). Haskell (1961) suggested that amplitude modulation is a more important component of the song than the underlying frequency spectra. Impulse rate modulation *(e.g.* Elsner 1974) was shown to be important in eliciting response from females of *Omocestus viridulus* (Linneaus) (Skovmand and Pedersen 1978), whereas the within -echeme structure, specifically the "main -pulse" duration to pause duration ratio, is important in *Chorthippus biguttulus* (von Helversen 1972) and *C. brunneus* (von Helversen and von Helversen 1981).

In gomphocerine bioacoustics female stridulation has often been used as a response criterion (Skovmand and Pedersen 1978, 1983, von Helversen 1972). Crucially, Butlin *et al.* (1985) and Green (1987) demonstrated that stridulating females of *C. brunneus* are significantly more likely to mate than females that do not respond to natural calling song. Although phonotaxis is perhaps a more clear cut measure of response, Eiriksson (1987) reported that in *Omocestus viridulus* (Linneaus) separate phonotaxis and stridulation experiments yielded similar results.

An equally important question which this paper addresses is: if females vary in responsiveness and selectivity of songs responded to, is there any heritable component to the variation? Most intra-specific studies have concentrated of finding the mean female preference and have not investigated heterogeneity in preference in much detail (but see Hedrick 1986).

The evolution of signal-receiver systems whether through "genetic coupling" or coevolution (see Butlin and Ritchie 1989 for a recent review) requires the presence of heritable variation in the receiver's (usually female's) preference (or selectivity) for the signal. Also, many models of sexual selection through female choice, both Fisherian and adaptive, assume that female preferences vary genetically *(e.g.*, Lande 1981, Nichols and Butlin 1989, for a review see Bradbury and Andersson 1987). Since this assumption is the basic premise of these models, it must be tested.

Nevertheless, even though there have only been a handful of studies thus far. genetic variation of insect female mating preferences has been found, *e.g.*, in the ladybird *Adalia bipunctata* (Linnaeus). (Majerus et al. 1982) and *Drosophila (e.g.*, Thoday and Gibson 1962). Unfortunately, the cues used for female choice in these two taxa have not been identified. In this paper a powerful technique for investigating genetic heterogeneity (iso-female lines) is used to try to answer this second question. Here, iso-female lines (Hosgood and Parsons 1976, Ehrman and Parsons 1981) are derived from singly mated females, and matings within these lines are allowed to occur at random. Consistent variation among lines in responsiveness and selectivity persisting through three generations will be indicative of the presence of genetic variation in the initial population.

MATERIALS AND METHODS

I shall describe an experiment which investigated female response to, and selectivity for, a number of different synthesized calling songs, and also the presence of additive genetic variation in both response and selectivity using iso-female lines tested in the parental (GP), G1, and G2 generations.

The calling song of *Chorthippus brunneus* consists of a number of chirps (or echemes: Broughton 1976) which are produced by the impacts of stridulatory pegs on the hind femur against modified wing veins (ie stridulation). When a male sings, a nearby receptive female may respond by stridulating in return. A duet of alternating male and female echemes results during which the insects orientate towards each other. The male may attempt a copulation; if unsuccessful he will invariably attempt to remount, but may produce the quieter courtship song before he does so.

Song synthesis

Ten artificial calling songs were generated using the Music System^{r} software on an Apple IIe computer (Fig. 1). Figure 2a shows a natural calling song echeme which consists of a number of syllables. Although the structure of the echeme is quite regular, the composite syllables vary in length and amplitude. Therefore, one refers to the mean syllable length of the echeme (= echeme length/number of syllables: Butlin *et al.* 1985). By definition, then, a syllable contains a pause between rises in amplitude. The parameters for each song model (Fig. 2a,b) are shown in Table 1. Each song model was organised into a song series consisting of 5 twenty-one-second calling songs (Fig. 1).

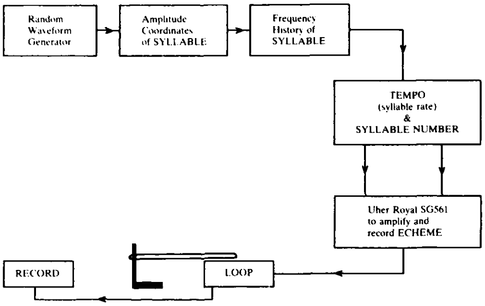

Fig. 1.—Artificial song synthesis. Calling songs consist of a number of echemes containing syllables. A syllable was constructed for each song model by specifying a "noisy" random waveform and amplitude coordinates through time. The frequencies chosen were the 4 highest intensity harmonics (Haskell 1957) of the real song and were constant throughout the syllable. A tempo and syllable number were specified which together with the constructed syllable produced one echeme. The echeme was amplified and recorded in stereo. A tape loop with a mono echeme was made and a 21 s song of 10 echemes was recorded. Continous tape loops of syllables and of white noise were made for CS and W, respectively, and the songs were created by recording the loop for 21 s. A song series for each model was constructed consisting of 5 songs with song interval of 1.5 min. The interval between two consecutive song series was 5 min.

Song models
A. Song Structure Alteration

1. White Noise (W). Both the (21s.) calling song and the interval between successive calling songs (1.5 min.) contain continuous white noise, which acts as a general control.

2. Continuous syllables (CS) throughout the song were used to ascertain whether amplitude modulation itself is important in eliciting response (Haskell 1961).

B. Gross Echeme Structure Alteration

3. Constant Song (C). As with all subsequent songs C contained an echeme length (EL), syllable number (SN) and mean syllable length (SL) in the natural song range recorded between 25 - 28°C (*e.g.*, Butlin *et al.* 1985, Charalambous 1990).

4. Echemes of White Noise (WC). This type of song has been widely used by von Helversen (1972) and von Helversen and von Helversen (1983). It was used to test whether the presence of echemes is a crucial song component. The overall response to WC can be compared with that to CS to ask if the presence of syllables or echemes is of greater importance.

5. Triplet Structure (T). Butlin and Hewitt (1988) reported that males who achieved the greatest mating success tended to have syllables (of intermediate length) arranged in triplets. The maximum amplitude of a syllable is 100% (as in CS, C described previously and song models HSP, LSP, HA and LA described below). In the Triplet echeme the syllables are arranged in six sets of triplets of descending amplitude (the first syllable of the triplet at 99% of maximum amplitude, the next at 66% and the third at 33%).

6. Busnel (B). Busnel (1963) posited

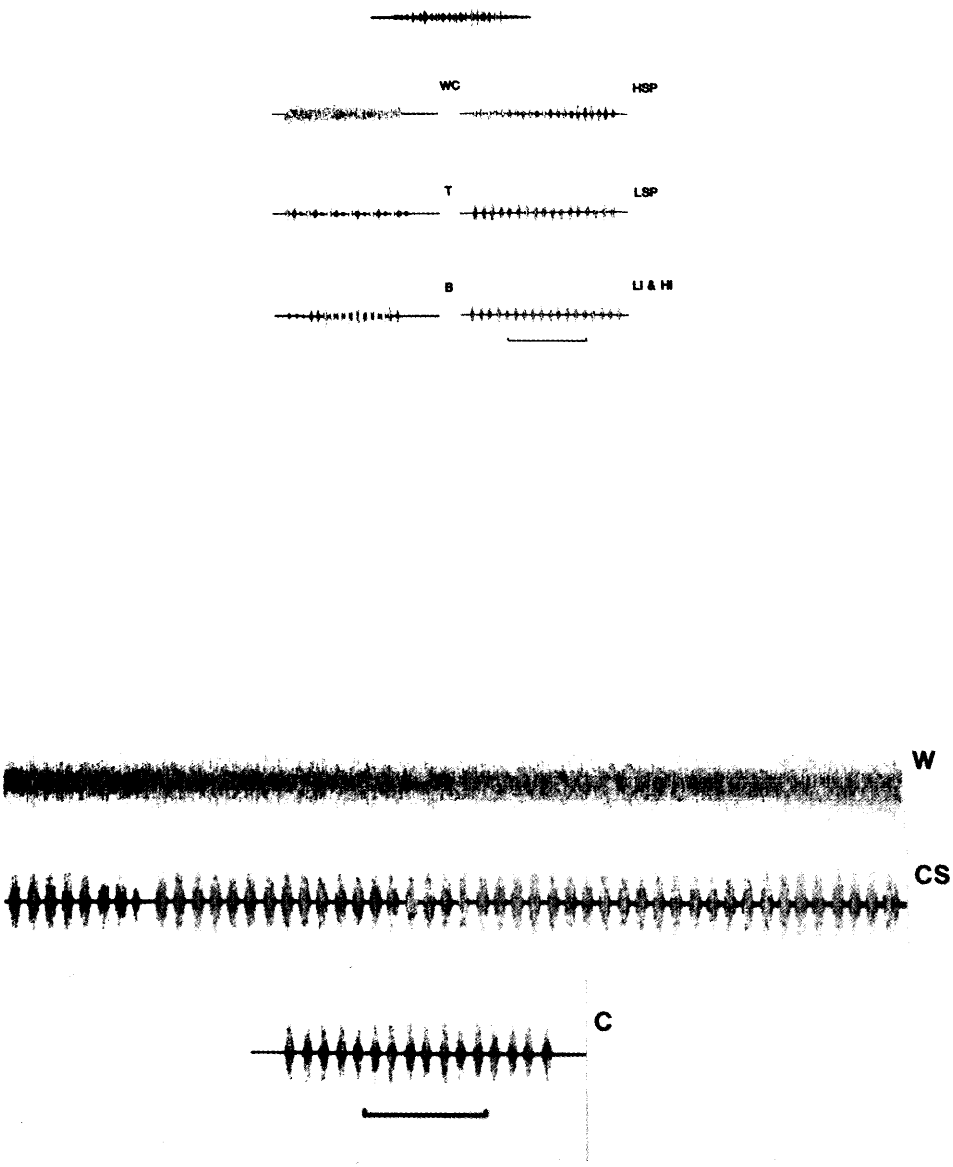

Fig. 2.—Synthesized song models, recorded on a Uher Royal SG561 and played through a 150-50,000 Hz high-low pass filter into a Mingograf 34T paper trace machine. Sensitivity is 10 Volts. Time is on the horizontal axis: the lines mark 0.2 s in real time. Amplitude is on the vertical axis. See text for details.

a) Shown clockwise from the top are a natural echeme, consisting of syllables, recorded between 25-28° C. HSP, LSP, LI and HI (same structure), B (sensitivity is 10-50V, syllables rise and fall in amplitude), T, WC.

b) Top: W, Middle: CS, Bottom: C, constant amplitude echeme (0.5 V sensitivity) shown in relation to song structure models above.

that the rate of of build-up of amplitude may be important. This song has a slower rate of build up and decay than all other song models containing echemes, which attack and decay instantly. The rates of build up and decay in B are not symmetrical; the decay is much more abrupt.

C. Within-Echeme Structure Alteration

Von Helversen and von Helversen (1983) demonstrated that the ratio of the amount of sound to the amount of pause (sound-to-pause ratio duration) in echemes is important in eliciting responses from females of *Chorthippus biguttulus* (Linnaeus). The equivalent of *C. biguttulus* echeme sound-to-pause ratio duration in *C. brunneus* is syllable sound-to-pause ratio duration (Elsner 1974). In these models, the sound duration per syllable is kept constant, but, the pause before the next rise in amplitude (*i.e*, the beginning of the next syllable) is altered (Table 1).

7. High sound-to-pause ratio echemes (HSP).

8. Low sound-to-pause ratio echemes (LSP).

D. Sound Level Alteration

In acoustic species, rather than making an active choice between the songs of males, females may just passively move up a sound gradient towards the male who sings loudest (Parker, 1983). The sound levels of the following models are therefore different (see Table 1):

9. Low intensity echemes (LI).

10. High intensity echemes (HI).

Testing

All grasshoppers were reared under similar temperature regimes on 12:12hr light:dark cycles. Each day, eclosing adult males were isolated from females in a separate insectary to ensure female virginity and acoustic naivety. Adults were uniquely marked with spots of oil paint and females had their wings cut off at the base to avoid acoustical communication among females whilst testing. Like males, females produce a "response song" by stridulation. Therefore cutting off the wings effectively silenced them. However, since males and females alternate stridulations for some time, it is easy to see, by constant scanning, which females are stridulating in response to the synthesized songs. Cutting the wings off does not apparently affect female receptivity (i.e, the age at which a female first begins responding: Charalambous 1990, or ability to stridulate (personal observation).

Prior to the start of testing young adult females were housed in a large Harris locust cage.

Females were tested when 5, 6, 7, and 8 days old. Each female was placed in a plastic cylindrical cell (3" ×1") with fresh grass, *Dactylis*, and enclosed at both ends by fine

Table 1.—Synthesized echeme parameters for song models. All song models have a duration of 21 s. Where echemes are present, the interval between echemes is 1.9 s. The sound level (when it reached the females) was 55 dB for all models except LI (50 dB) and HI (60 dB).

	SONG MODELS							
Echeme Parameters	W	CS	WC	C, B	T	HSP	LSP	LI, HI
echeme length (ms)	—	—	310	300	335	370	370	390
syllable number	—	cont	—	16	18	21	17	18
sound/syllable (ms)	—	10	10	10	10	10	10	10
pause/syllable (ms)	—	8.75	8.75	8.75	8.75	6.42	10.29	8.75

cont: continous syllables

cotton mesh. This arrangement provided an unobstructed view of the female. All females were placed in wooden apparatus containing holes for the cells. The holes were arranged in a hexagonal fashion so that all females (except females at the edge) were surrounded by six others 4.5 cm away. The spaces between the cells were filled with cotton wool and packing material so that females could not see each other. This also reduced the likelihood of substrate borne vibrations. Thus the only means of communication between females not experimentally reduced was pheromonal. The apparatus was lit on one side with four 40 W bulbs and from above by diffuse ceiling lighting. A speaker (RS components: 8 ohms, and 16 cm diameter) was placed 1.5 m from the other side of the apparatus. On each testing day there were two 1.75 hr trials. After each day's trials, all females were kept in a large Harris locust cage overnight. In each of the trials the ten model song series were played in random order. All trials were carried out within the temperature range of the simulated songs (25-28° C). The first trial was started 30 min. after the last female had been placed in the apparatus. Females were constantly scanned and those that stridulated to a minimum of 4 synthesized echemes (or 4 times in the case of W and CS) were scored as having responded. A female that stridulated to any or all of the 5 songs in a song series was given a score of 1. Thus females had 2 independent opportunities per day to respond to each song model, and 8 opportunities in 4 days. Data was analysed for total response per female over 4 days.

Iso-female lines
Parental generation (GP)

F1 egg pods from grasshoppers collected on the University of East Anglia Campus, Norwich, UK., in July 1986 were stored at 4°C for 3 months and incubated at 26°C to break diapause. The pods were hatched in Harris locust cages under 40 W bulbs. Grasshoppers were fed every two days with freshly cut *Dactylis glomerata*. After testing on day 8, 60 females were mated with randomly chosen virgin males. All pods were collected.

First generation (G1)

21 G1 lines were reared in medium Dutt cages (15 cm diameter × 30 cm high) and placed under banks of 40 W light bulbs. The position of each cage was randomised every two days during feeding. A number of females (from 1 to 6) in each line were each mated with a virgin male sibling. Pods from each pair were collected.

Second generation (G2)

Each of the 21 G2 lines was hatched in a large Harris locust cage and illuminated with 40 W bulbs. Grasshoppers were fed with *Dactylis glomerata* grown in a greenhouse. Of the 21 lines brought out, only 6 produced a usable number of daughters for testing (ranging from 2 to 9).

Statistical Analyses

The design of the playback experiment was «no choice» since females were subjected to only one song model at a time. Thus, the response to one song model is independent of response to others and can be analysed using generalised linear models (GLMs, with binomial errors and logit tranformations, which are robust to unequal sample sizes). Principal Component Analysis (PCA) was used to investigate the pattern of females response covariation among song models. Robust multivariate Jackknife allocation tests (Sokal and Rohlf 1981) were used to investigate variation among G1 and G2 lines. Analyses were carried out using the GENSTAT statistical package (copyright Lawes Agricultural Trust 1977).

RESULTS

Calling song and female response
Parental generation (GP)

36% (44/122) of females responded to artificial song, which is similar to the response to playback of natural song (Green 1987). The number of responses per female (maximum = 8) is low to all models (Table 2). There was significant variation in the proportion of females responding to the different song models (G = 45.86, df = 9, $P<0.001$). The most marked effect was discrimination against W (the control) and CS. A G-Test shows an equal distribution of females responding to the 8 other song models (G = 12.83 df = 7, NS). Thus, the presence of the echeme (eg WC) in the calling song is more important in eliciting response than the presence of syllables (CS). Females do not differentiate between song models which differ only in the within-echeme structure or in amplitude (HSP, LSP, C, B, WC, T, LI and HI). Similar results were obtained with principal component analysis, where PC1 revealed general responsiveness to all song models (except W and CS).

Generation 1 (G1)

88% (103/117) of females responded, and in general they each responded more than in GP (Table 2). GLMs (Table 3) for each song model reveal variation among lines in number of responses to W, CS, WC and T, but not to the other models (means and sd are shown in Table 2). The variation in response to W is due to females in only one line (line 3) responding (mean = 0.143, sd=0.378, N=7). Variation associated with CS and WC is due mainly to some lines not responding since repeating the GLMs on responding lines only does not indicate differential response (Table 4, CS: $F_{5,27}=1.01$ NS; WC: $F_{12,56}=1.00$ NS). Line 1 contributes greatly to the variation in T, as there is no variation between lines when line 1 is omitted (GLM, $F_{19,77}=1.34$ NS). As in the parental generation there is a relative lack of response to W (white noise: 20/21 lines not responding), CS (continuous syllables: 15/21 lines) and, to some extent WC (echemes of white noise: 9/21 lines).

Generation 2 (G2)

Of the 57% (33/58) of females that responded, none responded to W or CS. Con-

Table 2.—Basic univariate statistics for the number of females responding to each model (in GP) and mean response to each of the model songs for all generations (pooled for all lines in G1 and G2). n = number of females responding.

		SONG MODELS									
Generation		W	CS	C	WC	T	B	HSP	LSP	LI	HI
Gp (n=44)	No. females responding	3	2	19	10	7	25	12	17	23	11
	No. responses										
Gp (n=44)	Mean	0.091	0.023	0.568	0.273	0.568	0.910	0.523	0.682	0.955	0.410
	St. Dev.	0.362	0.151	0.846	0.544	0.900	1.158	1.151	1.157	1.220	0.787
G1 (n=103)	Mean	0.001	0.174	3.220	0.285	2.485	3.136	3.233	3.573	3.417	3.165
	St. Dev.	0.020	0.463	2.020	0.552	1.727	1.864	1.965	2.164	1.793	2.126
G2 (n=33)	Mean	0.000	0.000	1.303	0.006	1.212	1.394	1.697	1.636	1.787	1.878
	St. Dev.	0.000	0.000	1.234	0.194	1.163	1.296	1.324	1.425	1.256	1.354

Table 3.—Variation among lines in the number of responses (maximum = 8) to each song model in G1. The deviance ratio from GLM is approximately distributed as the variance ratio F.

Song Model	Mean Deviance Ratio	$P_{29,72}$
W	5.50	<0.001
CS	4.64	<0.001
C	1.20	NS
WC	2.35	<0.01
T	2.06	<0.025
B	1.29	NS
HSP	1.08	NS
LSP	1.28	NS
LI	1.62	NS
HI	1.17	NS

Table 4.—Variation among lines in the number of responses to the model songs CS, WC and T in G1. Means (standard deviations) shown.

		SONG MODELS		
		CS	WC	T
Iso-female line	Number of Females Responding	Mean (sd)	Mean (sd)	Mean (sd)
1	6	0	0	0
2	3	0	0	1.333 (1.53)
3	7	1.000 (1.527)	1.000 (1.29)	2.714 (1.704)
4	6	0.500 (0.837)	0	4.167 (2.316)
5	5	0.400 (0.548)	0	1.200 (1.643)
6	9	0	0.111 (0.333)	1.333 (1.323)
7	5	0	0.200 (0.447)	3.400 (2.700)
8	7	0.142 (0.380)	0	1.286 (1.497)
9	5	0	0.600 (0.894)	3.200 (2.387)
10	5	0	0.400 (0.548)	1.000 (1.225)
11	5	0	0.200 (0.447)	3.600 (1.949)
12	2	0	0.500 (0.707)	1.500 (2.121)
13	5	0	0.600 (1.341)	2.000 (1.581)
14	2	0	0	2.500 (2.121)
15	6	0	0.333 (0.516)	4.667 (2.800)
16	4	0.250 (0.500)	0.750 (0.500)	2.750 (0.500)
17	6	0	0.167 (0.408)	3.333 (1.366)
18	6	0	0.167 (0.408)	3.667 (3.141)
19	2	0	0	2.500 (3.536)
20	3	0	0	2.333 (0.577)
21	4	0.750 (0.500)	0.750 (0.500)	3.500 (2.082)

sequently, these song models are not included in further analyses. The 6 lines varied significantly in response to all the models (Table 5) except HSP and LSP (means and sd in Table 2). Lines varied in the number of responses given to B, LI, and HI. A repeated GLM omitting lines that did not respond suggests that lines are also differing in the number of responses given to C and T (for C: $F_{4,25}=3.54$, $P<0.025$; for T: $F_{3,24}=3.13$ $P<0.05$, but borderline). Of the 5 G1 lines responding to WC, only line 11 responded in G2. It now appears therefore that the within-echeme structure is important in eliciting responses.

Is variation between lines heritable?

A Jackknife classification successfully allocated only 3/103 G1 females to the correct lines which is not significantly different from a random allocation. However, 22 out of the 33 (66%) G2 females were allocated correctly. The 99% confidence limits for successful allocation where n=33 are 0.44%-0.86%.

Although the Jackknife suggests that G2 lines are varying significantly, it does not weight the distribution of responses to the song models by the number of responses each female makes. A more informative approach would be to compare the behaviour of the lines using PCA which takes the number of responses made by each female into account. Also, by comparing generations genetic variation among lines can be investigated. Consistent variation among lines across generations indicates the presence of additive genetic variation, whereas more variation within lines than among lines would indicate a large between-generation component.

Rather than analyse lines across GP-G1-G2, GP-G1 and G1-G2 were compared separately in order to maximize the number of lines and individuals in the analysis. For the GP-G1 comparison, a parent-offspring regression was performed on principal component scores. For the G1-G2 comparison a GLM was used to investigate the presence of environmental and additive genetic variation in principal component scores. Principal component scores were derived from PCAs performed on the pooled generation data sets of the number of responses given by females to the ten song models (excluding W and CS for G1-G2).

The GP-G1 parent-offspring regression gave non-significant heritability (additive genetic variation) estimates of 0.57 ± 0.095 for PC1 (responsiveness) and 0.07 ± 0.029 for PC2 (selectivity, $h^2=2x$ slope: Falconer 1981).

A highly significant generation effect in responsiveness (PC1) was present in the G1-G2 comparison (Table 6). Since the among-line variation was not significant, there is no evidence of additive genetic variation in responsiveness (PC1) or selectivity (PC2).

How does response vary between generations?

For all females tested in both G1 and G2 the increased variation in the number of model songs responded to and number of responses made can be explained by the differing proportion of non-responsive females among lines (Table 7). Having shown in the previous section that no additive genetic variation is present in selectivity (PC2), more appropriate analyses can be performed to investigate responsiveness. GLMs (Table 7) reveal a significant effect of generations for the total number of responses made; but with this taken into account there is still variation among lines. A similar generation effect is seen in the number of song models responded to (Table 7), but again there is significant variation among lines. The fact that there is consistent variation among lines across generations suggests additive genetic variation in the total number of responses given and in the number of song models eliciting a response. However, since the total number of responses made is highly correlated with the number of song models responded to (G1 $r=0.84$, $df=101$, $P<0.001$; G2 $r=0.753$, $df=31$, $p<0.001$), the additive ge-

Table 5.—Mean number of responses (and standard deviations) to song models that vary significantly among G2 lines. n is the number of females responding to at least one song. Significance values for GLMs (with binomial errors) are ***, p=<0.001; **, p=0.025–0.01; *, p<0.05

	ISO-FEMALE LINE						
Song Models	8	6	10	11	18	9	Deviance Ratio
C	0	0.20(0.5)	2.40(1.70)	1.80(1.64)	0	1.13(1.13)	4.01**
WC	0	0	0	0.4(0.54)	0	0	10.77***
T	0	0.40(0.54)	2.30(1.90)	1.00(1.23)	3.00(0.00)	0.50(0.53)	4.15**
B	0.67(1.15)	0.60(0.54)	2.80(1.90)	1.80(2.04)	1.00(0.00)	0.25(0.46)	3.70**
LI	0.30(0.60)	0.60(0.90)	2.70(1.50)	3.00(1.25)	2.50(0.70)	1.00(0.75)	3.63**
HI	0.66(0.60)	0.80(0.54)	3.30(1.70)	1.60(1.95)	1.00(0.00)	1.63(1.41)	2.75*
n	3	5	10	5	2	8	

Table 6.—GLMs of principal components 1 and 2 for the pooled G1 and G2 data for the number of responses to all song models (except W and CS). Generations and Lines are fitted in turn.

	Principal component 1			Principal component 2		
GLM	F	df	P	F	df	P
+gen	11.15	1,68	<0.001	0.27	1,68	NS
+line	1.74	5,63	0.25–0.1NS	1.24	5,63	NS
+gen. line			NS	2.81	5,58	<0.05

Table 7.—Variation between lines in G1 and G2 for the number of songs responded to and the total number of responses made by females for the subset of those that responded, and all the females tested. Also shown are generalised linear models fitting generations and lines as factors, with the means (and standard deviations) for each generation. DR is the deviance ratio.

Generation	N	No. songs responded to			Total number of responses made		
		DR	df	P	DR	df	P
G1 (responding)	103	1.80	20,82	<0.05$^+$	1.70	20,82	NS
(all tested)	117	2.07	20,97	<0.05	2.09	20,97	<0.05
G2 (responding)	33	2.06	5,27	NS	3.45	5,27	<0.025
(all tested)	58	5.33	5,45	<0.001	6.99	5,45	<0.001
GLM G1/G2 responding[1]							
+gen		6.09	1,68	<0.025	11.86	1,68	<0.001
+line		3.26	5,63	<0.025	3.14	5,63	<0.025
+gen. line				NS			NS
G1 mean (sd)			6.027 (1.63)			20.47 (13.42)	
G2 mean (sd)			4.788 (2.37)			10.94 (9.94)	

$^+$ indicates borderline significance.

[1] G1 N=36, G2 N=33; Responses to W and CS (only ocurring in G1) are omitted.

netic variation present is mainly in general responsiveness.

The large effect of generations is partly due to five out of six G2 lines not responding to WC. It is difficult to explain this as a purely environmental effect since care was taken in the methodology to replicate conditions for all generations.

DISCUSSION

Which song components elicit female response?

In the base population (GP) the number of females responding to each of the 10 simulated songs suggests that the presence of echemes in the song is more important than amplitude modulation (CS). Von Helversen (1972) suggested that in *Chorthippus biguttulus* an internal echeme structure is not crucial in eliciting response. Since the number of females responding to WC did not differ significantly from C, T, B, HSP, LSP, LI and HI, the present work supports von Helversen's suggestion.

No songs emerged as being preferred over the others. It remains possible, however, that there are small differences in female selectivity which could be detected with larger sample sizes.

In the songs with echemes, the echeme length, syllable number and syllable length were parameters altered in different combinations. Perhaps testing females with model songs varying more in echeme length might have caused differential response. However, von Helversen (1972) demonstrated in *C. biguttulus* that as long as the echeme length is above the minimum (1.2s) females do not discriminate it further. In fact it was the sound-to-pause duration ratio that was important in eliciting responses (von Helversen and von Helversen 1983). Intervals (more probably perceived as sound-to-pause ratios) are not unlikely candidates for discrimination: Bennet-Clark and Ewing (1969) showed that pulse interval is a species recognition parameter for some sibling *Drosophila* species.

In the later generations, a more detailed within-echeme structure was required to elicit responses. G1 lines discriminated against the control W, CS, and also WC. Thus a syllabic structure to the echeme was important in G1, and more so in G2 where only one line responded to WC. The amplitude variation throughout the echeme and song intensity were also important in eliciting response: G2 lines varied in the number of responses given to C, T, B, LA, and HA.

In the natural situation many successful courtships incorporate a large amount of «courtship song» Is courtship song, which is only sung in the presence of females, a more likely candidate for female discrimination? Green (1987) showed that the syllable rate and echeme structure of courtship song is not different from calling song, and thus there is no apparent reason why females should discriminate syllabic structure between these two songs differently. Throughout, courtship, then, females are exposed to consistent within-echeme information through both calling and courtship songs.

Iso-female line variation and genetics of response

The non-significant heritability of PC1 (responsiveness) and PC2 (selectivity) for the GP-G1 comparison is due in part to the fact that some G1 lines responded to model songs, whereas their mothers did not respond at all (4/21 G1 lines), suggesting that the presence of the large generational effect may possibly be swamping any additive genetic variation present. The G1-G2 generation effect mainly entailed G1 females being more responsive than G2 females. This G1 responsiveness may have been due to better rearing conditions. Lack of variation among lines in G1-G2 (Table 7) may partly be due to small sample sizes since a trend was present ($p=0.25-0.1$). However, significant variation among lines across generations G1 and G2 (suggesting the presence of additive genetic variation) was found for the total number of responses made and the number of song models responded to (Table 7).

Consistent variation among lines across generations suggests some genetic heterogeneity in the base population. Hoikkala (1985) attributes a genetic origin to iso-female strain variation in *Drosophila littoralis* (Meigen) for male song characters. Carson (1985) demonstrated iso-female variation in the number of foreleg tibial cilia in males of *Drosophila silvestris* (Perkins), which was known to vary genetically (Carson and Lande 1984). Iso-female strain variation in Swallowtail butterflies for oviposition preference (Thompson 1988a) was later confirmed to have a genetic basis (1988b).

However, variation among lines might be partly the result of differing environmental rearing conditions for each separately reared line. Therefore, a more sensitive method for investigating whether additive genetic variation exists in female responsiveness and selectivity is a divergent artificial selection experiment (Charalambous, unpublished data). If response to selection is successful, divergent lines can be crossed to make possible a detailed genetic analysis of selectivity and response (Mather and Jinks 1972).

Response to calling song and selectivity

The experiment described suggests that although a heritable component to female responsiveness (but not selectivity) is present, it is subject to large amounts of environmental variation. For example, consider the following. In all generations females were tested when 5, 6, 7, and 8 days old. In a congeneric species females become unreceptive when they are about to oviposit, at age 8 or 9 days (Hartmann and Loher 1974). Responsiveness is related to receptivity. For some reason such as poor food quality, G2 (and also GP) females might not mature sexually as quickly as G1 females. Consequently, the receptivity window for G2 females might have been much reduced. It is also interesting to note that components of the male calling song are subject to a large amount of environmental variation (Butlin and Hewitt 1986). Furthermore, environmental variation, will be even more severe under the relatively less constant field conditions.

Ultimately, the results of the investigation into the selectivity of response can be considered in two ways. Firstly, that females could be selective but due to the design of the experiment, small sample size or extreme environmental variation in rearing seperate generations, this was not reflected in the results. Of course, response stridulation might not actually be the correct "choice" criterion to use. However, of the female *Chorthippus brunneus* behavioural reportoire, it is the most obvious cue to use. Secondly, that females are not as selective as parental investment theory (Trivers 1972), for example, would predict. Evidently, though, the male-female "alternation song" represents some sort of choice and the experiment did reveal that females discriminate against songs that do not have a chirp structure.

Which of the two arguments is correct is still open to debate. However, experiments in the field (Charalambous, 1990) indicate that individual components of male song are not correlated with mating success. This lends some support to the second argument that females are not very selective. If females are not selective, then why does response to the male song, leading to the "alternation song", persist? There are both adaptive and non adaptive explanations which could be invoked.

It has often been noted that only mature, receptive females respond to calling song (reviewed by Haskell 1961) and that responding females are more likely to mate (Butlin *et al.* 1985, Green 1987). Also, males who sing more achieve a higher mating success (Butlin *et al.* 1985). Therefore in an adaptive context, response stridulations may function as a receptivity cue, and together with the "alternation song" may be used in mate location but not mate choice. The fact that genetic variation exists does not mean that response is under selection. At present, response stridulations may be selectively neutral: perhaps a remnant of past history. Alternately, response stridulations may be correlated with another female phenotypic character under selection, or even the male song, through linkage disequilbria.

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Mating behavior across a hybrid zone in *Chorthippus parallelus* (Zetterstedt)

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ABSTRACT

Two subspecies of the grasshopper, *Chorthippus parallelus* (Zetterstedt), form a hybrid zone in the Pyrenees. In the laboratory, hybrid males are sterile and behavioral differences between the subspecies are sufficient to produce assortative mating. Changes across the zone in the songs of the males, female preferences, and the pattern and fitness consequences of assortative mating are described. Behavioral isolation does not seem greatly increased following hybridization, as would be predicted by the Reinforcement Model of Speciation.

Key Words: Mating behavior, hybrid zone, grasshopper, *Chorthippus parallelus*, reinforcement, speciation.

Regions of hybridization connect many closely related orthopteran taxa (Hewitt, 1988; Shaw *et al.*, 1988; Harrison, 1986). Most of these hybrid zones seem to have been initiated when the forms came into contact following a period of allopatric differentiation and persist as a result of dispersal and selection against hybrid genotypes (Barton and Hewitt, 1985). Gene flow across such zones may be significant, especially for genes not strongly selected against. It seems sensible, therefore, to consider hybrid zones as intraspecific phenomena. However, they play an important role in some theories of speciation because full reproductive isolation might be expected to evolve as an adaptive response to deleterious hybridization (Wallace, 1889; Dobzhansky, 1976). If common, we would expect to find evidence of the exaggeration (or "reinforcement") of the behavioral differences that cause pre-mating isolation between subspecies at hybrid zones. However, this idea is contentious due to difficulties modeling the process and a lack of strong empirical evidence (*e.g.*, Paterson, 1985; Butlin, 1987; Coyne and Orr, 1989).

We have been studying a hybrid zone in the grasshopper *Chorthippus parallelus* (Zetterstedt) and have examined male and female variation in behavioral characters and patterns of assortment between populations. We have also examined the consequences of assortment within the hybrid zone. We believe this particular hybrid zone is one of the best-studied examples of its type. We would like, therefore, to take the opportunity to draw together our different approaches to this problem, and give an overview of all the results to date.

THE HYBRID ZONE

Chorthippus parallelus is a common European species of acridid grasshopper. The typical subspecies *C. p. parallelus* is replaced in Spain by *C. p. erythropus,* which is characterised by redder hind tibiae (Reynolds, 1980). There is a hybrid zone between them in the Pyrenees, and they exhibit clines in morphology, allozymes, and chromosomal markers (Butlin and Hewitt, 1985a,b; Gosalvez *et al.,* 1988). Figure 1 shows the morphological transition through the Col de la Quillane, Pyrenees-Orientales.

When the two subspecies are crossed in the laboratory, the resulting male offspring are sterile (Hewitt *et al.,* 1987), indicating strong selection against hybrids where they first come into contact. There is clearly potential for reinforcement.

This animal readily lends itself to behavioral studies. It can be collected in the field, brought into the laboratory, and eggs collected, allowed to hatch, and experimented upon the following spring. There is a complication that may influence results. The usually rare long-winged forms (or macropters), especially of *C. p. parallelus,* become common in the laboratory (Ritchie *et al.,* 1988).

MALE SONG CHARACTERS

The most noticeable feature of *C. parallelus'* mating behavior is the male song. Two main song types are involved, a calling song, which a male sings at any time, and a courtship song, which is produced by a male in contact with a female. Differences between the song types occur, mainly in the timing, or rate of calling, and the structure of the courtship song, which is more elaborate in *C. p. erythropus* than in *C. p. parallelus.* Figure 2 shows how these characters change through the Col de la Quillane. There is no evidence of any increased divergence in the area of hybridization.

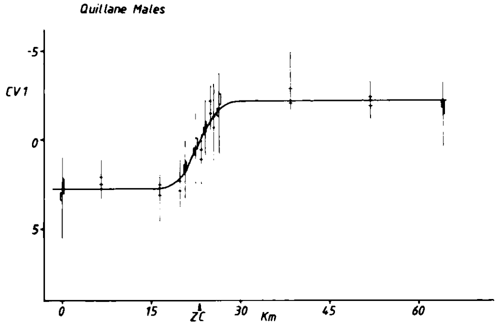

Figure 1. The cline in the first canonical variate of male morphology through the Col de la Quillane. *C. p. parallelus* is to the left, and the zone center is indicated. The character most responsible for CV1 is the number of stridulatory pegs. Bars are ranges and standard errors (some populations have been sampled twice). The line is a fitted tanh curve.

In order to assess whether these song differences are of any behavioral significance, a series of assortative mating experiments was carried out using males made unable to sing by the removal of their wings (Ritchie, 1990). We expected lower levels of assortative mating between females and these males, but found that virgin female *C. p. erythropus* could distinguish between the "mute" males of each subspecies as readily as singing ones. However, the removal of antennae in both sexes prevented assortative mating. Contrastingly, with *C. p. parallelus* females, assortment persisted despite the loss of antennae but is possibly reduced in the absence of song stimuli (an unfortunate interaction with wing morph confused the pattern in this last case (Table 1)).

These results indicate a change in the relative importance of song and pheromonal or tactile stimuli, or both, between these closely related subspecies. The frequency with which males call differs between the subspecies in the manner one would expect following such divergence (Butlin and Hewitt, 1985b). This series of experiments casts doubt on the use of male song differences as a measure of likely mating behavior and serves as a warning to experimenters about the interpretation of observed behavior.

FEMALE PREFERENCES

Despite our uncertainty about which male characters are involved with assortative mating, we can examine how the preferences of females for the two types of males vary across the hybrid zone. In principle, any variation in assortment which females show when offered an identical selection of males should reflect underlying differences in preference. For example, if a transect was made through the hybrid zone, and each resulting female was offered the same combination of potential male mates from pure populations, variation in assortment should reflect variation in female preferences because the confounding male factors are held constant.

Such an experiment has been carried out. Eggs were collected from populations spanning the hybrid zone at the Col de la Quillane and hatched in the laboratory. Pairs of young virgin females were confined in cages with a pure male of each subspecies matched for age and wing morph, and the identity of the first male mating with either female was noted. Some non-virgin matings were also scored. The pure males were ei-

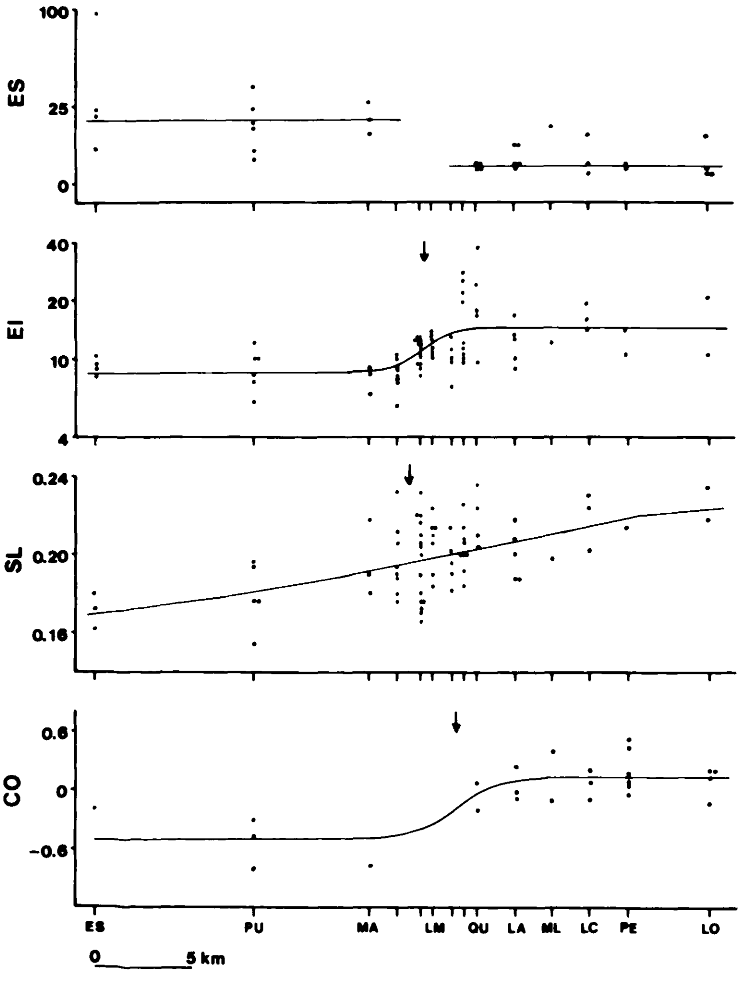

Figure 2. The clines in song characters through the Col de la Quillane. These are (top) chirps per sequence, gaps between chirps, syllable lengths, and structure of courtship song. Points are means from each individual. Lines are fitted tanh curves (no hybrid individuals were measured for chirps per sequence).

Table 1.—The number of homogametic (Hom) and heterogametic (Het) matings between normal individuals; following the removal of the antennae of both sexes; following the removal of males' wings; and following the removal of both wings and antennae. M = matings involving macropterous males, B = those involving brachypterous males. ($G = 13.43$, df = 3, $p > 0.0001$ for *C. p. erythropus females;* with *C. p. parallelus* females, male wing morph had a confounding effect: $G = 9.192$, df = 1, $p < 0.001$).

	Cpc		Cpp(M)		Cpp(B)	
	Hom	Het	Hom	Het	Hom	Het
Normal	17	1	13	7	8	2
Antennae	9	8	15	3	11	2
Wings	17	3	9	8	8	3
Both	9	8	4	3	3	0

ther from the Col du Pourtalet, Pyrenees Atlantique or from the purest populations of Quillane (though the females were not given a choice involving males from their own population). In all, over 500 females from 16 populations were tested, resulting in copulation around 700 times. In order to obtain this number of matings, the experiment was carried out on three separate occasions. Several populations were repeatedly sampled in the three trials in order to allow us to test for variation amongst the different trials. No such variation was found, which allows us to combine all the results.

Figure 3 shows how the proportion of females mating with the pure *C. p. parallelus* male varied across the hybrid zone ($\chi^2 = 32.23$, df=15, $p<0.006$). Though any preferences shown tend to be weak, there is a clear transition around the location of the morphological cline. However, two of the pure *C. p. parallelus* populations failed to show any preferences, possibly indicating an inverse cline on that side of the zone, with the strongest preferences for *C. p. parallelus* males occurring close to the zone. The *C. p. erythropus* side of the transect has an unfortunate sampling gap near the hybrid zone.

These results are difficult to interpret. If the increased preferences are due to reinforcement, they would be expected to occur within the zone rather than outside it, and similar results would be expected from the *C. p. erythropus* side of the zone. Attempts to fit curves to the data to distinguish statistically whether a simple transition or inverse cline fits best have proved ambiguous (Butlin and Ritchie, in press.). More females should be sampled, but this is the strongest suggestion yet of reinforcement in the zone.

ASSORTATIVE MATING

Variation between populations in both male and female components of mating behavior should result in assortative mating between the populations. This can be examined in the laboratory by combining laboratory reared males and females from the two populations in a large cage and scoring the resulting mating pattern. Such relatively simple experiments have been carried out between four pairs of populations from the Col de la Quillane. These consist of a pair from within the hybrid zone, another from the edges of the cline in morphology, a pair 16 km from the zone, and a final pair some 30 km from the zone. The last pair should be sufficiently far from the zone to represent the original allopatric populations. The varying levels of assortment that result are seen in Figs. 4 and 5.

The trends are slightly obscured by differences between the females of different wing morphs in one of the populations. In part, this may be a problem associated with the age at which brachypterous females mate (Ritchie *et al.*, 1989). Excepting these brachypters, the results indicate fairly strong assortment between all populations except those within the hybrid zone. The purest pair show the greatest assortment when virgin but discriminate less strongly when remating (compare Figs. 4 and 5). Amongst combined virgin and non-virgin matings the greatest level of assortment occurs at the edge of the zone though these populations are not significantly more isolated than are the pure pair. There does not appear to have been any major increase in behavioral isolation between populations at the hybrid zone.

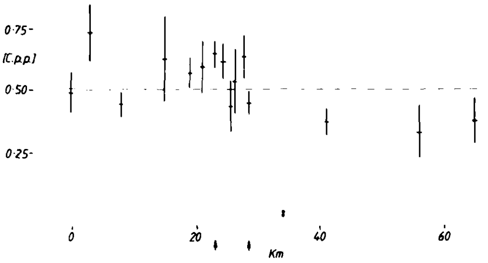

Figure 3. The cline in the proportion of females mating with the *C. p. parallelus* reference male through the Col de la Quillane. Arrows indicate the edges of the morphological cline, and the broken line is at 0.5 (*i.e.*, random mating). Bars are standard errors, and the two spots immediately to the right of the cline represent a sample of only two females.

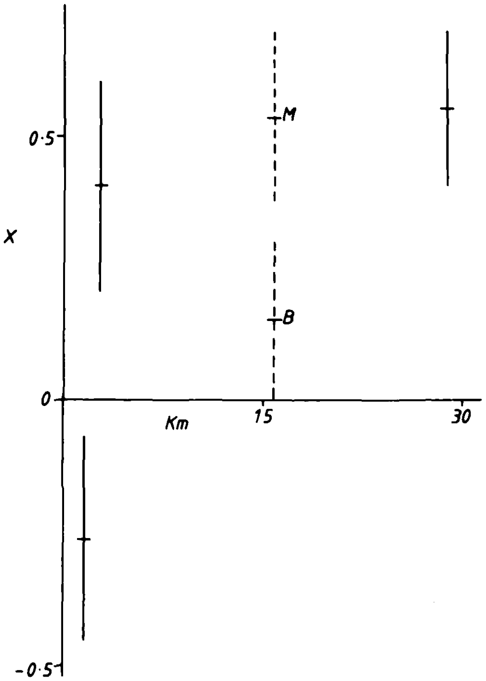

Figure 4. Behavioral isolation (X) between four population pairs from the Col de la Quillane plotted against mean distance to the zone center. Bars are standard errors. Brachypterous (B) and macropterous (M) females assort differently for one population. X is calculated from virgin matings only.

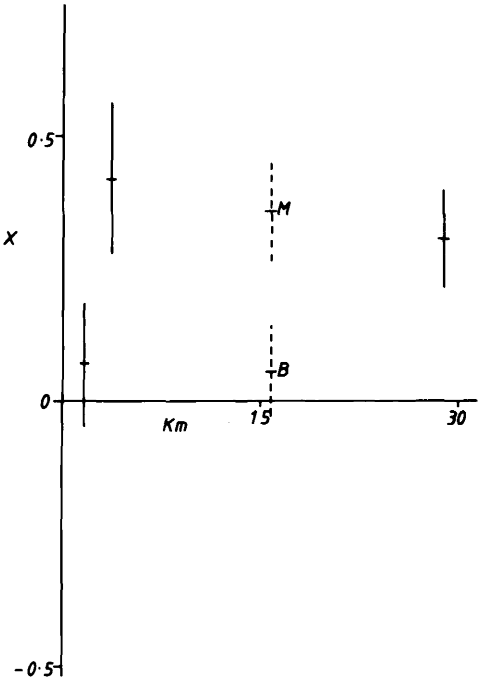

Figure 5. As with Fig. 4, but X is calculated from combined virgin and nonvirgin matings.

