

FLORIDA ENTOMOLOGIST

(An International Journal for the Americas)

Volume 69, No. 1

March, 1986

TABLE OF CONTENTS

Announcement 69th annual meeting and call for papers	i
THE FLORIDA ENTOMOLOGICAL SOCIETY'S FIRST CARIBBEAN CONFERENCE OF ENTOMOLOGY	1
POPENOE, H.— <i>The International Dimensions of Florida Agriculture: A Syn- opsis</i>	3
BRAITHWAITE, C. W. D.— <i>IICA Plant Protection Programme in the Caribbean A Case of Technical Cooperation in Agricultural Development Assist- ance</i>	5
SHANKLAND, D. L., AND H. N. NIGG— <i>An Environmental Toxicology Program for Florida</i>	15
HOLLIS, W. L.— <i>Cooperative Industry Efforts with Developing Countries to Im- prove Agrochemical Registration, Labeling and Education and Training Programs</i>	21
KING, A. H.— <i>Latin American Entomological Serials</i>	30
<hr/>	
SYMPOSIUM: INSECT BEHAVIORAL ECOLOGY—85	
WALKER, T. J.— <i>Stochastic Polyphenism: Coping With Uncertainty</i>	46
RAUSHER, M. D.— <i>Competition, Frequency-Dependent Selection, and Diap- pause in Battus philenor Butterflies</i>	63
MCNEIL, J. N.— <i>Calling Behavior: Can It Be Used to Identify Migratory Species of Moths?</i>	78
QUINN, J. S., AND S. K. SAKALUK— <i>Prezygotic Male Reproductive Effort in Insects: Why do Males Provide More Than Sperm?</i>	84
PIERCE, J. D., JR.— <i>A Review of Tool Use in Insects</i>	95
MORIN, J. G.— <i>"Firefleas" of the Sea: Luminescent Signaling in Marine Ostra- code Crustaceans</i>	105
TURNER, M. E.— <i>Multiple Mating, Sperm Competition and the Fertility Com- ponent of Fitness in Drosophila pseudoobscura</i>	121
LLOYD, J. E.— <i>Behavior Ecology Milestones</i>	129
<hr/>	
SYMPOSIUM: USE OF PHEROMONES IN TROPICAL CROPS	
MITCHELL, E. R.— <i>Preface</i>	131
MITCHELL, E. R.— <i>Pheromones: As the Glamour and Glitter Fade—The Real Work Begins</i>	132
SILVAIN, J. F.— <i>Use of Pheromone Traps as a Warning System Against Attacks of Spodoptera frugiperda Larvae in French Guiana</i>	139
DICKERSON, W. A.— <i>Grandlure: Use in Boll Weevil Control and Eradication Programs in the United States</i>	147
WHITCOMB, W. H., AND R. M. MARENGO— <i>Use of Pheromones in Boll Weevil Detection and Control Program in Paraguay</i>	153
SIVINSKI, J. M., AND C. O. CALKINS— <i>Pheromones and Parapheromones in the Control of Tephritids</i>	157

Continued on Back Cover

Published by The Florida Entomological Society

FLORIDA ENTOMOLOGICAL SOCIETY

OFFICERS FOR 1985-86

<i>President</i>	D. H. Habeck
<i>President-Elect</i>	D. J. Schuster
<i>Vice-President</i>	J. L. Taylor
<i>Secretary</i>	E. R. Mitchell
<i>Treasurer</i>	A. C. Knapp

<i>Other Members of the Executive Committee</i>	}	M. L. Wright, Jr.
		J. E. Eger, Jr.
		R. C. Bullock
		G. Mathurin
		A. Gettman
		C. G. Witherington
	J. R. McLaughlin	

PUBLICATIONS COMMITTEE

<i>Editor</i>	J. R. McLaughlin
<i>Associate Editors</i>	A. Ali
	C. S. Barfield
	J. B. Heppner
	M. D. Hubbard
	O. Sosa, Jr.
	H. V. Weems, Jr.
	W. W. Wirth
<i>Business Manager</i>	A. C. Knapp

FLORIDA ENTOMOLOGIST is issued quarterly—March, June, September, and December. Subscription price to non-members is \$30.00 per year in advance, \$7.50 per copy. Membership in the Florida Entomological Society, including subscription to *Florida Entomologist*, is \$25 per year for regular membership and \$10 per year for students. Inquires regarding membership, subscriptions, and page charges should be addressed to the Business Manager, P. O. Box 7326, Winter Haven, FL 33883-7326. *Florida Entomologist* is entered as second class matter at the Post Office in DeLeon Springs and Winter Haven, FL.