VARIATION WITHIN POPULATIONS

The method adopted so far in looking for reinforcement (*i.e.*, seeking inverse clines) is typical of such studies. However, this approach could be flawed when one examines a stable hybrid zone. If hybrid populations are composed of distinct assorting genotypes, a cline in population means through the zone might indicate a smooth transition from the one region to the other even though some distinction is maintained within the hybrid zone. The pattern of assortative mating *within* hybrid populations is, therefore, potentially more important than is a transect of population means. If reinforcement has occurred, assortative mating within hybrid populations should prevent the expression of hybrid dysfunction. If assortative mating had evolved within the zone in response to sterility of the hybrid male offspring, the sons of females from hybrid populations forced to mate at random would be expected to have poorer quality testes than those of females allowed to choose their own mates. Other aspects of fitness such as viability might also be reduced. Such factors have not been measured accurately on laboratory Fl hybrids.

We have measured a range of fitness parameters of the offspring of laboratory reared hybrid zone females who were either assigned a male at random or allowed to "choose" their own mate from a cage containing many potential mates. Each female was allowed only a single mating, and the same males were used for both groups of females. Eggs laid by the females were collected and subsequently analyzed. Three egg pods from each of 50 females were examined, and the results are shown in Table 2. There are no significant differences in any of the fitness measures. The testes of the sons of both groups of females are morphologically indistinguishable from those of pure populations and capable of delivering sperm.

Table 2.—Fitness parameters measured on the offspring of hybrid females either assigned a male at random or allowed to "choose" their own mate. Standard errors are shown in brackets; there are no significant differences.

Fitness parameter	Assorting females	Randomly mating females
% egg pods hatching	100	94
Days until hatching	17.06 (0.96)	16.21 (0.48)
No. hatching per egg pod	4.77 (0.42)	4.81 (0.39)
Days until adult	23.69 (0.56)	23.20 (0.47)
Mean survival per family	0.769 (0.039)	0.840 (0.037)
Testes:		
Follicle length	2.613 (0.057)	2.535 (0.050)
Follicle width (mm)	0.355 (0.009)	0.345 (0.009)

DISCUSSION

This study arose out of the need to test the Reinforcement Model of Speciation, an hypothesis which, despite its popularity, lacks empirical supporting evidence and has recently been subjected to criticism (*e.g.*, Paterson, 1985; Butlin, 1987). There is no strong evidence suggesting that behavioral isolation between the two subspecies examined here has been enhanced following hybridization. However, *C. p. parallelus* females from near the zone may show increased preferences for *C. p. parallelus* males. None of the other approaches taken imply successful reinforcement. Furthermore, the clines for all the behavioral characters examined are of widths similar to the morphological transition. Given the likely age of this zone and the organisms' dispersal, this is the approximate width expected of a neutral character (Hewitt *et al.*, 1988), implying that any increased preferences fail to counteract the gene flow of the other behavioral characters.

The results of the study of fitness within a hybrid population provide no evidence that assortative mating prevents the expression of any sort of dysfunction. One unexpected result of our studies within both hybrid and pure populations is that we have consistently failed to detect any dysfunction within hybrid populations from the field. This is despite the results from our laboratory crosses. There seem to be three obvious explanations a) we have failed to sample the center of the zone for the genes affecting unfitness; b) the relevant characters are polygenic, and there is a wide zone of many recombinant genotypes, each affecting dysfunction only a very little (imperceptably so); or c) there has been selection for modifier genes counteracting the unfitness within the zone. Possibility a) has not been supported by repeated sampling of testes through the zone failing to detect any reduction in fertility (in prep.). We have initiated crossing schemes across the zone which should allow us to distinguish between possibilities b) and c), either of which would presumably substantially reduce the possibility of reinforcement.

We conclude that selection by reinforcement may act on some characters in the hybrid zone but does not significantly restrict gene flow. This process is but one of several possible outcomes of deleterious hybridization that should be considered when one attempts to understand these intriguing phenomena.

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Effect of temperature on the acoustic signals of *Pterophylla beltrani* (Bolívar and Bolívar) and *Pterophylla robertsi* (Hebard) (Tettigoniidae: Pseudophyllinae)

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ABSTRACT

The effect of temperature on pulse rate per second, phrase rate per minute and length of phrase intervals of the acoustic signals of two Mexican species of *Pterophylla* (Tettigoniidae: Pseudophyllinae) was studied. *Pterophylla beltrani* (Bolivar and Bolivar) and *Pterophylla robertsi* (Hebard) acoustic signals were recorded over a temperature range of 19-33°C. In both species, there was a positive correlation between temperature and pulse rate per second and phrase rate per minute; there was negative correlation between temperature and length of phrase intervals. All three signal variables are adequately described as linear functions of temperature. *P. beltrani* acoustic signals were faster than those of *P. robertsi* at all temperatures.

Key words: *Pterophylla,* acoustic signals, temperature.

INTRODUCTION

Acoustic signals are one of the most important and elaborate communication systems in the more evolutionarily complex groups of animals such as arthropods, anurans, birds and mammals (Alexander, 1960, 1967, 1968; Mayr, 1963; Sebeok, 1977; Doherty and Gerhardt, 1984; Doherty, 1985). Some acoustic signals often are part of the Specific Mate Recognition System (SMRS) (see Paterson, 1978, 1980, 1985) and as such, act to attract males and/or females for the purpose of mating. Acoustic signals can also be used for aggregation, territory and home range marking (repellents), alarm and disturbance, aggression, etc. (Alexander, 1960, 1967, 1968; Dumortier, 1963; Claridge, 1985).

To function as a SMRS the signals need to be stereotyped and species specific. These signals should be resistent to change because of the coadaptation between males and females and the stabilizing selection to which the acoustic communication system is subject (see Paterson, 1978, 1980, 1985; Passmore, 1981). Nevertheless, acoustic signals do change by the action of various environmental and genetic factors, which are responsible for intraspecific and interspecific variation (see Walker, 1957, 1962 a,b; Doherty, 1985; Doherty and Hoy, 1985; Claridge et al., 1983, 1985; West-Eberhard, 1983; Barrientos, 1988).

Three environmental factors are known to influence the nature of the acoustic signals. These are temperature, acoustic signals of other animals, and humidity. Other factors such as light intensity, wind, rain and mechanical disturbance are important in determining whether the acoustic signals are produced or not, but they do not have a direct effect on the nature of the acoustic signals emitted (Walker, 1962 a,b; 1975). Amongst all environmental factors, temperature has the most universal effect on acoustic signals. Most commonly, it speeds up the signals by shortening certain temporal parameters. For example, in *Gryllus bimaculatus* (Doherty, 1985) syllable and chirp repetition rates increase linearly with increasing temperatures; in *Oecanthus* spp (Walker, 1957) pulse rate varies directly with temperature. It has been stressed that, although pulse rate may be characteristic for a species at a given temperature, individuals of two species displaying acoustic signals at different temperatures may have identical pulse rates (Walker, 1962a).

The present work was designed to investigate the relationship between tem perature and acoustic signals in *Pterophylla beltrani* (Bolivar & Bolivar) and *Pterophylla robertsi* (Hebard). It was carried out as part of an extensive study of the acoustic signals and taxonomy of Mexican *Pterophylla*. *P. beltrani* and *P. robertsi* are allopatric species but are often confused because of their very similar morphology. The acoustic signals of both species are made up of predominantly 2-pulse phrases (Barrientos, 1988). The most important parameters used to distinguish between them are: phrase rate per minute, length of the first pulse and length of pulse intervals. *P. beltrani* produces more phrases per minute, longer first pulses and shorter pulse intervals than *P. robertsi* (Barrientos, 1988).

MATERIALS AND METHODS

P. beltrani and *P. robertsi* occur in northeastern and eastcentral Mexico, respectively. Adult specimens of both species were collected in the field during the summer of 1986. The collection sites (Fig. 1) are as follows:

P. beltrani: Santiago, Nuevo León. Horsetail Falls, between the villages of Nogalera and Puerto Genovevo. Type locality. Elevation 840-1160 m.

P. robertsi: Ciudad del Maiz, San Luis Potosí. Village of Platanitos. Type locality. Elevation 1100 m.

The specimens were brought to Cardiff and kept in wood-framed, gauze-covered cages (1.0x0.25x0.25 m), at a density of 10-15 males or females per cage. They were fed on fresh oak leaves (*Quercus* species). Water was supplied twice daily by spraying the cages with a mist spray. Cultures were maintained at 25±1°C in the insectary of University of Wales, College of Cardiff.

The recording was carried out in a sound proofed, temperature controlled room of ca. 2x3 m. Prior to the recording sessions the insects were allowed at least 2 h to adjust to the recording room temperature. A total of 26 males of *P. beltrani* and 7 of *P. robertsi* were recorded (only males produce SMRS acoustic signals). However, the number of males recorded at each temperature was variable. Recording temperatures ranged from 10-33°C. Experimental temperatures were increased gradually every two or three days, once enough males had been recorded at certain temperature. Relative humidity ranged from 60-70%.

To record the acoustic signals a wood framed gauze-covered cage containing the males was placed in the recording room; when a male sang he was placed in a recording box (0.40x0.40x0.40 m) made of 5 cm thick sponge. The box reduced sound reverberation and contained the males. Each recorded male was labelled on its femur with a key number to keep track of all its recordings.

Acoustic signals were recorded on magnetic tapes using a Nagra Kudeleski, 4.2 tape recorder at a tape speed of 38.1 cm/s. A Sennheisser MKH 110 microphone was inserted in the roof of the sponge box. Recorded signals were analysed by playing back the tapes at a tape speed of 9.52 cm/s and making oscillogram traces on a Siemens Mingograf 34. From the traces the pulse

Fig. 1.—Map of Mexico to show the collection sites of *P. beltrani* and *P. robestri.*

rate per second, phrase rate per minute and length of phrase intervals were measured. Variables were determined from up to 10 samples of 5-20s recordings for each individual. Regression analyses were performed using each individual's mean at different temperatures.

RESULTS

The effect of temperature on pulse rate per second, phrase rate per minute and length of phrase intervals for *P. beltrani* and *P. robertsi* is given in Tables 1-3 and Figures 2-4. Both species showed a positive linear correlation between temperature and pulse rate per second and phrase rate per minute; there is negative linear correlation between temperature and length of phrase intervals.

P. beltrani produced signals over a greater temperature range (19.5-33°C) than *P. robertsi* (21-28°C). Above or below the acoustically active range males of both species remained inactive. For any given temperature, *P. beltrani* exhibited faster pulse and phrase rates and shorter phrase intervals than *P. robertsi.*

DISCUSSION AND CONCLUSIONS

The results of the present work agree with previous studies on the effect of temperature upon the acoustic communication signals of most poikilothermic animals. That is, the repetition rates of signals at high temperatures are higher than at low temperatures (see Walker, 1957, 1975; Gerhardt and Mudry, 1980; Doherty and Hoy, 1985). Variation of an acoustic signal with temperature affects its effectiveness as a SMRS. In order that a SMRS remains effective the effect of temperature on signal production by the sender must be similar to

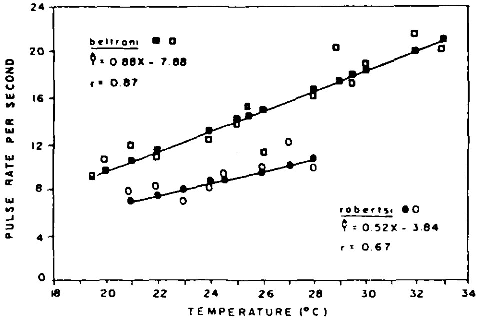

Fig. 2.—Effect of temperature on pulse rate of *P. beltrani* (□observed; ■expected values) and *P. roberstri* (○ observed; ● expected values) acoustic signals.

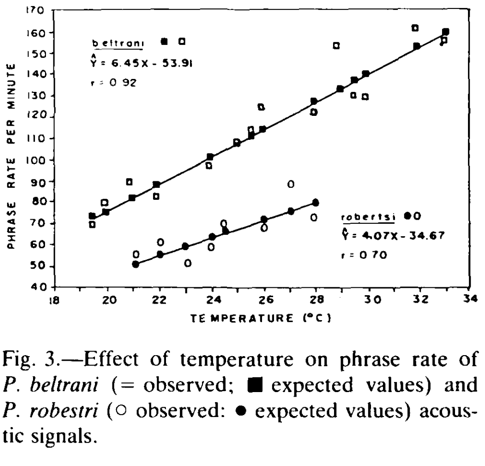

Fig. 3.—Effect of temperature on phrase rate of *P. beltrani* (= observed; ■ expected values) and *P. robestri* (○ observed: ● expected values) acoustic signals.

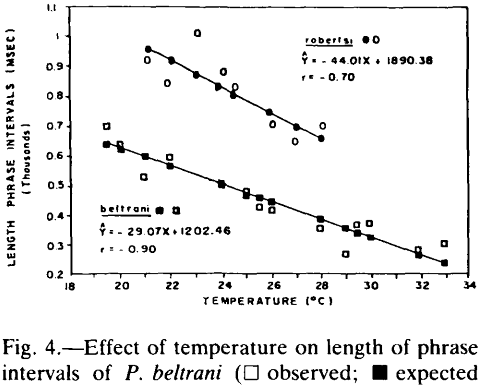

Fig. 4.—Effect of temperature on length of phrase intervals of *P. beltrani* (□ observed; ■ expected values) and *P. robersti* (○ observed; ● expected values) acoustic signals.

the effect of temperature on signal recognition by the receiver. This means that sender and receiver are coordinated or matched (temperature-coupled; Gerhardt, 1978). *P. beltrani* and *P. robertsi* showed large variation of their acoustic signals with temperature. How this variation affects their acoustic communication system is not known. It would be interesting to determine to what extent males and females of *Pterophylla* spp. are temperature coupled and what are the parameters of the acoustic signals that are important in the process of recognition. Although, temperature coupling has been demonstrated in many species, *e.g.*, *Oeanthus quadripunctatus* and *O. nigricornis* (Walker, 1957); *Gryllus bimaculatus* (Doherty and Huber, 1983; Doherty, 1985); *Hyla versicolor* and *H. chysoscelis* (Gerhardt, 1978; 1982) it may not be the only way to maintain effective communication at different temperatures. Recognition in the receiver may be based on signal properties that are not affected by temperature e.g., *Chorthippus biguttulus* (Helversen, 1972) and *Gryllus bimaculatus* (Doherty, 1985).

The effect of temperature on acoustic signals of crickets and katydids has been described in several groups. Walker (1962b) described the relationship between temperature and pulse rate for 19 species of crickets. He showed that for all species the rate of change in pulse rate could be expressed as a linear function of temperature. A similar relationship between temperature and pulse rate or phrase rate has been described for *Pterophylla camellifolia* (Shaw, 1968); *Atlanticus* species (Walker, 1975) and *Gryllus bimaculatus* (Doherty, 1985), among others.

Although, acoustic signals of *P. beltrani* and *P. robertsi* can be distinguished on the basis of temporal parameters (phrase rate per minute, pulse rate per second, etc.) they may produce a similar pulse rate at different temperatures. However, these species do not overlap in their distribution area. Acoustic signals of *P. beltrani* are faster than *P. robertsi* at any given temperature (see Tables 1-2). The range of activity for each species is also different, 19-33°C in

P. beltrani and 21-28°C in *P. robertsi*. Although, only seven males of *P. robertsi* were studied, the above differences reflect most probably their adaptations to different distribution areas.

The three variables studied were those that have been demonstrated to be important in discriminating between the different species and populations of *Pterophylla* (Barrientos, 1988). For each species the relation between temperature and variables is well described by linear equations which are useful for predicting values of any of the three variables at any given tem perature. They also could be useful for correcting acoustic signals' variables to a standard temperature in field studies and in comparative studies of allopatric populations and populations at different altitudes throughout the range of the species.

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Analysis of the maze behavior of adult cockroaches (*Periplaneta americana* L.) maintained under constant light since eclosion

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ABSTRACT

Previous studies with *Periplaneta americana* varying light/dark (LD) timing have dealt almost exclusively with the rhythm entrainment of locomotor activity. In the present study we analyze the stress of photoperiod on this behavior by means of a complex maze model selected from computer-generated series.

We used two groups of newly hatched nymphs under photoperiod conditions of 12L:12D and 24L:0D respectively. The adults resulting from them were subsequently maze tested.

The observed exploration, antennae grooming, and side displacement rates were similar in both groups. However, the time employed in the maze course was significantly longer in the LD 24:0 group, while their speed, course length, success in choosing the right way, and final arrival frequencies were strikingly lower. In addition, all animals of group 12L:12D learned the maze situation, while none of group 24L:0D did.

These results suggest that the 24:0 photoperiod seriously alters the behavioral patterns of *P. americana*. We observed a decrease in the maze starting line which disrupts exploratory behavior.

Key words: maze, *Periplaneta*, constant-light, behavior.

INTRODUCTION

There are few published papers on the behavior of a cockroach inside a maze since the works of Chauvin (1947) that have studied the maze exploration with *Blattella germanica*, and Longo (1964) training cockroaches *(Nauphoeta cinerea)* to turn in a maze either left or right and then repeatedly reversing the discrimination.

It is well known that alterations of the photoperiod induce behavioral (Harker, 1956, 1958; Lipton & Sutherland 1970) and physiological (Harker, 1961; Cymborowsky, 1971; Lukat, 1978) changes in cockroaches. An extreme example is the effect of continuous illumination (24L:0D) on *Periplaneta americana* during development, resulting in accelerated growth and maturation (Solomon *et al.*, 1977) and important behavioral alterations: irritability, hyperactivity in light, inactivity in dark, etc. (Mateu, 1989).

This paper deals with one aspect of altered behavior.

MATERIAL AND METHODS

Animals

We used 18 individuals of *Periplaneta americana*. The insects were reared in our laboratory in glass bottles with an "ad libitum" supply of water and food (Purina Dog Chow), at 25 ±1° C and 60 ± 5% RH.

Maze

The maze model was selected from 60 models generated by a computer. The maze was a rectangular box with black, wooden walls and a metacrylate base, with 30 L-shaped elements superimposed and two cubicles used as start and arrival points (see figure. 1).

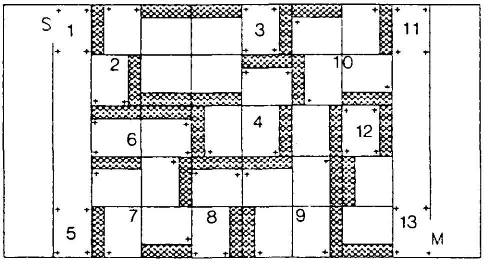

Figure 1.—Sketch of the maze plan and the 13 "influence sections". S=Start, M=Arrival.

Treatment

Eight nymphs (CLNymphs group) were reared under continuous light (24L:0D) since eclosion to adults, and then were individually tried in the maze.

The control group was 10 similar nymphs that were exposed to a 12L:12D photoperiod during development.

The maze was divided in 13 "influence sections" (figure. 1); crossing from one to the next involves a decision (choice between several options), and it was considered as "right" if the arrival was nearer after it.

There were a cotton rag soaked in beer and a piece of apple in the arrival as stimulus for the insects to run the maze.

The test was performed under red light, at the same time in both groups, corresponding to the last three hours of the scotophase of the 12L:12D cycle.

The animals ran individually in the maze twice a day for a maximum period of 3 minutes each run. The trial time since they left the start till they reached the arrival was measured for each run; in a failure, the maximum period of 3 minutes was registered.

The travel speed was calculated consider-

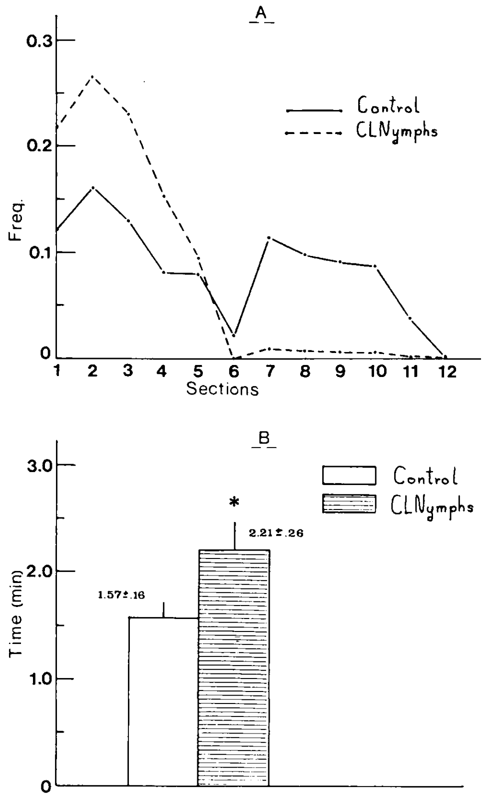

Figure 2.—Results for the variables, a) crossing frequencies for each section, b) run time. (*: $p<0.05$)

ing the length of the run and the time employed to travel along it.

Each animal was tested every day until it crossed the maze successfully for two consecutive days —four runs— ("Learning" conditions).

Statistical analysis

The Student t-test was used to compare parametric variables (time, length, and speed of the run) and the Mann-Whitney U-test for the non-parametric variables ("right" frequency, successful arrival frequency, individual maze sections crossing frequency). The arithmetic mean ± standard error figures are listed for the first test and only orientative arithmetic mean for the second.

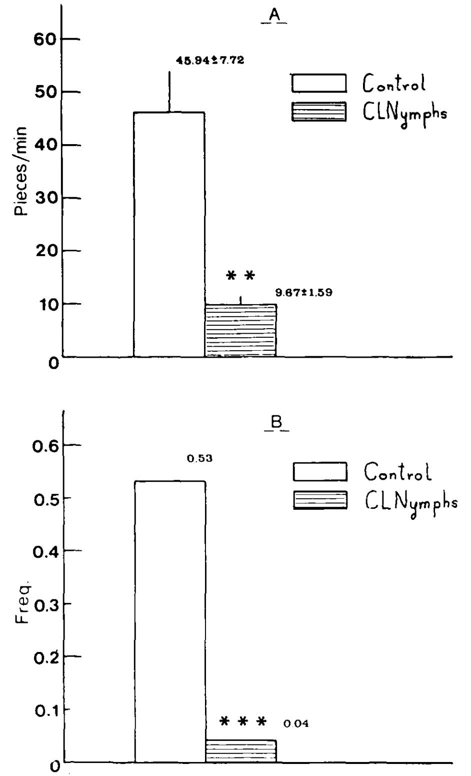

Figure 3.—Results for the variables, a) speed, b) right frequencies. (**: $p<0.01$; ***: $p<0.001$).

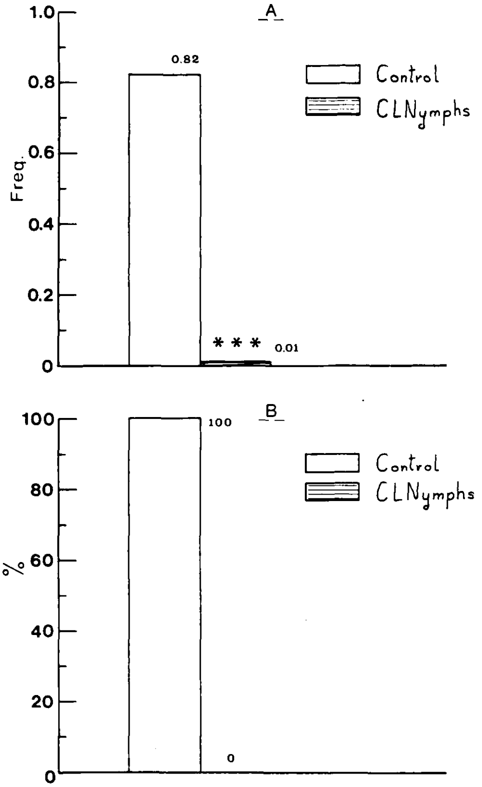

Figure 4.—Results for the variables, a) successful arrival frequencies, b) percentage of pre-established "learning" conditions. (***: $p<0.001$)

RESULTS

Figure 2a shows opposite search behavior for both groups, as in the "first part" of the maze (sections 1 to 5), crossing frequencies are very high for the CLNymphs experimental group and very low for the control group. Differences are significant in almost every case (1: $p<0.001$, 2: $p<0.001$, 3: $p<0.05$, 4: $p<0.05$); on the other hand, there is a significant inversion in the data for the "second part" (sections 6 to 13) in almost every case (6: $p<0.001$, 7: $p<0.001$, 8: $p<0.001$, 9: $p<0.001$, 10: $p<0.001$, 11: $p<0.001$).

The animals of the CLNymphs experimental group need more time for the run (figure. 2b): $t=2.29$ ($p<0.05$) and are slower (figure. 3a) than the control group animals: $t=3.56$ ($p<0.01$). Slower animals also use shorter itineraries: $t=13.76$ ($p<0.001$).

"Right" frequencies (figure. 3b) are much smaller for the CLNymphs group ($U=0$, $p<0.001$), as well as the successful arrival frequencies ($U=0$, $p<0.001$) (figure. 4a).

The differences in complying with the pre-established test conditions (figure. 4b) reflect the relationships betwen both groups.

DISCUSSION

The environmental lighting has a great influence on the insect behavior. Many species show a behavioral rhythmicity synchronized according to light: dark cycles. Cockroaches show a strong circadian rhythm in their locomotor activity (Lipton & Sutherland, 1970). Other behaviors, of a more specific kind such as feeding and drinking are rhythmic too and are related to locomotor activity.

In LL conditions *P. americana* shows for a few days a carryover entrained rhythm from previous LD conditions but an increased activity. The animals under continuous lighting since eclosion have an accelerated growth process as pointed out by Solomon *et al.* (1977) and corroborated by us (unpublished data). It is clear from our results that a parallel, gradual increase in irritability occurs.

The exploratory behavior of the CLNymphs group is deeply altered in comparison with the control group. The low tendency to explore the maze or even to enter it can be interpreted as an important reduction of the general activity (including antennae movements), opposite to hyperactivity in presence of light. That extreme passivity inside a dark maze is so high that it inhibits the learning possibilities.

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Food selection in the Acridoidea, or grasshoppers, of the Sierra de Cazorla (Spain)

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ABSTRACT

Del Cerro (1978) provided a recent discussion and a species list (1980) of the Orthopteroidea (including Acridoidea or grasshoppers) of the Sierra de Cazorla, one of the most interesting regions of the Iberian Peninsula. Some years after del Cerro's report, the author spent a week in ten different localities of the region collecting materials for analysis of the crop contents, feculae, and mouthpart adaptations of 14 species encountered there. An improved understanding of the insects' food selection in nature was obtained thereby, along with information on the incidence of late-season mandibular wear.

Key words: behavior, Cazorla (Spain), distribution, feculae, feeding, gut content, mandibular wear.

INTRODUCTION

The Sierra de Cazorla, a mountain chain situated in the east of Jaen Province, southeast Spain, is one of the most interesting regions of the Iberian Peninsula because of the richness and diversity of its biota. Becerra (1898), who worked in the adjacent Sierra de Segura, provided the first species list (a total of 15 orthopteroids) from the region. Ragge (1965) listed 47 orthopteroids from Cazorla in his report based on two expeditions of British Museum (Nat. Hist.) personnel. Del Cerro (1978) provided a more recent discussion in his unpublished doctoral dissertation. He subsequently (1980) published his list of 85 orthopteroid species (including 31 acridoids).

Some years after del Cerro's report, the author spent a week in early October collecting and experimenting on the grasshoppers of Cazorla. Collections were made at 10 different localities. No additional species were found to add to the existing list except for a possible *Stauroderus* sp. However, the first feeding data for regional representatives were amassed extending information contained in an earlier co-authored paper (Gangwere and Morales, 1973) on feeding in Iberian orthopteroids.

COLLECTION LOCALITIES

These included the following meadow, roadside field, scrub, and other open situations shown in Fig. 1:

1) Cabeza del Tejo. 1,500 m
2) Collado del Calvario ± 1,000 m
3) Coto Moreno, Piscifactoría. 700 m
4) Casa Forestal, El Vadillo. 1,200 m
5) Fuente Acero. 1,500 m
6) Fuente Moreno ± 900 m
7) Nava Criada
8) Nava del Espino. 1,420 m
9) Las Navillas. 1,100 m
10) Poyo Manquillo. 1,360 m

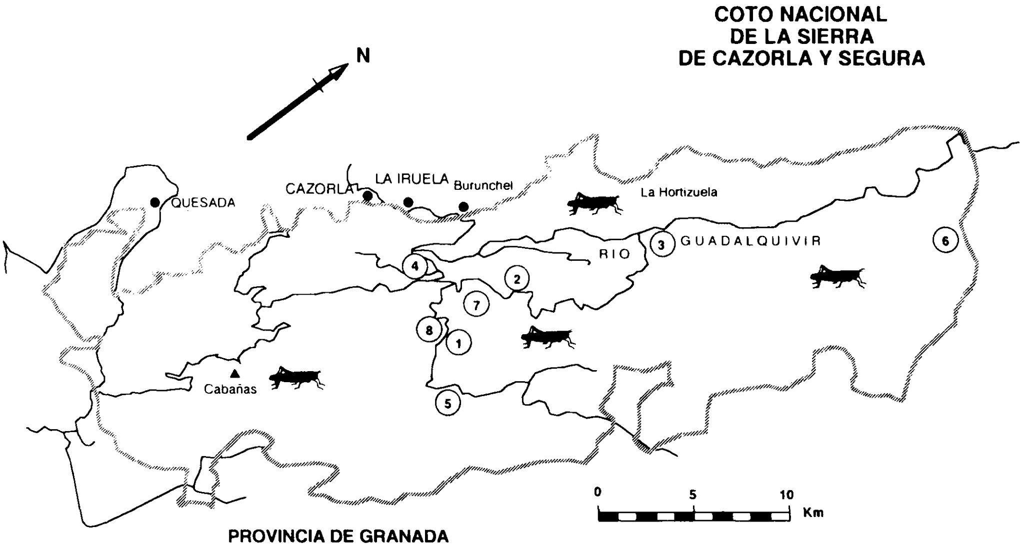

Figure 1. Collection localities.

METHODS AND RESULTS

The insects were field determined and placed within individual, labeled paper cones as described in Gangwere (1969) in which they lived for some days, defecating frequently. The cones were later opened in the laboratory and the insects retrieved, along with their accumulated feculae. The insects were relaxed and their mouthparts spread, studied *in situ*, and removed for more detailed examination by standard methods (Gangwere, 1965, 1969). The feculae were collected, classified to type (Gangwere, 1962), made into permanent microscope preparations using polyvinyl alcohol (PVA) mounting medium, and analyzed microscopically by standard methods (Gangwere, 1962, 1969). Up to nine insect specimens and multiple feculae of each species were studied. An annotated list follows.

Pamphagidae: Pamphaginae

Eumigus punctatus (Bolivar). Two species of this geophilous Mediterranean genus, *E. punctatus* (Bolivar) and *E. monticolus* (Rambur), have been recorded from the region, but both are probably referable to the former (Llorente, personal communication). The single female nymph of the taxon was collected at locality 6. Its Type IB feculae consisted of dicot remains. Based on earlier studies, the mouthpart adaptation is forbivorous-type.

Catantopidae: Catantopinae

Platyphyma giornae (Rossi). This brachypterous Mediterranean phytophile was found in localities 4, 8, and 10. Its feculae were Type IC, consisting of fibrous dicot remains. The mandibles were forbivorous-type, sometimes worn.

Catantopidae: Calliptaminae

Calliptamus spp. Two species of this widespread Palearctic genus, *C. italicus* L. and *C. b. barbarus* (L.), are known from Cazorla, and both were collected. The former was taken at localities 1, 3, and 4 and the latter at locality 5. The two insects, both phytophilous, are similar and often misidentified. The amassed data were similar. The feculae were Type IC, appropriate to the dicot gut content. The mandibles were forbivorous-type and usually worn.

Acrididae: Locustinae

Locusta migratoria (L.). A single individual of the solitary phase of this Old World plague locust, a phytophile, was captured at locality 3. Its Type IA feculae consisted of grass. The graminivorous-type mandibles were worn.

Oedipoda c. coerulescens (L.) (= *O. iberica* Bolivar). This Mediterranean geophile is relatively widespread in Spain on bare or sparsely vegetated, sunny fields or scrub. In Cazorla, it was taken in localities 1, 2, 3, 4, and 5. Its Type IC, occasionally 1B, feculae consisted of dicot, sometimes fibrous material. The mouthpart adaptation was forbivorous-toward-herbivorous type, with the dentes often worn.

Acrotylus spp. Two species of this geophilous Mediterranean genus. *A. insubricus* (Scopoli) and *A. patruelis* (Herrich-Schaffer), are recorded from Cazorla. Both were taken during this study. The former was captured in localities 1, 5, and 7 and the latter in locality 3. Both are common among patches of vegetation in sandy, sunny places. Their feeding data varied slightly. *Acrotylus insubricus* generally yielded Type IB feculae, the content of which included appreciable grass, and the sometimes-worn mandibles were graminivorous-type; *A. patruelis* defecated partly Type IB and partly Type IC feculae and included mostly dicot remains.

Aiolopus strepens (Latreille). This Mediterranean phytophile frequents meadows, cultivated fields, and other open situations elsewhere in Spain. In Cazorla, it was collected in locality 3. Its fibrous Type IB feculae consisted mostly of grass. The mandibles were graminivorous-type and visibly worn.

Dociostaurus g. genei (Ocskay). This widespread Palearctic species, like *A. strepens,* is a phytophile that frequents dry, sunny places. It was found in localities 3 and 9 in Cazorla. Its feculae were Types IB and IC, composed mostly of dicot remains. The IB pellets contained some fibrous, presumably grass material. The graminivorous-type mandibles were worn.

Omocestus panteli (Bolivar). This phytophilous meadow form endemic to Spain was found on low vegetation in localities 3, 8, and 10 in Cazorla. Its usually Type IA, occasionally Type 1B, feculae were distinctive because of their diminutive, slender, attenuate form. Their content was entirely grass. The graminivorous-type mandibles were often worn.

Chorthippus dorsatus (Zetterstedt). This phytophilous grasshopper is a Palearctic meadow inhabitant that, in Cazorla, was found in localities 7 and 8. The feculae were Type 1A. The gut content was grass. The mouthpart adaptation was graminivorous-type. The mandibles were worn.

Euchorthippus pulvinatus gallicus Maran. Another Palearctic phytophile, this grasshopper is ubiquitous in somewhat lush, open places throughout much of the Iberian Peninsula. In Cazorla, it was taken in localities 2, 3, 8, and 10. Its Type IA feculae consisted of grass. The mandibles were graminivorous-type and worn.

Stauroderus sp. The identity of this grasshopper, widespread in Cazorla, remains uncertain. It keys neither to *Stenobothrus* nor to *Chorthippus,* both of which genera are variable and taxonomically troublesome. The insect is probably referable to *Stauroderus scalaris* (Fischer-Waldheim). If so, this is a new record for Cazorla. For the present, it seems best to label the insect *Stauroderus* sp., while it is undergoing examination by specialists. It was collected in localities 1, 3, 4, 7, and 8 in Cazorla. Its Type IA feculae consisted of grass. The graminivorous-type mandibles were generally worn.

SUMMARY AND CONCLUSIONS

The majority of the Cazorlan grasshoppers studied consists of staunch graminophiles/graminivores *(Aiolopus strepens, Chorthippus dorsatus, Euchorthippus pulvi-*

natus gallicus, Locusta migratoria, Omocestus panteli, Stauroderus sp.) or of modified graminivores that may include a dicot component in the diet (*Acrotylus insubricus, A. patruelis, Dociostaurus g. genei*). The remainder consists of dicot feeders *(Calliptamus italicus, C. b. barbarus, Eumigus punctatus, Oedipoda c. coerulescens, Platyphyma giornae)* that eat forbs or occasionally leaves of woody plants. (Data are lacking to determine proportionate use, but forbs predominate, probably representing 90% or more of the diet). These results are consistent with those reported earlier in Spain (Gangwere and Morales, 1973).

The study took place in October. This is late in the season, a time when most grasshoppers of Cazorla were approaching the end of their lives. Their tegmina and wings were often frayed and sometimes parts of their appendages missing. Mandibular wear similar to that documented by Chapman (1964) was evident in over two-thirds of them. Surprisingly, there was no appreciable difference noted in the wear shown by the graminivores studied (which eat tough, silica-laden foods) as opposed to the forbivores (which take a presumably less abrasive diet).

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Food selection and feeding behavior in the species of *Neobarrettia* Rehn, 1901, a New World genus of predacious katydid (Orthoptera: Tettigoniidae)

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ABSTRACT

This study of food selection and feeding behavior in the species of the listrosceline genus *Neobarrettia* was undertaken to elucidate the behavioral factors that control their geographic and ecologic distribution in the thorn forest and thorn scrub communities of Mexico and southwestern United States. The investigation consisted of 1) analysis of crop contents, 2) differential feeding tests, 3) food restriction experiments, and 4) behavioral observations. *Neobarrettia* were found to be aggressive predators that specialize on medium-sized, relatively slow-moving, lightly armored insect prey. Occasionally they scavenge on dead insects, and rarely they may prey on small vertebrates. Given the opportunity, they are cannibalistic on smaller, weakened, or dying individuals of their own kind. It is unlikely that they feed on plants in nature though, under laboratory conditions, they may be induced to eat lettuce, cabbage, and certain flowers (probably for their water content), on which sustenance they can survive for a time. Slight interspecific differences in behavior between *N. victoriae* and *N. spinosa* were noted. These may be sufficient to account for their sympatry. The other known case of overlap, that between *N. hakippah* and *N. sinaloae*, may be explicable on the basis of differential habitat occupancy where the populations come together or on the basis of differential hatching, growth, and, therefore, nymphal size (the larger individuals eliminating the smaller).

Key words: behavior, feeding/predation, *Neobarrettia*, Orthoptera: Tettigoniidae: Listroscelinae.

INTRODUCTION

Little is known of the food habits and feeding behavior of the species of the genus *Neobarrettia* Rehn, 1901. This genus was revised by Cohn (1965). As Cohn noted, these katydids exhibit an early stage in the development of carnivory. They appear to be representatives of a primitive stock originating close to the divergence of the Listroscelinae from the Saginae. For purposes of the present study, they are interesting because a comparative analysis of species promises to explain certain cases of geographic contiguity and displacement as well as some cases of sympatry.

The nine species within the genus *Neobarrettia* (including the species of the synonymized genus *Rehnia)* are recorded from southern Mexico, through southwestern Texas and Oklahoma, up into Kansas, and over into New Mexico. All are arid land inhabitants of thorn forest and thorn scrub whose further dispersal is apparently blocked by grassland, oak woodland, and humid tropical forest barriers (Cohn, 1965). Of the six species groups, one having two species *(N. sinaloae* and *N. hakippah)* is commonly found on shrubs within disturbed (frequently ruderal) habitats along the northwestern coastal plain of Mexico; another (including only *N. cremnobates)* occupies shrubs within certain restricted barrancas of west central Mexico; a third with two species *(N. pulchella* and *N. bambalio)* occupies shrubby desert vegetation within certain restricted localities of southeastern Mexico; a fourth (only *N. victoriae)* is widespread in shrubby, mesquite-supporting habitats of northeastern Mexico through western Texas and Oklahoma into southern Kansas; a fifth includes a species *(N. vannifera)* found in thorn forest within a restricted locality of eastern Mexico and a species *(N. spinosa)* widespread northward within the mesquite and thorn scrub of northeastern Mexico and western Texas; while the sixth group (only *N. imperfecta)* lives on weedy or shrubby vegetation especially along roadsides within the Rio Balsas Basin, near Chilpancingo, in southern Mexico (Cohn, 1965).

METHODS AND RESULTS

This report is based on the following laboratory activities designed to confirm and supplement data amassed during Cohn's studies:

Analysis of Crop Contents. These analyses were performed to disclose any identifiable animal and plant remains within alcohol-preserved adult male, adult female, and nymphal (2nd-5th instar) specimens of all species except *N. vannifera.* In the laboratory, the crops were dissected from several specimens of each of the above stages, opened, and the contents emptied onto microscope slides. The slides were then analyzed by procedures given in Gangwere (1961, 1969). The crops of both adults.and immatures were exclusively of insect remains except for a small undeterminable plant content found in one specimen. The usual content included fragments of body and head sclerites and appendages, setae, and spines of insects, rarely determinable to order. No additional analyses were conducted after the preliminary studies because of the method's failure to yield more useful information.

Differential Feeding Studies. These tests involved the comparative selectivity of *Neobarrettia* species housed in individual cylindrical screen cages 230 mm high × 100 mm wide and given access to different assortments of food in approximately equal amounts. The relative amounts consumed over a period of some days were taken as an index of selection (Gangwere, 1961). A total of 35 tests involving 6 separate test series and 41 potential foods was carried out. *N. victoriae* and *N. spinosa* were subjected to four test series each: 1) meat/carrion (horse meat and dead flies), plant products, and plants, 2) plant products, plants, and prey; 3) plants only, and 4) prey only. Assorted *N. bambalio, N. pulchella, N. vannifera, N. victoriae,* and *N. spinosa* were subjected to two additional test series: 5) meat/carrion and plants and 6) plant products, plants, and prey. The results are summarized in Table I in which feeder identity is indicated except in series 5 and 6.

The katydids rejected all plants and plant parts offered in the differential feeding experiments except once when pine needles were possibly eaten and a few occasions when certain foods high in water content (flowers of *Anemone virginiana,* fruits of apple, grape, and blueberry, and lettuce leaves) were eaten sparingly. The insects took bran and oat flakes infrequently but meat/carrion somewhat more often. They readily accepted as prey most insects offered except for boxelder bugs and adult mealworm beetles (both of such low preference value that they were sometimes rejected outright). (See Appendix I for a listing of foods.)

Food Restriction Experiments. These tests were carried out on katydids caged as above but given access to plant materials only or to animal materials only so as to ascertain survival. Unfortunately, the stock of

Table I.—Differential Feeding Tests

(Code: we = well eaten; e = eaten; le = lightly eaten; n = nibbled; v = vegetative parts (mostly leaves); f = flowers; fr = fruits)

N. victoriae

On Meat/Carrion, Plant Products, & Plants (2 Tests on 3 Animals Each):
Horsemeat we> bran & oats e> rejected: *Chenopodium album* v, *Echinochloa crusgalli* vf, *Morus rubra* v, *Poa compressa* vf, *Polygonum* sp. vf, *Plantago major* vf, *Taraxacum officinale* vf, *Trifolium pratense* v, & *Tropaeolum majus* vf

On Plant Products, Plants, & Prey (8 Tests on 2-3 Animals Each):
Acheta domesticus, Conocephalus strictus, Melanoplus sp., *Musca domestica,* & larval *Tenebrio molitor* we> *Leptocoris trivittatus* e> bran, oats, *Lactuca sativa* v, *Pyrus malus* fr, *Vaccinium* sp. fr, *Vitis* sp. fr n*> rejected: adult *Tenebrio molitor*

On Plants Only (2 Tests on ? Animals Each):
Anemone virginiana fe> rejected: *Achillea millefolium* v, *Ambrosia artemisiifolia* v, *Asclepias syriaca* vf, *Gnaphalium obtusifolium* v, *Monarda fistulosa* vf, *Sassafras albidum* v, *Solidago juncea* vf, *Verbascum thapsus* v, *Vernonia altissima* vf, & *Zea mays* v

On Prey Only (7 Tests on 1-3 Animals Each):
Acheta domesticus, 3rd instar *Chortophaga viridifasciata, Melanoplus femurrubrum, M. keeleri luridus, M. scudderi, & Musca domestica* we> *Leptocoris trivittatus* e> *rejected: adult & larval Tenebrio* sp.

N. spinosa

On Meat/Carrion, Plant Products, & Plants (2 Tests on 10 Animals Each):
Horsemeat we> bran & oats e> rejected: *Chenopodium album* v, *Echinochloa crusgalli* vf, *Morus rubra* v, *Plantago major* vf, *Poa compressa* vf, *Polygonum* sp. vf, *Taraxacum officinale* vf, *Trifolium pratense* v, & *Tropaeolum majus* vf

On Plant Products, Plants, & Prey (8 Tests on 1-8 Animals Each):
Acheta domesticus we> larval *Tenebrio molitor* e> *Encoptolophus sordidus* & *Melanoplus femurrubrum* e> *Lactuca sativa* v, *Pyrus malus fr, bran, & oats e*>* *Vaccinium* sp. fr n*> rejected: *Conocephalus strictus, Leptocoris trivittatus, Musca domestica,* & adult *Tenebrio molitor*

On Plants Only (1 Test on ? Animals):
Rejected: *Asclepias syriaca* vf, *Gnaphalium obtusifolium* vf, *Monarda fistulosa* v, *Sassafras albidum* v, *Solidago juncea* vf, *Verbascum thapsus* v, & *Vernonia altissima* vf

On Prey Only (1 Test on 2 Animals):
Musca domestica e> rejected: *Leptocoris trivittatus* & adult *Tenebrio molitor*

N. spp.

On Meat/Carrion & Plants (1 Test on 4 Animals):
Dead *Musca domestica* e> *Pinus* sp. v e*> rejected: *Ilex* sp. vfr

On Plant Products, Plants, & Prey (3 Tests on 11-28 Animals Each):
Acheta domesticus we> rejected: *Lactuca sativa* v & oats

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* This record/these records is/are questionable.

living *Neobarrettia* available for restriction experiments was so limited that definitive tests could not be completed. However, there were enough animals to maintain a half dozen on plant foods (lettuce or cabbage supplemented by oat flakes) and another half dozen on animal foods (horse meat, ham, liverwurst, *etc.*, whichever was on hand in the laboratory). The katydids preferred lettuce to oat flakes and horse meat to ham and other meats. They ignored liverwurst in favor of the wet cotton of the water receptacles. The two test groups were maintained on their respective diet for well over a month (Oct. 6 through Nov. 12) before the experiment was terminated to put the animals to other uses. Surprisingly, short-term survival in the two groups was little different, attrition being negligible in each (1-2 animals).

Behavioral Observations. The activities of caged individuals were observed for several hours at a time, day and night, in hopes of elucidating specific differences in aggressiveness, perceptivity, food choice, feeding behavior, or feeding periodicity. Large numbers of individual prey or plants were given them, and the katydids' response was noted. (See Appendix I.)

Confronted with potential prey, the predators often rear backward on the mid and hindlegs, spread the mandibles, and extend the forelegs high over the head. They sometimes spread the wings in typical defensive posture. From this position, they pounce on the prey using the mandibles like forceps and the spinous legs to pin down the victim until it can be picked up and held by the foretibiae and tarsi, held flexed over the femora. The midlegs often help hold the prey, while the hindlegs support the downward-hanging predator from the vegetation or sides of the cage. The leg parts in contact with the prey include the first (basal) and second pulvilli and occasionally the terminal tibial spines. The pretarsi are held at an angle from the prey.

The prey is killed by a few bites whereupon the predator begins feeding on whatever body region is conveniently located (whether head, neck, thorax, or abdomen) according to the victim's position when caught. During eating, the katydid's maxillary palpi lightly tap on the food, while the labial palpi merely brush against it or tap it lightly. The labrum and labium are passively displaced toward their base by the food, but the labrum is also lifted (levated) and pulled toward its base by internal musculature. The mandibles make 17-20 regular strokes per 15 sec during simultaneous incision and mastication, while the laciniae and galeae alternate with them. This is typical piercing behavior (Gangwere, 1960). The katydid consumes all body parts except for wing, leg, antennal, and other fragments that accidentally fall to the ground. These are ignored thereafter except under starvation pressure. Feeding duration varies from less than 2 min (for consumption of an entire house fly) to 5 or more min (for consumption of an adult grasshopper or cricket). Feeding is followed by careful grooming of the mouthparts, legs, and other body parts.