Authors should consult "Instructions to Authors" on the inside cover of all recent issues while preparing manuscripts or notes. When submitting a paper or note to the Editor, please send the *original* manuscript, *original* figures and tables, and *3 copies* of the entire paper. Include an abstract and title in Spanish, if possible. Upon receipt, manuscripts and notes are acknowledged by the Editor and assigned to an appropriate Associate Editor who will make every effort to recruit peer reviewers *not* employed by the same agency or institution as the authors(s). Reviews from individuals working out-of-state or in nearby countries (e.g. Canada, Mexico, and others) will be obtained where possible. Page charges are assessed for printed articles.

Manuscripts and other editorial matter should be sent to the Editor, JOHN R. McLAUGHLIN, 4628 NW 40th Street, Gainesville, FL 32606.

This issue mailed May 23, 1986

THE 69th ANNUAL MEETING OF THE
FLORIDA ENTOMOLOGICAL SOCIETY
ANNOUNCEMENT AND CALL FOR PAPERS

The Florida Entomological Society will hold its 69th Annual Meeting on 6-8 August 1986 at the Sheraton Sand Key Hotel, Clearwater Beach, Florida. The location is 1160 Gulf Boulevard, Clearwater Beach, Florida 33515; telephone—1-813-595-1611. Room rates will be \$66.00 either single or double. Pre-registration and registration fees will be released in the June, 1986 *Florida Entomologist* and the April Newsletter.

Since many will present papers please copy the sheet and submit before 1 June 1986, to:

JAMES L. TAYLOR, Chairman
Program Committee, FES
P. O. Box 1893
Sanford, Florida 32771
Phone: 1-305-322-5716

Eight minutes will be allotted for presentation of oral papers, with 2 minutes for discussion. In addition, there will be a separate session for members who may elect to present a Project (or Poster) Exhibit. The three oral student papers judged to be the best on content and delivery will be awarded monetary prizes during the meeting. Student authors *must* be Florida Entomological Society Members and *must* be registered for the meeting.

- Oral Presentation
- Project Exhibit Session
(Poster Session)
- Student Paper

Return to: James L. Taylor
Merck & Co.
P. O. Box 1893
Sanford, FL 32771

DEADLINE: 1 June 1986

Author's Name _____

Title of Paper _____

Affiliation and Address _____

of the First _____

(Presenting) Author _____

Abstract: *Must* be Provided. Do *not* use more than 75 words.

All submitted papers should be designed to be 8 minutes long with 2 minutes for discussion; visual materials must be restricted to 2x2 slides or overhead projector transparencies.

THE FLORIDA ENTOMOLOGICAL SOCIETY'S
FIRST CARIBBEAN CONFERENCE OF ENTOMOLOGY
August 5-8, 1985

Ocho Rios, Jamaica, West Indies

Some came to enjoy the splendor of Jamaica, others to share entomological information and discuss common interests in insect biology and control, but all were treated to an incredible potpourri of Caribbean agriculture. We advisedly selected Ocho Rios, Jamaica, as the site for the first meeting because of the Jamaicans' desire to participate, the relevance of their agriculture to other areas of the Caribbean, the relative political neutrality and security of the country, and the availability of required logistical services. Aesthetic appeal also was important, along with a diversity of associated activities such as field trips to see crops and their associated harmful and beneficial insects, natural sites for collecting insects, and existing entomological collections and expertise. Our ambitious objectives for this pioneering meeting were to strengthen professional relationships with colleagues in entomology and plant protection, foster collaboration among Caribbean, Latin American, and U. S. scientists, encourage the exchange of scientific information on tropical and subtropical entomology as it impinges on agricultural production and product protection, expose practitioners to the technical problems and singular opportunities associated with developing tropical agriculture, and ultimately evaluate the Caribbean Conference and determine if others should be held. From the onset, we felt that the potential pay-offs of such a meeting could be enormous.