Katydids given access to moist cotton drink somewhat differently than they feed. Their labrum and labium are displaced toward the base by the cotton mass which the palpi occasionally tap, while the galeae and laciniae close on the cotton to squeeze out water. The mandibles may also close on the wet mass.

The nocturnally active, thamnophilous katydids move about somewhat clumsily and deliberately but can lunge at prey. They are relatively poor at capturing small, lively insects such as house flies. They apparently specialize in capturing medium-sized, slow-moving, weak insects such as juvenile katydids or crickets. They scavenge less readily than they prey on potential food insects suggesting that movement enhances the likelihood of feeding. Given the opportunity, they are cannibalistic on smaller individuals of their own kind, especially when starved or given access to newly molted, weakened, incapacitated, or moribund potential prey.

DISCUSSION

Neobarrettia victoriae has been recorded eating grasshoppers in both laboratory

Appendix I
Potential Foods Offered to *Neobarrettia* spp.
(All Tests & Observations)

Meat/Carrion

Musca domestica L./common house fly, dead (Diptera: Muscidae)

Neobarrettia sp., dead (Orthoptera: Tettigoniidae)

Ham

Horsemeat, commercial

Liverwurst

Plant Products

Bran flakes

Chicken mash

Oat flakes

Plants/Plant Parts

Achillea millefolium L./common yarrow (Compositae)

Ambrosia artemisiifolia L./common ragweed (Compositae)

Anemone virginiana L./thimbleweed (Ranunculaceae)

Asclepias syriaca L./common milkweed (Asclepiadaceae)

Brassica oleracea var. *capitata* L./cabbage (Cruciferae)

Chenopodium album L./lamb's quarters (Chenopodiaceae)

Echinochloa crusgalli (L.)/barnyard-grass (Gramineae)

Gnaphalium obtusifolium L./catfoot (Compositae)

Ilex sp./holly (Aquifoliaceae)

Lactuca sativa L./lettuce (Compositae)

Monarda fistulosa L./wild bergamot (Labiatae)

Morus rubra L./mulberry (Moraceae)

Pinus sp./pine (Pinaceae)

Plantago major L./common plantain (Plantaginaceae)

Poa compressa L./Canada bluegrass (Gramineae)

Polygonum sp./smartweed (Polygonaceae)

Pyrus malus L./apple (Rosaceae)

Sassafras albidum Nees/white sassafras (Lauraceae)

Solidago juncea Ait./goldenrod (Compositae)

Taraxacum officinale Weber/common dandelion (Compositae)

Trifolium pratense L./red clover (Leguminosae)

Tropaeolum majus L./garden nasturtium (Tropaeolaceae)

Vaccinium sp./blueberry (Ericaceae)

Verbascum thapsus L./mullein (Scrophulariaceae)

Vernonia altissima Nutt./ironweed (Compositae)

Vitis sp./grape (Vitaceae)

Zea mays L./corn (Gramineae)

Prey: Orthoptera

Acheta domesticus (L.)/house cricket (Gryllidae)

Arphia p. pseudonietana (Thomas)/red-winged grasshopper (Acrididae)

Atlanticus testaceus (Scudder)/short-legged shield-bearer (Tettigoniidae)

Chortophaga viridifasciata (De G.)/green-striped grasshopper (Acrididae)

Conocephalus strictus (Scudder)/straight-lanced meadow katydid (Tettigoniidae)

Encoptolophus s. sordidus (Burmeister)/dusky grasshopper (Acrididae)

Melanoplus fr. femurrubrum (De G.)/red-legged grasshopper (Acrididae)

Melanoplus keeleri luridus (Dodge)/broad-necked grasshopper (Acrididae)

Melanoplus scudderi (Uhler)/Scudder's short-winged grasshopper (Acrididae)

Melanoplus sp. (Acrididae)

Nemobius sp./ground cricket (Gryllidae)

Neobarrettia spp. (Tettigoniidae)

Schistocerca emarginata (Scudder)/bird locust (Acrididae)

Scudderia sp./bush katydid (Tettigoniidae)

Prey: Other Insects

Apis mellifera L./honey bee (Hymenoptera: Apidae)

Argynnine sp./fritillary (Lepidoptera: Nymphalidae)

Asilid sp./assassin fly (Diptera)

Bombus sp./bumble bee (Hymenoptera: Apidae)

Appendix I
Potential Foods Offered to *Neobarrettia* spp.
(All Tests & Observations)

Cantharid sp./soldier beetle (Coleoptera)
Chrysopa sp./lacewing (Neuroptera: Chrysopidae)
Chrysops sp./deer fly (Diptera: Tabanidae)
Cicindela sp./tiger beetle (Coleoptera: Cicindelidae)
Dragonfly sp. (Odonata)
Leptocoris trivittatus (Say)/boxelder bug (Hemiptera: Lygaeidae)
Limenitis archippus (Cramer)/viceroy (Lepidoptera: Nymphalidae)
Meloid sp./blister beetle (Coleoptera)
Musca domestica (L.)/common house fly (Diptera: Muscidae)
Pentatomid sp./stink bug (Hemiptera)
Pieris rapae (L.)/cabbage butterfly (Lepidoptera: Pieridae)
Satyrid sp./wood nymph (Lepidoptera)
Scarab sp. (Coleoptera: Scarabaeidae)
Tenebrio molitor L./yellow mealworm (Coleoptera: Tenebrionidae)
Tibicen sp./cicada (Homoptera: Cicadidae)

Prey: Vertebrates
Bufo americanus Holbrook/American toad (Amphibia: Bufonidae)
Hyla versicolor Le Conte/gray tree frog (Amphibia: Hylidae)

(Tinkham, 1944) and field (Cohn, 1965). The field records involved a female that consumed a *Mermiria* sp. almost as large as itself and a male that took a *Campylacantha* sp. *Neobarrettia spinosa* has been recorded preying on a cicada and cannibalizing an adult female of its own species, and a *N. hakippah* has been noted eating a carabid beetle (Cohn, 1965). The cannibalistic tendency of *N. spinosa* (under the synonym *cerberus)* has been discussed (Tinkham, 1944). Apparently the only records involving other listrosceline katydids are of *Phisis* (Cheesman, 1927), *Decolya* and *Phisis* (Henry, 1932), and *Beiericolya* (Kaltenbach, 1968). These genera, like *Neobarrettia,* have highly modified legs used in the capture of living insects for food.

Even casual examination of the structure of *Neobarrettia* (its carnivorous-type mandibles, globose, protruding eyes, elongate forelegs with long ventral spines and spurs, *etc.)* suggests that they are carnivores that seldom, if ever, accept plants as food. Nonetheless, they were given access to a variety of potential food plants in this study to determine the latitude of their response. The plants used were, unfortunately, ones commonly available in Michigan and not representative of the thorn forest, scrub, weedy field, ruderal, and desert flora of Mexico and southwestern United States. The insects refused the leaves and flowers of virtually every grass, forb, and woody plant offered, even under starvation pressure. Lettuce and certain flowers and fruits were a partial exception, doubtlessly for their water content rather than as food items. Some of the fruit eating or nibbling recorded in Table I is probably an artifact, attributable not to *Neobarrettia* but to crickets or possibly other potential prey caged with them; the methods used were inadequate to cancel out the effect of this variable.

Certain *Neobarrettia* species are confined within given plant associations and replace one another geographically, either overlapping slightly or being contiguous across narrow zones (Cohn, 1965). Clearly, it is not the vegetation itself that determines their habitat occupancy but their independent response to the same environmental factors that influence plant distribution. While it is impossible to measure all environmental parameters responsible for *Neobarrettia* distribution, analysis of selected, limited factors such as feeding seemed promising-hence this laboratory study.

Are the species of *Neobarrettia* carnivores that cannot survive indefinitely on a vegetable diet? Do they exhibit interspecific differences in food habit and behavior? If not, is competition responsible for the remarkable contiguity that Cohn noted in certain species?

1) Are the species of *Neobarrettia* carnivores that cannot survive indefinitely on a vegetable diet? The answer is a qualified *yes.* Though short-term laboratory maintenance of *Neobarrettia* species on vegetation alone is possible, it is unlikely that they eat vegetation in nature. They appear to be staunch carnivores that are aggressively predacious on medium-size, relatively slow-moving, lightly armored insect prey captured by lunging at them. On occasion, they even attack, kill, and eat small vertebrates such as the tree frogs and small toads offered in this study. They apparently find house flies and some other potential insect prey too small and active for ready capture, adult mealworm beetles and some other insects too heavily armored for successful attack, and boxelder bugs, adult mealworm beetles, and some other insects too odoriferous or distasteful to eat, even under starvation pressure. They are not effective scavengers. They usually leave unconsumed legs, wings, and other dropped body parts which suggests a preference for living, moving prey. They may be maintained, however, on horsemeat, chicken mash, bran and oat flakes, *etc.*, in the absence of living prey, and they scavenge on dead flies and cannibalize the dead and dying of their own kind. Such behavior, attributable to the pressures of hunger, is surely atypical in nature.

2) Do *Neobarrettia* species exhibit any obvious interspecific differences in food habits and behavior? The answer is a qualified *no*. The only behavioral difference noted is a tendency of *N. spinosa* to be less agile than *N. victoriae* and the other smaller species. It also spends more time resting on the cage floor in large cages than do the remaining species. *Neobarrettia victoriae* is sympatric with *N. spinosa* over much of its range. The two occupy the same habitat and sometimes even the same shrub in the area of overlap (Cohn, 1965). Perhaps the slight disparity noted between the two *Neobarrettia* species is sufficient to account for their ability to live side by side.

3) Is competition responsible for the remarkable contiguity of *Neobarrettia* species, as observed by Cohn? Again, the answer is a qualified *yes,* at least with respect to *N. hakippah,* the northern species of the northwest coast of Mexico, and *N. sinaloae,* the southern species of the same region. The two populations are separated by river except in a few places where the northern species has gained a foothold on the southern bank. Here, it is restricted to weedy or brushy fields, while the southern relative is located within the adjacent thorn forest. However, within two miles north or south of the river, where each lives alone, each occupies all available *Neobarrettia* habitats including weedy fields, brushy fields, and thorn forest (Cohn, 1965). Since the two insects are behaviorally similar and because of the tendency of *Neobarrettia* species to attack, kill, and eat smaller insects that they are able to catch and overpower, the plausible explanation is direct competition, with one eliminating the other where they come together. Thus, the northern species is the successful competitor in the brushy fields of the south bank and the southern species the successful one in the adjacent thorn forests. Or perhaps differential hatching and growth contribute to a larger nymphal size in one or the other species according to the habitat occupied (Cohn, 1965).

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Ecological components of a hybrid zone in the grasshopper *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae)

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ABSTRACT

1. Gene flow and hence the shape of a cline between subspecies will depend on the dispersal rate of the organism, for a given level of selection. This, in turn, will be modified by its spatial distribution. This paper investigates both factors in the Pyrenean grasshopper *C. parallelus*.

2. A significant correlation between habitat type, as defined by a multivariate classification (TWINSPAN), and grasshopper density was detected. This relationship was used to make inferences about the patchiness of the grasshopper distribution at the Col du Pourtalet.

3. Dispersal experiments yielded a daily dispersal estimate of 7.09 m day^{-1}, equivalent to 31.7 m gen^{-1} and in close agreement with a previous study involving a different technique. There is a tendency approaching significance for males to move further than females.

4. The results are discussed with reference to gene flow and the development of the hybrid zone following the end of the last cold stage (c 10000 BP). A comparison is made with another contact region further east.

Key words: Hybrid zone, gene flow, vegetation classification, dispersal, migration, paleobiology.

INTRODUCTION

The hybrid zone between *Chorthippus parallelus parallelus* and *C. p. erythropus* follows the Pyrenean ridge (Butlin & Hewitt, 1985a & b; Hewitt *et. al.*, 1988; Hewitt, 1988). The two races were isolated and diverged in allopatry during the last ice age; they now meet in the lower cols of the central Pyrenees and along a broader front in the western foothills. The subspecies differ in a number of characters including redness of the hind tibiae, number of stridulatory pegs, components of courtship and calling song (Butlin & Hewitt, 1985b), sex chromosome nucleolar organiser region, chromosome banding (Gosálvez *et. al.*, 1988) and allozymes (Butlin & Hewitt, 1985a). Crosses between pure *C. p. parallelus* and *C. p. erythropus* result in sterile male offspring (Hewitt *et. al.*, 1987). This hybrid disadvantage indicates that this is a tension zone (Key, 1974; Barton & Hewitt, 1985), *i.e.* it is maintained by a balance between introgression and selection against hybrids.

For a given level of selection, gene flow, and hence the shape of the clines between subspecies, will be inherently dependent on the dispersal rate of the grasshopper. This will, in turn, be influenced by environmental factors including population density and habitat type and distribution. The importance of spatial population structuring to gene flow has been recognised through modelling (Lande, 1979; Barton & Hewitt, 1981; Barton & Rouhani, 1987; Nichols, 1989). The consideration of dispersal rates and population distribution in the light of these results will aid our understanding of the processes involved in the development and maintenance of this zone.

STUDY SITE

Field work was undertaken at one of the contact regions, the Col du Pourtalet (1790m) in the Pyrenees Occidentales (0°25'W, 42°50'N). The col represents a narrow corridor through which gene flow between the subspecies occurs. The valley is heavily grazed with *Chorthippus parallelus* occurring in most areas below 2000m. The pasture flora of the region is diverse although dominated by *Festuca* spp., *Agrostis* spp. and *Nardus stricta*. Alpine species become abundant at higher altitudes.

METHODS

1. Grasshopper distribution

Although widely distributed *C. parallelus* reaches high densities at only a limited number of sites. The aim of this study was to investigate this density pattern, with particular regard to the degree of patchiness exhibited. There are two possible approaches to the mapping of this grasshopper's distribution. The first involves extensive sampling of the area of interest until a satisfactory picture is obtained. Alternatively, knowledge of the habitat preferences of the species can be used to provide estimates of the likely density occurring in an area with particular ecological characteristics. This second method has the advantage of allowing the distribution pattern over a large area to be predicted from a small number of sample sites where the density is accurately known. By deriving a vegetation type-density relationship one also gains the advantage of being able to map density from aerial photographs and satellite images.

The flora of an area is generally a good indicator of a wide range of environmental variables, and may be used effectively to describe a habitat type (eg. Nichols & Hewitt, 1986). The vegetation will reflect features of the prevailing climate, altitude, aspect, soil type and degree of disturbance, all of which have a potential influence on grasshopper density. Furthermore, the flora will reflect the conditions of the whole year, including those which may have an important influence on embryo development and hatch rate (Richards & Waloff, 1954).

During August of 1987 and 1988 data were collected from a total of 83 16m^2 quadrats. Sample sites were chosen to cover the whole range of altitude and aspect where *C. parallelus* is found. These sites are shown in Fig. 1. The quadrat used was considered of sufficient size to encompass small scale heterogeneity in the vegetation and to provide a reliable density estimate. Within each quadrat the presence and abundance of each plant species were recorded and an absolute grasshopper count made. The area was rapidly enclosed with a net pegged at the base to prevent escapes and searched until a 5 minute 'no find' period was reached. In practice this usually meant 10 to 15 minutes of intensive searching.

TWINSPAN (two-way indicator species analysis; Hill, 1979) was the chosen method of classification. This polythetic, divisive technique assigns quadrats containing similar species assemblages to the same class. This method uses a separate ordination of species among samples for each division, thus incorporating all the major axes of variation. The most valuable species in any multivariate analysis will be those that allow discrimination between classes, *i.e.*, those that are not too widespread and also not rare, and therefore potentially distributed as a result of random events (Greig-Smith, 1983). TWINSPAN overcomes the problems of domination of the ordination by a few species and allows rarities to be down-weighted.

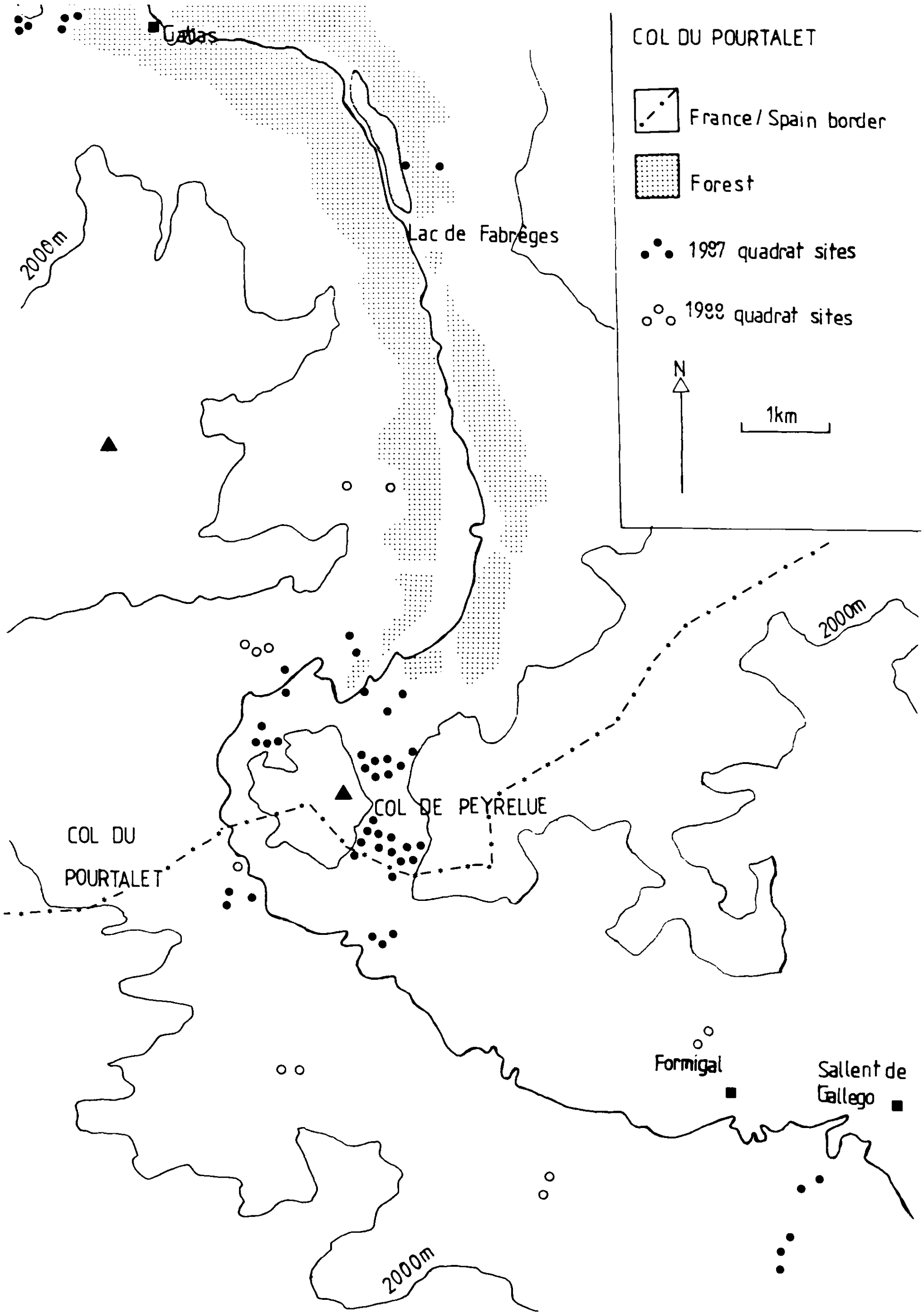

Figure 1.—Map of the Col du Pourtalet illustrating the area under 2000m inhabited by *C. parallelus*. The hybrid zone follows the France/Spain border.

Dispersal experiments

In August 1988, two lush pasture sites known to support moderately high densities of *C. parallelus* were chosen. A grid 16 × 32m was marked into 4 × 4m squares; the resulting 32 squares could be scored in a morning. The shape of the search area is important in determining the efficiency of recapture, epecially the chance of detecting long distance migrants (Barton & Hewitt, 1982). With the rectangular shape used there was a fair chance of recording movements up to 30m or so, whilst most of the displacements of 8m or less should have occurred within the grid. From the work of Aikman and Hewitt (1972) a mean daily dispersal rate of the order of 1.7m was expected.

At dawn, when the grasshoppers were still cold and immobile, they were given a grid square-specific mark with oil paint on the thorax. The insects were kept cold in an insulated box while the paint hardened and then immediately released at the centre of their home square. This method was planned to minimise agitation dispersal, and the insects showed no sign of agitation on release. Other workers have released from one or a few central points (eg. Aikman & Hewitt, 1972; Barton & Hewitt, 1982). Although this method is convenient as it allows individuals to be marked *en masse* off site, the possible effects of transplantation and especially crowding on movement cannot be ignored.

Six days later the area was methodically searched by workers walking through each grid square in a fixed zig-zag pattern. The positions of marked individuals were recorded. This recapture was also undertaken in the early morning before the grasshoppers were fully active. Although repeated scoring would obviously yield more data, particularly about the way dispersal varies with the age of the population, it was very important to keep disturbance to a minimum. By scoring once extensive trampling was avoided.

On analysis the recapture efficiency and variance in the distance moved (σ^2) were calculated.

RESULTS

1. Vegetation classification

Hill's (1979) TWINSPAN uses reciprocal averaging to ordinate stands in species space. 'Differential species', which characterise the opposite ends of the ordination and represent those species with clear ecological preferences, are identified and used to refine the ordination. The data are treated in this manner for each level of the classification and dichotomies made. The hierarchy for the first 3 levels of division and the associated indicator species are shown in Table 1.

From the environmental requirements of the indicator species it is possible to deduce the ecological character of each vegetation class. Classes I and II are lush, wet meadows and sites of stream flushes characterised by marsh marigold and sedge species. Classes III and IV are typically pasture sites, where floristic composition appears to be related to the intensity of grazing and the diversity of forb species, while class III consists of very closely grazed areas with low herbage. Classes V and VI are high altitude sites whose flora include alpine species. In contrast class VII consists of a few dry, montane quadrats with shrubby vegetation. The major underlying variables appear to be moisture and altitude.

2. Relationship with density

The density of *C. parallelus* within the $16m^2$ quadrats varied between 0 and 150 (a maximum of 9.4 grasshoppers m^{-2}). The highest densities were always found in the wet grassy areas that often occurred as discrete patches or as narrow bands along stream sides.

Although there is a great deal of noise in the data (Table 2) a one way analysis of variance compensating for missing values reveals a highly significant effect of vegetation class on density ($F=7.85$, $p<0.001$). This pattern could be the result of habitat preference; grasshoppers could be actively

Table 1.—The indicator species for the 2 primary (A, B) and 4 secondary (a, b) dichotomies are shown. Classes I to VII are produced by minor divisions at level 3.

Table of major TWINSPAN divisions

A *Trifolium pratense, Ranunculus acris, Plantago media.*
  (a) Wet meadows and stream flushes:
  Carex flacca, Caltha palustris, Prunella vulgaris.
    I. *Leontodon montanus, Hieracium pilosella, Cynosurus cristatus, Plantago media, Carex flacca.*
    II. *Carex* spp., *Ranunculus acris.*

  (b) Lowland pastures:
  Galium verum, Lotus corniculatus, Achillea millefolia, Scabiosa pyrenaeica.
    III. *Merendera montana.*
    IV. *Plantago lanceolata, Agrostis capillaris, Leontodon montanus, Rhianthus* sp.

B *Festuca* sp., *Trifolium alpinum.*
  (a) Alpine and montane sites.
  Trifolium alpinum.
    V. indicator species as for division B(a).
    VI. *Matricaria matricoides.*

  (b) Rocky, arid sites.
  Vicia pyrenaica, Arctostaphylous uva-ursi, Paeonia officinalis.
    VII. indicator species as for division B(b).

Table 2.—Density (no, of grasshoppers per 16m^2 quadrat) data classified by TWINSPAN group.

Vegetation Class	I	II	III	IV	V	VI	VII
Mean density	38.1	47.7	19.2	29.0	12.8	8.7	4.7
Standard error	12.3	12.7	3.4	6.5	4.8	1.4	2.3
No. of quadrats	7	12	24	26	8	3	3

seeking these moist grassy places. The data could also reflect the distribution of oviposition sites. Or else they could reflect those areas where hatching and/or survival is more successful. This latter explanation seems less likely; for although the pattern of nymph distribution has been linked to oviposition site, the relationship disappears as the nymphs age (Richards & Waloff, 1954).

If the dispersal behaviour of this grasshopper differed among habitats, as it does in some other insects (Gilbert & Singer, 1973; Dobzhansky *et al.*, 1979), a patchy distribution would result. The 'unfavourable' vegetation classes may represent those habitats where dispersal is fast.

3. Dispersal estimates

There are a number of possible fates that may befall the marked grasshoppers. Obviously a proportion will be recaptured within the search area. Of those remaining, some may have been overlooked, perhaps in areas of denser grass or because they had lost their mark, others could have moved out of the search area or have died.

Considering the above possible outcomes, the recapture rate for adults was encouragingly high. Of the 72 adults marked at site 1, 38 (52.3%) were recaptured in the search area. In 1988 the snow melt was delayed resulting in late emergence of *C. parallelus* and, as a consequence, low adult density at the time of this experiment; only 22 adults were marked at site 2 of which 11 were recaptured. A summary of the dispersal data is shown graphically in Fig. 2.

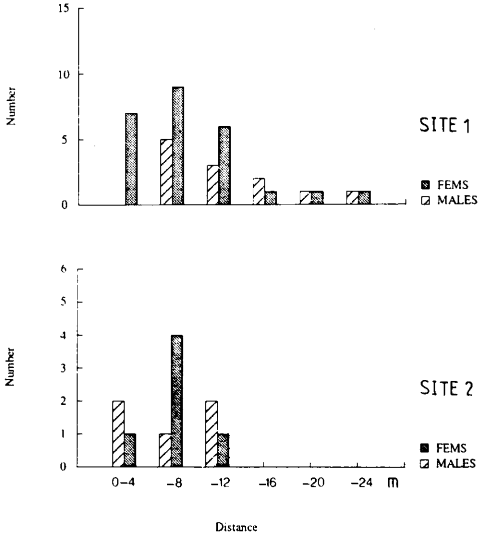

Figure 2.—The distribution of distances moved after 6 days, showing both sexes at the tow sites.

The simplest model for grasshopper dispersal is a two-dimensional random walk which assumes that a grasshopper's displacement is undirected, independent of other individuals and of a constant rate. This will produce an expanding normal distribution centred on the point of release. In this experiment grasshoppers were released from multiple positions in a rectangular matrix, a situation which can be analysed by considering a circular area, divided into a number of concentric annuli of equal width which is superimposed over the square from which each movement is initiated (Mason, 1988 & this volume). Displacement is measured as movement from the centre of the circle to the annulus that overlaps the square in which the grasshopper was recaptured.

The probability of a grasshopper moving into one annulus will depend on the square root of the number of days of dispersal and the daily dispersal rate, σ. The probability that the grasshopper is then seen within the search area requires the calculation of the fraction of the annulus that falls within the search area (since large annuli will lie partly outside it) and the sight rate (Mason, this volume). The involvement of both of these components in the analysis means the possibility of grasshoppers moving out of the search area and of being overlooked are considered. Maximum likelihood estimates of daily dispersal and the sight rate were computed (GENSTAT optimization facility).

Figure 3 shows the maximum likelihood contours for these parameters. The range of values occurring within 2 maximum likelihood units of the optima are tabulated (Table 3) along with the square root of the second derivative which is equivalent to the standard error.

Site 1

The data from site 1 yielded a value of σ of 7.90 m day^{-1}. Extrapolating this value over the assumed effective adult life span of 20 days, the root mean square value gives an estimate of 31.7 m gen^{-1}. This result, from the combined male and female data, is in close agreement with that obtained by Aikman and Hewitt (1972) with methodology contrasting in its release strategy (central release) and disturbance potential (grasshoppers were transplanted). In spite of the differences in experimental approach and method of analysis, their estimate of 33.7 m gen^{-1} does not differ significantly from that obtained here (based on $D=0.078$ yd hr^{-1}). This suggests that the dispersal behaviour of this organism is not readily

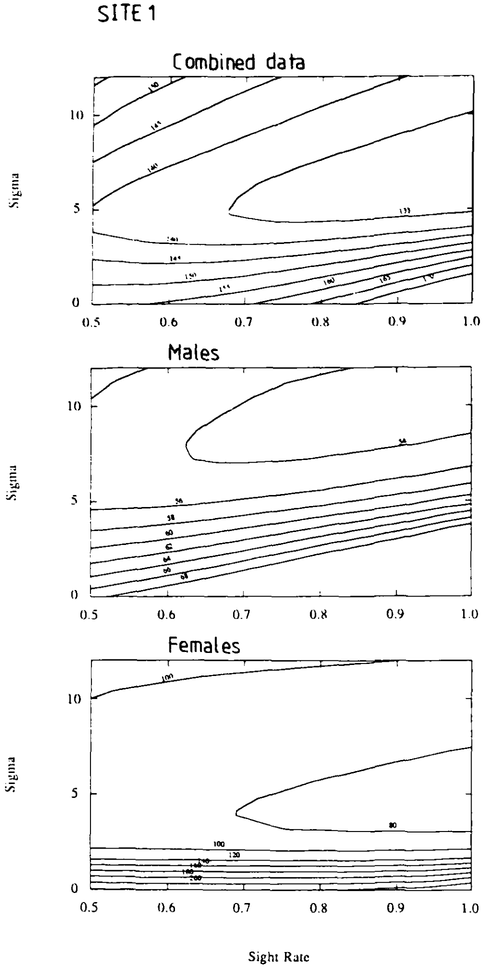

Figure 3.—Results from the optimization analysis. Maximum likelihood contours are shown for a range of values of the daily dispersal distance (σ) and the sight rate. Data are from site 1.

disrupted by human interference and may even be quite constant over a range of conditions (see also Mason, 1988).

Comparison of the sexes

There is a strong suggestion that males disperse further than females, although this difference is not quite significant since there is overlap of 0.1 likelihood units. The upper limit for male dispersal is high, indicating that more males have moved out of the grid. The males are smaller and lighter than the females and are effective at jumping (Richards & Waloff, 1954). Their large surface area to volume ratio should cause them to heat up more rapidly in the sun allowing activity when the females may still be sluggish. The larger females will lose heat slower but the males' advantage may override this effect. Males were often observed singing, congregated on banks facing into the sun. If males are actively seeking out these warm prominent positions for the purpose of female attraction, this behaviour may enhance any difference in the amount of radiation absorbed and vagility.

For both sexes a recapture efficiency within the search area of almost 100% best fits the model. The field workers were experienced in searching for and trapping this grasshopper and it is likely that few of these cold, slow moving, brightly marked individuals were overlooked. However the same confidence cannot be attached to the recapture of males as to females. Males are smaller, therefore more easily hidden, and tend to jump when disturbed, a fact reflected in the more diffuse sight rate estimate which includes values lower than 50%. Although females are more cryptic, as they tend to drop into the grass, the search intensity was sufficient to locate most of them (70% recapture; sight rate=0.99).

Site 2

The small number of displacements recorded at site 2 made it impossible to analyse the sexes separately. The optimization procedure reveals a broad range of likely values for σ and the sight rate; there is no evidence that dispersal differs between the 2 sites. Under the constraints of the model, the most parsimonious interpretation of the few data obtained at this site involves a high level of human error, *ie.* a low sight rate, however, there is no reason why the search efficiency should be lower at this site. The alternative explanation, suggested by the maximum σ of >10m day^{-1} is that a larger proportion of individuals are di-

Table 3.—The best estimates of A, dispersal σ (in metres) and B, the sight rate for the 2 sites.

A. Daily Movement.

	σ day^{-1}	Range (2ML)	S.E.
Site 1 Males	11.27	5.82 - >14.00	—
Females	4.27	3.45 - 5.91	1.060
Combined	7.09	4.64 - 8.73	1.785
Site 2 Combined	4.18	2.73 - >10.00	1.254

B. Sight Rate

	Sight rate	Range (2ML)	S.E.
Site 1 Males	0.99	<0.50 - 1.00	—
Females	0.99	0.82 - 1.00	0.146
Combined	0.99	0.73 - 1.00	0.168
Site 2 Combined	0.64	0.34 - 1.00	0.151

spersing out of the grid. This is a possibility since this site was heavily disturbed by grazing cattle during the course of the experiment. The environments of the 2 sites were different; a quadrat taken in site 1 revealed it to be class IV habitat, whereas site 2 is class II. However, both are favourable habitats (Table 2) and one might expect the dispersal to be similar in each. If this is the case an external influence, such as unequal levels of disturbance during the experiment, may need to be invoked to account for any difference between the sites.

Validity of assumptions

In the case of site 1 males and site 2 the failure of the analysis to define a small window of likely values is a result of the poor fit of the data to the model. The data set for site 2 was too small to be approximated to a normal distribution. The failure of the optimization on the male data, which precluded the computation of standard errors (Table 3), had the same cause. No male displacement was less than 3m, the peak occurring between 4 and 8m (Fig. 2). This, combined with the observation that only 46% of those marked were recaptured (*cf.* 70% of females) suggests that the distribution of movements may be flattened. This does not invalidate the above analysis, but helps to explain the finer resolution obtained for female dispersal.

DISCUSSION

The two features of the ecology of *C. parallelus* investigated here, its distribution and its dispersal behaviour, provide vital information likely to affect the pattern and rate of gene flow between the two subspecies.

At the Col du Pourtalet the habitat structure results in a mosaic of densities, with high concentrations of grasshoppers in wet flushes on the valley sides and close to streams. Towards the middle of the season the intervening pasture dries out and running water becomes scarce at low altitudes; moist areas become havens surrounded by inhospitable, arid grassland. Dispersal in these parched areas may be significantly faster than the 7.09m day^{-1} calculated above. This would result in the distribution pattern observed (Table 2). Habitat preference and active searching for moist areas could be involved. Such accelerated movement between favourable areas could also conceivably occur after disturbance by sheep and other large mammals, and thus may cause the actual dispersal through the region to be even faster.

Ritchie (1988) calculated the width of the cline in stridulatory peg number at this col to be 8.76km (derived from the maximum slope of the best fitting tanh curve [Barton & Hewitt, 1985]). This is significantly wider than at another contact zone further east, Col de la Quillane, with a width of 3.02 km. The data currently available indicate that the clines in the other characters are also narrower at Quillane (Hewitt, 1988). The steepest transition occurs in the polymorphism for a nucleolar organising region on the X chromosome ($\leq$ 4km at Pourtalet; ~ 0.6km at Quillane. [Hewitt *et al.*, 1988]). The narrowness of this zone argues strongly that it is maintained by a balance between hybrid dysfunction and dispersal (Barton & Hewitt, 1985). The effective selection on the X-NOR cline at Quillane was calculated as 2% based on $\sigma = 30$ m gen $^{-1}$ (Hewitt *et al.*, 1988).

If the data from the Col du Pourtalet are applied to the same Barton-Hewitt (1985) equation $w = \sqrt{8\sigma^2 / s}$, where w is the width of the cline, s, the selection acting against heterozygotes, becomes of the order of 0.02%. The shallower cline at Pourtalet suggests selection against hybrid combinations here is weaker. It is not impossible that the *C. parallelus* from the east and west Pyrenees have diverged, resulting in the reduced fitness of individuals hybrid for the X-NOR at Quillane (Hewitt *et al.* 1988).

Alternatively, if selection is the same at both cols, the cline width could be related to the contrasting environments of Pourtalet and Quillane. Pourtalet is higher, narrower and wetter with only small areas of broken forest to the north, whilst the Col de la Quillane has been less extensively cleared and grasshopper habitat is broken up by forests and arable fields. This latter habitat distribution may well retard gene flow.

Other characters (*e.g.*, peg number at Pourtalet; esterase-2 and song syllable length at Quillane) change more gradually, over distances of 10-20km (Butlin & Hewitt, 1985a & b), and are likely to be selectively neutral (Hewitt, 1989). If this is the case we may be observing neutral diffusion at the 2 sites (Endler, 1977). However, Endler's diffusion equation, $T = 0.35(w/\sigma^2)$ where T is the time since contact, predicts contact during the last ice age, which is clearly impossible (Hewitt, 1989). Even the consideration of a more rapid dispersal suggested by the male data gives a contact time of 31 500 BP for a 15km cline, which is still much earlier than the probable contact time (Hewitt, 1988 & 1989; Hewitt *et al.*, 1988).

In order to account for this anomaly it is necessary to consider two factors. The first is the underestimation of the rate of dispersal, and the second involves the historical aspects of this contact.

1. Underestimation of dispersal

One major problem with the mark-recapture approach is the possible loss of long-distance migrants (see Aikman & Hewitt, 1972; Taylor, 1978; Barton & Hewitt, 1982; Slatkin, 1985). Those few individuals which move a long distance will increase the level of gene flow. In this study a 20m border around the search area was checked for dispersants. That few were found indicates that the bulk of movements were accounted for, but no attempt was made to retrieve grasshoppers moving beyond this 20m boundary.

Another point worthy of consideration is the comparability of dispersal recorded today in continuous habitat with that of an advancing population during colonization and contact. Dispersal into virgin territory may well be more rapid. In patchy populations subject to local colonization and extinction gene flow has been shown to be fast (Lande, 1979; Nichols, 1984; Nichols *et al.*, this volume; Slatkin, 1985). The advancing front would have consisted of just such framented populations. This process of colonization of patches of available habitat by a few individuals, followed by rapid expansion and domination of that area, may have been sufficient to produce the effective dispersal rate of 100m gen^{-1} required to account for a neutral cline of 15km (Hewitt, 1989). There is evidence from coleopteran fossils (Coope, 1977) of extremely rapid colonization after the last ice age although this is a more vagile taxon.

The same process may be operating on a smaller scale at Pourtalet today. Favourable habitat may extend to unusually high altitudes during wet years. The random colonization of these high flushes may allow rapid gene flow as ephemeral subpopulations become dominated by a few gene combinations through founder events (as modelled by Nichols, 1989). The dense forest cover at the Col de la Quillane and the resulting disjunct population structure may preclude such processes or prevent them from having a marked effect.

2. Historical considerations

There is evidence from beetle fossils (Atkinson *et al.*, 1987, see Hewitt, 1988) that the improvement in climate occurred in two waves, first in 13000 BP and again at 10500 BP. Man colonized the lower cols soon after this amelioration and may have preceded the grasshoppers (Bahn, 1985; Hewitt, 1988). There is an ancient tradition of transhumance across the Pyrenees which suggests the pastures at Pourtalet may have a long history. From the present vegetation of Quillane it appears that no major clearances were made for the purpose of grazing animals; ancient pastures are present at high altitudes only. Thus, in spite of its altitude and cooler climate, contact may have occurred at Pourtalet first as a result of man's activities. This may, in part, account for the wider clines at Pourtalet.

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A quantitative ecology of Orthopteran communities on Pyrenean grasslands above timberline (Huesca, Spain)

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ABSTRACT

In this paper the structure of different orthopteran communities living in grasslands above timberline, in the central-western Pyrenees (Huesca, Spain), is compared. The work is based on a quantitative sampling method utilized during 1987 in ten plots ranging from 1,500 to 2,400 m of altitude in order to obtain density, biomass, and diversity data.

Epigeic activity in those communities is reduced to four-five months in a year. The adult grasshoppers begin appearing in early July. Sixteen species (4 Ensifera and 12 Caelifera) have been found. In 1987 grasshopper density reached 200 individuals per m^2. Important differences are noted between plots below 2,000 m of altitude (which have the highest density and the most common species) and plots above 2,000 m (where densities are always low and the species are well adapted to high altitude).

Key words: Orthopteran communities, population density, altitudinal gradient, Pyrenean pasturelands (Spain).

INTRODUCTION

Orthoptera, particularly Acrididae, are excellent indicators of different ecological factors (Gueguen *et al.*, 1980; Pfadt, 1982). The extent to which they may be so in the Pyrenees is here investigated.

In the grasslands above timberline in the central-western Pyrenees, between approximately 1,600 and 2,000 m of elevation, areas kept as pastures by human and cattle influence, Acrididae are the invertebrates with the highest biomass (Isern & Pedrocchi 1988). Most populations exhibit important yearly changes. Acrididae have only one generation in a year. They pass the unfavorable season as eggs, hatching in May or June, the adults living until early November. Above 2,000 m the vegetative period is shorter, and the grasshoppers there have low density values (Isern & Pedrocchi, 1987).

In this paper we compare some grassland orthopteran communities in places from 1,640 to 2,400 m during a year of high density, 1987. We used quantitative methods to obtain density, biomass, and diversity data and related them to differences in altitude, grazing, and plant communities. This study is part of the CSIC Project "Utilización y Conservación de Recursos Naturales de Montaña ante la Evolución de la Gestión Ganadera", ID-608.

DESCRIPTION OF AREA

The study area consists of pastures above timberline near Jaca (Spanish Pyrenees, lat. 42° 45′ N, long. 0° 31′ W). This is a medium-high montane environment with a nearly continental climate although notably affected by oceanic influences.

Ten plots were selected reflecting three altitudinal series (Fig. 1):

Series A (Plots 1 to 4). At the headwaters of the Lubierre River (Borau Valley), facing southward, from timberline to near

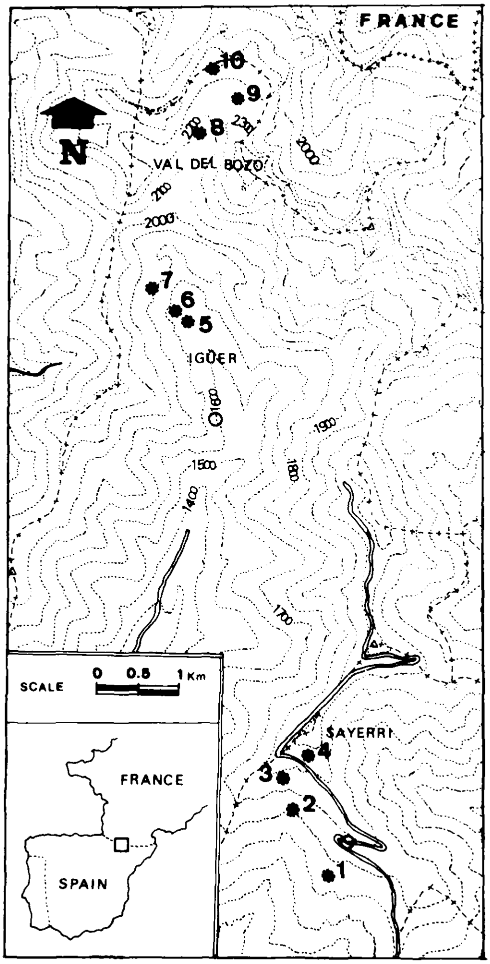

Figure 1.—Study area: in Borau and Aísa Valleys (Huesca, Spain). In black asterisks, all the study plots: Series A (Plots 1, 2, 3, and 4), Series B (Plots 5, 6, and 7), and Series C (Plots 8, 9, and 10). White circles represent the nearest weather stations.

the summit (Sayerri) (1,660 to 1,990 m a.s.l.);

Series B (Plots 5 to 7). From the bottom to mid slope along the high part of the Aísa Valley (Igüer), facing eastward (between 1,640 and 1,815 m);

Series C (Plots 8 to 10). The headwaters of the Aísa Valley (Val del Bozo), either at the bottom (Plots 8 and 9) or near the crest divide (Plot 10), facing southeastward (from 2,190 to 2,400 m).

The soils are deep (down to 1 m in all plots), except Number 10 which is stony. They are brown and decalcified in Plots 1 to 7 and subalpine rankers in Plots 8 to 10. The parent rock is Eocene sandy flysch in Plots 1 to 7 and Cretaceous sandstones in Plots 8 to 10.

During 1987, the annual recorded rainfall (no January data) in nearby weather stations (Fig. 1) was 762 mm in Borau Valley (Series A) and 1,062 mm in Aísa Valley (Series B).

In 1986, some studies on plant ecology were carried out in the area (Remón & Alvera 1988). Estimated production ranged from 430 g/m^2 (at 1,600 m) to 49 (at 2,260 m) in summer. Production and consumption by cattle were higher in Series A (except Plot 4, that is ungrazed) than in Series B and C. Ruminant grazing consumption ranged from 0 (Plots 4 and 10) to near 80% of total production. Plot 6 is only grazed in years of low production. Plots 8 and 9 are grazed by sheep.

Table 1 relates elevation to the principal plant species of the different plots.

METHODS

In 1987, quantitative sampling of grasshoppers in the pastures of Aísa and Borau was carried out during the five months from June 1 to October 21.

Biocenometers of 1 m^2 (adapted by Pedrocchi [1985] from Lamotte, 1969) were used. Each of the ten plots was sampled each fortnight and the grasshoppers (Ensifera and Caelifera) of 5 m^2 were collected. The material was kept in 70% alcohol and the adult forms determined by species following Harz's codes (1969 & 1975).

Grasshopper population density was directly determined from the biocenometer data. Averages and standard deviation (s) were calculated for each sample (n=5). Grasshopper population biomass was then indirectly determined from the body length measurement (L) of each individual. It was converted in dry weight at 105 °C (W) by means of: $W = a L^3$ (in Margalef, 1974), with Ensifera = 18.07^6 g/mm^3 (n=10;

Table 1.—Elevation (m.a.s.l.) and the main plant species in the study plots.

PLOT	ELEVATION	MAIN SPECIES
1	1,660	*Festuca gr. rubra, Gallium verum, Nardus stricta*
2	1,730	*F. gr. rubra, N. stricta, Agrostis capillaris*
3	1,870	*Trifolium alpinum, F. gr. rubra, N. stricta*
4	1,990	*Festuca eskia, T. alpinum*
5	1,640	*N. stricta, F. gr. rubra, T. alpinum*
6	1,680	*Festuca paniculata, Carex montana*
7	1,815	*N. stricta, F. gr. rubra, Thymus gr. praecox*
8	2,190	*T. alpinum, N. stricta*
9	2,260	*N. stricta, T. alpinum, Plantago alpina*
10	2,400	*Carex sempervirens, F. eskia*

$s=2.67^6$) and Caelifera= 7.99^6 g/mm^3 ($n=50$; $s=1.28^6$).

Species diversity was calculated for each of the plots to obtain the Shannon-Weaver index: H'= − pi In pi (Magurran 1988).

RESULTS AND DISCUSSION

Density: Biomass

Table 2 shows the average density and biomass data, and ratio to adults resulting from sampling Ensifera and Caelifera in the ten study plots.

Plots below 2,000 m (Series A and B) are dealt with separately from the higher plots (Series C). First, the Ensifera (Tettigoniidae and Gryllidae) are treated and then Caelifera (Catantopidae and Acrididae), the main group in these pastures. The total sample size was 16,935 individuals.

Series A and B

Ensifera

In as much as Gryllidae and Tettigoniidae formed only 0.70% of the total sample, their low density assured that the quantitative results on them were of low statistical significance.

Gryllid species were only found in Plot 1, at 1,660 m, close to timberline. Their maximal density value was 0.6 ind./m^2. Tettigoniid numbers were relatively high in Plot 3 (1,870 m) and in Plot 6 (1,680 m), where the maximal density value, 2.4 ind./m^2 in mid July, was reached. These two plots also had the highest biomass, with maximal values of 0.23 and 1.13 g/m^2, respectively.

Caelifera

Acridids composed 99.15% of the total sample. They are, ecologically speaking, the most important group in the pastures because of their consumption of grass and their acceleration of nutrient recycling (Isern *et al.*, 1989).