We were welcomed to the island on Tuesday morning, August 5, by Dr. Osmond Tomlinson, Custos of St. Ann Parish including Ocho Rios, who piqued our curiosity about current and historical associations among countries that lie within or border the Caribbean. This provocative introduction, the keynote address, and four invitational papers preceded a symposium on the "Biology and Control of Coffee Pests" organized and presided over by Ms. Janice Reid of Jamaica. Topics included the coffee berry borer, other pests of coffee, and both chemical and biological control. Submitted papers on crop protection moderated by Dr. Gary Leibeck followed describing the coffee leaf-miner in Puerto Rico; pink bollworm in Peru; mites in Central America and the West Indies; the potato tuber moth in Venezuela; *Liriomyza*, weevils, fruit flies, and insecticide testing in Florida; and cultural and chemical control of bean slug in Honduras. The afternoon was consumed by concurrent sessions with Dr. Russ Mizell's urban entomology and Dr. Emil Moherek's crop protection papers opposite those on citrus and medical entomology moderated by Dr. Bob Bullock and Dr. Arshad Ali, respectively. The exceptionally wide range of subjects were presented by speakers from Guadeloupe, Canada, Jamaica, Cayman Islands, and the U.S. The traditional "Behavioral Ecology" symposium produced by Dr. Jim Lloyd and "Student Paper Contest" officiated by Dr. Nan-yo Su on Wednesday were accompanied by poster exhibits and Dr. Everett Mitchell's symposium on the "Use of Pheromones in Tropical Crops". Thursday morning was devoted to "Biological Control" under Dr. Fred Bennett and "Crop Protection in Small Farm Systems" with Dr. Keith Andrews. Of the 98 non-student papers listed in the program, 33 were from other than U.S. with participation by a total of 14 countries.

One of the highlights of the meeting was a Thursday afternoon and evening "Citrus Tour" organized by Dr. Joe Knapp and conducted by Dr. Villi Bent. We traveled south through the central highlands of Middlesex to groves near Linstead. There we gathered in the field to meet Mr. Walter van Whervin, the Ministry of Agriculture's Chief of Plant Protection. Others present from Jamaica included Mr. David McConnell (Chair-

man, United Estates Limited), Mr. Mark McConnell (Managing Director, United Estates Limited), Mr. Robert Clarke (Manager, Worthy Park Farms), Mr. Winston Miller (Manager, Winston A. B. Miller, Ltd.), Mr. Ken Newman (Managing Director, Wakefield Farms, Ltd.), Mr. S. S. Stons (Project Manager, Citrus Rehabilitation Scheme), Mr. Crook (Expatriate Advisor), Mr. L. A. Bell (Extension & Research Officer), Mr. Amir (Expatriate Advisor, World Bank Fund), Mr. W. E. Tavares (Field Manager, United Estates, Ltd.), and Mr. L. V. Bowie (Ass't. Field Manager, United Estates, Ltd.). After this brief but impressive ceremony, the owners (David, Peter, Stuart and Mark McConnell) showed us fields of orange trees, sugarcane, and coconut palms. Among other things, they explained cultural practices and experiments designed to control the citrus root weevil. Our next stop was a nursery for citrus and tropical fruit, such as guava and passionfruit, that supplied the plants for new groves. Finally, we entered the St. Thomas-Ye-Vale Valley that had such a severe infestation of citrus root weevils that we were able to collect specimens merely by walking around the trees. On the way home, to our surprise and delight, our hosts treated us to a veritable feast of delicate meat pies and pastry served with hand-squeezed orange and tropical fruit juices. The tour was enjoyed and appreciated by all as a special experience in agriculture, science, natural history, and Jamaican hospitality.