Density was lower in the plots of Series A than in those of Series B (ratio 1:2.4). Average density values ranged from 17.4 ind./m^2 in Plot 2 (1,730 m) to 89.0 in Plot 7 (1,815 m). All species have only one generation per year. In 1987 hatching happened in mid May, and the first adult grasshoppers appeared in early July. In general, the maximal density value was reached during the last days of June or the beginning of July. The values were recorded as follows: 45.6 ind./m^2 (Plot 1), 48.2 (Plot 2), 84.0 (Plot 3), 157.2 (Plot 4), 211.6 (Plot 5), 124.8 (Plot 6) and 257.0 ind./m^2 (Plot 7) (the highest value recorded). At the end of August or beginning of September practically 100% of the grasshoppers were adults. The life cycle was completed by the end of October.

Table 2.—Average values of density (x), standard deviation (s), biomass, and ratio to adult (% A) in eleven samples (I-XI) and ten experimental plots (1-10), during 1987, in the study of Orthoptera (Ensifera and Caelifera) in pyrenean grassland above timberline, in Borau (Series A) and Aísa (Series B and C) valleys. Density in number of individuals/m^2 (n = 5); biomass in g/m^2; ratio to adults in %. Samples were done each fortnight from June 1 to October 21.

SAMPLES	I				II				III				IV				V			
PLOTS	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A
Series A	x	s			x	s			x	s			x	s			x	s		
1 Ensifera	0.6	0.9	0.0	33.3	0.0				0.2	0.4	0.0	100.0	0.0				0.4	0.5	0.0	0.0
Caelifera	45.6	29.9	0.1	0.0	45.6	22.5	0.1	0.0	34.2	15.5	0.3	1.7	15.6	7.8	0.3	26.9	35.4	10.5	1.2	65.5
2 Ensifera	0.4	0.5	0.0	0.0	0.0				0.0				0.2	0.4	0.0	0.0	0.2	0.4	0.0	0.0
Caelifera	23.0	8.5	0.0	0.0	13.6	8.2	0.0	0.0	48.2	26.1	0.2	0.0	31.2	11.3	0.4	3.2	31.4	12.4	0.8	26.6
3 Ensifera	0.6	0.9	0.0	0.0	2.2	1.9	0.0	0.0	2.2	1.9	0.1	0.0	0.2	0.4	0.0	0.0	1.6	1.7	0.1	12.5
Caelifera	82.4	28.9	0.2	0.0	84.0	26.2	0.3	0.0	67.6	37.2	0.9	7.7	36.6	23.0	0.8	29.0	51.6	20.5	1.6	44.9
4 Ensifera	0.4				0.2	0.4	0.0	0.0	0.2	0.4	0.0	0.0	0.2	0.4	0.1	100.0	0.2	0.4	0.1	100.0
Caelifera	157.2	33.0	1.0	0.0	22.4	15.4	0.2	0.0	82.2	16.3	3.5	31.0	65.6	15.1	4.0	66.7	37.0	6.1	2.5	75.5
Series B																				
5 Ensifera	0.2	0.4	0.0	0.0	0.0				0.0				0.0				0.0			
Caelifera	116.0	63.8	0.2	0.0	191.8	87.1	0.4	0.0	211.6	66.5	1.9	1.4	47.2	22.1	1.1	33.2	25.6	4.0	0.8	51.6
6 Ensifera	1.0	1.7	0.1	0.0	1.2	1.6	0.1	0.0	0.8	0.8	0.1	0.0	1.2	0.8	0.4	66.7	2.4	2.1	1.1	50.0
Caelifera	98.4	54.9	0.2	0.0	100.0	53.3	0.3	0.0	124.8	36.1	1.9	5.1	113.8	12.3	3.4	33.1	71.6	16.2	2.3	42.6
7 Ensifera	0.2	0.4	0.0	0.0	0.2	0.4	0.0	0.0	0.0				0.2	0.4	0.1	0.0	0.2	0.4	0.0	0.0
Caelifera	257.0	102.4	0.6	0.0	199.8	21.9	0.9	0.0	211.6	69.5	2.9	6.0	162.4	45.6	4.1	48.8	48.4	23.4	1.6	75.7
Series C																				
8 Ensifera					0.0				0.0				0.0				0.0			
Caelifera					0.0				0.0				0.0				0.0			
9 Ensifera					0.0				0.0				0.0				0.0			
Caelifera					0.0				0.0				0.0				1.2	1.3	0.0	0.0
10 Ensifera					0.0				0.0				0.0				0.0			
Caelifera					0.0				0.0				0.0				0.0			

Table 2.—(Contd.).

VI				VII				VIII				IX				X				XI			
Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A	Density		Biom.	%A
x	s			x	s			x	s			x	s			x	s			x	s		
2.0	1.4	0.1	10.0	0.0				0.6	0.9	0.1	66.7	0.2	0.4	0.0	0.0	0.0				0.0			
21.8	5.9	1.1	90.8	14.2	5.7	0.6	100,0	13.4	3.6	0.7	100.0	5.4	3.0	0.4	100.0	3.4	2.4	0.2	100.0	1.4	1.3	0.1	100.0
0.0				0.0				0.0				0.0				0.0				0.0			
19.2	10.5	0.9	74.0	10.2	4.0	0.5	94.1	8.4	5.4	0.5	100.0	5.4	0.9	0.4	100.0	1.4	1.3	0.1	100.0	0.0			
1.0	0.7	0.2	20.0	1.0	0.7	0.2	80.0	0.4	0.5	0.1	100.0	0.4	0.5	0.0	50.0	0.2	0.4	0.1	100.0	0.0			
43.4	6.6	2.4	65.7	22.0	6.2	0.9	92.7	9.0	3.3	0.6	97.8	2.8	2.3	0.2	92.9	0.2	0.4	0.0	100.0	0.0			
0.0				0.2	0.4	0.2	100.0	0.0				0.0				0.0				0.0			
28.4	9.9	2.2	91.5	19.6	6.7	1.5	96.9	16.6	7.4	1.3	98.8	5.2	1.1	0.4	100.0	1.0	0.7	0.1	100.0	0.0			
0.0				0.0				0.0				0.0				0.0							
18.6	4.2	0.9	91.4	4.2	2.8	0.2	95.2	3.0	3.2	0.2	100.0	2.6	0.9	0.1	100.0	0.0							
0.2	0.4	0.1	100.0	0.0				0.0				0.0				0.0							
47.4	19.1	2.4	85.6	19.0	8.0	1.0	96.8	6.8	3.2	0.4	100.0	3.6	3.6	0.2	94.4	0.0							
0.0				0.2	0.4	0.1	100.0	0.0				0.0				0.0							
8.0	4.5	0.4	77.5	1.8	0.8	0.1	88.9	0.4	0.9	0.0	100.0	0.2	0.4	0.0	100.0	0.0							
0.0				0.0				0.0				0.0											
0.2	0.4	0.0	0.0	0.2	0.4	0.0	100.0	0.0				0.0											
0.0				0.0				0.0				0.0											
0.4	0.9	0.0	0.0	0.4	0.5	0.0	0.0	0.6	0.9	0.0	100.0	0.4	0.5	0.0	50.0								
0.0				0.0				0.0				0.0											
0.0				0.2	0.4	0.0	0.0	1.4	1.1	0.0	28.6	0.0											

Density was higher in 1987 than in 1986. The average increase in Series A was 59% and in Series, B 130% with a total average increase of 95%. Density was higher in 1986 than in 1985 in the same or nearby plots. The average increase in Series B, the only common sampled plots, was 278% (Isern, 1988). the density in 1988 was similar to that in 1985 (Plot 7, the only sampled), meaning a decrease of 95% in relation to 1987 (unpublished data). Interannual changes are due to the regulation of predators (consumers, parasites), and more importantly environmental factors.

In 1986, as in 1987, density was lower in the plots of Series A (Sayerri) than in those of Series B (Igüer) (ratio 1:1.7) (Isern 1988). The Sayerri pastures being grazed by cattle more than those of Aísa suggests a relationship between grazing and Acridid density, but we are not able to separate this from other possible factors.

During the summer of 1987 the change of acridid biomass of the seven plots followed a similar model. At the beginning of June very low biomass values (ranging from 0.03 to 0.98 g/m^2) were recorded. The maximal values were reached during the beginning of July or the beginning of August. The values were recorded as follows: 1.15 g/m^2 (Plot 1), 0.94 (Plot 2), 2.41 (Plot 3), 4.03 (Plot 4), 1.89 (Plot 5), 3.35 (Plot 6) and 4.10 (Plot 7).

Series C

In plots above 2,000 m no species of Ensifera were collected, due to their rapid dispersity in relation to the elevation (Marty, 1969).

Caelifera

In as much as Caelifera (Acrididae and Catantopidae) composed 0.15% of the total sample, their low density assured that the quantitative results on them were of low statistical significance.

First hatching took place at the end of July, more than two months later than in plots below 2,000 m. The first adults were found at the end of August or the beginning of September.

In mid September a grasshopper population of 71.43% of immature individuals was recorded in plot 10. In the next sampling, at the end of September, no orthopteran was found. In the last year, 1986 (unpublished data), only adults were found until late October. This data allows us to presume that, in some years such as 1987, the grasshoppers cannot finish their life cycle due to unfavorable weather. Two possible hypothesis could explain this: unfavourable weather conditions in late summer force the young grasshoppers to hibernate until the following year when they finish their life cycle, or, some individuals die without reproducing.

The highest average density was found in Plot 9, followed by Plot 10 and Plot 8. The maximal density values were recorded as follows: 1.4 ind/m^2 (Plot 10), 1.2 (Plot 9) and 0.2 (Plot 8).

Density was slightly higher in 1986 than in 1987 (43% in average). As in 1986, the highest density values were recorded in Plot 9, followed by Plot 10 and Plot 8 (Isern, 1988).

During 1987, the maximal biomass values recorded were 0.03 g/m^2 (Plots 9 and 10) and 0.01 (Plot 8).

DIVERSITY: STRUCTURE OF COMMUNITIES

Table 3 includes the list of orthopteran species. Figure 2 shows the total number of each species (adult forms) collected in each of the ten plots, species richness, and species diversity. Sixteen species (4 Ensifera and 12 Caelifera) have been found.

With reference to the beginning of this section, to show some general results we demonstrate separately the results of each plot series: first the number of species and species diversity; secondly the presence of species in all plots (common species), and the species caught in only one of the plots (we consider these rare species (R) when only one individual is found); and finally the most abundant species in each plot.

Table 3.—Species list of Orthoptera collected in grasslands above timberline in Borau and Aísa valleys (Pyrenees, Huesca, Spain), elevations from 1600 to 2400 m.

ENSIFERA	
Tettigoniidae	*Decticus verrucivorus* (L.) *Platycleis albopunctata hispanica* Zeun. *Steropleurus catalaunicus* Bol.
Gryllidae	*Gryllus campestris* L.
CAELIFERA	
Catantopidae	*Cophopodisma pyrenaea* (Fisch.)
Acrididae	*Starodeurus scalaris* (Fisch.-Wald.) *Chorthipus brunneus-biguttulus-mollis gr.* *Chothippus dorsatus* (Zett.) *Chothippus parallelus* (Zett.) *Stenobothrus lineatus* (Panz.) *Stenobothrus stigmaticus* (Ramb.) *Stenobothrus nigromaculatus* (H.-S.) *Omocestus haemorrhoidalis* (Charp.) *Omocestus panteli* (Bol.) *Mymeleotettix maculatus hispanicus* Harz *Aeropus sibiricus* (L.)

The same structure of all the orthopteran communities above 2,000 m typically showed low diversity and two or three very abundant species with a density higher than 80%. Density values for some species increased with elevation between certain thresholds: *Stenobothrus stigmaticus, S. nigromaculatus,* and *Aeropus sibiricus.* However for other species, they decreased: *Chorthippus brunneus-biguttulus-mollis* gr., *Omocestus panteli, O. haemorrhoidalis,* and all the Ensifera species.

Series A

Fourteen species had been found in the plots of Borau valley, species richness reaching a level of seven in Plots 1 and 2, and nine in Plots 3 and 4. Although the structure of the community was quite different, diversity values were very similar, ranging from 1.16 to 1.29.

The species of *S. stigmaticus, O. haemorrhoidalis, Chorthippus parallelus,* and *C. brunneus-biguttulus-mollis* gr., were common in all plots. Others were found only in one, as *Gryllus campestris* (Plot 1), *Steropleurus catalaunicus* (Plot 3, R), *Chorthippus dorsatus* (Plot 2, R), *Myrmeleotettix maculatus* (Plot 4) and *A. sibiricus* (Plot 4).

Stenobothrus stigmaticus and *O. haemorrhoidalis* were found to be the most abundant species in the similarly structured communities of the first three plots.

The distinguishing factors of Plot 4 compared with plots below 2,000 m were the abundance of *S. nigromaculatus* and *A. sibiricus.* These differences will now be discussed.

The ungrazed *Festuca eskia* communities (the site of Plot 4) contained a peculiar structure of orthopteran community, hosting a different amount and densities of species of comparatively greater body weight. Plant diversity and plant species richness were low (mainly *F. eskia* and *Trifolium alpinum).* In the Pyrenees, Defaut (1978/79) related grasshopper distribution to plant communities; Gueguen *et al.* (1980) in relation to plant community structure.

In order to presume that a relationship between orthopteran communities and orthopteran nourishing preferences exists, an analysis of plant epidermis in faeces was done (unpublished data). The first results indicated certain food preferences. The most abundant species of this plot, *S. nigromaculatus,* preferred *F. eskia* (100%, n=5). *A. sibiricus,* the following one, preferred *T. alpinum* (presence in 6 of 7 analyses, one with 100%), but would also eat *F. eskia* (presence in 3 of the 7 analyses), and other plant species.

Research of plant covering, an especially

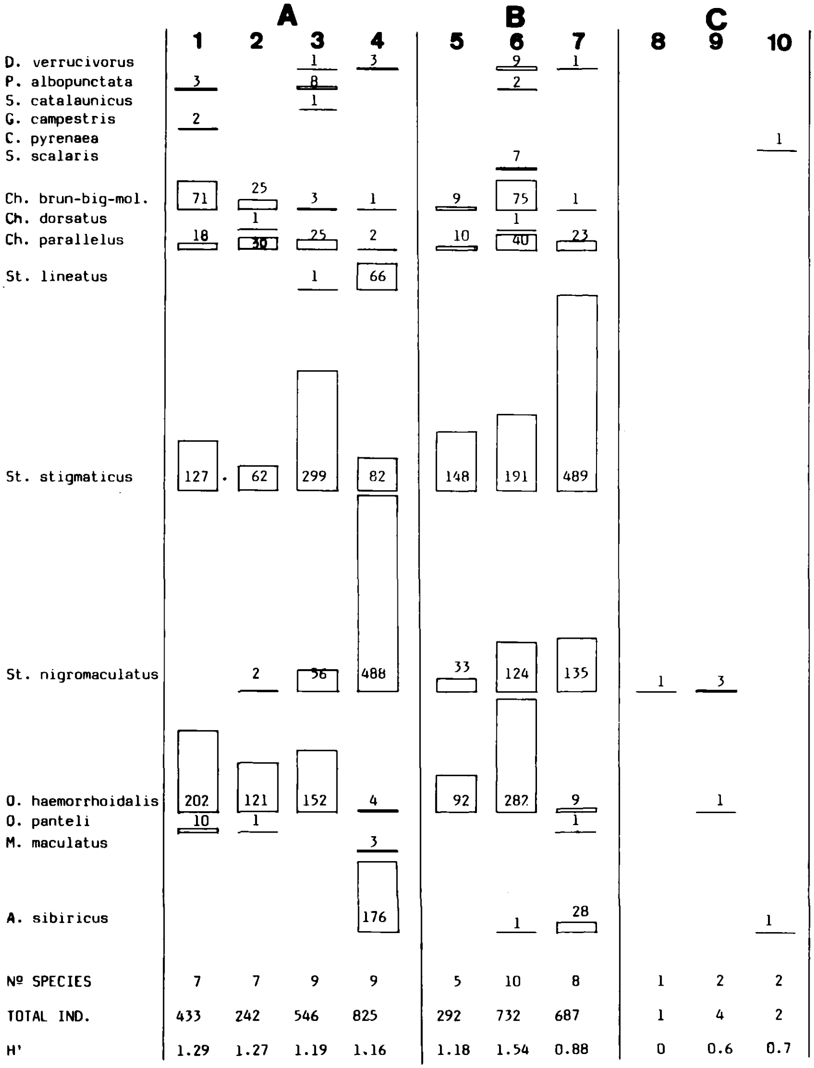

Figure 2.—Species composition of plots in Series A, B, and C. Number of adults of each species collected in all the 1987 samplings, species richness (n.º species), total number of individuals (total ind.) and diversity values (H').

important factor for *A. sibiricus*, indicated the species preference for both bare ground, necessary for egg laying and warming up (Voisin 1986a), and vegetation, as it exists in the typical structure of small terraces in *F. eskia*. *M. maculatus*, a species only found in this plot, also prefers places with low covering (Gueguen *et al.*, 1980). In the Alps, a negative effect of sheep grazing on *A. sibiricus* populations was found, the result mainly effecting an early mortality (Gueguen & Gueguen, 1987). Voisin (1986b) and other authors found a relationship between a high density of this species and bare ground caused by over grazing. Therefore the abundance of *A. sibiricus* in the community with *F. eskia* would be explained by two main factors: no grazing, and the peculiar structure of community in small terraces, with relatively low plant covering.

Series B

Eleven species had been found in the Plots of Igüer (Aísa Valley), species richness reaching a level of five in plot 5, eight in Plot 7, and ten in Plot 6. Diversity values were more extreme than in Series A, ranging from 0.88 (Plot 7) to 1.54 (Plot 6).

The common species were the same as in Series A in addition to *S. nigromaculatus.* Found only in one plot were *Platycleis albopunctata* (Plot 6), *Staurodeurus scalaris* (Plot 6), *Omocestus panteli* (Plot 7, R), and *Ch. dorsatus* (Plot 6, R).

Plot 7 community structure was determined by the abundance of the species *S. stigmaticus.*

Plots 5 and 6 showed a similar orthopteran community structure, but complexity was higher in the latter. The differences will now be discussed.

Because of the decrease of grazing pressure, the *Nardion* communities (the site of Plot 5) are being occupied by *Festuca paniculata,* Plot 6 being placed in a community with this plant. The highest complexity reached was reflected by grasshoppers as an increase of species richness, diversity, and density values. Species richness in Plot 6 was twice that in Plot 5, with five coincidental species (keeping the highest density values). The most abundant species in both plots were *O. haemorrhoidalis* and *S. stigmaticus.* Diversity values were 1.54 in Plot 6 and 1.18 in Plot 5, and density values higher in Plot 6 than in Plot 5.

Series C

Only four species had been found in plots above 2,000 m, in the "Val del Bozo" (Aísa valley), three of which can also be found at lower altitudes *(S. nigromaculatus, O. haemorrhoidalis,* and *A. sibiricus). Cophopodisma pyrenaea,* only collected once as an adult at 2,400 m (Plot 4), had also been found in young states in the two plots of 8 and 9 but never below 2,000 m. The low density assured that the diversity values on those plots were of low significance.

CONCLUSION

Pastures above timberline of the central-western Pyrenees, at altitudes lower than 2,000 m, contain unstable populations of Orthoptera primary consumers (Acrididae) of significant yearly changes. In the event of a population explosion, as in 1987, individuals play an important role in the consuming and acceleration of the nutrient recycling in the ecosystem. All species have only one generation a year with a life cycle duration of, approximately, four and a half months.

Environmental factors rather than predators seem to control populations.

Common species below 2,000 m are *Stenobothrus stigmaticus, Chorthippus parallelus, Omocestus haemorrhoidalis,* and *Chorthippus brunneus-biguttulus-mollis* gr.

Density values of some species increase with elevation between thresholds: *S. stigmaticus, Stenobothrus nigromaculatus* and *Aeropus sibiricus.* Others, on the contrary, decrease: *Ch. brunneus-biguttulus-mollis* gr., *Omocestus panteli, O. haemorrhoidalis,* and all species of Ensifera.

Above 2,000 m only Caelifera is present with very low density values. The short vegetative period can stop the life cycles: grasshoppers hibernate in young states, or even die. It is possible that in these grasslands, depending on species, both strategies were used.

Cophopodisma pyrenaea have been found only above 2,000 m of elevation, its apterism being well-adapted to alpine environment. This, and the fact that orthopteran populations in this zone do not have important changes, indicate, in spite of being grazed by sheep, that here communities are more stable and well adapted to short vegetative period and unfavourable weather.

A decrease in grazing pressure may indirectly produce changes in orthopteran communities through the increase of species richness, density, and diversity values.

The peculiar structure of grasshopper communities living in zones containing *Festuca eskia* is related to characteristics of the plant community (species composition in relation to food preferences), with plant covering, and no grazing, favouring the species *A. sibiricus*.

Geographic factors are not an important explanation of the differences between orthopteran communities from nearby zones. Grasshoppers have enough capacity for settlement; therefore differences may be due to ecological factors.

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Dispersal in the alpine grasshopper, *Podisma pedestris* (L.): old and new wine in old bottles

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ABSTRACT

Previous investigations of dispersal in *Podisma pedestris* (L.) have involved the central release of marked animals and their subsequent recapture at distances from their origin. The present study is concerned with the dispersal of grasshoppers that were individually marked, released where found, and subsequently searched for on a daily basis. A novel analysis, of general use for other such studies, is employed to produce estimates of daily dispersal distances for early and late instar nymphs and adults of both sexes. Comparisons are made between the classes. Nymphs are demonstrated to be capable of considerable movement, contrary to previous assumptions concerning this species, and estimates for adults are found to be higher than previous published values. The problem of the existence of a home range is considered.

Key words: *Podisma pedestris,* dispersal, home range.

INTRODUCTION

There have been several studies of dispersal in the alpine grasshopper *Podisma pedestris* (L.), including those of Barton and Hewitt (1982) and Nichols (1984). These have typically involved releasing a large number of grasshoppers from a central point and searching for them after a number of days. Estimates of dispersal distance per generation are then derived based on the assumption of 20 days adult dispersal. For the purposes of these studies, dispersal was assumed to be undirected, independent of other grasshoppers, and occurring at a constant rate: a two-dimensional random walk. These studies were unable to ascertain the contribution of nymphs to lifetime dispersal or to establish whether there was differential dispersal between the sexes.

In this paper I tackle this old problem anew. An experimental design is described whereby freshly-marked grasshoppers are replaced where they were found and daily searches made to allow the possibility of multiple observations of individuals. A novel analysis is developed to estimate dispersal rate in different age classes for both sexes, and the assumption of dispersal by two-dimensional random walk is examined.

METHODS

The study site is a gentle north-facing slope (ca. 20°) at the foot of the Cime du Plan Tendasque, above Castérine, in the

Alpes Maritimes, France. The habitat consists predominantly of short grass, with some patches of bare earth and protruding rock, interspersed sporadically among which are thistle, false gentian, globe flower, thyme and young larch trees. This area was selected due to the abundance of *Podisma* nymphs and the lack of vegetational cover.

A 20x20 m grid, divided into 1 m squares, was marked out with string and pegs. Only a 6x2 m strip, unsuitable for grasshoppers, was not sampled.

Grasshoppers were marked almost daily in the afternoon between 20 July and 10 August 1985. Individuals were caught by hand during systematic searches of the grid. Using oil paints, a unique color code was applied to each animal. After the details of sex, instar, and location had been recorded, the marked grasshoppers were released in the same place that they first had been seen.

Daily searches of the grid were made between 21 July and 20 August 1985, usually between 1000 and 1100 hr, when the animals were becoming active and noticeable but had probably not moved very far that day. Their location was recorded.

RESULTS

A total of 1,192 individual markings were applied during the period. Many of these markings will have been made on successive instars of the same grasshopper, because marks are lost when nymphs moult. Field data are in the form of the 1 m square coordinates of individuals on one or more days. In the analysis of movement, information from different individuals in different squares is combined to provide a general estimate of dispersal rate. The movements were classified according to the following scheme. A 27 m radius circle, divided into 9 concentric annuli, each 3 m wide, is superimposed over the square from which movement begins, and displacement is measured in terms of the annulus in which movement is concluded (Fig. 1).

Marked grasshoppers may have one of several fates. Some individuals will be seen again within the dispersal area on at least one other occasion, but many will never be seen again due to movement out of the area, death, or loss of markings. The following model is developed to take these factors into account.

Assuming that dispersal follows a two-dimensional normal distribution, the probability, probin (n), of a grasshopper moving into annulus n is a function of the product of the square root of the number of days of dispersal, $t^{-1/2}$, and the daily dispersal rate, σ:

$$\mathrm{probin}(n) = \mathrm{NPI}(n_{\mathrm{out}} / (\sigma \cdot t^{-1/2})) - (\mathrm{NPI}(n_{\mathrm{in}} / (\sigma \cdot t^{-1/2})),$$

where NPI is the normal probability integral and n_{out} and n_{in} are respectively the radial distances from the center to the outer and inner edges of the annulus.

Because the largest annulus of the overlaid circle must encompass the diagonal distance across the dispersal grid, only a fraction of the area of many of the annuli will overlap the area of the grid itself. This fraction depends on the grid square the particular annulus is centered upon. This fraction, fraction(n), of the whole of each annulus, n, that falls within the search area is calculated for each square. The grid was 20 × 20 m, comprising 400 one meter squares. It can be seen that there are only 100 unique positions with respect to the fraction of annuli that overlap the search area (Fig. 1) as long as the unsearched area is disregarded. This simplification will not affect estimates of dispersal unless sightings are aggregated near to the 'missing' squares (which is not the case) although it will lead to a reduction in the sight rate.

The probability, seen(n), that the grasshopper both moves to the region of an annulus which overlaps the search area and is seen is given by:

$$\mathrm{seen}(n) = \mathrm{probin}(n) \cdot \mathrm{fraction}(n) \cdot \cdot \mathrm{sightrate},$$

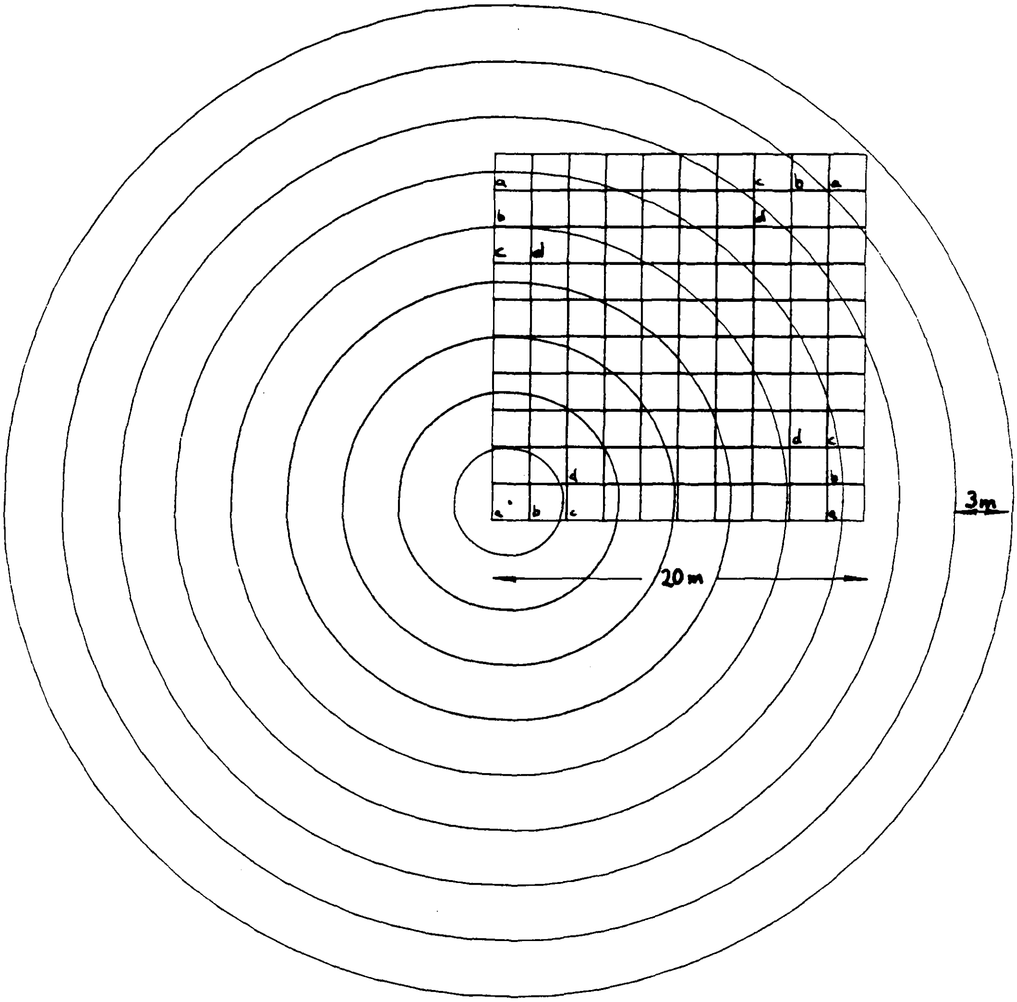

Figure 1. Representation of measurement of movement within dispersal grid by superimposition of concentric annuli. The area of many of the annuli lies outside the dispersal area. Lower case letters illustrate examples of squares with identical amounts of overlap by annuli.

where sightrate is the overall search efficiency for the area.

The probability, lostprob(n), of missing a grasshopper that is present in annulus n is:

$$\text{probin}(n) \cdot (1-\text{sightrate}),$$

while that of missing an animal, because it has moved out of the search area, is:

$$p(\text{missout}) = 1 - \Sigma(\text{probin}(n)).$$

The number of movements from each effective square into each annulus is summed. Every pair of observations of an individual is included. For example, if a grasshopper is seen on three successive days, both the movements between the first and second days and the second and third days are included in the totals, but are treated as independent events. Maximum likelihood estimates of daily dispersal distance and sight rate, together with the respective square root of the second derivative (equivalent to a standard error), were derived using the optimization directive in version 4 of the GENSTAT statistical package. The analysis has been applied to movements over time periods up to 7 days between observations, for young (2nd and 3rd instar) and old (4th and 5th instar) nymphs and adults of both sexes (Table 1).

Although dispersal estimates for both sexes of the two age classes of nymphs are significantly lower than those for the adults, they are far from negligible. Despite being smaller, early instar female nymphs move farther than late instar females, whereas the older male nymphs move farther than do young nymphs.

Table 1.—Optimized daily dispersal distances and sight rates.

Time interval between sightings /days	Daily σ/m		Sight rate	
	Estimate	S.E.	Estimate	S.E.
(a) 2nd & 3rd instar female nymphs				
1	5.288	0.450	0.446	0.032
2	5.454	0.676	0.437	0.043
3	4.745	0.798	0.287	0.039
4	5.183	1.660	0.150	0.038
(b) 4th & 5th instar female nymphs				
1	4.510	0.276	0.536	0.026
2	3.594	0.284	0.320	0.024
3	2.763	0.291	0.229	0.023
4	3.026	0.405	0.191	0.024
6	3.655	1.047	0.092	0.022
7	3.777	1.337	0.082	0.024
(c) Adult females				
1	7.153	0.777	0.528	0.043
2	5.160	0.721	0.368	0.041
3	6.254	1.516	0.382	0.071
4	5.416	1.313	0.382	0.071
6	4.046	1.196	0.192	0.045
(d) 2nd & 3rd instar male nymphs				
1	4.013	0.441	0.455	0.043
(e) 4th & 5th instar male nymphs				
1	5.305	0.405	0.571	0.034
(f) Adult males				
1	9.498	1.393	0.677	0.072
2	9.298	2.522	0.692	0.147
3	7.252	2.044	0.600	0.131

The possibility of making comparisons between sexes is limited by the fact that observations sufficient to give a precise estimate are available only for the 1-day interval for young and old males. However, from these comparisons it appears that young female nymphs move significantly farther than do young male nymphs, while the trend is reversed for the two classes of old nymphs. The impression gained from field observation that adult males are more mobile than adult females is borne out by the respective dispersal estimates despite relatively large standard errors.

The tendency of the dispersal estimates to decrease as the time interval between successive observations increases might be explained by the effect of agitation dispersal (Aikman and Hewitt, 1972) following a grasshopper's initial marking. Although this would affect estimates for all time periods, it would have greatest influence on the single-day interval because a much greater proportion of individuals were seen on the day after they had been marked than on 2 or more days after marking. However, it might also indicate that grasshoppers have a home range and therefore their movement is not well described as a random walk over longer periods of time. With the exception of young female nymphs, values of σ are greater for a 1-day time interval than for longer intervals in all classes where comparisons are possible. Due to the increasing standard error associated with the dispersal estimates, such a trend cannot be established for any of the classes although there is a hint of such a trend in old female nymphs and in both sexes of adults.

Table 2.—Examples of corresponding root mean square values of dispersal over an effective adult life of 20 days based on daily estimates.

Class	Time interval between sigthings / days	Daily σ / m	R.M.S. σ m gen^{+1}
Adult females	2	5.160	23.076
	3	6.254	27.969
Adult males	2	9.298	41.582
	3	7.252	32.432

DISCUSSION

The combination of the intensive, repeated sampling of the experimental method and the powerful analysis used gives rise to the most precise estimates of *Podisma* dispersal yet achieved. The general utility of such a method thus becomes apparent. It is less clear whether the technique might be generally suitable for demonstrating the existence of a home range because the diminishing number of observations made between greater time intervals gives rise to increasing standard error.

In this study, separate dispersal estimates were obtained for different combinations of age and sex for the first time. Previous published studies have not demonstrated such differences. Both Barton and Hewitt (1982) and Nichols (1984) assume an effective adult life of 20 days, from which they derive lifetime dispersal estimates of 20.7 m gen^{-1} and 14.1 m gen^{-1}, respectively. Applying the same criteria to the grasshoppers in this study gives typically higher values (Table 2). Furthermore, the two previous studies assumed negligible nymphal dispersal. Having demonstrated that this is erroneous then under the assumptions of dispersal by random walk, the values will be underestimates. Assuming that grasshoppers go through one instar each week and that the effective adult life is indeed 20 days, then the equivalent lifetime dispersal for grasshoppers in this study would be 30.97 m gen^{-1} for females (based upon estimates for a 2-day interval) and 47.39 m gen^{-1} for males (based upon the single-day time interval). These considerably higher values than those previously published suggest that patterns of movement in *Podisma* are more complicated than we had previously thought.

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Limited introgression through orthopteran hybrid zones

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ABSTRACT

Hybrid zones in Orthoptera are generally very narrow compared with the species range, and this is due to the insects' low dispersal, the young age of the zones, and the unfitness of hybrid genomes. There are instances where introgression is higher than expected from these factors. These are discussed in the light of the effects on gene flow and the mixing of genomes of (i) a patchy environment; (ii) the interdigitation of distinct specific habitats; (iii) the initial conditions of secondary postglacial contact; and (iv) the subsequent unhitching in population bottlenecks of genes and characters during Holocene changes in distribution. Apparently many racial and subspecific genomes remain largely distinct, despite free hybridization. It is argued that the ranges of these genomes are moved by major changes in climate, and the effects of repeated long glaciations with short interglacials on the genomic substructure of species are considered.

Key words: Hybrid zone, gene flow, introgression, clines, biogeography, paleobiology.

AFTER THE ICE

As the climate warmed and the ice retreated after the last glaciation some 14,000 years ago, organisms which had their distributions compressed towards the tropics expanded out into the now temperate regions. Consequently, the present distributions of species including grasshoppers, crickets and their allies, in Europe, North America, southern Australia, and southern South America will have been generated from then. Hybrid zones, where different species, subspecies, and races meet parapatrically and hybridize, are being discovered all through these regions and must therefore be recent in origin (Hewitt, 1985, 1988). Hybrid zones are also found in the tropics, but here their origins are more difficult to deduce (Endler, 1982; Mayr and O'Hara 1986). The Orthoptera provide some classical examples of hybrid zones (White, 1957) and some of the best researched (Barton and Hewitt, 1985). The size, numbers, habitats, life styles, and experimental facility of these insects recommend them for studies on the many evolutionary questions that can be approached through hybrid zones.

As they expanded out from their Ice Age refugia, the genetically distinct forms would have met and, if their individual mate recognition systems were still sufficiently compatible, would have hybridized. What would then have happened? We would expect the alleles of genes for which the two forms differ to gradually introgress over subsequent generations, to produce progressively shallower clines. The extent of this introgression will depend on the length of time and the dispersal of the organism; it will be slowed down and even stopped by selection against the heterozygotes, hybrids, and recombinants of coadapted gene complexes. Table 1 contains some Orthopteran hybrid zones where we have reasonable information on their width. Some of them are very narrow indeed when compared with the range of the organism. For example, those in *Caledia, Podisma, and Vandiemenella* are less than 1 km wide, while the distribution for each species is several thousand kilometers. Even in *Chorthippus* and *Gryllus* the zones are only tens of kms wide in species ranges of 3,000 km. Moreover this relative narrowness is a more general feature of hybrid zones, including those of butterflies, amphibia, small mammals, and birds (Hewitt, 1988).

HOW WIDE SHOULD ZONES BE?

The width of a hybrid zone and the extent of introgression will be determined by several factors, which may be described under dispersal, age and selection. The dispersal of the species will depend on its vagility and fecundity and this may vary between habitat types. It will depend also on the patchiness and connectedness of these different types of environment and also on the species' own density, which in turn will have been produced by these previous factors. Furthermore, in mammals and plants, dispersal may be hindered or prevented by difficulties with establishment in a new society or closed sward; but this seems an unlikely problem for grasshoppers. The more generations of organisms that have dispersed in the time elapsed since contact, the wider should be the zone. However, introgression will be retarded if the heterozygous hybrids and recombinants are less fit than the parental genotypes, since natural selection will tend to purify hybrid populations in favour of the more frequent type.

Table 1.—Width of Orthopteran Hybrid Zones.

Species Range	Character	Width km	Hybrid Fitness	References
Vandiemenella viatica (S. Australia ~ 1000 km)	19/24xy 17/19 K. Is 17/24xy 17/19 Keith	~0.01 ~0.02 ~0.20 ~0.40	v. low (1/102) low (3/38) hybrids (6/20) few hybrids (5/41)	Mrongovius 1975 White 1978
Podisma pedestris (Alps-USSR 800 km-300 km)	xo/xy	0.1-0.8 varies	50-80 % lab & field	Barton and Hewitt 1985 Nichols and Hewitt 1988
Caledia captiva (E. Australia > 300 km)	Chrom invs Allozymes	0.35-0.80 (mtDNA rDNA not coincident)	F_2 inviable Bx 50 %	Shaw *et al.* 1985 Marchant *et al.* 1988
Chorthippus parallelus (Pyrenees-W. Europe ~ 3000 km)	Allozymes Song Strid. pegs Echeme Int NOR	20 ~15-20 2-9 1.4 ~0.6	F_1♂ sterile Bx♂ partly Sterile	Butlin and Hewitt 1985 Hewitt *et al.* 1988
Gryllus pennsylvanicus/firmus (NES. USA ~ 2000 km)	Morphology Allozyme Behaviour mtDNA	~40 mosaic	*Gf* ♀ x *Gp* ♂ Sterile	Rand and Harrison 1989 Harrison and Rand 1989
Allonemobius fasciatus/socius E. USA ~ 2000 km)	Allozymes	5-200? mosaic?	*As* ♀ x *Af* ♂ less fit F_2 poor	Howard 1986

Even alleles which are equally fit (neutral) will be slowed down by association or linkage with other loci that are actually creating the tension zone of dispersal and selection (Barton and Hewitt, 1981, 1985).

We may begin analysis of this complex causation by measuring simple individual dispersal distances through mark/recapture experiments. However, this has been done in only a few cases so far. We have field dispersal estimates for *Podisma pedestris* (L) and *Chorthippus parallelus* (Zetterstedt) in the order of 20-30 metres/generation (s.d. parent-offspring distance) (Aikman and Hewitt, 1972; Barton and Hewitt, 1982). If we argue that the zones formed about 8000 BP in the mountains, then using Endler's (1977) diffusion equation for neutral clines [$T = 0.35\ (w/d)^2$ where T is the time since contact, w is cline width (1/max slope), and d is dispersal], we expect the zone width to be about 3 km. The Alpine zone for the X chromosome in *Podisma pedestris* is only 800 m wide in most places, and this means that selection must be operating against the chromosomal heterozygote, unless the zone had formed just 560 years ago. In some places it is less wide, which is probably due to hybrid unfitness interacting with the coincidence of the zone with very strong barriers to dispersal. On the other hand, in *Chorthippus parallelus* the Pyrenean zone for the allozyme Est 2 and song syllable length are some 20 km wide or more which is something of a paradox and requires a closer examination of dispersal for its resolution.

PATCHES, CLIMATE, AND MAN

Firstly, the measures of dispersal are in largely favourable habitats and the equation is for essentially continuous diffusion. We need to estimate dispersal in unfavourable habitats —this will not be easy. Furthermore, the environment in reality is an irregular patchwork of favourable und unfavourable vegetations, and dispersal through such patchy regions of variable density and population size may well be considerably faster. For example, in *Podisma pedestris* from Seyne-les-Alpes, detailed studies of the distribution of the grasshoppers and genotypes through the hybrid zone reveal how small pockets of each karyotype may survive amongst each other in marginal regions of patchy low density, producing a considerably wider zone (Nichols and Hewitt, 1986). Just 2 km further along the same zone in more continuous favourable habitat, the zone is a narrow, fairly smooth cline. To quantify the significance of this factor in determining the width of hybrid zones, we need pertinent dispersal and distribution measures on these grasshopper species coupled with realistic computer modelling, and these are in hand.

Secondly, the expectation of a zone only 3 km wide in *Chorthippus parallelus* is based on a simple postglacial range expansion and meeting in the Pyrenean cols. The initial contacts may well have been spasmodic and complex. Genotypes may intermingle much more at low density; long distance migrants at the leading edge may penetrate and establish populations well into the sparse fringe of the other subspecies range. The climate would have been varying from year to year so that having crossed the col in a good season, they may have had several poor seasons of low density in which their frequency might increase by chance. Several other detailed interactions are possible in a secondary contact such as this, and all of these require closer attention.

Thirdly, in considering the development of hybrid zones after the last glaciation, we must not forget the activities of *Homo sapiens* L; there is evidence from a number of zones where these seem to have caused a change in composition or position (Hewitt, 1989). E.g. In the fire ants *Solenopsis richteri* Forel and *S. invicta* Buren, a hybrid zone has recently been created by the introduction of these species to Mississippi (Ross *et al.*, 1987). Man was hunting actively around the Pyrenees as the ice age ended and followed his quarry up into the mountains as conditions improved (Bahn, 1985). Indeed, there is a long tradition of transhumance across the Pyrenees, and it is quite possible that grasshoppers were carried over the cols by herders in both directions. We have seen grasshoppers carried on sheep and have one or two anomalous samples at Col du Pourtalet which are rather difficult to explain in any other way! It also seems that high altitude pasturage was established early after the conditions improved sufficiently, while the valleys leading up to the cols remained forested until recent times. Indeed, the Val d'Ossau and Val d'Aude still present formidable forest barriers to grasshopper dispersal. Under such conditions hybrid populations may have become established without a high level influx of the two pure subspecies.

Perhaps we may best summarise these deliberations by emphasising that using the simple diffusion model to produce a cline over 20 km wide at Col du Pourtalet requires that the flightless *Chorthippus parallelus* disperses on average 132 m each generation, where this is the standard deviation of the distribution of parent-offspring distances. I feel that this most likely includes exceptional successful long distance migrants, whatever their mode of transport!

MOSAIC HABITATS

The preceding discussion of gene flow through a hybrid zone has so far ignored that the parapatric taxa may be suited to different habitats found on either side. Where this occurs the structure, shape and width of the zone will be affected. There are few clear indications of this in the literature, although it has not often been tested and may well be involved in a number of zones along with hybrid and recombinant unfitness (Barton and Hewitt, 1985; Hewitt, 1988). If the two forms are closely adapted to the two distinct habitats, then we would expect their distribution to follow closely the habitat arrangement. Rand and Harrison (1989) are involved in the analysis of a nice example of this in the cricket genus *Gryllus*. *Gryllus pennsylvanicus* Burmeister from the N.E. USA is found on loamy soils and forms a hybrid zone with *G. firmus* Scudder which occurs on sandy soils from the East Coast. Around New Haven, Connecticut, ridges of loam from the north interdigitate with sandy riverbeds draining south. The two species differ in morphology (e.g. ovipositor length), allozymes, and mitochondrial DNA, and within the hybrid zone neighbouring samples from loam and sand largely preserve these differences. There is some asymmetrical introgression of *G. pennsylvanicus* mtDNA into essentially *G. firmus* genotypes on sandy soil, which is explained by asymmetric reproductive isolation, such that crosses of *G.p* ♀ x *G.f.* ♂ are fertile but not the reciprocal. Interestingly, this asymmetry is also found between loam and sand populations.

The species overlap and the mosaic zone is some 40 km across, which is narrow compared with the species range. If crickets can be found in places where two soil types come into sharp contact, the local hybrid zone may well by very narrow because of the strong selection against hybrids and low individual dispersal —reported at 10 m (Harrison and Rand, 1989). It is difficult to judge how common such mosaic habitat parapatry may be; a similar case to this is reported in the newts, *Triturus cristatus* Laur. and *T. marmoratus* Latr., in N.W. France, where differences in their habitats and life styles are important in determining a broad geographically complex overlap (Wallis and Arnzen, 1989). In the North American ground cricket genus, *Allonemobius,* there is a long zone of overlap varying in width from 5 km to possibly over 100 km. Where the suitable and preferred habitats are widely intermingled, the zone is broader than where they are juxtaposed (Howard, 1986). Furthermore, from allozyme differences it appears that hybridization and introgression are less where the zone is broader.

Significantly, in all these cases of mosaic zones, the two parapatric forms are still quite distinct despite intermingling of habitats and hybridization.

UNHITCHING OF CLINES

Hybrid zones, including those in the Orthoptera, characteristically comprise many coincident clines (Barton and Hewitt, 1985;

Hewitt, 1989). Literally only a handful of possible exceptions are found in the literature. There are good reasons for this coincidence, the most important being the secondary contact of coadapted genomes that have diverged at many loci. Thus the gene clines are coincident at the formation of the zone, and interactive alleles recombined away from their racial fellows are less fit in the other genomic background (Hewitt, 1989). However, effectively neutral alleles in time may become recombined away from any selected zonal genes and may then diffuse into each other's ranges. This introgression will be symmetrical maintaining coincidence, unless there is some other factor, such as mating asymmetry as in *Gryllus,* which drives one morph. It is much more difficult for causative zonal loci to become unhitched from each other, particularly where they involve heterozygote and recombinant unfitness. However, it is difficult to escape the conclusion that such reassortment occurred in the evolution of the eumastacid *Vandiemenella viatica* complex in South Australia (Hewitt, 1979) and recent molecular studies in the acridid *Caledia captiva* Walk. from eastern Australia have provided a superb new example (Shaw *et al.*, 1988; Marchant, 1988; Marchant *et al.*, 1988).

Extensive studies over 15 years have revealed a narrow hybrid zone between two very distinct karyotypes —'Torresian' and 'Moreton' involving complete F_2 and partial backcross breakdown due to recombination of their genomic differences. The changeover of chromosomal, allozymic, mitochondrial DNA, and nuclear ribosomal DNA characters from Torresian to Moreton is coincident. However, some Moreton allozyme, mtDNA, and rDNA markers are found a considerable distance north in some Torresian populations —viz.— mtDNA ~ 250 km, allozymes ~ 350 km, rDNA ~ 450 km. It is not possible to envisage simple introgression by diffusive dispersal over such distances, and the most likely explanation, cogently argued by Marchant *et al.*, (1988), is that the zone has moved south since the last glaciation leaving a trail of Moreton markers in areas of the Torresian subspecies. As has been argued for *Vandiemanella viatica* Key (Hewitt, 1979) and *Mus musculus domesticus* Rutty (Gyllensten and Wilson, 1987) the unhitching most probably occurred by the chance survival of a reassorted genome in a bottlenecked population. In *Caledia* one such population with the Torresian genome and Moreton mtDNA seems to have expanded into the present Moreton mtDNA "introgression" area (Marchant *et al.*, 1988). The unhitching of Moreton rDNA is geographically more extensive and not fixed, and this would require several such events. Indeed, it may well involve biased gene conversion of Torresian to Moreton ribosomal restriction fragment length pattern (Arnold *et al.*, 1988).

Why have several such cases been reported recently? Perhaps mtDNA can become reassorted more readily because it is not linked to nuclear genes, and some of these chromosomal loci are negatively heterotic and hence would tend to hold each other in the zone. Of course there are a growing number of cases where the mtDNA does change coincidentally at the zone (Harrison, 1989) including other regions of the *Caledia* and *Mus* zones (Marchant *et al.*, 1988; Vanleberghe *et al.*, 1989). It simply may be that geographically extensive surveys and the discrimination afforded by new molecular techniques are now allowing us to discern these fascinating variants from the major pattern. It is significant that introgressed allozyme markers as well as mtDNA and rDNA ones were found in *Caledia.*

HYBRID ZONES AND SPECIES SUBSTRUCTURE

The preceding consideration of the better studied Orthopteran hybrid zones shows that over a range of habitat forms and even with occasional unhitching there is very little gene flow through them, despite 800 years of hybridization. This is also true for zones in many other organisms, although the zones may be somewhat wider in more mobile animals (Fig. 1). Zones

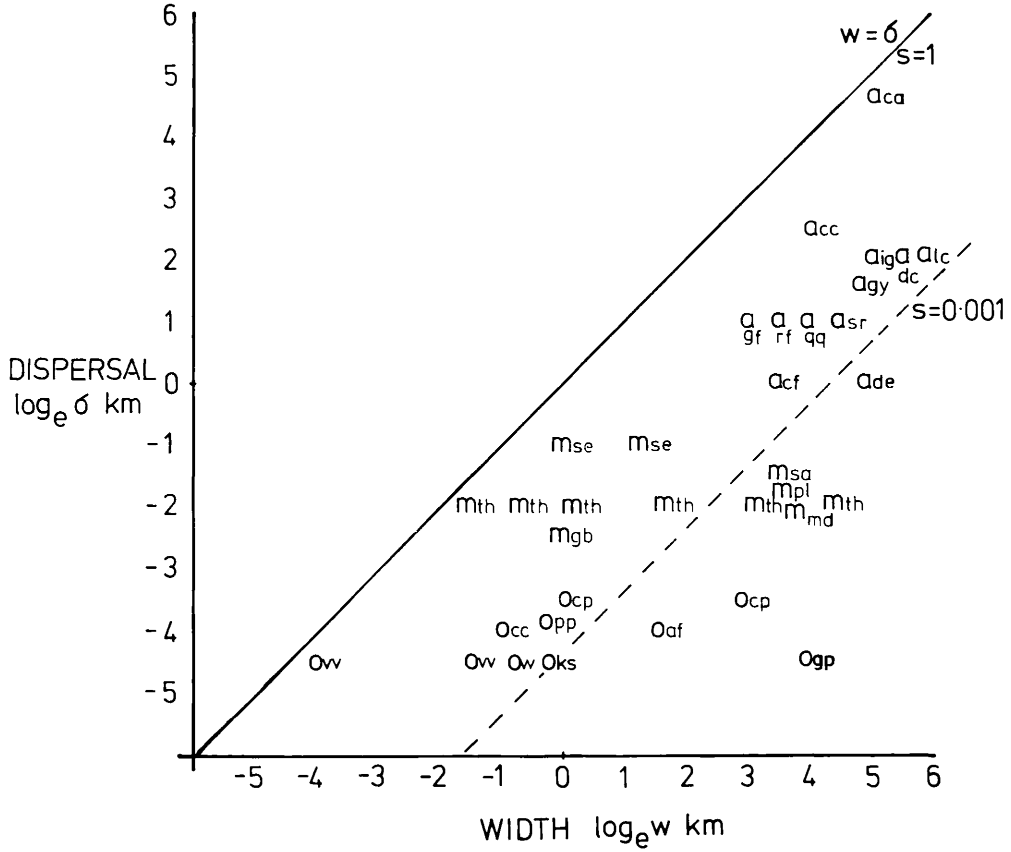

Figure 1. A plot of dispersal (σ) against width (w) of hybrid zones in Orthoptera (o), Small mammals (m) and Birds (a), where the width is fairly well known. Dispersal estimates are available for some species (*) although some require futher examination. Species legend: o = Orthoptera, vv = *Vandiemenalla viatica* complex (see Table 1), ks = *Keyacris scurra*, gp = *Gryllus pennsylvanicus/firmus**, cc = *Caledia captiva**, pp = *Podisma pedestris**, af-*Allonemobius fasciatus/socius*, cp = *Chorthippus parallelus*;* m = Mammalia, gb = *Geomys bursarius/lutescens**, th = *Thomomys bottae** complex, md = *Mus domesticus/musculus*, pl = *Peromyscus leucopus**, sa = *Sorex araneus**, se = *Spalax ehrenbergi**, complex; a = Aves, cf = *Campylorhynchus rufinucha*, de = *Dendroica coronata**, gf = *Galbula ruficauda*, ref = *Ramphocelus flammigerus*, qq = *Quiscalus quiscula*, sr = *Sturnella magna/neglecta*, gy = *Gymnorhina tibicen/hypoleuca*, ig = *Icterus galbula*, dc = *Daphoenositta chrysoptera*, le = *Lanius collurio/phoenicuroides*, cc = *Corvus corone**, ca = *Colaptes auratus/cafer**. The diagonal is where hybrids are completely sterile (s = 1) so that the width of the zone is equal to the dispersal; the dotted line gives the width of tension zones caused by various dispersals where selection against the hybrids is weak (s = 0.001).

may also be more transient in organisms whose life style is more ephemeral or cosmopolitan and whose habitats are more dispersed or variable (Hewitt, in press). Consequently, in many groups the genomes of races and subspecies will remain distinct for many thousands of generations —quite possibly right through an interglacial. The major reorganization in species substructure will have come about during the range expansions and contractions caused by large climatic changes. With the onset of an ice age the distributions of species now living in northern temperate regions will have moved south and into refugia, and many genomes will have gone extinct. After an ice age those surviving will have expanded north again. These major cycles are overlaid with smaller ones, so that over recent geological time —2 million years— surviving genomes will have been subject to many cycles of contraction and expansion. The refugia and leading edges of these moving genome ranges may well have provided many opportunities for divergence and substructuring (Hewitt, 1988, 1989): effective population sizes would have been small and realized fecundity high, so that new mutants and recombinants may become fixed more rapidly and spread. If such a mutant is negatively heterotic, then it will have a much greater chance of establishment than in a system with large effective population size. As these diverged genomes expanded, they could form a hybrid zone when they met.

EFFECTS OF THE LAST 20,000 YEARS

We have most information about the last 20,000 years —the late Pleistocene and present Holocene— and this comes from a variety of biological and geological sources. Consider for example *Chorthippus parallelus,* some 18,000 BP in the depth of the last glaciation; pollen analysis (Huntley and Birks, 1983) suggests that in Western Europe the vegetation which supports this species at present was to be found only as far north as southern Spain and possibly southern Italy (Fig. 2). Farther east we have less data but suitable habitats probably occurred beyond the Balkans. There appears to have been a rapid warming around 14,500 BP, and *Chorthippus parallelus* would have expanded northwards as the vegetation became suitable. The grass species on which it lives may well have advanced significantly faster than the trees which form the major part of pollen analysis of vegetational changes, and the high insolation which was driving the melting of the ice may well have created warm summer ground conditions a long way north. The speed of advance of some insects is indeed very rapid, as evidenced by the luminary work by Coope (1979) on fossil beetles. In fact, the distribution of beetle species deduced from remains in stratigraphic cores has revealed new details of the warming, and in particular has shown that after the initial dramatic warming a severe cold reversal occurred around 12,000-10,500 BP followed by another rapid warming to postglacial conditions (Atkinson *et al.*, 1987). It seems that these insects made rapid advances —and retreats— in response to relatively short term fluctuations in climate. Grasshoppers should also do this, and it is a pity that they are not better preserved in these deposits, but the speed of their advance after this cold period must have been quite rapid in order to reach England before the rising seas cut the Channel to the North Sea (Hewitt, in press). This narrow stretch of water is a real barrier to dispersal (Ragge, 1968, 1988). It was cut around 8,000 BP, and grasshoppers must have travelled at between 200 to 500 m/year to cover the 1,000 km distance —depending on maximal and minimal (5,000 to 2,000) years expansion period. The occasional macropterous female may have greatly influenced this.

Such a scenario has important implications for the genome structure of the species (Hewitt, 1988, 1989). The genome expanding will come from populations at the edge of the ice age distribution of the species, and the speed of the advance means that essentially one of very few genome variants may cover most of the new territory. In the case of *C. parallelus,* genomes from the south of Spain, Italy and the Balkans will have advanced and met in the Pyrenees, where they formed a hybrid zone because they had diverged to produce sufficient incompatibility. Whilst some genetics change and local adaptation will have occurred since they expanded, it seems that the taxa disperse to places they can reach and where their genomes will allow them to survive. This concept of the movement of a relatively non-evolving genome to track the environments to which it is suited is an important tenet in biopaleoclimatic reconstruction (Coope, 1979). It raises some intriguing genetic and paleontologic questions!

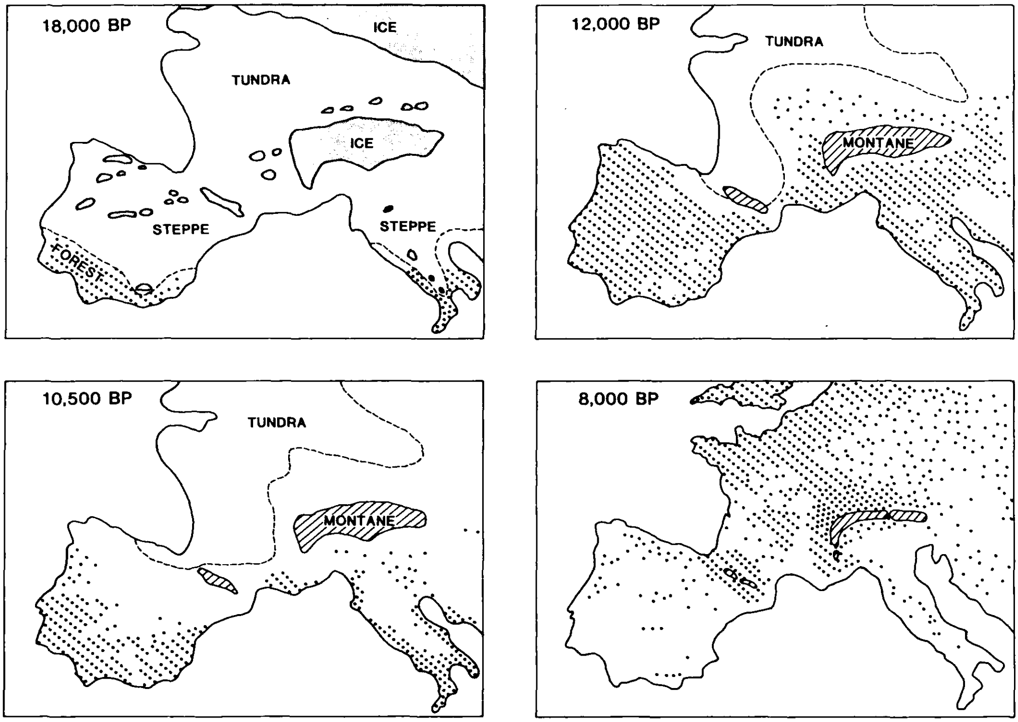

Figure 2. Proposed distribution of grasshoppers such as *Chorthippus parallelus* which survived in refugia in southern Spain and Italy at various stages in the postglacial warming, including the 10,500 BP reversal. It is based primarily on vegetation distribution deduced from pollen analysis.

The dynamics of the leading edge of expansion also has some interesting implications. Such population systems will be characterised by a few migrants colonizing small pockets of suitable habitat in a 'rolling-stepping-stone' model, which will produce bottlenecking and genetic drift. Climatic fluctuations and reversals will amplify this, producing an oscillating patchy distribution of suitable locations. This could produce homozygosity, and there is some evidence from northern mammals for this (Sage and Wolff, 1986). It could also promote genomic divergence by the fixation of negatively heterotic mutations in isolates, and the multiple karyotypic races of *Mus* and *Sorex* in Northern Europe may be in part a result of this (Hewitt, 1989).

Not only may this rapid expansion involve few genomes, but also only some species. There is increasing evidence (Adams and Woodward, 1989) of a relative paucity in the Northern American and European floras as compared with that of N.E. Asia, and this is attibutable to the effects of greater glaciation on these regions which then require recolonisation. This also implies that biotas and communities are not at equilibrium and the still changing natural distributions of many species support this (Huntley and Birks, 1983; Bartleim & Prentice, 1989).

EARLIER GLACIAL CYCLES

The previous Ipswichian Interglacial was around 120,000 BP, and there have been some short, less warm interstadials interrupting the glacial in between, in which insects advanced and retreated (Coope, 1977). Over the last 2 million years there have been some 20 glacials and interglacials each with their interstadials, so that Northern Temperate species have been subject to many range shifts and cycles of contraction and expansion. Mutations which occur in contracted populations may spread out later, forming hybrid zones where they meet, and repeated cycles could accumulate these to produce subspecies with complex hybrid zones, and maybe even species (Hewitt, 1988, 1989).

Whilst we concern ourselves with current and recent distributions, it is worth reflecting that most of the last 2 million years have been ice age —the warm interglacials comprising only a small fraction of that time. Consequently the distributions of temperate species usually will have been compressed to the subtropics. For Western European species the Mediterranean Sea, the Straits of Gibraltar and North Africa will have played crucial roles. During the many interstadials the Pyrenees and Alps may have been important barriers. Mexico and Florida, along with the Rockies and Appalachians, are formative features in North America. Clearly, we need better data on pollen and beetle distributions from these glacial ranges to assess the details of this process. It is already apparent that different interstadials produced different asssemblages of beetles; the ranges of species were not the same each time. There is obviously a chance element in this, but also the physical factors responsible for the climatic cycles —ice volume, insolation, orbital eccentricity, tilt and perihelion (Bartlein and Prentice, 1989) —were different and would produce different refugia and different patterns of expansion and contraction. The genetic substructure of current species would seem to have had a long, variable and distant history —they do not appear equilibrated and are affected by chance events.

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Chromosome structure in hybrid zones of *Chorthippus parallelus parallelus* and *Chorthippus parallelus erythropus*

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ABSTRACT

Chorthippus parallelus parallelus and *Chorthippus parallelus erythropus* form hybrid zones in different Pyrenean passes. The extent of these zones can be determined by analyzing morphology, courtship behaviour and stridulatory pegs and through cytogenetic analyses of pure and hybrid populations. To date, two hybrid zones have been analyzed in detail (Col de Portalet and Col de Quillane). In both cases we have observed differences between the two races in the number and behaviour of the nucleolar organizer regions (NOR) located on the sex chromosome. These regions contain the genes that code for ribosomal RNA.

The role of these sex chromosome genes in hybrid male sterility and the structure and maintenance of such zones are discussed.

Key words: hybrid zones, insect cytogenetics.

INTRODUCTION

A more extensive analysis of chromosome variation in relation to geographic distribution has been carried out in Insecta than in any other group of organisms (White, 1973 for review). Such analysis shows that populations of many species are mixtures of individuals with differently constructed chromosomes. As more detailed results are produced, using highly specific chromosome markers, the more differences we find between these chromosome systems. These studies reveal a considerable underlying variabity which is reflected between individuals, populations, races and subspecies.

Chromosome differences between closely related populations within the same species can give rise to complex chromosome interactions when the individuals are allowed to cross breed. If they produce viable individuals, the level of heterozygosity in the «hybrid form» is increased with respect to the parents. The behaviour of the chromosomes during the cell cycle or components such as meiosis may be affected although the magnitude of the chromosome change in the hybrid may have no relation to the viability of the hybrid. The subsequent survival of the hybrid offspring then depends on the various components of natural selection. Clearly, the fitness of these individuals may be modified in different ways according to the degree and nature of heterozygosity in the hybrid.

Cases of natural contacts between closely related populations and subspecies, with the subsequent production of considerable heterozygosity, can be analyzed in hybrid zones. Hybrid zones, using the terminology of Barton and Hewitt (1985), are narrow regions in which genetically distinct populations, meet, mate and produce hybrids. Hybrid zones are found in a wide variety of organism including plants, insects and vertebrates (Barton and Hewitt, 1985 for review).

Several previous papers (Butlin and Hewitt, 1985 a,b; Hewitt *et. al.*, 1987, 1988; Gosálvez *et. al.*, 1988), as well as some included in this volume, describe different aspects of a contact zone between two subspecies of the meadow grasshopper *Chorthippus parallelus*. This contact zone is found along the Pyrenees between France and Spain and is probably the result of the postglacial spread of two subspecies of this genus; *Chorthippus parallelus parallelus (Cp parallelus)* is widespread through western Europe and *Chorthippus parallelus erythropus (Cp erythropus)* is an Iberian endemic. These were probably formed from the glacial splitting of a common ancestor into refugia with divergence to subspecies (Hewitt, 1989).

We would like, in the present paper to review some aspects of the chromosome system of both subspecies in an attempt to understand the genetic basis of the evolution and maintenance of the whole hybrid zone in the Pyrenees as well as the peculiarities of the contact region in individual valleys.

The methods and techniques used for chromosome analysis of similar material have been previously reported (López-Fernández and Gosálvez, 1981) and some have been slightly modified from those reported by Gosálvez *et al.*, (1987), particularly those concerning restriction endonucleases.

THE CHROMOSOMES: SIMILARITIES AND DIFFERENCES

The basic chromosome complement

The chromosome complement is similar in both subspecies, and comprises 16 autosomes of different sizes plus an XX ♀/XO ♂ sex determining mechanism. The three long pairs are submetacentric (L1-L3), while the remainder (M4 to S8, including the X chromosome), display terminal centromeres (John and Hewitt, 1966).

Localization and nature of heterochromatin

The heterochromatin in *Cp parallelus* is quite similar to that found in *Cp erythropus*. C-banding plus Giemsa in *Cp parallelus* shows pericentromeric heterochromatin in all the chromosomes (fig. 1a,d). Additionally, terminal C-bands are present in all the acrocentric chromosomes and in the shorter arms of L2 and L3 chromosomes (fig.1a). Most of these bands are polymorphic for size and presence/absence of segments (John and Hewitt, 1966; Westerman, 1969). Interstitial bands are found in the short and long arm of the L3 and in the M4 chromosome. Medium and short chromosomes show similar polymorphisms for distal heterochromatin in both subspecies.

The X chromosome differs significantly between the two subspecies. Thus, while *Cp parallelus*-X shows a distal heterochromatic band (fig. 1a), this is replaced in the *Cp erythropus*-X by a prominent interstitial one (fig.1d).

Similar results are obtained if the slides are processed for C-banding and stained with Acridine Orange (fig. 1b,c,e and compare 1d with 1e). The main difference is that the pericentromeric band in the chromosome L2 of *Cp erythropus* is expanded into two closed bands, one of them is stained light green while the other is intense green. Both bands are easily visible in very condensed chromosomes. Intense green fluorescence is also observed in the distal band of the L3 chromosome in both species

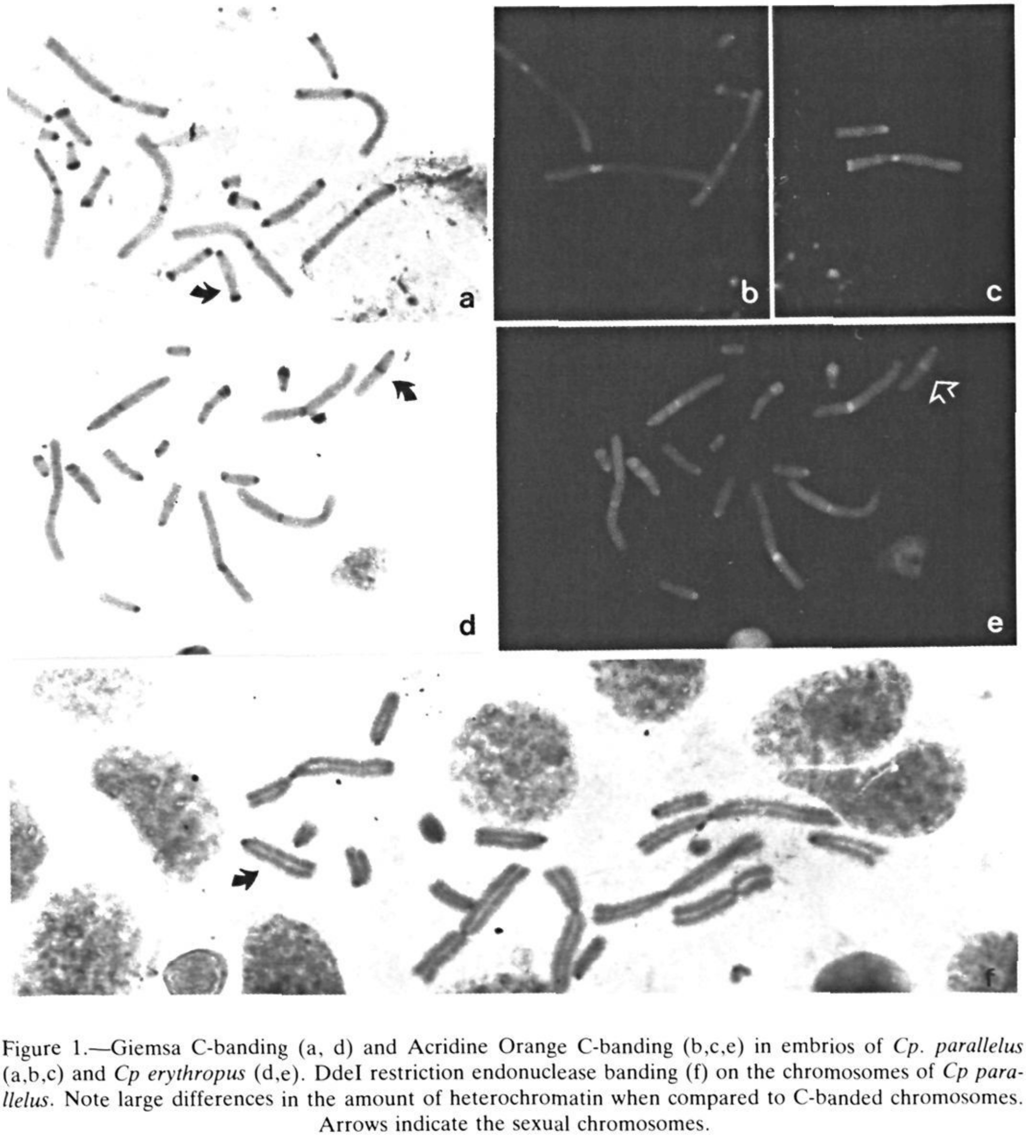

Figure 1.—Giemsa C-banding (a, d) and Acridine Orange C-banding (b,c,e) in embrios of *Cp. parallelus* (a,b,c) and *Cp erythropus* (d,e). DdeI restriction endonuclease banding (f) on the chromosomes of *Cp parallelus*. Note large differences in the amount of heterochromatin when compared to C-banded chromosomes. Arrows indicate the sexual chromosomes.

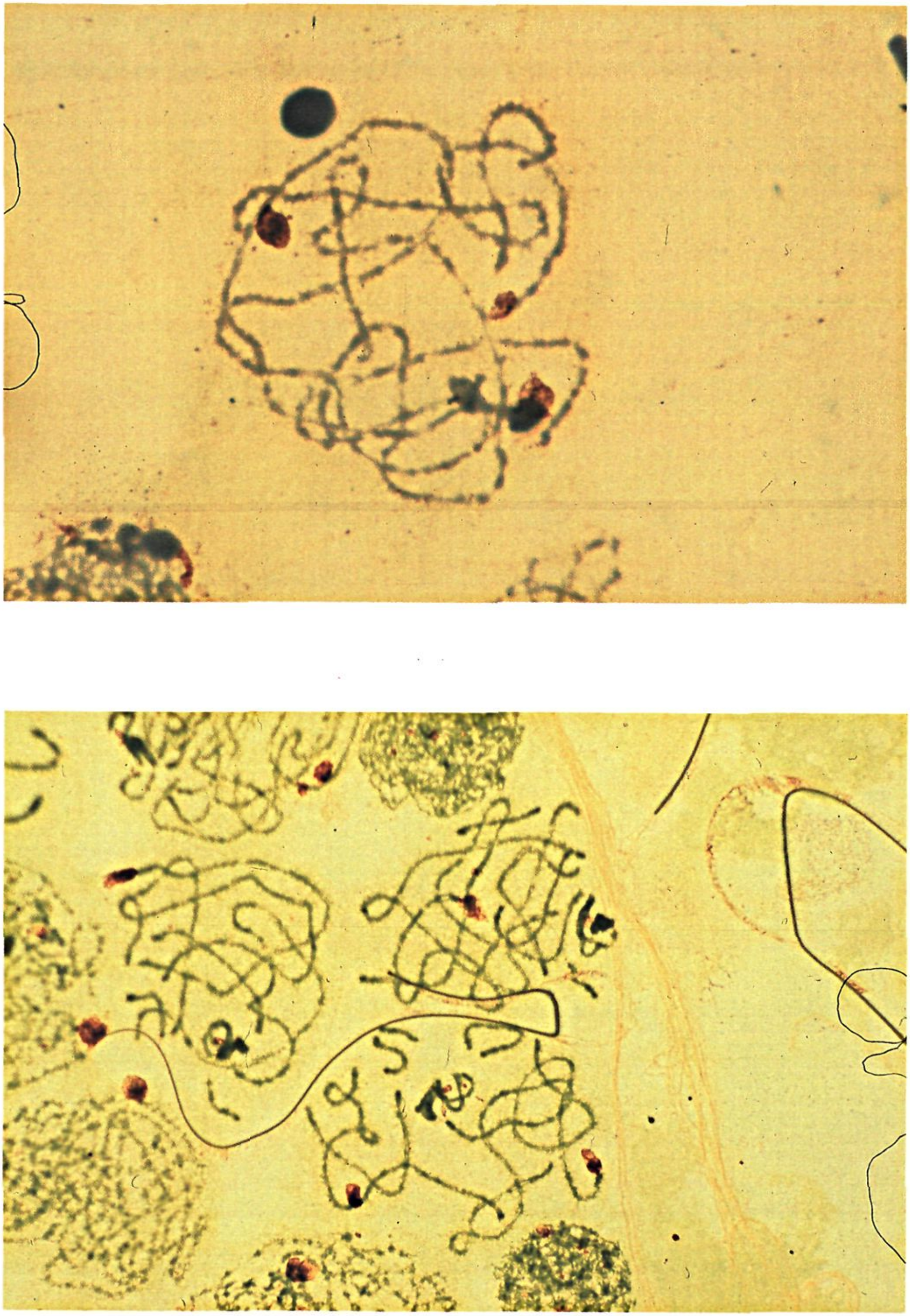

Figure 2.—Silver staining in early prophases of *Cp parallelus* (a) and *Cp erythropus* (b).

(fig. 1c) and in the distal band of the X in *Cp parallelus*. All these bands correspond to heterochromatin associated with active Nucleolar Organizer Regions (NORs). The rest of the heterochromatic regions are dull green.

The most useful pattern of bands to distinguish both subspecies is that shown by the X chromosome. This chromosome in *Cp parallelus* shows a distal positive C-band which gives intense green fluorescence when stained with Acridine Orange; this band is absent in *Cp erythropus*.

Chromomycin A_3 is a fluorochrome that binds specifically to GC-rich DNA. The level of fluorescence on the chromosomes can be enhanced when counterstained with Distamycin A (DA). The use of this method revealed that all the heterochromatin present in both subspecies is particularly GC rich.

Diamidino phenyl-indol (DAPI) counterstained with DA is a battery of compounds revealing AT enriched DNAs. If DA/DAPI is used, a nonspecific pattern of bright bands is obtained. Only unstained regions (gaps) are evident in those regions which are particularly rich in GC base pairs (Gosálvez *et. al.*, 1988).

Restriction endonucleases banding

Restriction endonucleases (RE) are enzymes capable of cleaving double-helix DNA at specific sites, and have recently proven very useful in investigating the structure of chromosomes in fixed cytological preparations. A characteristic longitudinal differentiation has been found in mammalian chromosomes (Mezzanotte *et al.*, 1983) and also in grasshopper chromosomes (Gosálvez *et. al.*, 1987; López-Fernández *et. al.*, 1988). Since the pattern of bands obtained may not be identical to that obtained by other techniques, different REs have been assayed on the chromosomes of both subspecies to look for additional chromosome markers. The following REs were used on mitotic chromosomes from embryos: Alu I (AGCT), Msp I (CCGG), Hpa II (CCGG), Mbo I (GATC), Sau 3A (GATC), Dde I (CTNAG), Hinf I (GANTC) and Hae III (GGCC).

Most of the REs used produce a total digestion of both eu- and heterochromatin with the subsequent absence of longitudinal differentiation. On the other hand, enzymes such as Dde I (CTNAG) digested all the euchromatin, all the distal heterochromatin and a part of the pericentric heterochromatin. Only small blocks of heterochromatin remain undigested in the centromere of each chromosome. In fact, the band obtained is smaller to that of C-bands (compare fig. 1a with fig. 1b). Whilst these results are of interest in showing the underlying heterochromatin heterogeneity between the centric and distal heterochromatin and that existing within each centromere, the technique unfortunatelly does not reveal differences between the two subspecies.

Nucleolar organizing regions

Silver staining can be used on meiocytes of males to successfully localize those NORs that were active in previous interphases (Miller *et al.* 1976; Rufas and Gosálvez, 1982). Using silver staining we found that while *Cp parallelus* has three NORs on two submetacentric chromosomes (L2, L3) and on the X chromosome, *Cp erythropus* does not have active NOR on the X (fig. 2). This provides a clear chromosomal marker to distinguish between both subspecies and has been used to score its frequency throughout the hybrid zone in Col de Portalet. This frequency changes from pure *Cp parallelus* (three silver precipitates per meiocyte) to pure *Cp erythropus* (two silver precipitates per meiocyte), and in populations in the hybrid zone it is possible to find male individuals with two and individuals with three silver precipitate per cell. The frequency distribution fits with that expected for male individuals carrying either X-*parallelus or X-erythropus*. Details of frequencies at Col de Quillane and Col the Portalet were given elsewhere (Hewitt *et. al.*, 1989) and a part of these data from Col the Portalet together with new data are given in fig. 3.

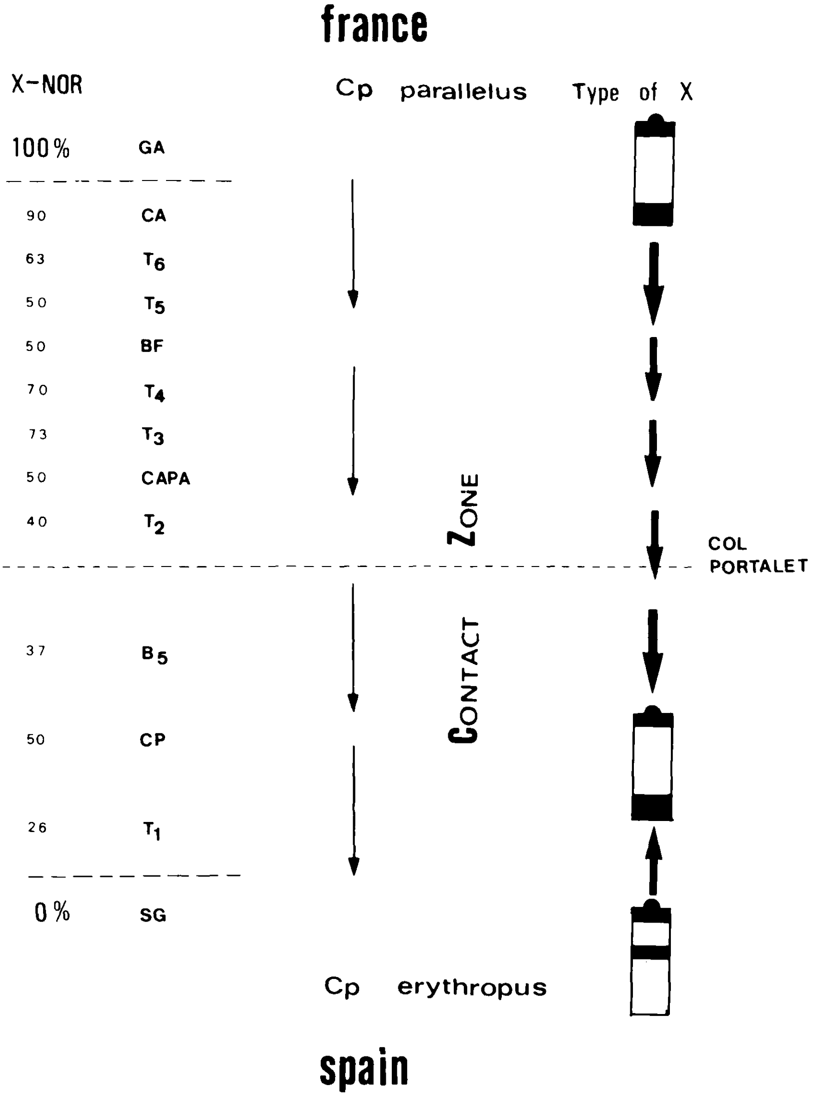

Figure 3.—A distribution of frequencies of individuals with active X-NOR and type of sexual chromosome present in populations from the contact zone in Col de Portalet.

As stated above, differences in NORs from individuals of the hybrid zone corresponds to a cline of nucleolar organizing-X or not organizing-X. This would be pressumed to be directly related to presence of X-*parallelus,* which has active NOR in the pure race, or X-*erythropus* which has not. However, further analysis shows that this is not the case in Col the Portalet. In fact, all the individuals analyzed by Acridine Orange and C-banding plus Giemsa show an X chromosome corresponding to the *parallelus* type in the center of the contact zone.

These results indicate two important new possibilities: i) the control of ribosomal genes in the sex chromosome is apparently disrupted in individuals in the hybrid zone.

ii) the *parallelus* sex chromosome has possibly introgressed on the Spanish side of the Col.

F_1 hybrid males

In order to analyze the possible disruption of NOR activity in the X chromosome in hybrid individuals, and the role played by the autosomes in controlling the expression of X-NOR, pure female *Cp erythropus* were crossed with pure male *Cp parallelus* and *vice-versa*. The resulting F_1 males in both cases are sterile because of testis dysfunction (Hewitt *et. al.*, 1987) but nucleolar activity could be monitored by silver staining in interphase somatic cells.

The results were very different in the two cases. When a female *Cp erythropus* was used as the parent, the number of nucleoli were stable from cell to cell (four per cell i.e. one for each autosome). In contrast, great variability in the number of active NORs was found when the female parent was *Cp parallelus*. In this case the number of nucleoli varies from 1 to 8 (Gosálvez *et. al.*, in preparation).

These results indicate that: i) heterozygosity of all the autosomal set does not change the pattern of NOR activity and does not interfere with an X which normally does not organize nucleoli. ii) an X which organizes nucleoli interfers with a heterozygous set of autosomes and produces variable and presumably unbalanced amounts of rDNA activity.

Distribution of the hybrid zones and perspectives

The Pyrenees is a complex of valleys running North-South from its crest of high peaks in the central part whilst the western and eastern ends are lower and smoother. This particular configuration has been important for the spreading of both subspecies. Thus, places such as the mountains around Viella may exclude genetic flow between both subspecies, since these grasshoppers are seldom found higher than 2,000 m. We have found contact zones in valleys with similar characteristics to those of Col de Portalet. For example, to the west Col the Somport and Port de Larrau show intrapopulation variation with respect to the number of active NORs (Gosálvez and Hewitt, in preparation).

The post glacial contact of *Cp parallelus* from the north (France) and *Cp erythropus* from the south (Spain) would have occured first in the lower regions at the ends of the Pyrenees chain. We may therefore expect greater introgression to have occurred in these regions than in the central high cols where contact was probably much later. There are differences between Col de la Quillane and Col de Portalet in the width of clines for various characters (Hewitt *et. al.*, 1988) and it is important to study in detail more contacts along the Pyrenees to ascertain the reasons for any such differences in introgression.

On the other hand, our results suggest that the heterozygosity of hybrid genomes produced by recombination in the zone is causing abnormal nucleolar expression. It is possible that this is a cause of F_1 male testis dysfunction and consequently may be a major factor in this example of Haldane's Rule. It will be important to study this in more molecular detail, and to compare cols with zones of different width where NOR expression may be more or less controlled.

Currently, we are attempting to find new subspecific chromosome markers by using *in situ* hybridization. It is important for any genetic analysis of these diverged genomes to have such markers, and whilst allozyme and chromosome banding studies have given a few differences more are needed. We hope that these will be forthcoming soon.

ACKNOWLEDGEMENTS

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Chromosome divergence in *Podisma* Berthold through the Alps, Pyrenees and Sistema Ibérico

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ABSTRACT

The wingless genus *Podisma* L. reached western Europe during the Ice Ages and is now found in high mountains, viz., the Alps, Apennines, Pyrenees and Sistema Ibérico (Spain), from which latter Morales-Agacino described the species *P. ignatii*. By examining the chromosomes of these extant forms it may be possible to reconstruct their evolutionary history. Crosses between different forms have been analysed. There are at least two chromosomal races of *P. pedestris* L. in the Alps and a different one in the Pyrenees, and all are different from *P. ignatii*. The role of geographical isolation in producing these differences, and their role in speciation will be discussed. The application of molecular markers promises to shed light on these processes.

Key words: Cytogenetics, chromosomal races, hybrids, speciation.

INTRODUCTION

Allopatric and parapatric chromosomal variability has been widely discussed with respect to both plant and animal groups. Such distributions are interesting to a wide range of biologist, including taxonomists, cytogeneticists and zoologists, because of the obvious implications for speciation and evolution. Well studied cases include the genus *Clarkia* and *Gilia* in plants (See Grant, 1971), the black rat in animals (Yoshida, 1983 for a review) and the Australian morabine grasshoppers of the "viatica" group (White *et al.*, 1967; White, 1974; 1978).

The genus *Podisma* (Acrididae: Catantopinae) is particularly useful for these kind of studies because it provides clear examples of allopatric and parapatric chromosomal variation, both intra- and inter-specific, as well as one of the most fully analysed "hybrid zones" between two of the four described chromosomal types (Hewitt and Barton, 1980; Hewitt, 1985).

In this paper we examine the chromosomal divergence among different species and races from the western range of *Podisma* in Europe. We also consider the possible causes, origin and evolution of the observed differentiation.

THE DIMENSIONS OF THE GENUS

The genus *Podisma* is composed of several species of wingless mountain grasshoppers. One of them, *P. pedestris (L.)* is widely distributed in the mountain regions of Europe from Eastern USSR to the Pyrenees. This extensive distribution seems closely related to low temperature and food plants (Dreux, 1962; Nichols, 1984; Nichols & Hewitt, 1988). Three different chromosomal races have been found so far two in the Alps and a third in the Pyrenees (Gosálvez *et al.*, 1988a).

P. ignatii, in contrast is an endemic Iberian species with a distribution restricted to the Picos de Europa, Sistema Ibérico and Sistema Central (Morales-Agacino, 1950). Advances and retreats of the last Ice Age seem responsible for the present distribution. Both species probably separated from a common Podismini ancestor as long ago as the late Tertiary (Marty, 1969).

THE CHROMOSOMAL SYSTEM OF *PODISMA*

The basic chromosomal complement of the genus is 22 autosomes plus an X for males (2n=23) and 22 autosomes plus two Xs for females (2n=24), all of them acrocentric. Autosomes can be divided into 3 large (L1 to L3), 6 medium (M4 to M9) and two small (S10 and S11) sized pairs. Two different types of B-chromosomes have been reported in the Pyrenean and Alpine populations (Gosálvez *et al.*, 1980) ranging in number from 1 to 11 extra elements (Hewitt & John, 1972; Hewitt, 1975) (Fig. 1). A rearrangement involving the X-chromosome of *P. pedestris* has resulted in a race with 2n=22 (both male and female) in part of the Alps.

CHROMOSOMAL DIFFERENTIATION IN *P. PEDESTRIS:* ALPINE RACES

Two chromosomal races have been found in the French Alpes Maritimes: the XO race, which shows the standard acridid karyotype 2n = 22 + X, 2n = 22 + XX) all acrocentric) and a Neo-XY race (2n = 20 + NeoX + NeoY, and 2n = 20 + NeoX + NeoX). The Neo-XY karyotype involves a submetacentric Neo X chromosome originating from a centric fusion of the original X and a large autosome, apparently the L3 (John & Hewitt, 1970; Hewitt & John, 1972). This race is distributed in the Southern Alpes Maritimes. The two races meet and hybridize in a narrow «hybrid zone» that has been studied in detail for more than a decade. Its behavioural, morphological, allozymic, ecological and cytogenetical features have been reported (Barton & Hewitt, 1981a,b; Hewitt and Barton, 1980; Hewitt, 1985). There is proximal heterochromatin on all chromosomes of both XO and NeoXY races as well as in a distal position on all the medium sized chromosomes, as detected by Giemsa and Acridine Orange C-banding (Fig. 1, 2). All this heterochromatin seems to be highly Guanine-Cytosine (GC) rich, judging by its response to the Distamycin A/Chromomycin A3 (DA/CMA3) counterstaining (Fig. 4) (Westerman & Hewitt, 1985).

The number and position of the Nucleolar Organizer Regions (NORs) have been revealed by means of the silver staining technique (Gosálvez *et al.*, 1988a, b). In *P. pedestris* this information is useful not only in the characterization of the races, but also in the interpretation of the evolution of the group. We will focus our attention here in the X chromosome, the site of the main nucleolus in all the races and species of *Podisma,* because the technique is most consistent on this chromosome. The NORs on the other chromosomes are difficult to score because they become disorganized before diplotene, a condition unusual in grasshoppers (Rufas *et al.*, 1985).

Both the XO and the NeoXY races show substantial ribosomal DNA activity in a subterminal region of the X chromosome associated with a C-heterochromatic region which fluoresces differentially green when Acridine Orange C-banded (Fig. 1b and 4). In this way NORs can be located without using the more traditional silver staining technique. The Neo-XY race individuals show an additional small NOR close to the point of fusion (Fig. 1d and 4) (Gosálvez *et al.*, 1988a, b).

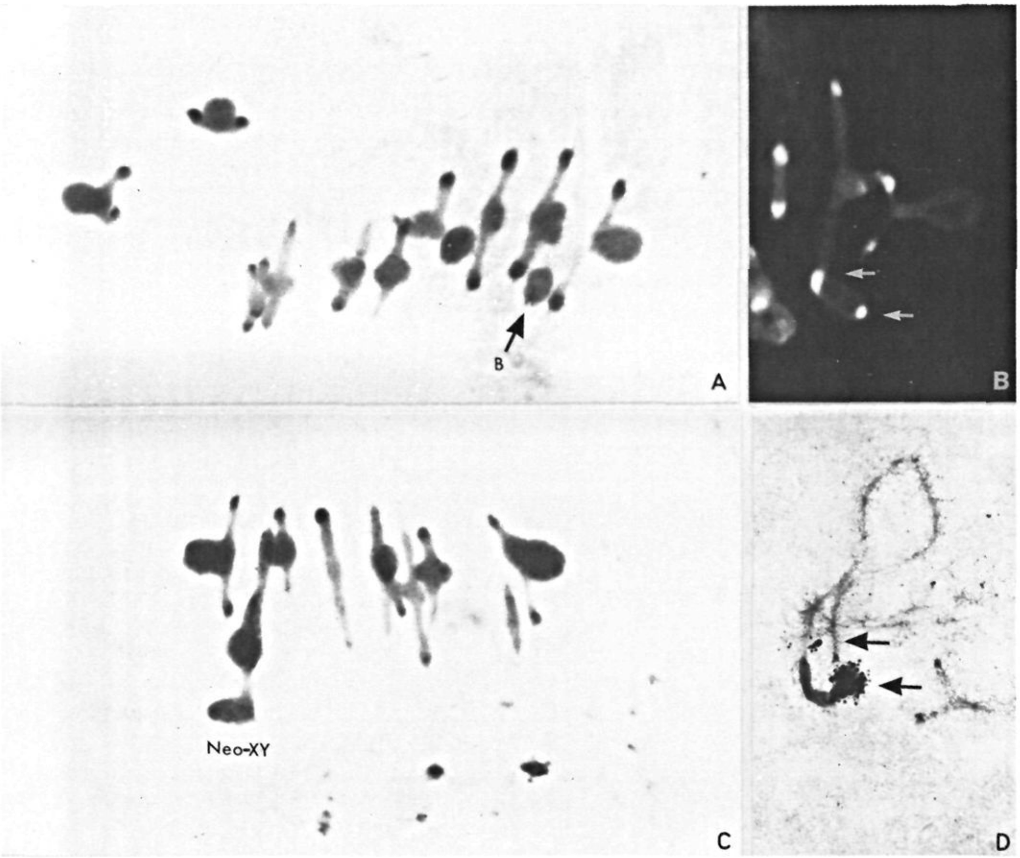

Figure 1.—The Alpine races of *Podisma pedestris*. a) Giemsa C-banded spermatocyte from XO race. Note the presence of proximal and terminal heterochromatin on the medium sized bivalents as well as the existence of a B-chromosome. b) Selected metaphase I NeoXY bivalent Acridine Orange C-banded. Arrows show the heterochromatin associated to the NORs, which fluoresces differentially in green after this treatment. c) Male meiocyte from a NeoXY male after Giemsa C-banding. d) Selected silver stained NeoXY diplotene bivalent showing the distal position of a main nucleolus in the fused X as well as the existence of ribosomal activity close to the fusion point (arrows) but in the autosomal arm.

THE PYRENEAN RACE

The Pyrenean populations of *Podisma* show some interesting differences in the distribution and composition of the heterochromatin, and the distribution and composition of the heterochromatin, and the localization of the main nucleolus on the X chromosome. All individuals studied have the standard acridoid sex chromosome system (*i.e.* XO/XX) but only the proximal heterochromatic bands are present. Each is larger than the corresponding Alpine band (Fig. 2). This paracentromeric heterochromatin seems composed of two narrow bands, of different DNA base pair composition. Thus there is positive response to Distamycin-A-DAPI (DA-DAPI) in the Adenine-Thymine (AT) rich band and to DA-CMA3 in the GC rich band (Fig. 4) (Gosálvez *et al.*, 1988a, b).

As with the Alpine races, there is a major NOR on the X chromosome, discernible with silver staining and with the Acridine Orange C-banding technique (Fig. 4) Gosálvez *et al.*, loc. cit.). It is however, in a proximal position.

PODISMA IGNATII

This Iberian endemism was described in 1950 by Morales-Agacino. The species distribution is restricted to the highest parts of the Sistema Ibérico and Sistema Central mountains as well as some localized areas of Cantabria. It is therefore the most distant representative of the genus from the original focus of dispersion, Siberia. Its distribution was probably determined by range expansions and contractions during glaciations.

When the above mentioned techniques are used on the chromosomes of *P. ignatii,* they disclose that amount and distribution of chromosomal C-heterochromatin resembles that of the Pyrenean race of *P. pedestris* (Fig. 4), whereas its composition resembles that of the Alpine races: there is positive response to the DA-CMA3 treatment, indicating a relatively rich GC DNA base composition (Figs. 3a and 4) (Gosálvez *et al.*, 1988b).

The position of the main NOR is again on the X chromosome; which seems to be a genomic characteristic of the genus. It is located in sub-distal position (Fig. 3b), similar to that reported for the Alpine *P. pedestris* races and is associated with a heterochromatic region which is the only terminal one in the complement (Figs. 3a and 4). This band is smaller than the corresponding one on the Alpine X, but shows up in the same way after Acridine Orange C-banding (Gosálvez *et al.*, loc. cit.).

THE HYBRIDS

Both natural and laboratory crosses between the races have been analyzed and detailed work has been carried out on the hybrid zone between the Alpine races of *P. pedestris* (*i.e.* the XO and NeoXY races). Hybrid individuals show low levels of hatching, development and survival (Barton and Hewitt, 1981 a,b; Nichols, 1984). The offspring of hybrid females collected from the zone show strong homogamy (Hewitt *et al.*, 1987). No ecological differences (Nichols and Hewitt, 1988) no allozyme differences (Halliday *et al.*, 1984) and no morphometric differentiation (Barton, 1979) have been found across the hybrid zone.

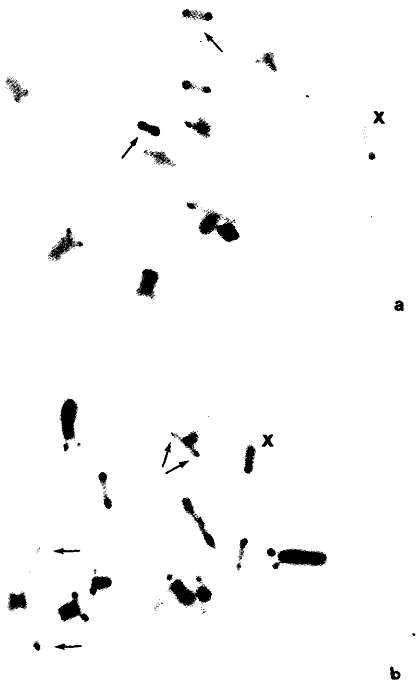

Figure 2.—The Giemsa C-banding of *Podisma pedestris.* a) Metaphase I bivalents from a Pyrenean individual. Large heterochromatic bands are proximally placed. b) Laboratory Pyrenean × Alpine male hybrid. Differences in the size of the proximal heterochromatin are evident, the smallest bands corresponding to the Alpine parental line, while the X shows the typical absence of distal heterochromatin of the Pyrenean populations (compare a and b).

There is racial divergence in the rDNA sequences between the XO and the NeoXY *P. pedestris* Alpine races (Dallas *et al.*, 1988) and differences in DNA content in their spermatids (Westerman *et al.*, 1987). However, neither male hybrids collected in the field nor those produced in the laboratory show the meiotic dysfunction or excess production of abnormal spermatids indicative of non-disjunction or severe karyotypic incompatibility and sterility. So it seems that other genic differences between the races are responsible for the low fitness of the hybrids and the maintenance of the hybrid zone.

Hybrid individuals between the Pyrenean race and the XO Alpine one, have been produced in the laboratory. These are viable and do not show irregularities affecting the meiotic process, despite their clear differences in composition, amount and distribution of the heterochromatin and differences in the main NOR position on the X chromosome (Fig. 2b) (Gosálvez *et al.*, 1988a, b).

To examine the hatch rate in crosses between the taxa, populations of 60-200 individuals were taken from 4 sites one from either side of the hybrid zone in the French Alps near Seyne les Alpes (XO and XY), and 2 from near Pto. de la Bonaigua in the Pyrenees (P1 and P2). They were brought into the laboratory and crossed in bulk locust cages in the combinations given in Table 1. The eggs were collected and reared using the method given in Nichols 1984. After incubation the unhatched eggs were dissected and the stage of development scored.

The Pyrenean/Alpine crosses produced viable offspring and some of the hybrid males were reared until adult so that their karyotype and spermatogenesis could be examined (see above). An analysis of deviance reveals no significant difference in the hatch rate of Pyrenean/Alpine hybrids from the intra-region crosses (see table 1). However, the high mortality in all crosses was sufficient to obscure even the reduced hatch rate between crosses between the XO and XY populations, so the test is not highly sensitive. Nevertheless this breeding experiment demonstrates that the Pyrenean/Alpine cross produces viable offspring in reasonable numbers. This is somewhat suprising in view of the marked karyotypic differentiation between these two regions.

An attempt to produce hybrid individuals between the Iberian endemic *P. ignatii* and the *P. pedestris* Pyrenean race was not successful but further attempts also involving the Alpine races could provide new data on the divergence within the genus.

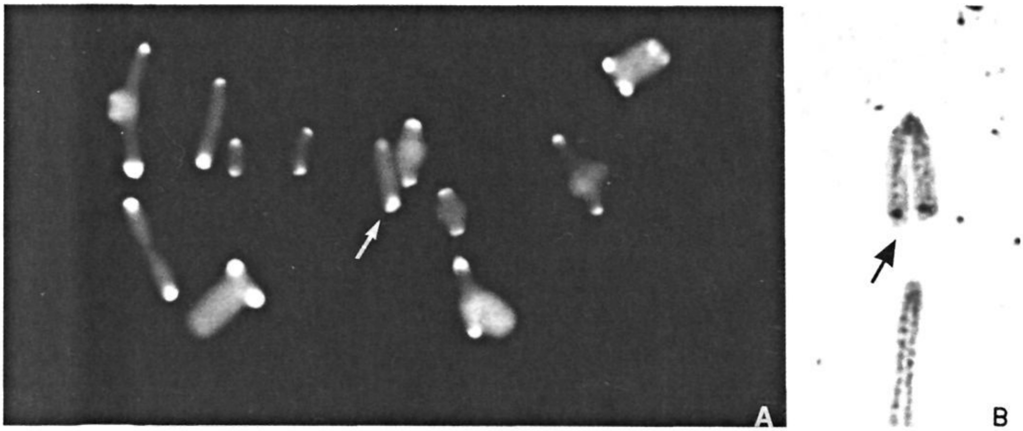

Figure 3.—*Podisma ignatii.* a) Distamycin-A/Chromomycin-A_3 (DA-CMA_3) staining of a methapase I male meiocyte showing the existence of large Guanine-Cytosine (GC) rich proximal heterochromatic bands in all the chromosomes excepting the X, where there is an extra terminal one (arrow) associated with a Nucleolar Organizer Region (NOR) as evidentiated by means of silver staining b).

Table 1.—Mortality rates in eggs from crosses between and within *Podisma taxa*. Populations used in the crosses came from Seyne les Alpes, the P1 and P2 from Puerto de la Boinagua in the Pyrenees.

Cross		No. Pods	Mean No. of Eggs	Mean No. not Developed	Mean No. Died Prediapause
Female	Male				
XO	XY	40	12.0	9.1	1.38
XY	XO	38	11.4	7.8	2.00
XY	XY	22	13.3	9.0	2.86
XO	XO	18	11.5	8.1	1.16
XO	P1	20	10.9	6.3	0.65
P1	XO	20	12.3	9.0	0.80
XY	P1	19	13.8	11.5	0.57
P1	XY	20	12.6	7.9	0.55
P2	XO	20	13.5	10.5	1.25
XO	P2	20	12.3	6.5	0.90
XY	P2	20	9.7	5.7	0.65
P2	XY	19	12.0	7.4	0.47

THE RACIAL AND INTERSPECIFIC DIVERGENCE OF *PODISMA:* GEOGRAPHICAL AND CHROMOSOMAL BASIS

The evolutionary diversification of the genus *Podisma* detailed above appears to have involved several aspects of the genome. A predominant role must be also attributed to geographical and climatic processes resulting in several rounds of isolation and expansion of ancestral populations. Genetic differences could accumulate at each round, eventually leading to the present allopatric, parapatric and endemic taxa (Hewitt, 1988).

It is assumed that the paleartic fauna colonized Western Europe during the Quaternary glaciations, *i.e.*, between 60,000 and 15,000 years B.P. (Uvarov, 1929). Successive advances and retreats probably caused isolations and reunions until a final ice retreat resulted in present conditions (14 to 9,000 years B.P.). The existence of the parapatric chromosomal XO and NeoXY races in the Alps seems to be due to a secondary contact between *Podisma* populations retaining the original XO system, and those coming from an isolate where the chromosomal rearrangement took place (Hewitt and John, 1972). During this period, the genomic divergence was enough to produce the low fitness of the hybrid individuals but not sufficient to be reflected in the morphology, the allozyme expression, the distribution and composition of the heterochromatin or the number and position of the NORs. Detailed features of the DNA, gene sequence and gene expression, must be responsible for the low fitness of hybrids.

The same geographical and climatic processes underlie the presence of a third race of *P. pedestris* in the Pyrenees. However, a different pathway of divergence must have been involved, since differences between the Pyrenean and Alpine XO populations involve heterochromatin distribution and composition, in addition to the main NOR position. The unexpected presence of AT rich heterochromatic paracentromeric subregions on this race has been interpreted as possible large duplications of some gene sequences (Gosálvez *et al.*, 1988a). Such duplications have been proposed to explain a similar phenomenon in another orthopteran, *Atractomorpha similis* (John et al., 1986). The difference in composition, as well as the absence of distal heterochromatic blocks on the medium sized chromosomes of the Pyrenean race may be important given the involvement of heterochromatin

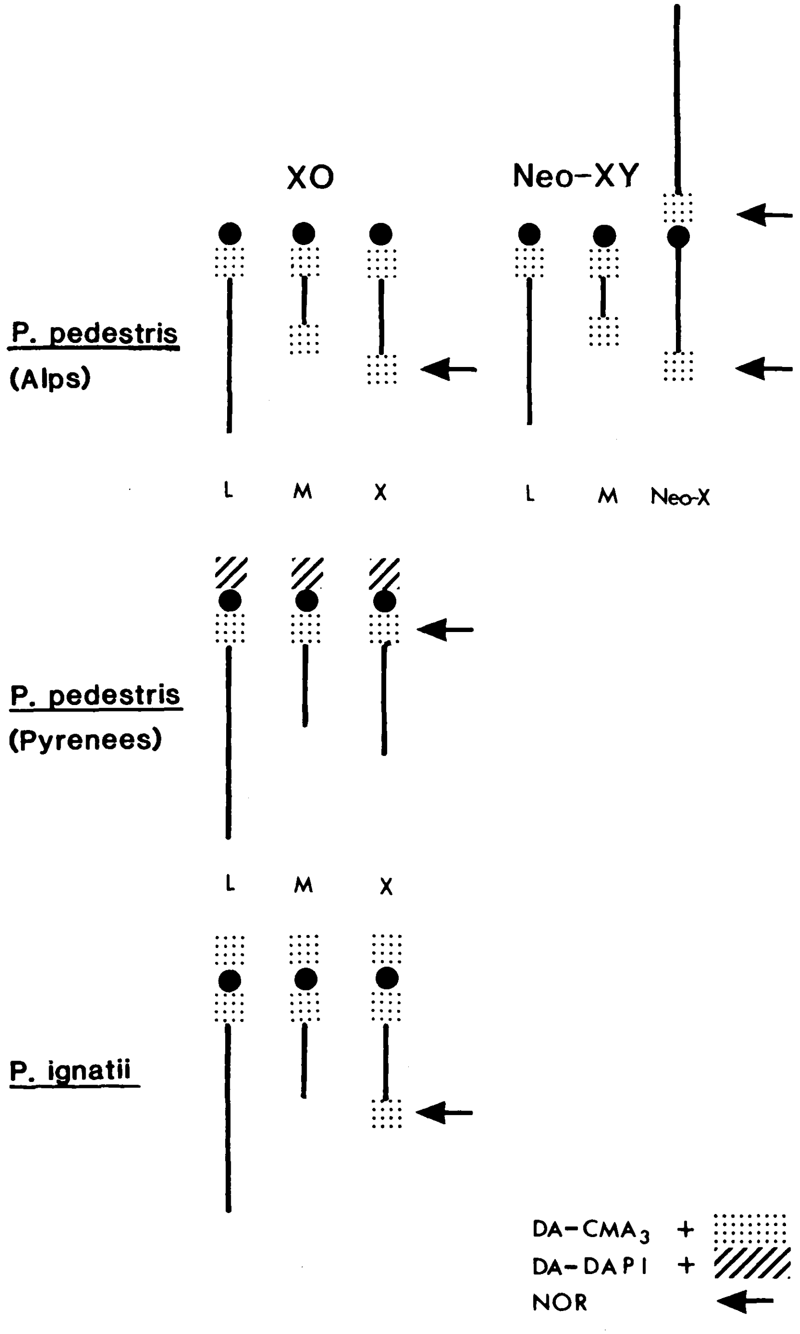

Figure 4.—Diagram showing the composition and distribution of the heterochromatin and the position of the main nucleolus on Large (L), medium (M) and X chromosomes of the *Podisma* taxa. Note the gross similarity between the *P. pedestris* Pyrenean race and *P. ignatii* autosomes. However, the X chromosome and the composition of the heterochromatin in the latter species is more similar to that of the Alpine *P. pedestris* individuals.

in chromosomal differentiation and speciation (White, 1978; Dover *et al.*, 1982; John, 1981; John *et al.*, 1985).

The Iberian endemic *P. ignatii* also has large paracentromeric heterochromatic regions but lacks distal heterochromatin suggesting a close evolutionary relationship with the *P. pedestris* Pyrenean race. However, all the proximal bands show only GC base pair richness, not the double AT and GC banding of the Pyrenean race. The large size of the Pyrenean and Iberian paracentromeric blocks may therefore be due to some concerted amplification mechanism operating on different sequences in the two forms to give a similar gross appearance. The evolutionary link between the Alpine and these other two forms is difficult to envisage, but we are reminded of the similar concerted rearrangements in the Australian grasshopper *Caledia captiva* (Shaw *et al.*, 1985).

General proximal GC rich heterochromatin seems to characterise the genus. In these most Western forms, DNA sequences in this position show a tendency for self amplification. This may include AT as well as GC rich sectors as in Pyrenean *P. pedestris*. However, the lack, of data from the Eastern *Podisma* makes it difficult to infer the ancestral distribution and composition of the heterochromatin. A similar study on the populations of Eastern Europe could throw new light on these remarkable features.

The X chromosome seems to be specially involved in the differentiation of races and species of this genus. There is a main NOR placed on a distal position on this chromosome, both in the Alpine races of *P. pedestris* and in the *P. ignatii* Iberian endemic. However, in the Pyrenean individuals, the ribosomal cistrons occupy a proximal position; there is no terminal heterochromatin, and the pericentromeric band seems larger than the equivalent one on the X-chromosome of the other taxa.

It is not known if this different NOR position in *P. pedestris* is the result of a major chromosomal inversion, or if the repositioning consists of a simple terminal deletion and dosage compensation by amplification of cryptic ribosomal sequences placed close to the X centromere. The existence of such cryptic sequences could account for the paracentromeric NOR activity detected in both Pyrenean and NeoXY populations which are geographically isolated.

The first inversion hypothesis could involve a fragile site close to the centromere, suggested by the autosomal fusion of the X in the Alpine NeoXY *P. pedestris* race. However, the existence of a Pyrenean population of *P. pedestris* in Valle de Arán, where some individuals show absence of nucleolar activity on the X chromosome (Gosálvez *et al.*, 1988b) cautions against such simple conclusions, and is a further demonstration of the lability of the X chromosome relative to the autosomes.

The X may be prone to change for many reasons: advantageous recessive mutants are expressed in males (Charlesworth *et al.*, 1987) and the dynamics of other types of allele are also affected by the hemizigous condition of the X in males (Rice, 1984). Additionally, the lower effective population size of the X may lead to rapid change (Avery, 1984). These and other reasons have been advanced to account for the major role of the X in reproductive isolation (*e.g.* Coyne and Charlesworth, 1986). Changes in the X could have repercussions throughout the genome, including karyotypic change.

Finally, there are no obvious genetic, morphologic or ecologic differences among the *Podisma* taxa. For this reason, the employment of new molecular techniques, such as chromosomal «in situ» hybridization or mitochondrial DNA analysis, may be the key to understanding chromosomal differentiation, racial and interspecific divergence and the patterns of evolution followed by *Podisma*.

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Supernumerary heterochromatic segments adjust recombination: effects on populations

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ABSTRACT

The presence of supernumerary heterochromatic segments has been described in different plant and animal species. Polymorphic systems due to the presence of supernumerary segments are widely represented among orthopteroid insects. In most cases where different karyomorphs within the same population have been compared, the variation in the heterochomatic content is closely associated with an altered chiasma distribution.

An example of this correlation is described for a monochiasmate bivalent of two species of grasshoppers: *Arcyptera fusca* and *Arcyptera tornosi*. Our results suggest that the standard pattern of chiasma distribution is dramatically altered by the structural heterozygosity of the bivalents rather than by the presence of heterochromatic segments themselves.

In this paper we discuss the validity of a model developed to assess the role of genetical recombination in natural populations and the evolutionary implications of these polymorphic systems.

Key words: polymorphism, supernumerary segments, chiasma distribution.

CHROMOSOME POLYMORPHISM INVOLVING SUPERNUMERARY SEGMENTS

The term *polymorphism* describes a situation in which «distinct karyomorphs differing in respect of the structure, number, or heterochromatic content of their chromosomes coexist within individual populations of a given species» (John, 1983).

In eukaryotes, and particularly in Orthoptera, the most common polymorphisms involve a spontaneous amplification of particular chromosome regions resulting in formation of supernumerary segments (John, 1983). Almost all of these segments consist of constitutive heterochromatin and are either pericentromeric or terminal in location within the chromosome (John, 1983). These segments, at least in grasshoppers, are usually associated with the smallest members within a chromosome complement (Hewitt, 1979).

Some populations are polymorphic for either the presence or size of supernumerary segments. Within such populations, one may find individuals that are homozygous for the absence of the segment (bb), heterozygous (bh) or homozygous for the presence of the segment (hh). In addition, if the segments vary in size, they may be heterozygous for the size of the segment (Hh).

Figure 1.—C-banded Anaphase-I showing the heterochromatic content of *Arcyptera fusca*.

In most analyzed cases, the karyomorph frequencies usually fit a Hardy-Weinberg ratio (Hewitt, 1979).

EFFECTS ON CHIASMATA ASSOCIATED WITH SUPERNUMERARY SEGMENTS AS EXEMPLIFIED BY *ARCYPTERA FUSCA* AND *ARCYPTERA TORNOSI*

Little is known about the heterochromatic nature of supernumerary segments and even less about their role in cellular physiology or chromosome structure and behavior. Nevertheless, a correlation has been reported between their presence in the genome of some organisms and modification of chiasma formation. This takes various forms. There may be a change in the basic pattern of chiasma distribution (John, 1981; García-Lafuente *et. al.*, 1983; Camacho *et. al.*, 1984; John and King, 1985; Navas-Castillo *et al.*, 1985; de la Torre *et. al.*, 1986; Cano, 1988), in mean cell chiasma frequency (John and Hewitt, 1966; Camacho *et. al.*, 1984), or between cell variance (Shaw, 1971 a, b). This means, as claimed by John (1981), that «there are grounds for arguing that one of the functions of the heterochromatin variations to be found in natural populations is the regulation of recombination and, through this, the regulation of the variation present within and between populations».

Arcyptera fusca and *Arcyptera tornosi* are two species of grasshopper where the correlation has been found. Both have a similar karyotype consisting of eleven pairs of autosomes (two long, six medium, and three small pairs) with an XO/XX sex chromosome system. The heterochromatic content of both chromosome complements as well as the associated polymorphic systems is encountered elsewhere (Gosálvez *et. al.*, 1981; de la Torre *et. al.*, 1986; see Fig. 1). Our interest is focused on the polymorphism of the distal supernumerary segments

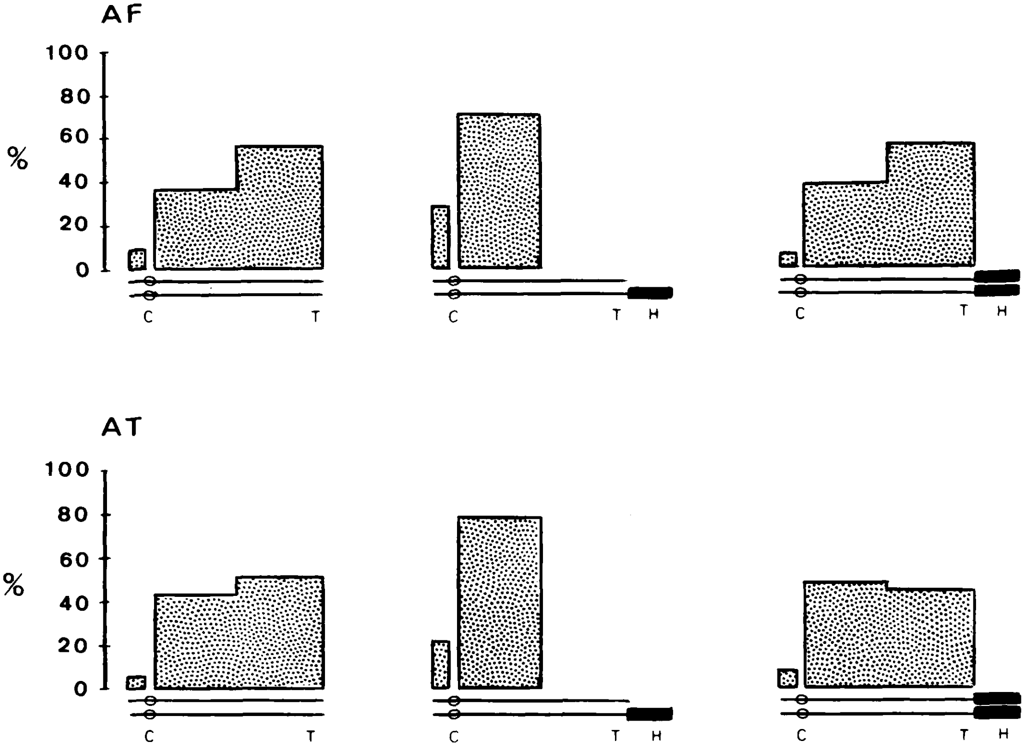

Figure 2.—Chiasma distribution in the S11 bivalents. AF represents the distribution of *Arcyptera fusca* according to the three karyomorphs. AT represents the distribution of *Arcyptera tornosi* according to the three karyomorphs.

associated with the smallest chromosome pair (S11), which has only one chiasma in both species. The supernumerary segments on this pair are positively C-banded and occur in the three different karyomorphs: bb (without heterochromatic segments), bh (with one heterochromatic segment), and hh (with two heterochromatic segments).

In all analyzed populations of *A. fusca* and *A. tornosi,* the observed frequencies of each karyomorph (genotypic frequencies) fit a Hardy-Weinberg ratio. When the frequencies for each chromosome kind (with and without supernumerary segment; *i.e.*, genic frequencies) were compared, significant differences were not found between populations. This applies both to *A. fusca* and *A. tornosi* (Tables 1 and 2).

The effect of supernumerary segments on the pattern of recombination in the S11 bivalent was ascertained by analyzing chiasma distribution in C-banded diplotene cells from male individuals with different combinations of supernumerary segments (bb, bh, and hh). Three different categories of chiasmata were scored in each: i) chiasmata placed in a short arm beyond the centromere, ii) proximal chiasmata, *i.e.*, near the centromere but placed in the long arm, iii) distal chiasmata, *i.e.*, near the telomere of the long arm.

No difference in the pattern of chiasma distribution was found in the species when individuals with the same karyomorph were compared. Therefore, the results can be aggregated to obtain a characteristic karyomorph pattern (Fig. 2). When comparing different karyomorphs, significant differences in the pattern of chiasma distribution were found in the structural heterozygotes (bh) vs. homozygotes (bb, hh) of both species (Table 3). In the heterozygous bi-

Table 1.—Distribution of the S11 karyomorphs (observed and expected) in the analyzed populations of *Arcyptera fusca*. The expected frequencies are calculated from the observed genic frequencies in the global population. Note the Hardy-Weinberg equilibrium.

Population	Number of Individuals	Observed					Expected		
		bb	bh	hh	p(b)	q(h)	bb	bh	hh
AF-I-80	16	10	5	1	0.78	0.22	11.43	4.19	0.38
AF-II-80	18	12	5	1	0.81	0.19	12.86	4.71	0.43
AF-III-80	25	18	7	0	0.86	0.14	17.85	6.55	0.60
AF-IV-80	17	14	3	0	0.91	0.08	12.14	4.45	0.41
AF-V-80	7	5	2	0	0.86	0.14	5.00	1.83	0.17
AF-VI-80	14	9	5	0	0.82	0.18	10.00	3.67	0.34
AF-VIII-80	27	22	5	0	0.91	0.09	19.28	7.07	0.65
AF-IX-80	10	8	2	0	0.90	0.10	7.14	2.62	0.24
AF-X-80	20	11	7	2	0.72	0.27	14.28	5.24	0.48
AF-XI-80	6	4	2	0	0.83	0.17	4.29	1.57	0.14
AF-XII-80	6	2	3	1	0.58	0.42	4.29	1.57	0.14
AF-XIX-80	14	7	7	0	0.75	0.25	10.00	3.67	0.34
AF-XX-82	17	13	4	0	0.88	0.12	12.14	4.45	0.41
AF-PLCH-82	15	11	3	1	0.83	0.17	10.71	3.93	0.36
AF-AG-82	14	11	3	0	0.89	0.11	10.00	3.67	0.34
AF-SG-82	7	3	3	1	0.64	0.36	5.00	1.83	0.17
AF-MP-82	9	9	0	0	1.00	0.00	6.43	2.36	0.22
AF-ALPES-I	26	23	3	0	0.94	0.06	18.57	6.81	0.62
Total	268	192	69	7	0.85	0.15			

$X^2 = 40.96$, N.S. $0.1922 < p < 0.1944$

Table 2.—Distribution of the S11 Karyomorphs (observed and expected) in the analyzed populations of *Arcyptera tornosi*. The expected frequencies are calculated from the observed genic frequencies in the global population. Note the Hardy-Weinberg equilibrium.

Population	Number of Individuals	Observed					Expected		
		bb	bh	hh	p(b)	q(h)	bb	bh	hh
AT-CP-81	16	11	4	1	0.81	0.19	9.16	5.89	0.95
AT-LH-82	9	5	4	0	0.78	0.22	5.15	3.31	0.53
AT-II-82	8	2	4	2	0.50	0.50	4.58	2.95	0.47
AT-III-82	13	10	3	0	0.88	0.12	7.44	4.79	0.77
AT-HE-82	14	8	6	0	0.79	0.21	8.01	6.16	0.83
AT-C-82	9	7	1	1	0.83	0.17	5.15	3.31	0.53
AT-SPII-81	15	10	5	0	0.83	0.17	8.59	5.52	0.89
AT-SPI-82	29	12	14	3	0.65	0.35	16.60	10.68	1.72
Total	113	65	41	7	0.76	0.24			

$X^2 = 18.85$, N.S., $p - 0.17$

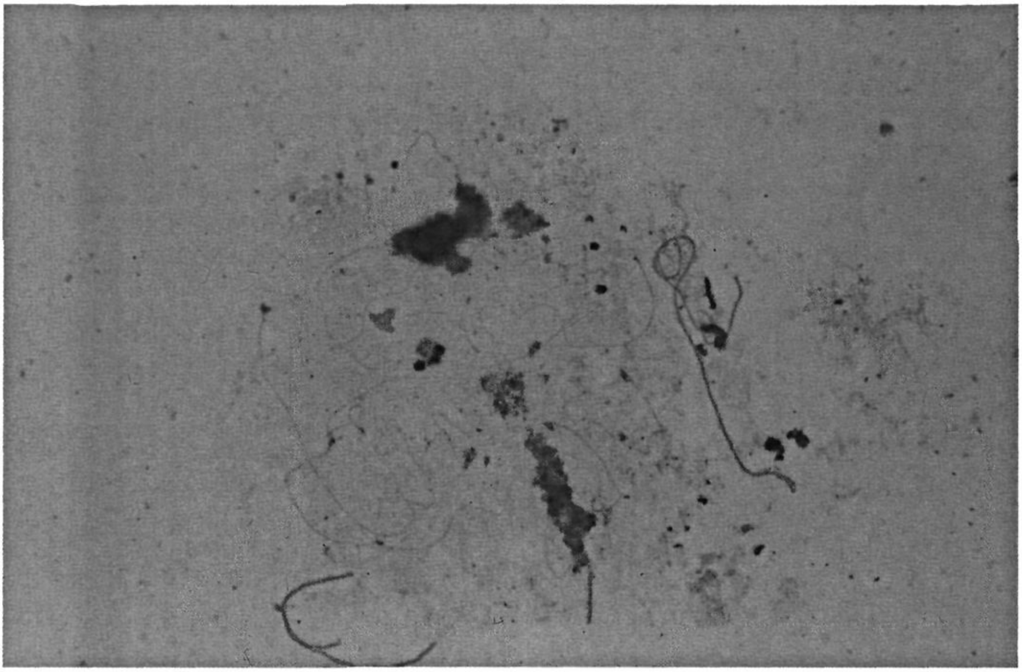

Figure 3.—Light micrographs of silver-stained pachytene SC surface spreads of *Arcyptera tornosi*. The chromosome pairing seems not affected by the presence of supernumerary segments in a heterozygous condition.

valents, no chiasmata were found in the distal region and an appreciable increase in proximal chiasma frequency was observed. However, there was no difference between the two homozygous forms (bb×hh) (Table 4). The observed differences in the pattern of chiasma distribution were not paralleled by an altered pattern of pairing in the heterozygous bivalents (Fig. 3).

In summary, from the above-described results, we conclude that: i) supernumerary segments in a homozygous condition do not modify the pattern of chiasma distribution characteristic of the basic homozygous S11 bivalent; and ii) supernumerary segments in a heterozygous condition readjust chiasma distribution, preventing chiasma formation in a large region next to the telomere (distal chromosome region).

The observed disturbances in the pattern of chiasma distribution associated with the presence of supernumerary segments could give rise to differences in the frequency of distinct recombinant gametes among different populations. Since the effect of each karyomorph is proved to be the same in all populations (*i.e.*, the supernumerary segment provokes an identical effect irrespective of the population), the expected differences would depend on the frequency of the supernumerary segment in each population. In any case, the greatest differences are predicted between populations with intermediate frequencies of supernumerary segment ($q = 0.5$) and fixed populations ($q = 1$ or 0). This reflects the differences in chiasma distribution between homozygotes and heterozygotes.

EVOLUTIONARY PERSPECTIVES: ORIGIN AND MAINTENANCE OF POLYMORPHIC SYSTEMS FOR SUPERNUMERARY SEGMENTS

Chromatin is said to be supernumerary when the organism can apparently develop normally in its absence (John, 1983). It is

Table 3.—Comparison of the chiasma distribution among the three different karyomorphs. Significant differences are observed in both *Arcyptera fusca* and *Arcyptera tornosi.*

Arcyptera fusca

Karyomorphs	Chiasmata Position			Total
	Short Arms	Proximal	Distal	
B. Homozygous (bb)	90 (147.15) 22.20	387 (491.01) 22.03	605 (443.94) 58.43	1082
Heterozygous (bh)	129 (60.79) 76.53	318 (202.85) 65.37	0 (183.40) 183.40	447
S. Homozygous (hh)	9 (20.13) 6.15	56 (67.16) 1.86	83 (60.72) 8.17	148
Total	228	761	688	1677

X^2= 444.14, S.; $p<0.01$

Arcyptera tornosi

Karyomorphs	Chiasmata Position			Total
	Short Arms	Proximal	Distal	
B. Homozygous (bb)	31 (66.99) 19.34	235 (309.21) 17.81	276 (165.85) 73.15	542
Heterozygous (bh)	90 (49.69) 32.71	312 (229.34) 29.79	0 (123.01) 123.01	402
S. Homozygous (hh)	7 (11.37) 1.68	44 (52.49) 1.37	41 (28.15) 5.86	92
Total	128	591	317	1036

X^2= 304.73, S.; $p<0.01$

Table 4.—Comparison between the chiasma distribution of both homozygous karyomorphs. No significant differences are observed in both Arcyptera fusca and Acryptera tornosi.

Arcyptera fusca

Karyomorphs	Chiasmata Position			Total
	Short Arms	Proximal	Distal	
B. Homozygous (bb)	90 (86.56) 0.14	387 (389.52) 0.02	605 (605.92) 0.00	1082
S. Homozygous (hh)	9 (11.84) 0.68	56 (53.28) 0.14	83 (82.88) 0.00	148
Total	99	443	688	1230

X^2=0.98, N.S., $o.5 < p < 0.7$

Arcyptera tornosi

Karyomorphs	Chiasmata Position			Total
	Short Arms	Proximal	Distal	
B. Homozygous (bb)	31 (32.52) 0.07	235 (238.48) 0.05	276 (271.00) 0.09	542
S. Homozygous (hh)	7 (5.52) 0.40	44 (40.48) 0.31	41 (46.00) 0.54	92
Total	38	279	317	634

X^2= 1.46, N.S., $0.3 < p < 0.05$

usually heterochromatic and occurs polymorphically in populations. Both characteristics suggest that it lacks function in the cell. But to say this leaves unanswered questions. How does it arise?, How are the polymorphisms maintained in nature, and why do they usually occur in a Hardy-Weinberg ratio?

Aside from the nature of the mutational events that give rise to supernumerary chromatin, let us consider what happens to a novel chromosome type with a supernumerary segment at its initial, very low frequency in the population. The most likely outcome is its loss. However, in a large number of species, such types occur at a stable frequency far higher than can be maintained by mutation. The stability and uniformity of polymorphism in *A. fusca* and *A. tornosi* argue against the supernumerary segments being inert and, hence, at the mercy of random events. It implies the possibility of some kind of positive selection.

One alternative awaiting validation is that the supernumerary segment presents certain adaptive advantages. However, this would eventually lead to fixation unless counterbalanced. What type of selection, compatible with our knowledge of the nature and effect of supernumerary heterochromatin could lead to the observed polymorphism?

In our opinion, the most plausible mechanism is one involving selection through the effect of supernumerary segments on recombination between genes lying on the adjacent distal chromosome region. By suppressing chiasma formation in this region, it would permit a number of coadapted genes to occur in the heterozygous state without subsequent disruption by recombination (Darlington and Mather's «supergenes», 1949). Crossing over and gene recombination would break them up. Thus, supernumerary segments would acquire selective advantage if they arise in chromosomes carrying valuable gene complexes. They could be merely one of the several genetic mechanisms which suppress recombination between coadapted gene complexes. The same argument has been postulated to explain the origin and maintenance of inversion polymorphisms in *Drosophila* and certain other organisms (Dobzhansky, 1951; Ford, 1965).

When the novel chromosome reaches a certain frequency in the population, structural homozygotes could appear. Two situations have been described with respect to chiasma distribution in structural homozygotes:

(a) Structural homozygotes could present a similar chiasma distribution to that shown by heterozygotes by suppression of recombination in the distal chromosome region (John, 1981).

(b) Structural homozygotes could present a chiasma distribution similar to that shown by basic homozygotes by a high frequency of chiasmata in the distal chromosome region *(A. fusca* and *A. tornosi).*

In both cases polymorphisms are generated, but their characteristics are different and their possibilities of stabilization and evolution are predictably different.

In the first case, the block of genes near the heterochromatin remains linked both in heterozygotes and structural homozygotes. Consequently, a hypothetical advantage would be preserved, but evolution would be slow depending on newly arisen infrequent mutational events.

The second case, which includes the polymorphic system discussed in this paper, is similar to inversion polymorphisms. Homozygous individuals experience a free recombination in the distal chromosome region, which would favor establishment of polymorphisms with local adaptations. Each locality would then be an outcome of a historic process of adaptation to the environment.

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Extra heterochromatin in acridoid grasshoppers

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ABSTRACT

Extra heterochromatin is found in two forms in the complements of acridoid grasshoppers. First, there are added free elements (B-chromosomes) and, second there are blocks of heterochromatin added to one or several pairs (heterochromatic segments). Both kinds of heterochromatin are major sources of chromosome change within grasshoppers and may be defined by two main characteristics. First, they are heterochromatic, which means they appear highly condensed during the whole cell cycle. Second, they are supernumerary since they represent extra material that is clearly dispensable to the organism itself in the sense that it can develop normally in its absence. Cytogenetic studies have provided extensive information on their incidence in natural populations, their rate of transmission, their effects on some nucleotypic characteristics, and their structural organization. However, the origin and possible biological roles of both kinds of chromosome mutation are still a mystery.

Key words: heterochromatin, chromosome polymorphisms, acridoid cytogenetics.

B-CHROMOSOMES: THE LONE RANGERS

B-chromosomes are additional elements of the standard chromosome complement that are not homologous with any other regular chromosome. They have no effect on the viability of the individual bearing them. They are supposed to be derived from some standard member of a karyotype so in their evolution any former homology has been lost (Jones and Rees, 1982). Extensive variation in size and morphology has been found in different acridoid species. An extreme case is that of the grasshopper *Eyprepocnemis plorans* (Charpentier) where up to 26 different types of B-chromosomes have been described (Henriques-Gil *et al.*, 1984). Most are derived from translocations, deletions or misdivisions. Upon application of C-banding technique (which reveals most of the constitutive heterochromatin), most B's show a homogeneous dark staining, although clear-cut differentiation in the form of complex banding patterns has been reported (Webb and Neuhaus, 1979).

One of the most striking features of B-chromosomes is their non-Mendelian modes of inheritance. This is commonly expressed in an accumulation process rather than in their elimination. B's usually exhibit non-disjunction during pre-meiotic mitosis and both meiotic divisions (Jones, 1985). This leads to the production of gametes that may contain a greater number of B's than the individual inherited. It is particularly important in the oocytes, where meiotic drive has been described (Hewitt, 1976; Cano and Santos, 1989).

However, whatever the number of B's, strict correlations with any qualitative exophenotypic effect in the affected individuals have rarely been described. This is also true for the commonly studied nucleotypic effects on the frequency and distribution of chiasmata and on the rate of abnormal spermatids where there is conflicting evidence in published results. Thus, B's may or may not affect chiasmata frequency (John, 1983), and their influence on increasing the number of abnormal spermatids is generally negligible, except in particular cases (Suja *et al.*, 1989).

These discrepancies make it difficult to ascribe a biological role for these mysterious extra elements and to explain their widespread presence in natural populations of grasshoppers. At present, most authors consider them to be parasitic or selfish elements (Östergren, 1945; Werren *et al.*, 1988). This means that their existence in natural populations depends upon a balance between the transmission rate and the reduced fertility or vigour of the carrier individuals. However, the significance of B-chromosome systems that have no accumulation mechanism is still under debate (Jones, 1985).

The origin of B's is one of the major questions not yet answered. Two main mechanisms have been hypothesized: they may derive from aneuploidy events, or they may appear as a consequence of chromosome rearrangements (White, 1973).

Whatever the mechanism, B's are supposed to undergo important changes in structure through rapid evolution. This inevitably leads to the disappearance of any former homology with the standard chromosomes and also to the genetic inactivation of the potential B, probably through a heterochromatinization process.

Although no significant molecular differences between a B-chromosome and the standard chromosomes have been reported (Dover and Henderson, 1976), the chromosome structure may be greatly altered. Such changes may impede the recognition of any former structural homology with the members of the standard complement when studied by means of most banding techniques used for chromosome differentiation. In fact, B's usually show exclusive banding patterns and even the most selective techniques also seem to be inappropriate to determine which was their source. For instance, after digesting chromosomes *in situ* with a great variety of restriction enzymes, B's show specific patterns that are not exhibited by either the X chromosome or the autosomes (J. Gosálvez, personal communication).

SUPERNUMERARY SEGMENTS: THE CROSS TO BEAR

Supernumerary segments are additional blocks of heterochromatin found in one or several chromosomes of a given complement. They vary strongly in size and position. In most cases they occur in a distal position close to the telomeres but they may occupy proximal, or interstitial regions within a chromosome.

Natural populations of several species of grasshoppers have been shown to possess this type of chromosome variation (Hewitt, 1979; John, 1983; Navas-Castillo *et al.*, 1986; Rufas *et al.*, 1986). In some cases they produce a complex polymorphic system due to the existence of different blocks in different chromosomes (John and King, 1983; García de la Vega *et al.*, 1986; Navas-Castillo *et al.*, 1987).

Supernumerary segments usually appear dark-stained after C-banding, thus demonstrating their heterochromatic nature. However, exceptions have been reported (see references in Camacho *et al.*, 1984).

Supernumerary segments have proved to be homogeneous in their effect on chiasma distribution within the affected bivalent (see Torre *et al.*, this volume). Particularly, in heterozygous individuals (*i.e.*, those with a heterochromatic segment in only one of the two homologues) the pattern of chiasma distribution is dramatically changed so that the chromosome region proximal of the block is almost devoid of recombination. This change is by itself an attractive evidence to learn about their biological role since one of the outcomes of such a change could be the promotion of a supergene in the proximity of the block (Torre *et al.*, 1987).

Current theory considers the origin of supernumerary segments to be found in a mechanism of unequal crossing-over although some authors have also pointed out that chromosome interchanges, particularly from pre-existing B-chromosomes, may also explain their appearance (White, 1973), or that some represent relics of euchromatic regions lost during chromosome evolution (Camacho and Cabrero, 1987).

Unequal crossing-over is the classical mechanism proposed to explain the origin of gene duplication. Recently, Rufas *et al.* (1988) suggested that in some cases unequal crossing-over may be observed in cytological preparations. This is explained by the peculiarities of the silver impregnation technique used for differentially staining chromosomes that reveals a chromatid core all along the chromatids. It has been suggested that this structure is an important element in chromosome organization during mitosis and meiosis (Rufas *et al.*, 1988). Silver staining also provides a reliable method to confidently analyze the position and number of chiasmata. This analysis has shown that certain kinds of heterochromatin (supernumerary segments) are involved in recombination events, and that unequal crossing-over occurs in both heterozygotes and homozygotes of a particular supernumerary segment (J. S. Rufas, personal communication).

This result indicates how supernumerary segments may undergo major decreases and increases in size from generation to generation. This, in turn, provides a simple, reliable explanation for the existence of certain complex systems of supernumerary segments in which one can find blocks of different size affecting the same chromosome pair. It also poses a question regarding the fate of supernumerary segments in populations: if supernumerary segments can evolve so rapidly and undergo important increases in size from generation to generation, is there a critical size of segment that, once exceeded, would impede normal development of the affected individual?

B-CHROMOSOMES AND SUPERNUMERARY SEGMENTS: THE INTEGRATION OF SUBVERSIVE ELEMENTS

Since B's and supernumerary segments are both dispensable and mainly heterochromatic, and because they are widespread among natural populations of grasshoppers, it is tempting to look for a link between both types of extra heterochromatin.

In fact, Ruiz-Rejón *et al.* (1987) have suggested that B's may undergo their integration into the standard complement and behave like supernumerary segments. This proposal is supported by experimental results obtained by, Henriques-Gil *et al.* (1983) in which B's of *Eyprepocnemis plorans* may be involved in chromosome interchange with both the X chromosome and the autosomes. In maize, similar chromosome rearrangements have contributed to the identification of the control elements within the B's that may be involved in their non-Mendelian transmission (see references in Jones, 1985). Such observations suggest a parallel behaviour of B's to that of the genetic mobile elements (transposons) that are able to integrate into host genomes.

Despite the fact that supernumerary segments could also originate through chromosome translocations of B's and standard chromosomes, the structural characteristics of both kinds of extra heterochromatin have made it difficult to establish any relationship between naturally occurring B's and supernumerary segments.

While supernumerary segments prove rather homogeneous in their staining characteristics when treated with different banding procedures (Camacho *et al.*, 1984; López-Fernández *et al.*, 1988), B's may show clear-cut differentiation all along their length and include bands absent from other members of the karyotype (Webb and Neuhaus, 1979; J. Gosálvez, personal communication).

The hypothetical integration of B's suggests that these extra elements may exist in independent (supernumerary chromosomes) or dependent (supernumerary segments) forms (Ruiz-Rejón *et al.*, 1987).

Supernumerary segments may be considered to be symbiotic with their host chromosomes in some way, while most B's are now considered parasitic. Supernumerary segments are not free elements, and their transmission depends on the chromosome that they have invaded. It is noteworthy that the molecular characteristics of the segments that colonize different autosomes in *Atractomorpha similis* (Bolívar) are identical (John *et al.*, 1986).

Supernumerary segments may increase their presence in populations through a heterotic effect because of selection of neighbouring genes among which recombination is commonly absent (Torre *et al.*, 1987; see also Torre *et al.*, this volume). This effect seems to stem from the impairment of the pairing of homologues at meiosis, or from the defective timing of such pairing, leading to the absence of the «recombination machinery» from those regions. In fact, Moens (1987) has shown correct pairing in a heterozygote bivalent of *Chloealtis conspersa* (Harris) containing a large distal heterochromatic block (see Fig. 8a, b, in Moens, 1987).

Accordingly, supernumerary segments should be of a size large enough to promote such effects (Rufas *et al.*, 1986; Navas-Castillo *et al.*, 1987). Those blocks that are small (*e. g.*, the distal heterochromatic bands found in many species) may not disrupt the pairing process, while those blocks that are too large may interfere with the normal process of chromosome replication or segregation and, hence, could be selected against.

If B's do indeed evolve into supernumerary segments, their size when integrating into a host chromosome could be a discriminatory characteristic for their stabilization in populations.

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Gene flow and the distribution of karyotypes in the alpine grasshopper *Podisma pedestris* (L.) (Orthoptera: Acrididae)

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ABSTRACT

Collections of the alpine grasshopper *Podisma pedestris* (L.) were made from a 600 m by 1200 m area adjacent to a chromosomal hybrid zone in the Alpes Maritimes. Throughout the area there was a low frequency of grasshoppers carrying a fused chromosome originating from the opposite side of the zone. The frequency did not follow the expected sigmoidal relationship with distance from the zone. Instead, the highest frequencies were found most distant from the zone. Changes in genetic architecture and in population structure are considered as possible explanations for this unusual distribution of karyotypes. A comparison for Gst at allozyme loci, and the fusion suggests that the fusion is negatively heterotic as it is in the zone. The unusually high frequency of the fusion is found in an area where the populations are sparse and subdivided. These are conditions in which low effective population size could facilitate genetic introgression across the hybrid zone.

Key words: *Podisma pedestris,* tension zone, shifting balance, effective population size, genetic introgression.

INTRODUCTION

Many species are divided by hybrid zones, defined as "narrow regions in which genetically distinct populations meet, mate, and produce hybrids" (Barton and Hewitt, 1985). Detailed surveys often reveal several zones that subdivide a single species (*e.g., Heliconius* butterflies, Turner, 1971; morabine grasshoppers, White *et al.*, 1967, Mrongovius, 1979; common shrews, Searle and Wilkinson, 1987). These zones may be greatly outnumbered by those that escape detection.

Our present concern is the hybrid zone in *Podisma pedestris.* It has been extensively studied for over 10 years (Hewitt and John, 1972; Hewitt, 1975; Barton and Hewitt, 1981; Nichols and Hewitt, 1988). It runs along the major ridge of the Alpes Maritimes in southern France. The race distributed to the south of the ridge bears an X chromosome which may have been derived from a Robertsonian fusion between the ancestral X and an autosome (Westerman and Hewitt, 1985; Bella *et al.* this volume). The zone runs where the 2 races would have met as their ranges expanded after the last ice age (Hewitt, 1975). This zone, as with most documented examples, appears to be maintained by selection against hybrids counteracting the gene flow between the two races (Barton and Hewitt, 1985; Hewitt, 1988). Key (1968) used the term "tension zones" to identify these phenomena. Tension zones can move from place to place until they become trapped in a position where the effects of gene flux from either side are balanced. This will often be in a region of low density, flanked on either side by denser populations (Hewitt, 1975). The tension zone in *Podisma pedestris* runs through regions of low population density for most of its length (Barton and Hewitt, 1981; Nichols and Hewitt, 1986), and there is evidence of the effect in several other tension zones (Table 1, Hewitt, 1986).

Very shallow density gradients (1/zone width) are sufficient to prevent the zone escaping from density traps, even if one homozygote has a selective advantage (Barton, 1979;, Hewitt and Barton, 1980). For this reason it was intriguing to discover that in certain marginal populations close to the western end of the zone, the chromosomal fusion appeared to have crossed a density trap, penetrating over 1 km into the range of the other race (Nichols and Hewitt, 1988). This preliminary evidence was from only three populations, and the frequencies of the fused chromosome were low (<0.01). Here we report on a more detailed mapping of genotypes in the area. Collections were made around the three populations to discover the frequency of the fused chromosome and the extent of its introgression. This information can be used to assess explanations for the origin and maintenance of the fusion away from the zone. The population structure might affect the extent of introgression by the fused chromosome (Nichols, 1989). For this reason allozyme frequencies were scored together with karyotype. The frequencies can then be used to characterize population structure (Slatkin and Barton, 1989), and to make comparisons between regions with different levels of introgression.

METHODS AND RESULTS

In August 1986 samples of grasshoppers were collected at intervals of 100 m in a 600 by 1200 m transect between the ski lodge at Chabanon and the hybrid zone to the South (Fig. 1). Each sample consisted of up to 12 males from a 20 m radius. The grasshoppers were dissected within a day of capture, and the testes fixed in 3:1 ethanol and ethanoic acid. After dissection, the bodies were initially stored in the field at -30°C, and subsequently transported back to the laboratory and kept at -70°C.

The karyotype was studied by examination of squashed preparations of testes stained with diproprionic orcein. The bodies were scored for the presence of 25 alleles at the seven polymorphic allozyme loci identified by Halliday *et al.* (1986) using cel-

Table 1.—A GLM to assess the direction and shape of the geographic change in the frequency of the chromosomal fusion.

Comparison A: a 2-dimensional multinomial ($x+x^2+y+y^2$) accounts for a significant proportion of the residual deviance.

Comparison B: there is no significant geographic variation in an east-west direction. Once the north-south trend is fitted, the residual deviance is not significantly greater than expected for a binomial variate (Chi^2 approximation $0.5<p<0.1$).

Comparison C: the north-south trend is significantly curvilinear.

Model⁺	Residual Deviance	df	Mean Change	df
A) $x + x^2 + y + y^2$	68.50	80	38.28	4 $p < 0.001$
B) $- x - x^2$	69.42	82	0.93	2 notsig.
C) $- y^2$	88.74	63	19.32	1 $p < 0.001$

+: x and y are the coordinates of a sample on the 100m grid from the northeastern corner of the transect (y:N-S; x:E-W).

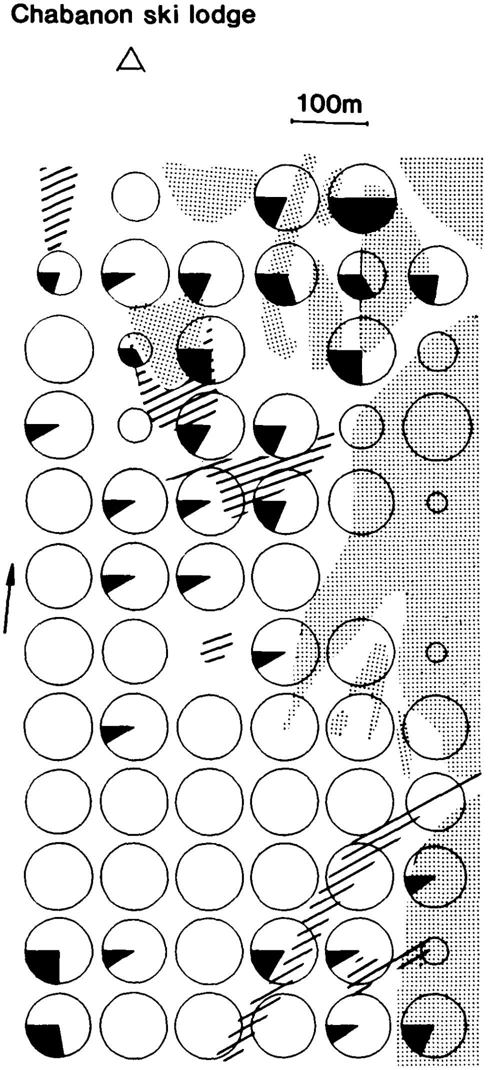

Figure 1. Map of karyotype distribution adjacent to the *Podisma* tension zone near Seyne Les Alpes, France. The area of the pie charts is proportional to sample size (maximum 12), and the dark sector is proportional to the frequency of the fused chromosomes. The wooded areas are represented by stippling and scree slopes by shading.

lulose acetate membrane electrophoresis (two amylase loci, two esterase loci, mallic enzyme, two phosphoglucomutase loci).

Figure 1 is a map of the distribution of karyotype frequencies. The frequency of the fused chromosome is highest in two areas: the southern end of the transect close to the hybrid zone, and the northeastern corner. The frequency appears to be lower in the centre. This trend is confirmed by an analysis of deviance (Table 1), which indicates that north-south change in karyotype frequency is significantly curvilinear ($p<0.001$). Elsewhere the karyotype frequency has been found to follow the sigmoid tanh curve predicted by a diffusion equation model (*e.g.*, Barton and Hewitt, 1981).

The variation in karyotype frequency among populations can be quantified using Nei's Gst (Nei and Chesser, 1983). The Gst value for the fusion (0.0664) is significantly greater than the combined value of all other loci (Table 2A). This greater variation in fusion frequency is not restricted to the proximity of the zone. It is found even when the 12 most southern populations are excluded (Table 2B). The northeastern area with the unexpectedly high fusion frequency is subdivided by bands of trees and scree slopes (Fig. 1), which are apparent barriers to grasshopper dispersal. However, the frequency variation at loci other than the chromosomal fusion, proves almost identical to that in the open area (Table 2C).

DISCUSSION

Based on preliminary studies, Nichols and Hewitt (1986) deduced that there is greater introgression of the chromosomal fusion across the hybrid zone in the marginal *Podisma* populations near Chabanon ski lodge. The present more detailed survey confirms that the introgression is over 1,500 m rather than the 400 m found elsewhere. Furthermore, the shape of the chromosomal cline is not a typical tanh curve. The frequency of the fusion rises significantly in the collections farthermost from the zone.

Why has the chromosomal fusion not been eliminated from the northeastern section of the surveyed area? Selection against heterozygotes should gradually eliminate it here because its frequency is less than 0.5, and so it will occur predominantly in hete-

Table 2.—Comparisons of Nei's Gst to determine if the frequency of the fusion is more variable than other alleles and if variation is greater in specific locations.

A) Over the whole transect, Gst for the fusion is significantly greater than Gst for the other loci ($p<0.001$)

Locus	Area+	Gst	Standard Error*
fusion	whole transect	0.0664	
otherloci	whole transect	0.0138	0.0037

B) Gst for the fusion in the area away from the zone is also significantly greater for the fusion ($p<0.001$)

Locus	Area+	Gst	Standard Error*
fusion	x = 1-6,y = 1-10	0.0820	
other loci	x = 1-6,y = 1-10	0.0168	0.0032

C) Gst for the allozyme loci is not significantly higher in the subdivided area (i) than in the central open area (ii)

Locus	Area +	Gst	Standard Error*
other loci	i) x = 1-4,y = 1-6	0.0071	0.0093
other loci	ii) x = 1-6,y = 7-10	0.0068	0.0065

+: x and y are the coordinates on the 100 m grid from the NE corner *: The standard error is calculated by jackknifing over loci

rozygotes. One possibility is that there is no selection against heterozygotes in this region. The selected loci could have been stripped from around the fusion by recombination with the unfused X, or the fusion could have a different origin from those which incur heterozygote disadvantage. However, the gene frequency variation argues against this explanation because the Gst is higher for the fusion than for the other loci, which is expected of a locus with selection against heterozygotes.

Heterozygote disadvantage tends to lead to fixation of one allele or the other. Like other modes of divergent selection it increases the variation among populations and, hence, inflates Gst. For most other types of selection, and for neutral loci, the expected value is a simple function of migration rate:

$$Gst \approx 1/(1+4Nm)$$

where Nm is the average number of migrants per deme.

This relationship can be derived from a range of population models, and appears to be quite robust (Slatkin and Barton, 1989). As the chromosomal fusion and allozyme loci were scored in the same individuals, they shared the same population structure including migration rate. The fusion's larger Gst value is, therefore, explicable by selection against the chromosomal heterozygotes.

Another potential explanation for the unusual karyotype distribution involves the effective population size (Ne). Nichols (1989) studied the effect of low Ne on the mixing of alleles in computer simulations. Figures 2 and 3 represent his results after 2,500 generations of introgression in a two-

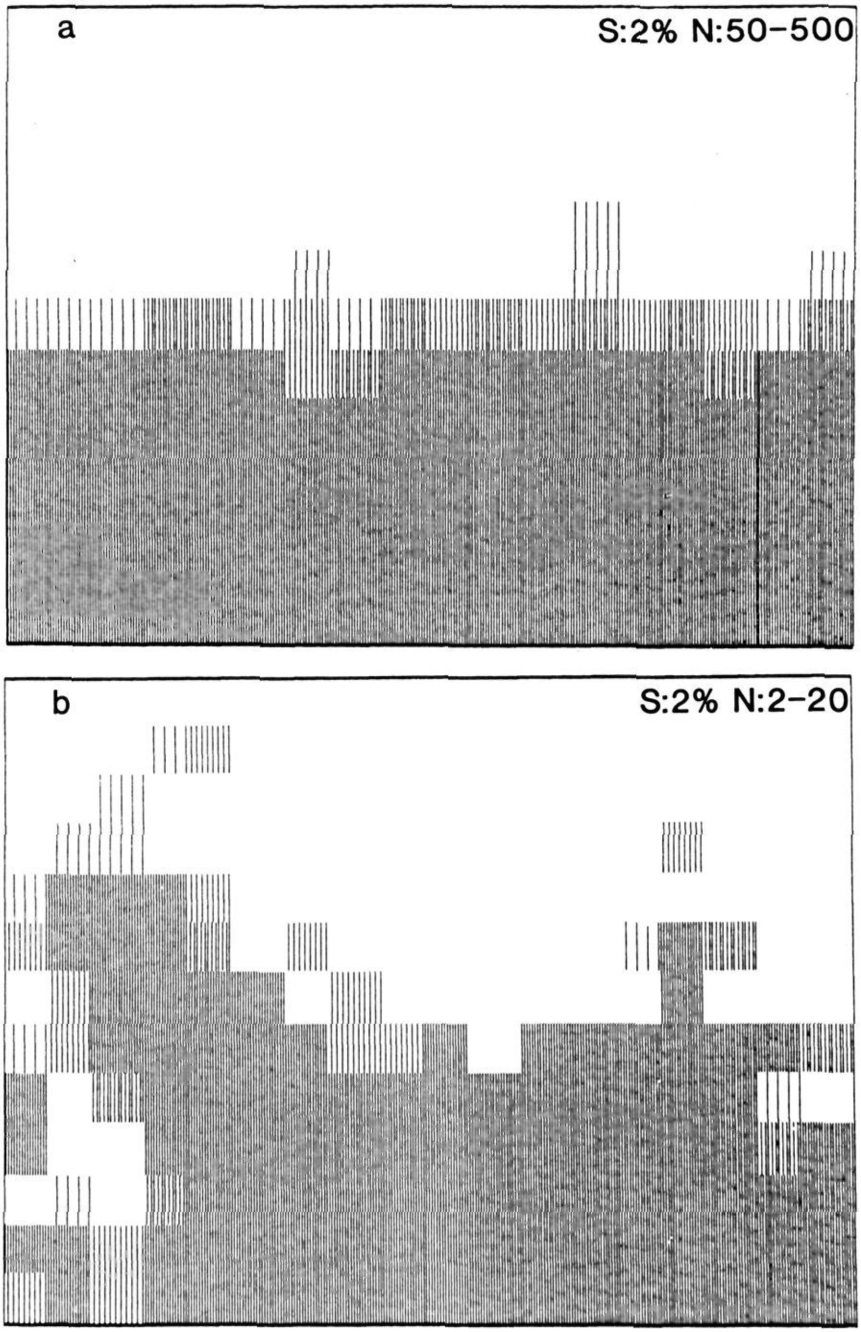

Figure 2. Maps of gene frequency in model tension zones after 2500 generations from two different simulations. Note the increased introgression at lower effective population size. The intensity of shading indicates the frequency of an allele in increments of 0.2. S is the selection against heterozygotes, and N is the range of deme sizes. The deme sizes are highest at the top and bottom of the map and lowest in the center. The simulation was initiated with the top and bottom halves of the area fixed for alternative alleles.

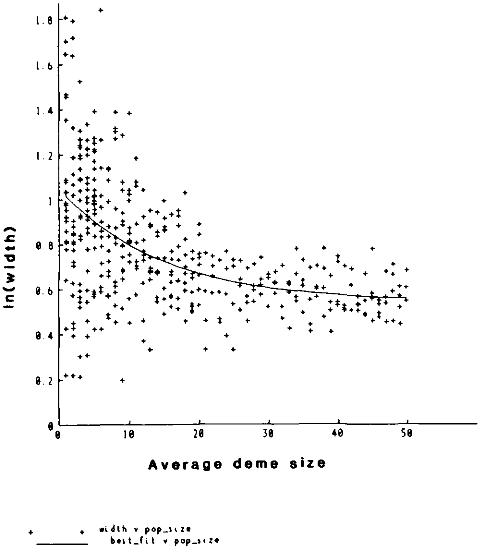

Figure 3. The relationship between tension zone width and the average number of individuals per deme in simulations. Note the logarithmic scale.

dimensional stepping-stone model with selection against heterozygotes. At low Ne, genetic drift can establish patches of an allele on the foreign side of a tension zone (Fig. 2). In such patches the allele escapes selection because it is locally abundant and so occurs predominantly in homozygotes. The allele can therefore persist away from the tension zone. As a result, an inverse relationship is found between Ne and zone width (Fig. 3). The greater introgression of the chromosomal fusion might therefore be explained if Ne were smaller in the Chabanon region.

At first sight, the karyotype distribution at Chabanon favours this explanation. The long-distance introgression is through areas which are wooded and subdivided by scree slopes (Fig. 1). Effective population size could be smaller in this region. However, the allozyme data do not support this conclusion. Gst proves no greater in the subdivided area than in the open area where the frequency of the fusion is low (Table 2C). The history of the area may provide a solution to the puzzle. There are gaps through the trees in the form of roads, teliski tracks, and pistes which were cleared when the ski lodge was built in the early 1970s (Fig. 1). The forest felling produced a large area of new habitat suitable for *Podisma*, which now supports thriving populations of it.

These new habitats would have been colonized from much smaller woodland clearings. The fusion may have persisted in the original clearings because of their small Ne. Now that the populations are larger, the fusion may be experiencing gradual elimination. However, because the selection against heterozygotes is less than 1% (Barton and Hewitt, 1981) the process may take hundreds of generations. If the selection were 0.5%, it would require nearly 1,300 generations for the frequency to decline from 0.4 to 0.01.

There may be other areas of long distance introgression of the *Podisma* karyotypes across the zone. A survey of areas where *Podisma* occurs in low population densities should disclose additional examples if the advanced hypothesis is sound. Past collections have concentrated on areas where *Podisma* is abundant. It may be that the tension zone is held in position by density traps in regions where *Podisma* is abundant, but in other, less populous regions there is more potential introgression.

This principle can be extended to species other than *Podisma,* to other loci, and to other gene complexes. For example, Wright's shifting balance mechanism (1988) envisages the involvement of small effective population size in the establishment of coadapted gene complexes. Once a favourable gene combination is established, it may be expected to spread because of greater gene flow from the demes where it is established. However, if a tension zone forms around the range of a new gene complex, its expansion could be restricted by density troughs. The example of *Podisma*'s karyotype suggests that, in regions where density is generally low, density traps will not be efficient. However, comparable density changes in densely populated regions will prevent zone movement.

Population density is not static. In most species it is profoundly affected by climatic fluctuations. The past climate has undergone broad changes as well as short-range fluctuations of shorter periods of 78 and 180 years (Dansgaard *et al.*, 1967). These coincide with tree-line fluctuations of 100-200 m in elevation (Wardle, 1974). Similar range shifts are seen in insects (*e.g.*, Coope, 1977). It follows that, although areas of low population density may be important in the local spread of coadapted gene complexes, the appropriate conditions do not last indefinitely. Nevertheless, they can last long enough for a gene complex to become established in part of the species range. Further spread from these bridgeheads is likely to be through range expansion. Major movements in species range, and the genomes comprising them, will arise from large-scale climatic change such as glaciations and interstadials (Hewitt, 1989). The initial geographic location and range of a genome will surely be affected by the long-range introgression discussed here and will strongly affect the fate of the genome in the subsequent cycles of range expansion and contraction.

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Effect of selection on wing dimorphism in the ground cricket *Dianemobius fascipes* (Walker)

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ABSTRACT

The ground cricket *Dianemobius fascipes* (Walker) is wing dimorphic, giving rise to a long-winged phenotype under crowded long-day conditions and to a short-winged one under either crowded or isolated short-day conditions, both at 25-27°C. The frequency of the long-winged form changed gradually in successive generations over several years under constant conditions (25-27°C, long days or equivalent photoperiodic regimes). In order to confirm the involvement of genetic factors in such changes, three selection lines were established: the L line was selected for long-winged under short day (LD 12:12 h), the S line for short-winged under long day (LD 13:11 h), and the C (control) line for long-winged under the long day and for short-winged under the short day in alternate generations. Even after 12-14 generations of selection neither the L nor the S line bred true, though the frequency of the selected form increased considerably in each. Reciprocal crosses were made between the 11th generation of the L line and the 13th generation of the S line. F1 and F2 progeny, and of the backcrosses were examined for the frequency of long-winged adults under both long and short days. They showed a graded variation in percentage of macroptery. Such hybrid responses, together with the gradual selective changes, suggest the involvement of a polygenic system. They might also be ascribed to a few allelic pairs of threshold genes determining the frequency of wing forms. If the latter is the case, at least two pairs of alleles (one sex chromosomal and the other autosomal) would be involved. The regression of offspring produced by various crosses on the parents suggests the existence of a maternal or cytoplasmic effect, although this was not indicated by the results of the reciprocal crosses L x S and S x L.

Key words: wing dimorphism, selection, genetics, cricket.

INTRODUCTION

The wing is a highly versatile structure in crickets. Its character state ranges from nil (aptery) to fully functional (macroptery) among different species (Masaki and Walker, 1987; Walker and Sivinski, 1986). Even in the same species, wing form may vary geographically (Harrison,1979; Masaki, 1973) and seasonally (Alexander, 1968). Wing form variation is particularly common in the ground cricket subfamily Nemobiinae, and most members of this group in the Japanese Islands are wing dimorphic (Tanaka, 1978; Tanaka *et al.*, 1976; Masaki, 1979; Masaki and Oyama, 1963; Masaki and Watari, 1989; unpublished observations). In the long-winged form, the hindwings when folded extend beyond the abdominal tip. In the short-winged form, the hindwings are vestigial, immovable flaps entirely covered by the forewings (Fig. 1). The two forms can also be distinguished by the size and shape of the forewings in the female and by the shapes of pronotum and acrotergite of the first abdominal segment in both sexes (Tanaka, 1985). At least during the early stage of adult life, the long winged form retains massive flight muscles, whereas the short-winged form has inconspicuous ones (Tanaka, 1985, 1986b; Roff, 1989).

Maintenance of the flight apparatus requires considerable metabolic costs and thereby may constrain other life functions such as egg production. In *Dianemobius mikado* (Shiraki) [formerly regarded as conspecific with *Pteronemobius taprobanensis* (Walker)] and *Allonemobius fasciatus* (De Geer), the functional wings of the long-winged form tend to delay egg production, which is promoted after shedding or artificial removal of the hindwings (Tanaka, 1976, 1986b). The long-winged females of *Gryllus firmus* (Scudder) lay eggs at a slower rate than do the short-winged ones, and this is regarded as "the cost of being able to fly" (Roff, 1984). Even though total fecundity is not changed, artificial dealation accelerates the rate of egg production in *Teleogryllus oceanicus* (Le Guillou) and *G. firmus* (Roff, 1989).

These observations may explain the retrogressive evolution of wings in crickets (Roff, 1986b, 1989). However, loss of flight ability decreases fitness when habitat conditions deteriorate, and migration by flight gives a higher probability of reproduction. Wing dimorphism, diphenism, and autonomous dealation, as found in many crickets are undoubtedly adaptive responses. These enable crickets to have different individuals

Figure 1. Long-winged (left) and short-winged pairs of *Dianemobius fascipes*. In each pair, the left specimen is female and the right one male.

or different phases with different flight and reproductive capabilities in adult life (Masaki and Walker, 1987). Such variation may be accomplished either through genetic or environmental means.

Genetic factors are responsible for the intraspecific variation in wing form in *Gryllus rubens* (Scudder) (Walker, 1986, 1987) and *G. firmus* (Roff, 1986a). Other environmental factors that induce variations in wing form include crowding in *Gryllodes supplicans* (Walker) (Arai, 1978a; McFarlane, 1966), *Velarifictorus micado* (Saussure) (Saeki, 1967a), *G. rubens* (Zera and Tiebel, 1988), temperature in *G. supplicans* (Arai, 1978b; McFarlane, 1962), *Pteronemobius nitidus* (Bolívar) (Tanaka, 1983), and photoperiod in *V. micado* (Saeki, (Mathad and McFarlane, 1968), *P. nitidus* 1967b), *G. supplicans* (Mathad and McFarlane, 1968), *P. nitidus* (Masaki and Oyama, 1963; Tanaka, 1978), *D. mikado* (Masaki, 1978, Tanaka *et al.*, 1976), *Dianemobius nigrofasciatus* (Matsumura), *Dianemobius fascipes* (Walker) (Masaki, 1973; Masaki, 1984; Masaki *et al.*, 1987; Masaki and Watari, 1989), and *A. fasciatus* (Tanaka, 1986a). These factors, particularly photoperiod, vary seasonally so that migration by flight may relate to seasonal adaptation. The warm season favours flight activity and tends to increase population density, and the cool season exerts the opposite effects. Daylength foretells this change. Any seasonal variation of wing form should, thus, be manifested in multivoltine species with two or more generations growing under different conditions of daylength.

The subtropical ground cricket, *Dianemobius fascipes* (Walker), is one such species. The physiological system determining its wing form is highly sensitive to photoperiod (Masaki and Watari, 1989), but our stock cultures of it also indicate the possibility of genetic control. If so, the cricket's wing-form characteristics would be subject to genetic change under the influence of natural selection. Therefore, the purpose of the present work is to show whether selection can produce strains of this ground cricket conspicuously different from one another in wing-form characteristics. If this is possible, this will enable us to cross different strains and investigate the genetic background of wing-form determination.

MATERIALS AND METHODS

Stock Cultures

Laboratory cultures were established with offspring of adults of *Dianemobius fascipes* collected from Ishigaki Island (24°N, 120°E) in October, 1973. They were kept in 2-litre jars and provided insect feed (Oriental Yeast Industry Co.) and carrot slices once a week. Water was supplied in a plastic vial plugged with cotton wool. The bottom of the jar was covered with dry sand, on which 4 sheets of corrugated filter paper (11 cm diameter) were piled to increase the available area. Usually 70-100 crickets were reared in each jar at 25-27°C in a controlled temperature room. Adults were transferred to a similar jar where they laid eggs in the cotton plug of a water-filled vial. The plugs containing eggs were removed once a week and kept in small plastic bottles until hatching.

Until 1980, groups of crickets in each generation were subjected to various light-dark cycles provided by a 6 or 10 W 'daylight' fluorescent tube to analyze the photoperiodic response. The offspring were usually obtained from those groups ovipositing earlier than others just to save time. Perhaps owing to this procedure, a gradual change in the frequency of wing forms occurred from generation to generation as described below. For further details of rearing methods, see Masaki and Watari (1989).

Wing-Form Selection

In order to maintain the genetic ability to become either short- or long-winged in response to photoperiod, a control (C) line was subjected to alternate selection. As shown in Fig. 2, short-winged adults were selected for under a short day of LD 12:12 h in one generation, long-winged ones un-

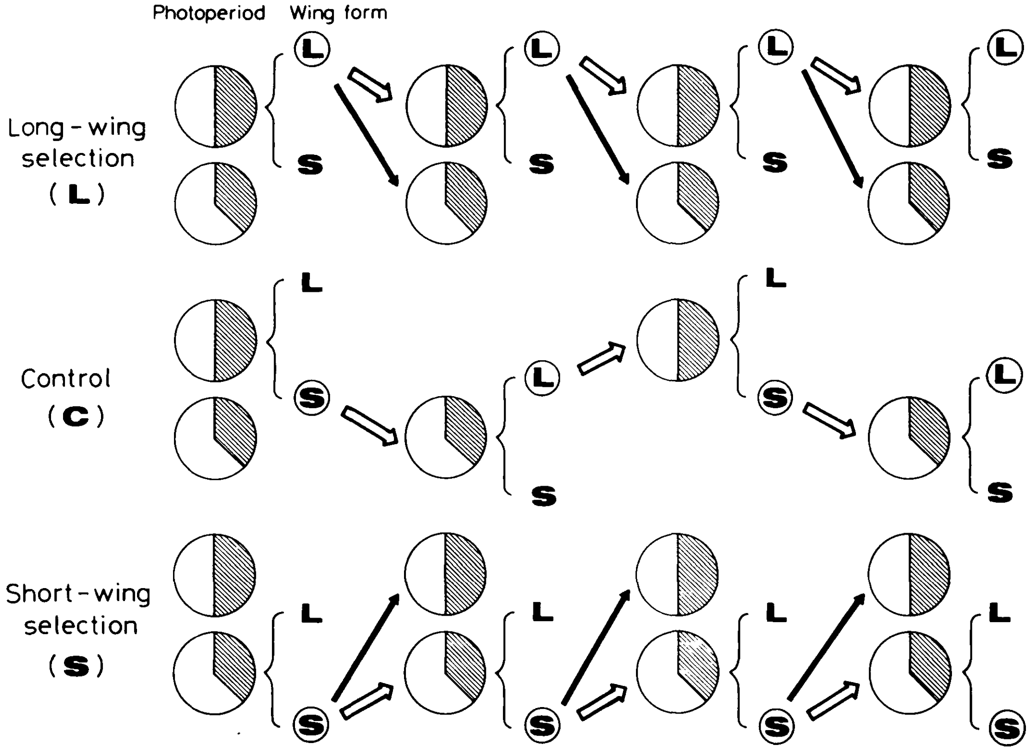

Figure 2. Scheme of selection for L (long-winged), S (short-winged), and C (control) lines of *Dianemobius fascipes*. L and S lines were reared in both short-day and long-day photoperiods. For the L line, offspring were obtained only from long-winged adults emerging in the short day; for the S line, only from short-winged adults emerging in the long day (hollow arrows); for the C line, selection for short-winged in the short day and selection for long-winged in the long day were alternated. The difference between the two photoperiods (LD 12:12 h and LD 13:11 h) is exaggerated in the fan diagram.

der a long day of LD 13:11 h in the next generation, and this was repeated. The 1 hour difference crossing the critical daylength (12 h 30 min) was originally highly effective in switching the wing form (Masaki and Watari, 1989).

Two other lines were selected for the long-winged and short-winged phenotypes, respectively. The long-wing selected (L) line was constantly kept under a short day of LD 12:12 h that had originally induced short-wing development in 90% of the individuals and the short-wing selected (S) line under a long day of LD 13:11 h that had originally favoured long-wing development (60-80%). Selection was 100% for each line.

In order to see any change in the responsiveness to photoperiod of each selection line, every generation was reared in both short and long days. In most cases 10 or more rearing groups as described above for the stock cultures were allotted to each selection line in each generation, but in a few generations only 4 to 8 groups were available. The rearing jars were examined every day, adults were removed and their wing forms recorded. The sample size for determining the percentage of macroptery ranged from about 250 to 1100 adults of both sexes. To obtain offspring in each line, 25 randomly chosen pairs of the selected wing form were allowed to oviposit in each rearing jar.

Crossing Experiments

Reciprocal crosses between the 11th generation of the L line and the 13th generation of the S line were made by means of mass breeding of 25 pairs. This was followed by all possible combinations of F2 crosses and backcrosses as mass breeding of 10-15 pairs. Usually, adults with the predominant wing phenotype in each parent group were randomly taken for crossing. The progeny from each cross were divided into two photoperiodic treatments, LD 12:12 h and LD 13:11 h. The sample size, i.e., the number of adults for determining the percentage of macroptery in the offspring of each cross, varied from 150 to 1000.

RESULTS

Decrease in Frequency of Long-Winged Forms over Generations

We kept laboratory cultures of *D. fascipes* for several years to study the photoperiodic response. Under the long-day conditions, the percentage of macroptery was high, exceeding 70-80% before 1978. Then it declined gradually over the next 10 generations or so and reached a low level of 20% in 1980 (Fig. 3). This became an obstacle in assessing the wing-form response to photoperiod. We suspected that a genetic change occurred possibly as a result of unintended selection owing to a difference in reproductive schedule between the wing forms (Tanaka, 1976, Roff, 1986a). In 1980, therefore, we started selection for the long-winged form in a photoperiod of LD 13:11 h and obtained positive results over the following several generations. The frequency of macroptery eventually restored the original level of about 70-80%.

Continuous selection for long-winged adults in a given photoperiod might enhance macroptery but modifies photoperiod sensitivity. In order to avoid this we selected for long-winged forms in LD 13:11 h and for short-winged ones in LD 12:12 h in alternate generations. This procedure somewhat decreased the frequency of long-winged crickets but maintained a 50-70% level in LD 13:11 h and a 10% or lower level in LD 12:12 h. Thus, we could assess the photoperiodic response with reasonable accuracy using the later generations of the

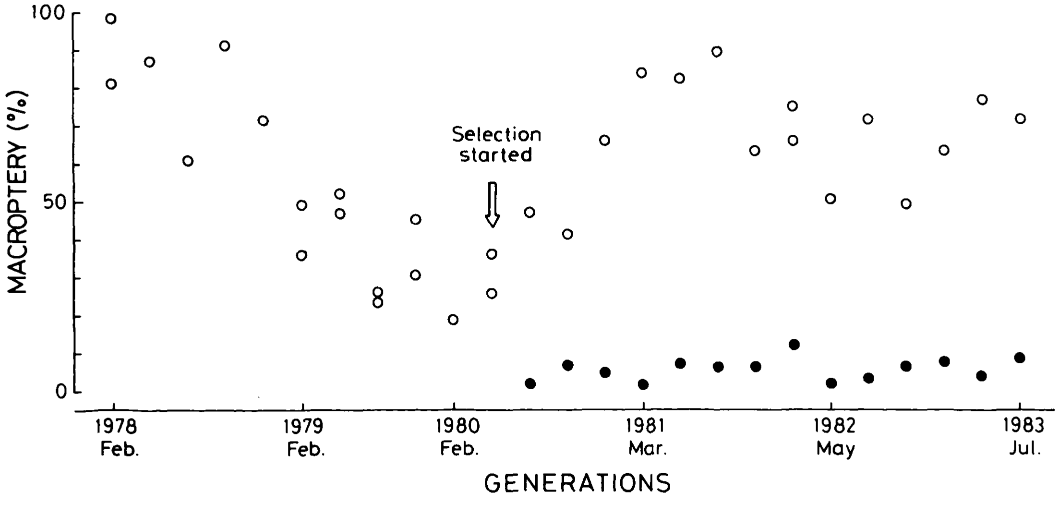

Figure 3. Change in proportion of long-winged adults under long-day conditions in a laboratory stock of *D. fascipes* over time under crowded conditions of rearing. Selection started in 1980. The hollow circles show percentages of long-winged adults in long days or equivalent photoperiodic regimes, and the closed circles those in short days. Sample size for each datum point is 100-1000.

laboratory stock. In order to understand wing polymorphism, however, it is important to investigate the extent to which wing-form frequency can vary with selection.

Selection for Long-Winged and Short-Winged Crickets

Selection proved effective in both directions, *i.e.*, increasing long-winged adults in the short day and short-winged adults in the long day (Figs. 4 and 5). In LD 12:12 h, the L line has already attained a percentage of macroptery as high as 60% by the second generation compared with only 20% in the original generation. It decreased again to about the original level in the following two generations, after which there was a steady rise to 70% around which level the later generations fluctuated. The S line, on the contrary, decreased its frequency of long-winged form to almost nil after 4 generations of selection, and this low level was maintained except for the 10th generation. The C (control=alternate selection) line came close to the level of the S line in certain generations but generally showed a higher incidence of long-winged forms.

In LD 13:11 h, the S line showed a gradual decrease in the frequency of long-winged form. The change in this line was impressive, from the original 60% to only about 5% in the 14th generation. By contrast, the L line was stabilized at about the 90% level, an increase of about 30% from the original response. The C line underwent no substantial change, and the performance of each generation fluctuated around a mean level of 60-70%.

Selection was thus effective in increasing long-winged adults, counteracting the short-day effect that otherwise suppressed long-wing development. It was also effective in increasing short-winged adults, counteracting the long-day effect that otherwise promoted long-wing development. The selection became apparent after several generations, but neither the L nor the S line bred true even after 12 (for the L line) or 14 (for the S line) generations.

These selective changes in the frequency of wing forms were associated with decreased responsiveness to photoperiod. This was not unexpected from the method of selection. The L line was selected for long-winged and the S line for short-winged in opposition to the actions of short days and long

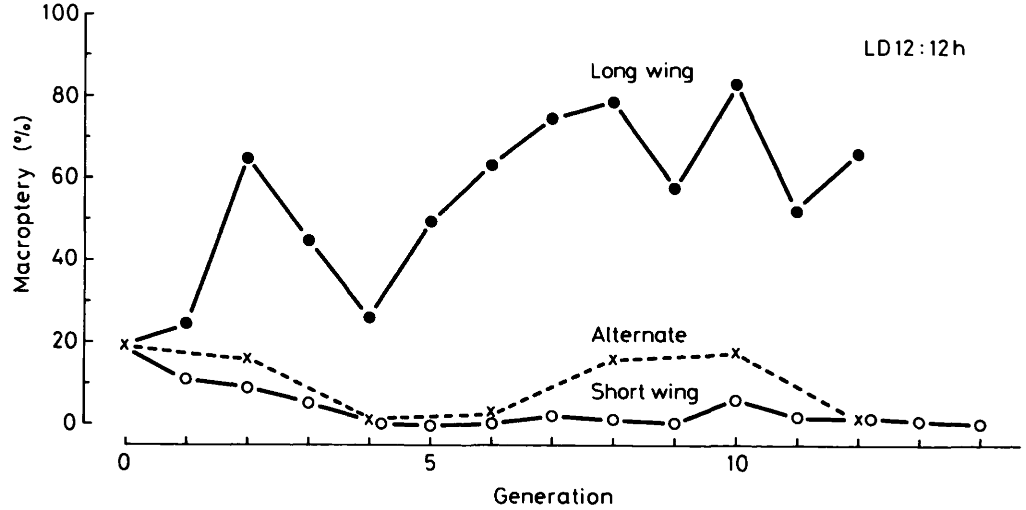

Figure 4. Changes over generations in percentage of long-winged crickets at LD 12:12 h of L (Long wing), S (Short wing), and C (Alternate) lines of *D. fascipes*. See Figure 2 for the procedure. Sample size for each datum point is 579-1116 in L line, 333-1096 in S line, and 269-552 in C line.

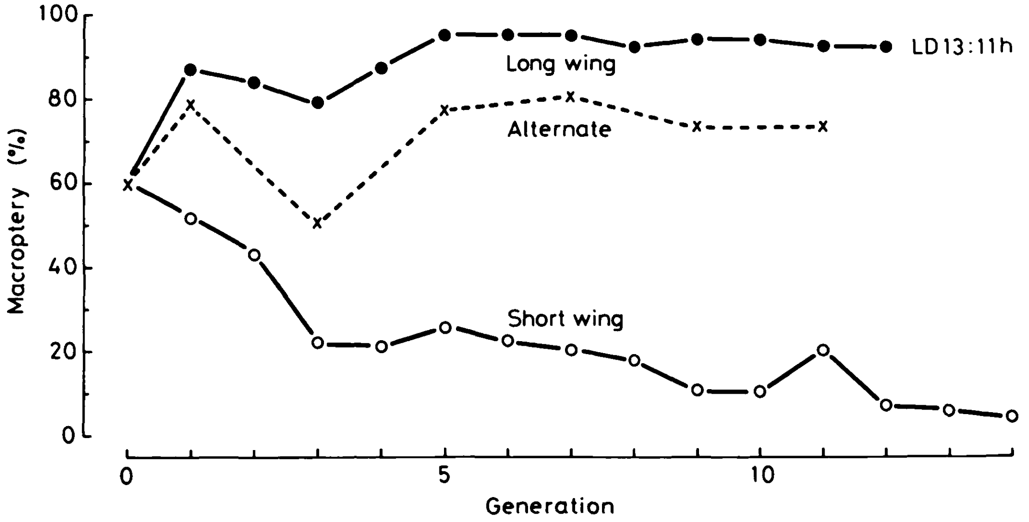

Figure 5. Changes over generations in percentage of long-winged crickets at LD 13:11 h of L (Long wing), S (Short wing), and C (Alternate) lines of *D. fascipes*. See Figure 2 for the procedure. Sample size for each datum point is 699-1075 in L line, 246-1102 in S line, and 320-844 in C line.

days, respectively. If the responsiveness to photoperiod is simply represented by the difference in frequency of long-winged forms between the long-day and short-day groups in each line, there would be similar decreasing trends in the responsiveness to photoperiod though the regression is statistically significant only in the S line. The C line with alternating selection does not show such a trend (Fig. 6).

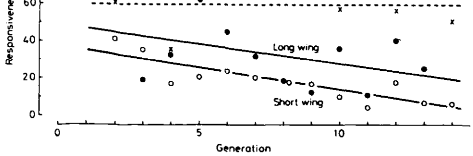

Figure 6. Change in responsiveness to photoperiod over generations in L (Long wing), S (Short wing), and C (Alternate) lines of *D. fascipes*. Responsiveness is represented by the difference between percentages of long-winged adults in LD 12:12 h and LD 13:11 h. The regression coefficient is statistically significant only for the S line ($t=6.11$, $df=12$, $p<0.001$).

Effect of Crossing on the Percentage of Macroptery

We made all possible combinations of the L and S lines and their hybrid offspring in F1, F2, and backcrosses. The results indicate that the percentage of long-winged forms is more or less proportional to the relative amounts of genetic materials derived from the L and S lines (Figs. 7, 8). Between L x L and S x S crosses there is a graded series of hybrid frequencies of long-winged adults, and the two photoperiodic series showed a close correlation (Fig. 9). Although each line was subjected to selection only under a fixed photoperiod, selection was effective in changing the liability to develop long wings but not the pattern of the photoperiodic response.

In many crosses the long-winged form was more common in the female than in the male offspring (Figs. 7, 8). This was the case in 9 and 13 out of 14 crosses in LD 12:12 h and LD 13:11 h, respectively. This may suggest the existence of a sex-linked factor as observed in other species of wing-dimorphic crickets (Walker, 1987; Zera and Tiebel, 1988; Roff, 1984, 1986a). L x S and

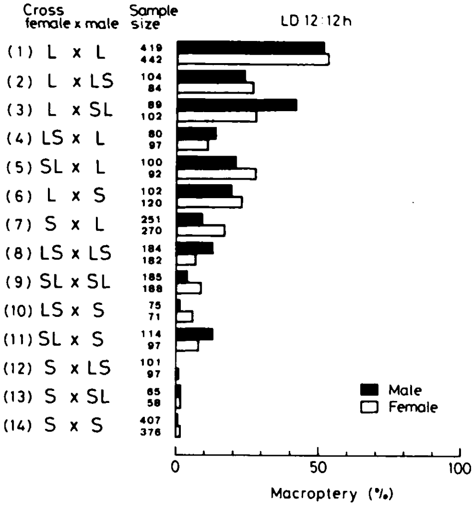

Figure 7. Percentages of long-winged crickets in F1 and F2 crosses between L and S lines and backcrosses under a short day.

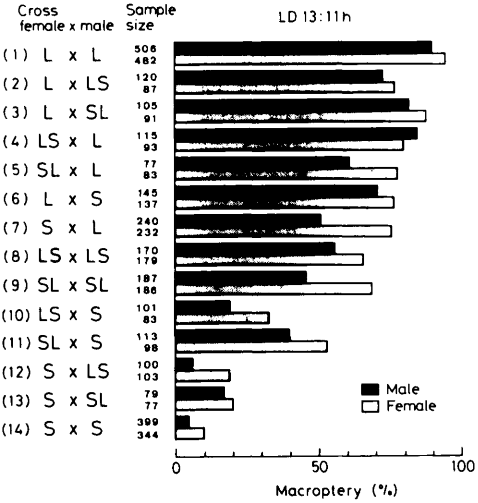

Figure 8. Percentages of long-winged crickets in F1 and F2 crosses between the L and S lines and backcrosses under a long day.

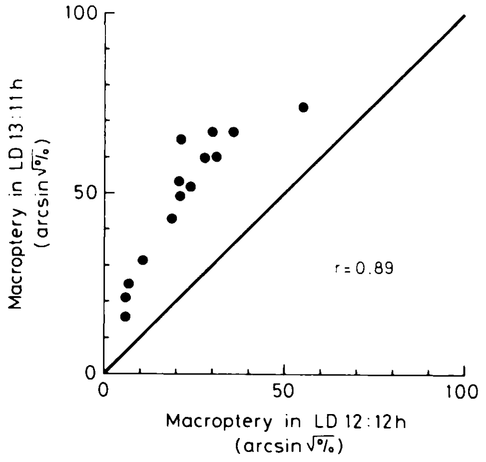

Figure 9. Correlation between frequencies (average of male and female data, arcsine transformed) of long-winged crickets in short days and long days obtained from various crosses of L and S lines of *D. fascipes*. See Figs. 7 and 8 for the types of crosses.

S x L should give daughters with the identical sets of genes but sons with different ones since the son's single X chromosome is derived from the mother. A significant difference in the proportion of long-winged adults occurs between the sexes in S x L (χ^2=29.7, P<0.01 in LD 13:11 h; χ^2=5.81, P<0.05 in LD 12:12 h) but not in L x S (χ^2=1.45, P>0.10 in LD 13:11 h; χ^2 = 0.30, P>0.25 in LD 12:12 h). In the latter case the son and daughter share the same set of autosomal and sex chromosomal genes derived from the L-line mother, but in the former cross the son lacks the sex chromosomal gene of the L line. On the other hand, the reciprocal crosses gave similar proportions of long-winged female offspring, and this might exclude the existence of a female cytoplasmic or yolk factor. As shown below, however, we obtained evidence for a maternal effect on wing form. Further investigation is necessary to confirm this point.

Regression of Offspring on Parents

Neither the time course of selective response nor the results of crossing between the selected lines suggests a simple Mendelian factor directly responsible for the expression of wing form. This situation could derive from a polygenic system. An alternative explanation could be the involvement of a relatively small number of threshold genes. Wing-form determination probably involves a threshold reaction (Zera and Tiebel, 1989; Roff, 1986b; Walker, 1986) controlled by genes not directly responsible for wing morphogenesis. In order to assess the genetic effect, we examined the regression of offspring frequencies (arcsine transformed) of long-winged form on those of parents.

Both the male and female offspring showed highly significant regression on mother and midparent [(mother + father)/2], and this accounted for 49-70% and 74- 86% of the variances of their frequencies of long-winged forms, respectively (Table 1). However, the regression on father was significant only in the female offspring reared under the short day, which accounted for only 20-32% of the variance. The regression coefficient took a larger value on the mother than on the father in both sexes, and its value on the mother was larger in the son than in the daughter. Although these trends were observed in both long and short days, none of the differences in regression coefficients between son and daughter and between mother and father were statistically significant. The midparent regression consistently took the largest value, probably due to both parents' genetic contribution to the frequency of the long-winged form in spite of the insignificant regression of the male offspring on the father.

This situation clearly required a simultaneous evaluation of the mother and father effects, so we made multiple regression analysis, taking the frequencies of the long-winged form (arcsine transformed) of the mother and father as independent variables and those of the son and daughter as dependent variables (Table 2). Most of the variance (87%) can be accounted for by the multiple regression on the male and female parents. Deletion of the effect of either parent from this component of the offspring variance leaves a significant portion of the variance that should be ascribed to the

Table 1.—Regressions of male and female offspring on parents in short and long days for percentage macroptery (arcsine transformed) in various crosses between L and S lines of *D. fascipes*. See Fig. 7 or 8 for the types of crosses involved.

	Regression of Y on X: b (r^2)		
X	Y, son	Y, daughter	t
LD 12:12			
Midparent	0.83(0.74)**	0.81(0.86)**	0.11 NS
Mother	0.61(0.70)**	0.54(0.66)**	0.46 NS
Father	0.31(0.21)NS	0.34(0.32)*	0.15 NS
LD 13:11			
Midparent	1.15(0.76)**	1.05(0.74)**	0.38 NS
Mother	0.64(0.55)**	0.56(0.49)**	0.35 NS
Father	0.36(0.20)NS	0.36(0.22)NS	0.02 NS
t values for comparison of regression coefficients in LD 13:11 h			
Midparent	1.37 NS	1.21 NS	
Mother	0.15 NS	0.11 NS	
Father	0.18 NS	0.03 NS	

b: regression coefficient.

r^2: proportion of the variance of Y attributable to regression. Regression is significant at **$P<0.01$ or *$P<0.05$ with df=12.

t tests the significance of difference between b's for son and daughter (right column) and for short and long days (lower section). All comparisons indicate no significant difference (NS) with df=24.

Table 2.—Multiple regression of offspring frequency (Y, arcsine transformed) of macroptery on mother (X1) and father (X2) in various crosses between L and S selected lines of *D. fascipes*. Data in LD 12:12 h and LD 13:11 h are pooled.

Items	df	Variance	Mean sq.	F
a. Male: $Y=0.64\ X1 + 0.35\ X2 - 7.02$ ($R^2=0.87$)				
Total	27	11419		
X1, X2	2	9943	4971	
Deviation	25	1476	59	
X1 alone	1	8010		
X2 after X1	1	1932		32.7**
X2 alone	1	3716		
X1 after X2	1	6227		105.5**
b. Female: $Y=0.61\ X1 + 0.41\ X2 - 4.24$ ($R^2=0.87$)				
Total	27	11719		
X1, X2	2	10213	5106	
Deviation	25	1506	60	
X1 alone	1	7577		
X2 after X1	1	2636		43.8**
X2 alone	1	4584		
X1 after X2	1	5629		93.4**

**$P>0.01$

R^2: proportion of variance attributable to the multiple regression.

other. This may indicate that genes derived from both parents give, at least to some extent, an additive effect.

The partial regression coefficients on the mother are 45 and 35% larger than those on the father in the male and female, respectively. In the male, this larger effect of the mother may support the hypothesis derived from the result shown in Figs. 7 and 8 [crosses (6) and (7)] that at least one locus on the X chromosome is involved since the female has XX and the male XO in this cricket (Ohmachi, 1938) and male's single X chromosome comes from the mother. However, the greater effect of the mother than the father on the female offspring cannot be explained by chromosomal genes only, since they receive X chromosomes as well as autosomes from both parents. Although no difference was found in the proportion of long-winged forms between the female offspring of the reciprocal crosses of the L and S lines (Figs. 7, 8), the results of regression analysis did not entirely exclude the possibility of a cytoplasmic effect.

DISCUSSION

Wing form in this ground cricket is highly sensitive to photoperiod and rearing density which may vary the percentage of macroptery from almost 0 to more than 70% (Masaki and Watari, 1989). Nevertheless, the present study suggests a high possibility of genetic variation in this wing-form control.

The selective advantage of the long-winged form may vary with the need for migration from habitats degraded by natural disasters or overcrowding. In the field, the proportion of the long-winged form in *D. fascipes* and other species of ground cricket seems low (unpublished observations), but this might be due to sampling biases. Sometimes long-winged ground crickets are attracted to light, and there is little doubt that they migrate by flight. The selective advantage of migratory flight may change in time and space which helps conserve the variability in the genetic background determining the frequency of long-winged forms.

Evidence for natural selection or genetic drift affecting the frequency of different wing forms has been found in *Gryllus firmus* associated with variation between different habitats (Harrison, 1979). In *Dianemobius nigrofasciatus* (formerly regarded as conspecific to *D. fascipes*) there is a latitudinal cline in the highest proportion of long-winged adults reared in a range of 12-16 h daylengths (Masaki, 1973). During several years of rearing, several tropical populations of *D. fascipes* consistently produced lower percentages of long-winged adults in all photoperiods between 11 and 16 h light per day (Masaki *et al.*, 1987 and unpublished observations) than the subtropical Ishigaki population (Masaki and Watari, 1989).

According to Walker's definition (1986) of different types of polymorphism, the wing dimorphism in *D. fascipes* seems at first sight to be conditional polyphenism because of the conspicuous photoperiodic and density control. However, we obtained neither 100% long-winged adults in a long-day photoperiod nor 100% short-winged adults in a short-day photoperiod. This incomplete photoperiodic switch of wing form cannot be ascribed to individual variation in the critical (=threshold) photoperiod. The response becomes saturated with about 70-80% long-winged in a non-selected line exposed to various photoperiods between 0 and 24 hr (Masaki and Watari, 1989). Selection shifts this saturation level, for the response curves of the L and S lines over a wide range of photoperiod show opposite shifts in height (T. Shimizu, unpublished observations).

The concerned genes are probably responsible for determining the ratio of the two wing forms but not wing morphogenesis itself. In the sense that they determine the probability for the adults being long winged, they might be regarded as stochastic genes (Walker, 1987). At the same time, they control, probably indirectly, the probability of response to environmental conditions such as photoperiod and population density and in this respect provide the background for conditional polyphenism. This mixture of polymorphism and polyphenism is clearly of selective advantage. It provides a means to cope with both predictable and unpredictable environmental change. The probability of fitness increasing through being able to fly (or inversely through being unable to fly) would vary seasonally, and yet the success of each morph at a given time of year is subject to stochastic fluctuation. If the probability remains nearly constant throughout the year, a purely stochastic polyphenism would be selected for. If it varies abruptly from 0 to 1 and *vice versa* at certain times of the year, a strictly conditional polyphenism could evolve. Considering the prevalence of gradual seasonal changes in most parts of the world, various mixtures of conditional polyphenism and stochastic polymorphism are probably commonly encountered in nature.

Although we selected the L and S lines for more than 10 generations under stringent conditions (100% selection in photoperiods suppressing the appearance of the selected form), pure lines that breed true were not obtained. The change in frequency of the selected forms was gradual over generations. Superficially, these features indicate the involvement of a polygenic system but do not contradict the hypothesis of a few threshold genes. If there are a few such genes, each of the alleles could produce in different frequencies both the selected and discarded phenotypes so that one or the other allele at each locus could not be selected out within a few generations. The rate of selection may depend on the difference in threshold between the alleles.

In *Gryllus rubens*, the macropterous and brachypterous morphs show clear differences in juvenile hormone esterase activity in the haemolymph during the last two nymphal instars. Since ester hydrolysis is thought to be the exclusive route of juvenile hormone degradation, this variation in esterase activity may play an important role in wing morph determination (Zera and Tiebel, 1988, 1989). At least one possible hypothesis is that the threshold genes determine the level of juvenile hormone esterase activity which, in turn, controls the frequency of the two wing forms although the possibility cannot be ruled out that the observed difference in esterase activity is not the cause but a result of wing-form determination. In *D. fascipes* and other species with photoperiod-sensitive wing diphenism, the effective level of the hormone may be affected by photoperiod through either the synthetic or degradative activity of particular enzymes.

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Phytohormone effects on the fertility, fecundity, and periodicity of egg laying in *Locusta migratoria* R. and F.

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ABSTRACT

Pairs of adult *Locusta migratoria* R. and F., reared from nymphs maintained under uniform conditions in the laboratory, were fed a dry defined diet initially devoid of unrefined plant material, to which dried ground wheat seedling leaves and one of three concentrations of a phytohormone (gibberellic acid, indoleacetic acid, kinetin, or abscisic acid) were added. The kind and concentration of ingested dietary plant hormone added to the diet were reflected in the number of egg pods produced, as well as the onset and periodicity of egg laying. Results obtained from the treatment groups varied significantly from those of the control groups fed fresh wheat seedlings or a defined diet with dried wheat leaves. These results provide evidence that reproductive performance in the African migratory locust is subject to direct influence by dietary phytohormones.

Key words: plant growth hormones, locust reproduction.

Generations of animal breeders were aware that animal fertility is dependent upon adequate nutrition long before physiologists were able to demonstrate experimentally this relationship. An extensive literature provides information on the essential nutrients for many animal species. More than 30 reviews concerning insect nutrition have appeared in the past 40 years according to Hagen *et al.* (1984). The discovery of the role of vitamins and trace elements led to the realization that not all dietary constituents are used solely as nutritional substrates providing metabolic building blocks, but can, in trace amounts, have regulatory significance in metabolism. In 1959 Gottfried Fraenkel concluded that most plants contain the essential carbohydrates, lipids, and proteins required by insects, yet between certain insect and host plant taxa some highly specific relationships have developed. These associations have apparently evolved as insects "cued in" to particular secondary plant substances (compounds synthesized by plants without any apparent essential role in metabolism). Numbers of these substances belonging to many classes of compounds have been identified and their relationships to insects established. They provide evidence for the enormous complexity of biochemical relationships that have evolved between insect herbivores and their hosts.

Nevertheless, there appears to be no clearly defined biochemical mechanism accounting for the significant and seemingly erratic changes that occur in the fertility of insects such as grasshoppers that feed on the same host plants from one year to the next. Adverse spring or winter temperature and moisture conditions are often given as the reason for the declining numbers in grasshopper populations in Montana, and drought is generally given as the basis for sudden outbreaks of rangeland grasshoppers. However, experiments designed to separate the direct influence of temperature on grasshopper reproductive success, apart from the influence that the growing temperature of the host plant might have on the grasshopper's physiology, demonstrated that the plant growth temperature significantly altered the rate of production of fertile eggs regardless of the temperature at which the insects were maintained (Visscher *et al.*, 1979). This finding suggested the possibility that changes in environmental condition might affect substances in the host plant with regulatory activities in the insects that ingest them. Plant growth hormones (PGHs) are substances belonging to five classes of chemical compounds that regulate the growth and reproductive physiology of plants. PGHs seemed ideal candidates for such a role in animals, first, because they are synthesized along metabolic pathways that are also present in animals, and, second, because they vary in kind and concentration in plants with changes in temperature, moisture, and daylength.

Experiments were carried out at Montana State University in which representative PGHs and western wheatgrass (*Agropyron smithii* Rydb.) were fed to a rangeland grasshopper, *Aulocara elliotti* (Thomas). Highly significant dose related differences were demonstrated in the growth, reproduction, and longevity of these acridids fed different PGHs (Visscher, 1980; 1982; 1983). In more recent experiments PGHs were fed to *A. elliotti* in a defined diet, and direct effects were observed on fecundity and egg viability (Visscher, 1987). Moreover, the rate of development, nymphal survival, onset of egg laying, and adult longevity were significantly affected by dietary PGHs.

The phase transformation of the African migratory locust (*Locusta migratoria* R. and F.) is characterized by similar changes. It was hypothesized, therefore, that phase changes in that species might be induced by dietary plant growth hormones. The herein reported experiment to test this possibility was conducted at Ege University in Bornova, Izmir, Turkey.

MATERIALS AND METHODS

Fifth-instar nymphs of *L. migratoria* were collected from a wild population at the old airport near Izmir and maintained in large screen cages to obtain egg pods. These were incubated to hatching and the resulting nymphs maintained on fresh wheat seedling leaves until the adult ecdysis. The first adult appeared on April 1. Single pairs of adults were isolated in cylindrical cages of clear plastic (21x40 cm) covered by screen lid tops and the bottom placed on sterile sand in aluminum pans (21.5x7.5 cm). A branch was placed vertically in the cage for perching. Distilled water was provided the locusts in urethane-stoppered vials (15x5 cm).

Groups of five-six adult pairs were assigned to each treatment group. Adults in Control Group I were fed fresh 10-15 day old wheat seedling leaves grown in a greenhouse with fluctuating light and temperature. The leaves were held upright in distilled water in vials (3.5x6 cm). Adults assigned to Control Group II were fed a defined diet, modified from Cavanagh (1963), with 20% dried ground wheat seedling leaves added. The mixture was moistened with distilled water and pressed into uniform pellets in electron microscope embedding molds (5x10x2.5mm). The food blocks were prepared and fed daily in plastic dishes placed on the bottom of the cages. The residual diet was removed each day at the time of feeding. Other groups of adults were fed one of three concentrations: 5, 25 or 50 ppm, of either gibberellic acid (GA_3), indole-3-acetic acid (IAA), kinetin, or abscisic acid (ABA) mixed with the food mixture. PGHs were dissolved in 1 ml of 95% ethanol before dilution with distilled water before they were mixed with the diet.

The cages were provided with moistened sand egg tubes for oviposition. The egg pods were removed daily, incubated at 32°C for 10 days, fixed in Bouin's solution, and stored in 70% ethanol pending microscopic study to determine the embryonic viability. Cages containing adults were maintained at long daylengths (16 hr light: 8 hr dark) at temperatures ranging from 38°C in daytime to 20°C at night with relative humidities ranging from 35 to 40%. A 40W incandescent light bulb above each cage, as well as fluorescent ceiling lights and south facing windows, provided light.

Data were analyzed statistically by multivariate analysis of variance or two-way Chi square contingency tests.

RESULTS AND DISCUSSION

Female *L. migratoria* normally lay their eggs in loosely formed pods in moistened sand, but when stressed may not follow normal egg laying behavior, depositing them instead on top of the sand. In nature these eggs would dessicate and fail to develop; hence, when this occurred in the laboratory, these pods were designated as "abnormal". Table 1 provides data on the number and type of egg pods produced (normal pods shown by solid ovals; abnormal pods by open ovals) according to time of deposition and treatment group. The oviposition dates of Control Groups I and II were similar, with adults fed dry defined diet (Control II) producing fewer pods (5) than were produced by females fed fresh wheat seedling leaves (Control I)(8), but both groups produced three abnormal egg pods. Females fed GA$_3$ at the 5 ppm concentration laid no egg pods. Those fed that hormone at 25 and 50 ppm produced three or two pods, respectively, all normal. Females fed kinetin at the 5 ppm concentration produced only one normal egg pod, whereas those fed the 25 ppm dose laid one normal and two abnormal egg pods. Females fed kinetin at the 50 ppm concentration laid four normal egg pods early in their reproductive period, none for a period of three weeks, then one final pod. Comparison of the total number of pods laid by females fed any PGH, combining the three doses in each treatment group, with the number of pods laid by females in the Control Groups (combining data for those Groups) revealed significant differences (P = .033).

Table 1.—Oviposition dates and number of egg pods laid by *Locusta Migratoria* fed young wheat leaves or defined diet with plant growth hormones.

Treatment Group	April 14-20	April 21-27	April/May 28-30; 1-4	May 5-11	May 12-18	May 19-25	May/June 26;01	Normal/ Abnormal Egg pods
Control I*	●	●●●	●○●●○	●○				8/3
Control II**	●	●●	○○	○●				5/3
GA$_3$-5 ppm								0/0
GA$_3$-25 ppm	●	●●						3/0
GA$_3$-50 ppm		●	●	2/0				
Kinetin-5 ppm						●	1/0	
Kinetin-25 ppm		●	○	○				1/2
Kinetin-50 ppm		●●●	●				●	5/0
IAA-5 ppm			○●	○○○	○○●	●●	4/9	
IAA-25 ppm			●	●●	○●	○●	●	6/2
IAA-50 ppm			●○					1/1
ABA-25 ppm				●				1/0
ABA-50 ppm	●	●●●●●	●●○					

* Control I diet: Fresh wheat seedling leaves.
** Control II diet: Defined diet with 20% dried wheat seedling leaf meal.
● = Normal egg pod.
○ = Egg pod laid outside the sand.

Adults fed IAA at all concentrations delayed their oviposition two weeks compared to the Control Group females and those fed GA_3 at the 25 ppm dose. One-way analysis of variance comparing combined data for the onset of egg laying for all IAA treatment groups to combined data from the two Control Groups showed the delayed onset of oviposition in IAA treated females to be significantly different from the Control Group females (P = .008). When egg laying did occur, females fed IAA at 5 ppm produced four normal and nine abnormal egg pods. Those fed the 25 ppm concentration produced six normal and two abnormal pods. Females fed diet containing 50 ppm of IAA laid only one normal and one abnormal egg pod.

Adult pairs fed ABA at the lowest concentration produced only abnormal egg pods, four in all. Females fed ABA at 25 ppm, however, produced only one normal egg pod in the fourth week of their reproductive lifespans. Females fed ABA at the 50 ppm concentration laid nine normal egg pods in a sequence similar to that demonstrated by Control Group I females. However, females fed the highest concentration of ABA ceased egg laying in three weeks, two weeks sooner than females in either Control Group.

Data concerning the number of females contributing egg pods or proving infertile are given in Table 2. These results demonstrate that fertility as well as fecundity was influenced by dietary PGHs. Only females fed ABA at 50 ppm surpassed females in Control Group I in production of normal egg pods. Females fed IAA at the 5 ppm concentration, on the contrary, produced the highest number of abnormal egg pods per female (Table 2).

Statistical analysis by the Chi Square Two-Way Contingency test revealed that females fed ABA at 5 ppm differed significantly (p = .03) from those in Control Group II with respect to the number of normal versus abnormal egg pods (Table 1). Similar comparison of the number of abnormal egg pods from females fed any PGH, combining data for all three concentrations, to combined data in the two Control Groups, demonstrated significant overall differences (P = .03). Small data samples and wide variability may account for the difficulty experienced in obtaining statistical significance from the results of other individual treatment groups.

Table 2.—Number of Egg Pods Laid by Female *Locusta migratoria* fed Plant Growth Hormones in a Defined Diet.

Treatment Group	Initial N.° of Adult Pairs	Fertile Females*	Mean N.° of Normal Pods	Egg Pods Abnormal Pods
Control I	6	3	1.34	0.50
Control II	6	2	0.83	0.50
GA_3-5 ppm	6	0	0.00	0.00
GA_3-25 ppm	6	1	0.50	0.00
GA_3-50 ppm	6	2	0.33	0.00
Kinetin-5 ppm	5	1	0.20	0.00
Kinetin-25 ppm	5	1	0.20	0.40
Kinetin-50 ppm	5	3	1.00	0.00
IAA-5 ppm	6	3	0.67	1.50
IAA-25 ppm	6	3	1.00	0.33
IAA-50 ppm	5	2	0.20	0.20
ABA-5 ppm	6	2	0.00	0.67
ABA-25 ppm	6	1	0.17	0.00
ABA-50 ppm	6	4	1.50	0.17

*Females laying any egg pods.

Because the kinds and concentrations of PGHs in host plants are variable, changing over the season as well as when plants experience unseasonal changes in environmental conditions, it can be speculated that the concentrations of GA_3, kinetin, and IAA that elicited significant inhibitory effects on egg laying behavior may have been physiologically or phenologically inappropriate to adult locusts. Moreover, because the PGHs were fed individually, no interacting effects of these substances on reproduction could be observed although such effects might be expected when the locusts feed on host plants. ABA, the drought-stress, senescence hormone of plants, inhibited egg production only at the two lower concentrations and seemed to accelerate that process at the highest concentration. Furthermore, the lifespans of females fed ABA at 50 ppm were shortened compared to those fed other PGH treatments. Significant differences were also observed in the longevity of adults fed PGHs in defined diet. These data and those pertaining to the viability of embryos from egg pods discussed here will be presented elsewhere.

The results presented here suggest that ingested plant growth hormones can affect the reproductive periodicity and may interfere, at certain concentrations, with behavioral patterns that result in normal egg pod production. Moreover, because PGHs were fed in absence of living plant material, the results provide evidence for direct metabolic effects of PGHs on the reproductive physiology of *L. migratoria*.

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Resúmenes

Abstracts

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Organisation phylétique, spatiale, et trophique des peuplements d'acridiens forestiers amazoniens

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De nombreux échantillonnages, tant en milieu forestier qu'en succession ont pu permettre d'approcher l'organisation spatiale et trophique des communautés d'Acridiens dans l'écosystème forestier amazonien, en relation avec la structure phylétique des peuplements. Les Ommatolampinae (20 à 30%), les Bactrophorinae (35 à 50%), les Proctolabinae (14 à 26% des espèces et 6 à 14% des effectifs) ainsi que les Romaleinae (10 à 15%) sont les groupes fondamentaux.

Les Ommatolampinae exploitent des milieux particuliers et sont davantage interstitiels.

Au contraire, les Bactrophorinae (constitués essentiellement par des éléments récents: Ophthalmolampini) et les Romaleinae (sous-famille plus ancienne) exploitent massivement la canopée. Les deux sous familles présentent le même schéma d'organisation fonctionnelle pour l'exploitation des couronnes (complémentarité entre consommateurs des arbres et des épiphytes assurée par des phylums particuliers, dans la même grande unité systématique). Romaleinae et Ophthalmolampini, dont les abondances et la diversification sont bien différentes et opposées, correspondent à un écosystème plus ancien et à un plus récent qui se superposent actuellement. L'ensemble du systéme, étendu à tout le bassin amazonien est plus complet dans les refuges du Napo et de Guyane, et les variations d'extension des deux groupes ont éte et sont toujours réglées par les modalités d'expansion de la forêt et les barrières à la dispersion.

Les Proctolabinae complètent cette organisation. Bien qu'importants dans certaines forêts non perturbées, ils sont surtout un élément fondamental de la régénération (stades tardifs). Par ce biais, la sous famille, d'origine septentrionale, s'introduit progressivement dans le bassin amazonien. Au contraire des autres composants, les Proctolabinae (Proctolabae, essentiellement *Poecilocloeus)* ne sont importants que dans l'ouest amazonien, peu d'espèces ayant franchi les barrières du centre de dispersion. Dans le sud-ouest amazonien, à forêts moins humides, moins riches en Ophthalmolampini des couronnes, le genre *Poecilocloeus* a formé, à côté des especes de la régénération, un groupe forestier qui, au nord de l'Amazone a donné un groupe de fin de succession.

A revision of the Mediterranean species of the genus *Acrotylus* Fieb

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In this paper the Mediterranean species of the genus *Acrotylus* Fieb, are reviewed. Four species are present in the area: *Acrotylus insubricus* (Scop.) (= *Acrotylus patruelis* A.A.), a widely distributed Afro-Mediterranean species; *Acrotylus maculatus* (Oliv.) (= *Acrotylus insubricus* A.A., *nec* Scopoli), a circum-Mediterranean species differentiated into two races, the north Mediterranean *maculatus* and the south Mediterranean *inficitus* (Walk.); *Acrotylus fischeri* Azam, a west Mediterranean species; and *Acrotylus longipes* (Charp.), and Afro-Mediterranean species.

Acoustic behavior of *Eremogryllus hammadae* and of *Notopleura saharica* (Orthoptera: Acrididae: Eremogryllinae)

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Males of the eremogrylline grasshoppers *Eremogryllus hammadae* and *Notopleura saharica* proclaim their presence by songs which are loud and long and have a wide spectrum of frequencies. The songs are conspicuous, but the grasshoppers are small and well-camouflaged; furthermore, they are capable of self-burial.

The calling song of these species is divided into 2 distinct parts: the body of the song and a 'coda'. The body of the song of *E. hammadae* is composed of complex chirps whose form can readily be related to the stridulatory movements of the legs.

In contrast, the body of the song of *N. saharica* consists (in addition to sounds produced by stridulation) of banging sounds produced by percussion and of hissing sounds which appear to result from air emission. The components of the song may vary from male to male and, in the same male, from song to song. The chirps of the coda vary in number but not in structure.

Under natural conditions, males of *E. hammadae* apparently maintain a distance from one another. However, under the conditions of confinement and relative crowding in laboratory cages, they may emit non-stereotyped sounds of communicative significance.

Aspects of defensive behavior of *Eurycantha calcarata* Lucas females and the evolution of scorpion mimicry in the Phasmida*

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Defensive behavior was studied in females of the New Guinea stick-insect *Eurycantha calcarata* Lucas, using *Chinchilla laniger* Molina (Rodentia) as predators. It was found that the females protected their black shiny ovipositor by placing it toward the substrate and using the hindlegs in active defense, instead of using scorpion mimicry, as reported earlier. The evolution of scorpion mimicry in female stick-insects equipped with an ovipositor is discussed.

* A travel grant from the Swedish Natural Science Research Council is acknowledged. A complete paper of this work is in press in Biol. Zent. bl., *108 (1989): 257-262.*

Defensive stridulation in *Heteropteryx dilatata* Parkinson (Phasmida)*

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Defensive behavior was studied in females of the Malayan stick-insect *Heteropteryx dilatata* Parkinson. It is a large insect, 165 mm in length and 50 g in body mass. It uses scorpion mimicry, red displays, active fighting, chemical defense secretion, and a powerful defense stridulation. The stridulation has a sound pressure level reaching almost 100 dB(A) with its maximum between 8-13 kHz. It consists of an initial strong clicking sound which is followed by a hissing sound. Presumably it mimics scorpions (and perhaps snakes) and is able to frighten birds and mammals.

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The origin of structural isolating mechanisms: Evidence from the distribution of structures

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Interspecific differences in genitalia and other male structures, so extensively used by taxonomists, are often thought to have arisen under selective pressures to prevent interspecific mating which might otherwise lead to inviable offspring. The alternative hypotheses are that such structures arose under selective pressure for more efficient mating (Eberhard) or for more efficient integration of the species population (Paterson).

Two cases of character divergence (reinforcement) in genitalic structure in the narrow area of overlap of species in the acridid genus *Barytettix* and the tettigoniid genus *Neobarrettia* are reviewed. In each case the isolating function is indirectly demonstrated, yet the structural modifications do not extend much beyond the zone of contact of the two species. In these cases, conditions which clearly represent "isolating mechanisms" seem to have negative selective value outside the immediate contact zone; thus the development of such structures as isolating mechanisms cannot explain their wide occurrence in other species beyond the range of contact with close relatives.

In most of the numerous species of the rhaphidophorid genus *Pristoceuthophilus*, genitalic and abdominal differences show little variation whether close relatives are broadly or narrowly sympatric or are parapatric. This is the case in three situations which are discussed. 1) close relatives with broadly overlapping ranges, in which the genitalic differences are uniform far beyond the overlap zone including distant populations that have probably been isolated since the last glaciation; 2) cave-associated species of restricted distribution which have highly distinctive structures and are surrounded by but not sympatric with, wide-ranging close relatives that are structurally unaffected by close proximity, and 3) closely related parapatric species with significant differences, which have the opportunity of invading each others' ranges but have failed to do so. In contrast, there are instances in this genus of extensive hybridization between populations that are distinctively different in genitalia and abdominal specialization which vary little over wide areas.

The parsimonious interpretation of the rhaphidophorid examples is that the structures play little role in interspecific segregation and consequently must have been developed for intraspecific mating efficiency. The alternative hypothesis that these were developed to prevent interspecific mating requires such *ad hoc* hypotheses as prior contact or rapid spread of the structure for which we find no evidence. We conclude that, although these structures sometimes could and in some cases probably do prevent mating, this is an accidental result of selection for other functions.

Evolution of Ectobiidae (Blattaria)

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The study of evolution in the Ectobiidae is based mainly on analysis of the internal cuticular structures of the male glandular pit.

Wing-Length polymorphism in grassland grasshoppers: Patterns of inheritance and fecundity differences in selected lines

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Phoetaliotes nebrascensis (Thomas) (Orthoptera: Acrididae) is a common univoltine grasshopper that exhibits wing-length polymorphism in populations found in Nebraska's sandhills grasslands. Although proportions of long-winged individuals are usually low (0.5-5.5%), 25% long-winged individuals are produced when eggs are hatched and reared in the laboratory under high density and low food quality conditions. One generation in selected lines is sufficient to demonstrate significant divergence between long × long and short × short crosses. Fecundity estimates also diverge and suggest that a significant reproductive cost is associated with the development and maintenance of long wings.

Homing navigation in territorial acridids

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Males of *Ligurotettix* spp. (Orthoptera: Acrididae: Gomphocerinae), territorial grasshopper species that defend individual host plant shrubs, home to their territories by memorizing landmarks. The insects are able to navigate toward high quality, chemically distinctive, recognizable shrubs via gustation though these plants are indistinguishable from a distance.

Acoustic communication and phonotaxis in *Steropleurus nobrei* (Bolivar)

J. C. HARTLEY

Both sexes of *Steropleurus nobrei* produce complex songs composed of several syllables. The male song is made up of 2-5 syllables of up to 10 tooth strikes, a long opening-syllable of 30-34 tooth strikes and a major closing-syllable where a similar number of teeth are struck in a slower and more deliberate manner. An average song of 6 syllables lasts 0.56 secs. The main song may be followed by 1-3 irregular after-syllables. The female song is initiated by the male call. It is composed of 3-8 variable syllables with a more irregular and slower tooth strike rate than that of the male.

Both sexes are able to perform phonotaxis on the call of the opposite partner in a duet. Males tend to move further and faster than females (3:1).

There are therefore 3 patterns of phonotaxis now known in the Ephippigerinae.

1. Reiteratively calling stationary males with silent females performing phonotaxis (1).
2. Occasionally calling males stimulated to frequent calling by responding female, female performing phonotaxis (1).
3. Occasionally calling males stimulated to frequent calling by responding female, either sex performing phonotaxis.

In evolutionary terms it may be more advantageous for the species if the female is less exposed than the male. In category 1 the male broadcasts his presence and the female becomes conspicuous when moving; in 2 acoustic exposure is minimised although the female still moves (nocturnally in known examples); in 3 *(S. nobrei)* while broadcasting may be restricted, female movement is also reduced, but females may perform phonotaxis if necessary. Both sexes of all ephippigerines may produce a stridulatory squawk when molested. This may have a defensive value as in *Mygalopsis* (2).

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Community ecology of Serengeti grasshoppers

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The Serengeti National Park in Tanzania protects nearly 15,000 km^2 of natural tropical grassland with a unique ecosystem of migrating ungulates. Little is known about its insect fauna, but grasshoppers have been shown to be major consumers during the wet season. An exploratory study involving 198 samples taken in different parts of the park and the adjoining areas resulted in collection of 77 species of Acridoidea. A Detrended Correspondence Analysis showed them to be grouped into a small number of communities whose distribution is determined by rainfall, drainage, and the impact of mammalian herbivores.

Attraction of *Melanoplus sanguinipes* (F.) to host plant odors and volatile compounds

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The attraction of a polyphagous grasshopper, *Melanoplus sanguinipes* (F.), to odors from intact and cut plant foliage or to volatile chemical components of odors was tested in a glass. Y-tube olfactometer. Individual insects were tested in groups of 10 last-instar nymphs or adults 1-2 weeks after ecdysis. The test insects were supplied water but no food for 24 hrs prior to testing. Humidified air was passed through the sample and control chambers at equal flow rates and then through the Y-tube to the holding chamber containing the test insect. Fresh plant foliage or growing plants were placed in the sample chamber, while solutions of volatile chemicals in water were metered at a constant rate into the sample air stream with a motor-driven syringe pump. Insects moving upwind were recorded after entering either the sample or control arm of the Y-tube. Both nymphs and adults were strongly attracted to cut, intact seedling foliage of perennial rye grass, wheat, and corn. Only the cut leaves of sorghum and alfalfa were significantly attractive. The major volatiles in rye grass odor, identified by GC-MS, were cis-3-hexenyl acetate, cis-3-hexen-1-ol, trans-2-hexenal, and 1-penten-3-ol. When chopped instead of intact leaves were sampled the amount of volatiles increased markedly, and many more compounds were detected. The major volatiles in rye grass odor when individually tested were significantly attractive to grasshoppers over humidified air but not to the degree of whole plant odor. However, when the volatile chemicals were mixed in proportions simulating the natural odor blend, a higher level of attractancy was observed that equaled grass odor. Testing a range of concentrations was important to establish an optimum level above the threshold of attractancy and below higher concentrations that were repellent.

Therefore, the five- and six-carbon unsaturated alcohols, esters, and aldehydes volatilizing from green plants in the proper blend and concentration range may play an important role as olfactory cues for attraction of grasshoppers to host plants.

Geographical variation and its taxonomic significance in the genus *Phisis* Stal, 1861, *S. Str.* (Grylloptera: Tettigonioidea)

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Geographical variation of morphological characters in the genus *Phisis* Stal, 1831, *s. str.* has been found at three levels: supraspecific, interspecific, and intraspecific. The supraspecific variation shows characteristic distribution patterns for the two species-groups involved. This suggests an earlier pattern of geographical separation and morphological differentiation. The interspecific variation in all species shows two typical distribution patterns: either highly endemic or widespread. Some of them show the direction of species differentiation and hence indicate a close evolutionary relationship among species. Some also suggest different dispersal routes, each having its own distributional territory. The current intraspecific variation in three widespread species provides reliable evidence for explaining their respective distribution patterns. All data presented strongly support the present taxonomic treatment and infer that the New Guinea-New Britain region is probably the epicenter of *Phisis* evolution and dispersal.

The importance of habitat type to grasshopper communities

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Habitat is a much-debated topic within ecological and entomological circles. Entomologists are frequently faced with pest management problems. All too often, applied entomologists working in a particular area of pest management find past habitat-related field research of limited value because the focus was too narrow or the work not replicated sufficiently to allow for extrapolation beyond a specific site or area. Their studies often include many pieces and parts without a view of the whole. Conversely, there are numerous global theories that, while providing material for debate and formulation of hypotheses, are not designed to answer the problems facing entomologists working in pest management.

In this paper will be reviewed recent work linking discrete grassland habitats with the complexity and structure of rangeland grasshopper communities in Montana, USA. Connections will be made between specific habitat types and historical rangeland grasshopper outbreaks. Lastly, the importance of the use of habitat types and rangeland pest management as well as community ecology will be discussed.

A preliminary record of orthopteroid insects of the Maldive Islands

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The orthopteroid fauna of the Maldive Islands in the Indian Ocean is poor. Orthopteroids known to occur in the Archipelago comprise eight species of cockroaches, most (if not all) of which have been introduced by human agency; a termite; four species of bush-crickets, all widely distributed elsewhere; a mole-cricket, also widely distributed; eight species of true crickets (with a possible ninth), at least two of them introduced; four widely dispersed species of grasshoppers; a groundhopper; and five species of earwigs, at least four of them introduced. If the list is extended to include the southernmost atoll of the Laccadive Islands, Minikoi, another cockroach, a mantid, another cricket, the Bombay locust, and possibly another groundhopper can be added. The Chagos Archipelago to the south has one more species of cockroach and another cricket that could occur in the Maldives. Most of the non-cosmopolitan orthopteroid fauna seems to be of southern Indian or Sri Lankan origin. No endemic species are known.

Orthopteroid insects as biocontrol agents - a brief review

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Insects may be employed as biocontrol agents to dispose of either animals (usually other insects) or plants that are regarded as being in some way undesirable. Orthopteroids are not among the insects that are generally thought of in this regard. Nevertheless, there has been some attempt to use them in the control of other organisms. Some account of their natural role in regulation will be given, together with on outline of historical examples of attempts to use orthopteroids, some rather dubious cases, and some apparent successes.

Origin of Western Mediterranean Pamphagidae: Tyrrhenian vicariance *versus* dispersion from North Africa

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Until recently many authors considered the Iberian and Sardo-Sicilian Pamphagidae as originating from North Africa stocks that dispersed northward. Evidence is presented here favoring an origin from a Paleotyrrhenian plate, both for Western European and Northern African Pamphagidae, whose stocks have assumed their present distribution after the plate break-down and drift of fragments eastward and southward.

New techniques for chromosome analysis in grasshoppers

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During recent years a certain number of techniques for chromosome analysis emmanating from advances of molecular biology have permitted a deeper understanding of chromosome structure.

In this poster we present the uses and possibilities that these techniques offer in the analysis of grasshopper chromosomes. This allows us to understand the mechanism involved in chromosome evolution and speciation.

A comparison of the orthopteroid insects of Lanzarote and La Palma, Canary Islands, Spain

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The orthopteroid fauna of the disparate, widely separated islands of Lanzarote and La Palma, Canary Islands, Spain, are compared. The species found in each are tabulated, and the insects' habitat preferences, seasonal occurrence, and feeding are discussed.

Does the neo XY sex-determining mechanism condemn the species to an evolutionary dead end?

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The majority of species of Orthoptera have an XO (male) - XX (female) chromosomal mechanism of sex determination. Some species change to a neo-XY system by means of an X-autosome fusion. If successful, the new mechanism becomes definitely established in the species and starts differentiation of the sex pair.

Five species belonging to three unrelated genera present characteristics of old X-autosome fusion and, at the same time, disturbances in the first meiotic prophase.

It is suggested that heterochromatinization of the XR arm in first meiotic prophase or even in late interphase interferes with the transcriptional processes that codify for proteins concerned with the chromosomal architecture. This could be the start of a series of events leading to the decadence and extinction of the species.

Katydids of the Peruvian Amazon (Orthoptera: Tettigoniidae)

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A faunistic study of the katydids of the Amazon Basin of Peru is underway, with surveys made in both the rainforest canopies and understories of three areas east of Iquitos in Loreto Province, northern Peru, and in Tambopata and Manu Forest Preserve in Madre de Dios, southeastern Peru. Prior to this study, 215 species had been reported from the entire country, including highland and coastal areas. We have identified so far 237 phena from the tropical rainforest regions of Peru alone, 96 (or ca. 40%) of which have been associated with already described species. The number of species of the following subfamilies are as follows: Agraeciinae, 17; Conocephalinae, 3; Copiphorinae, 26; Listrocelinae, 8; Pseudophyllinae, 83; Phaneropterinae, 110. Collecting methods at ground level (0-20 feet in the forest vertical profile) differed for each subfamily: most phaneropterines were collected at mercury vapor lights; most copiphorines and all conocephalines were collected by locating acoustical signalling males or by sweeping or by chance encounters; all other katydids (pseudophyllines, agraeciines, listrocelines, and occasionally other subfamilies already mentioned) were visually spotted and collected by hand at night. Canopy species were collected as part of a Smithsonian Biodiversity Research Project using fogging methods modified by Dr. Terry Irwin and associates of that institution.

In addition to surveying the fauna, studies are underway to understand the biology of many of these species. To date, few studies have been made on neotropical katydids. Our studies include predator-prey relationships, daily activity cycles, and pair formation behavior.

Insecticidal seed dressings for grasshopper control in cereal crops

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Recent studies of seed treatments for controlling grasshoppers at the Research Station in Saskatoon, Canada, included two consecutive years of greenhouse tests and two years of field experiments. Results of the green house test indicates that two of the five compounds used were promising, causing 89% and 73% mortality in third-instar grasshoppers (*Melanoplus sanguinipes* (Fabricius), in two days. Five-day tests in the field with the two selected compounds indicate dissimilar trends. Surviving grasshoppers were then treated for their susceptibility to deltamethrin as a contact insecticide. They showed a significantly greater susceptibility to this insecticide. A parallel experiment was conducted to determine the influence of interaction of seed treatments and cultivars on the biotic potential of surviving grasshoppers. Tests indicated that there was a significant interaction in the field.

Morphological and allozyme variation in French populations of *Ephippiger ephippiger* Fiebig (Orthoptera: Tettigonioidea)

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Ephippiger ephippiger Fiebig extends over Europe from Northern Spain to the Netherlands and from Northern Greece to Western Russia. The species is highly polymorphic, especially in Southern France (and Northern Spain) from which at least five taxa have been described. Accordingly, populations of *E. ephippiger* from this area have been the subject of an analysis of morphological characters and enzyme allele frequencies.

The structural characters studies (measurement of the body extremities and male appendages) usually show geographical clines notwithstanding variation within populations. These clines, however, vary from one another geographically. The same applies to the enzyme allele frequencies: variation is clinal and different for each enzyme. Although the genetic distances between populations are within the same range as the genetic distances between *E. terrestris* Yersin subspecies (Landman *et. al.*, 1989), it appears pointless to divide *E. ephippiger* into different taxa within the area of study. The taxa would be arbitrary and their geographic range highly restricted.

A new species of *Xerohippus* Uvarov, 1942 from Almeria, Spain (Orthoptera: Acrididae: Gomphocerinae)

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The genus *Xerohippus,* related to *Eremippus* and *Chorthippus,* was established by Uvarov on the basis of the following main characters: well developed tarsal arolia, distinctly ensiform antennae in both sexes, a pronotal swelling, ventral valves of the ovipositor without a basal tooth or other processes, and the M-area of the tegmina with a weak, often irregular intercalar vein without apparent stridulatory function.

In this paper, we describe a new species of the genus whose main external features are: the smallest size of all known species of the genus, lateral carinae of the pronotum roundly incavated in the prozona and convergent up to the anterior margin, a typical sulcus placed behind the middle, the tympanic opening three times longer than wide, and the tegmina reaching the apex of the hind femora.

The species is found in southeast Spain in dry sunny localities with short, sparse vegetation. The adult occurs from June to January. As all presently known species of this genus are from the oriental Mediterranean area, we name our new species *Xerohippus occidentalis.*

Studies of pathogens, a gap in the research on population dynamics and control of grasshoppers and locusts

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Grasshoppers and locusts are among the most serious insect pests of agriculture in Africa and elsewhere in the world. Studies on grasshoppers and locusts have recently made advances on a wide front (biology, damage surveys, outbreaks, chemical control methods, *etc.)*. However, there is little known about their parasitic microorganisms, some of which might be used in biological control. Our examinations fill this gap. The investigations of pathogens of the natural populations of grasshoppers and locusts made during a period from 1983 to 1987 in Tanzania and Yemen, A.R., revealed the occurrence of 33 new parasites belonging to entomopoxviruses (5), rickettsiae (3), amoebae (1), eugregarines (11) and microsporidians (13).

Large numbers of specimens of the Migratory locust, *Locusta migratoria* (250), Desert locust, *Schistocerca gregaria* (52), Elegant grasshopper, *Zonocerus elegans* (180), Ak grasshopper, *Poekilocerus buffonius-vittatus* (450), Grassland locusts, *Cataloipus fuscocoeruleipes* (815), *Cataloipus pulcher* (395), *Chortipes* sp. (40), *Catantops axillaris* (85), and other orthopterans (125) were collected at different sites in Tanzania and Yemen, A.R. This insect material was brought into the laboratories of the Tropical Pesticide Research Institute in Arusha (Tanzania) and the Yemen-German Plant Protection Project in Sana'a (Yemen, A.R.) and reared under laboratory conditions. The grasshoppers and locusts were successively (3-5 day intervals) examined for pathogens by means of light, Nomarski interference, and electron microscopy.

Among other microbial agents (rickettsiae, amoebae and microsporidians) —the eugregarines are typical gut commensals in that they do not produce any pathological effect in the host-animal— the entomopoxviruses have great potential as an alternative to chemical pesticides; they could hold a leading place in grasshopper and locust control. The entomopoxviruses have many positive features that suit them for biological control: highly pathogenic, chronic nature of disease, relatively easy production of occlusion bodies, and others. For global strategy, special attention should be paid to experiments on possible beneficial interactions between virus isolates (following dual or triple infection experiments) or combined use of entomopoxviruses with other microbial agents or chemical pesticides.

A classification of the Tettigoniinae of the world

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Eighty-two characters were assessed for more than 100 genera or Tettigoniinae to determine if there is any justification in retaining the Decticinae as a separate taxon. It was also considered opportune to determine the relationships of the group on a worldwide basis in light of recent revisionary studies of the group in the Southern Hemisphere. A phenetic procedure was used to formulate the analysis. Five distinct groups seem apparent from the study, and these are designated as tribes. They reflect reasonable zoogeographic congruence.

The Australian Saginae

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Recent studies by Kaltenbach have raised the question of the real relations between the Australian katydid genera usually ascribed to the Saginae and the typical Old World sagines. A comparative study is currently underway to determine these relations. Approaches and procedures will be discussed and characters used in the analysis will be illustrated.

Acoustic interaction in *Amblycorypha parvipennis* Stal (Orthoptera: Tettigoniidae: Phaneropterinae)

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Conspecific males of singing Orthoptera compete acoustically for females. This acoustic interaction (chorusing) may show predictable temporal relationships, such as alternation and synchrony, between song units of adjacent males. *Amblycorypha parvipennis* Stal is unique among the singing Orthoptera; adjacent singing males alternate and overlap song phrases (groups of phonatomes) and, where phrases overlap, phonatomes (sounds produced by single wingstrokes) are synchronized.

Shortening the distance between pairs of chorusing males alters their chorusing behavior. Compared to males singing 3.3 m apart, males 20 cm apart produce fewer phrases per unit time, longer intervals between phrases, and overlap a shorter portion of their partner phrases. A katydid may slow its phrase rate because it is inhibited by a longer portion of its partner's phrases falling between its own phrases. Males singing more slowly during chorusing than when soloing support the idea that males are inhibited from singing during much of the phrase of another katydid.

When a sound-producing ("ticking") female is present, paired males also alter their chorusing behavior. Males eventually chosen by females produce longer phrases and begin more phrases after the end of their partner's phrases (rather than overlapping them) than vice-versa.

Phaneropterine females typically tick at species-identifying intervals following song phrases of males. *Amblycorypha parvipennis* females are unique in that their ticks may fall in between phonatomes of males as well as follow the end of phrases. Synchrony of phonatomes probably helps males perceive alternated female ticks.

The possible adaptive values of the unique male-male and male-female acoustic interaction of *A. parvipennis* will be discussed.

The third form of *Anechura harmandi* (Burr) (Dermaptera: Forficulidae)

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Anechura harmandi (Burr) is known as a polymorphic species; that is, there are two kinds of male forceps, slender microlabia and thick macrolabia. They are often recognized taxonomically as forms *lewisi* and *harmandi,* respectively. In Japan only macrolabial adult males were collected from the west of Lake Biwa and Chugoku District, while the eastern populations in Chubu and Kanto Districts always consisted of microlabial, macrolabial, and intermediate forms.

On the other hand, a third form with a larger body and forceps and differing from the above in forceps morphology was found at Soeda in Kyusyu District. The forceps were as thick as macrolabia, longer than those of macro- and microlabia, intermediate between them in curvature or the inflection point of the forceps, and had the single-peaked or double-peaked process of the forceps. They differed from the double-peaked process in macrolabia and microlabia. Thus, the males from the Soeda population may be distinguished as a distinct third form.

The possible role of allometry in cricket speciation

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Although speciation is a crucial aspect of evolution potentially affecting our entire interpretation of nature, there is disagreement regarding the mechanism of speciation. Three alternative mechanisms are briefly reviewed: relational tuning, environmental tuning, and allometric speciation. Of these three mechanisms, allometric speciation is by far the least well studied. Some evidence justifying further investigation of consequences of the concept allometric speciation is discussed. It is argued that a detailed study of the possible role of allometry in speciation is desirable.

Some data concerning the pericentric inversion in the S_{11} chromosome of *Aiolopus strepens* Latreille in natural populations of Granada

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All seven analyzed populations of the grasshopper *Aiolopus strepens* Latreille showed variation in the morphology of the S_{11} chromosome caused by a pericentric inversion arising from a metacentric S_{11} from a standard subtelocentric one. The metacentric S_{11} chromosome showed a similar frequency in both sexes which was consistent with random segregation of the X chromosome and the heteromorphic S_{11} bivalent at the first meiotic division in heterozygous males. All populations showed a similar low frequency of metacentric S_{11} chromosomes, and genotypic frequencies were consistent with the Hardy-Weinberg equilibrium.

Several chromosome banding techniques (C, G, N, and fluorescence) demonstrated the presence of a paracentromeric band in all chromosomes besides an interstitial one in the L_3, M_9 and S_9 chromosomes. None of these banding patterns seems modified by the S_{11}-inversion except for the local change of position of its paracentromeric band.

Finally, the S_{11} inversion causes a decrease in mean chiasma frequency in heterozygous males and appears to have some influence on nucleolar organizing regions (NORs) activity.

C-Banding and fluorescence in species of the family Tetrigidae (Orthoptera: Tetrigoidea)

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We have analyzed the location and nature of constitutive heterochromatin in six species of the family Tetrigidae: *Mishtshenkotetrix brachyptera* (Lucas), *Paratettix meridionalis* (Rambur), *Tetrix bipunctata* (Linne), *T. bolivari* (Saulcy), *T. depressa* (Brisout), and *T. undulata* (Sowerby). All individuals were collected in the Sierra Nevada and the Sierra de Alfacar Mountains, Granada, southern Spain.

All specimens studied showed a C-banding pattern consisting of paracentromeric C-bands. We also obtained (except in *T. depressa)* reactions to treatment with the chromomyciny (R-bands) and DAPI (DA-DAPI bands) fluorochromes. These results lead us to reinterpret the possible nature of constitutive heterochromatin in the above-mentioned species.

A diversity of mantis ears: evolutionary implications*

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Some praying mantises possess an acute auditory sense mediated by a single tympanate auditory organ located in the ventral midline of the metathorax. This ear is sensitive almost exclusively to ultrasound. I have examined museum specimens representing 330 of the 400 mantis genera and have recorded physiological audiograms from 31 species (29 genera) to determine how much variation in ear structure and function exists within the suborder Mantodea.

At least 5 distinct anatomical types of metathoracic groove (the primary structural component of the ear) occur among mantises. Only one of these is consistently associated with sensitive ultrasonic hearing.

Two of the other groove types are found primarily in the females of species with strong sexual dimorphism in hearing. While such dimorphism is rare in other tympanate insect groups, it is present in 34% of the mantis genera sampled. These two types are widely but patchily distributed in the three largest families, and they may represent stages of secondary reduction of the ultrasound-sensitive ear.

A fourth type may represent the primitive condition for the metathoracic groove. It is found in the Chaeteesidae, a mantis showing many primitive traits. It resembles the groove of newly hatched nymphs as well as the homologous region of the primitive cockroach *Cryptocercus*. Its distribution (compared with that of the presumably derived ultrasound-sensitive ear) does not, however, fit well within existing taxonomic schemes for the Mantodea.

Both among taxa and within species that are sexually dimorphic in hearing, a strong correlation often exists between the presence of long, presumably functional wings and ultrasonic hearing (the converse also holds). This finding supports the hypothesis that hearing in mantises serves as part of a defensive system against echolocating, insectivorous bats.

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