At the traditional "Bull Session", we had an opportunity to ask those in attendance to fill out a brief questionnaire and carry on a rather lengthy discussion about how they would evaluate this first international venture. In summary, the group responding there (and later) voiced overwhelming support for the Florida Entomological Society to continue to hold periodic meetings in the Caribbean Basin. Instead of every 5 years, most felt that a 3 year schedule was even better.

It occurred to us that most of the stated objectives of the Caribbean Conference were accomplished and that this success should be documented. Therefore, we assembled the keynote address, opening invitational papers and a listing of "Latin American Entomological Serials" into a single unit for publication in *Florida Entomologist*. Dr. Hugh Poponoe put in perspective the commonality of agriculture in countries that share the Caribbean, Dr. Chelston Brathwaite identified the primary agricultural institutions of the Caribbean and briefly discussed the functions of each, efforts to effectively monitor and control hazardous chemical waste in Florida, a relevant problem for other areas of the Caribbean, were described by Drs. Dan Shankland & Herb Nigg, and an international "crisis" in pesticide development, production, and regulation in developing countries was exposed by Dr. Bill Hollis. The serials list was compiled by Ms. Ann King. We sincerely thank all the participants for their contributions to this first international Caribbean Conference on Entomology.

C. S. Barfield and N. C. Leppla
Local Arrangements Committee

THE INTERNATIONAL DIMENSIONS OF
FLORIDA AGRICULTURE:
A SYNOPSIS

H. L. POPENOE

Director for the Center for Tropical Agriculture
University of Florida
Institute of Food and Agricultural Sciences
Gainesville, Florida 32611 USA

ABSTRACT

There are very close bonds that exist among agricultural scientists and practitioners in the Caribbean Basin. Florida shares a common ecology and common crops with Caribbean nations to a greater degree than with most states in the contiguous United States. Thus, continuing and emerging entomological problems in Florida require sharing of information and cooperative research efforts with other members of the Caribbean community.

RESUMEN

Existen estrechos vínculos entre los científicos agrícolas y practicantes en el área del Caribe. La Florida comparte una ecología y cultivos en común con naciones del Caribe en un mayor grado que con la mayoría de los estados contiguos de los Estados Unidos. De aquí que continuos y salientes problemas entomológicos en la Florida requieren el intercambio de información y esfuerzos cooperativos de investigación con otros miembros de la comunidad del Caribe.

We truly live in an interdependent world. In entomology, perhaps more than any other science related to agriculture, both our problems and their solutions are often to be found in some other country. This is especially true throughout the Caribbean Basin where a large number of tropical and sub-tropical countries are in close proximity. The United States is clearly represented in the region through the state of Florida. This explains, to a great extent, Florida's affinity to the Caribbean and underscores the importance of international programs (Fig. 1).

Florida is a peninsula surrounded by water. It doesn't share common ecology or common crops with other states. We actually have more in common agriculturally with nations to the south than with most states in the contiguous United States. Thus, since Florida shares agricultural and urban problems related to entomology with virtually every country in the Caribbean, information is shared across international boundaries.

An opportunity exists for us to conduct cooperative research on incipient pests, those that have been controlled or eradicated but remain a constant threat, and even some that are currently of unknown importance. Hopefully, these activities will continue to serve as an early warning system and prepare researchers to deal with damaging insects that are detected within our borders. The international dimension of this work allows us to be prepared for the current and potential realities of introduced agricultural pests.

In Florida agriculture, entomologists have been repeatedly called on to solve novel problems, in record time, to save growers, producers and consumers estimated millions of dollars. This phenomenon has become an expectation rather than an extraordinary feat. Through the cooperative efforts of our international programs we are often able



Fig. 1. Caribbean Basin Map emphasizing the proximity of Florida. (Source unknown)

to anticipate problems before they emerge and predict the outcome of available insect control practices. This shared knowledge and the collaboration of international scientists has proven its worth time and again.

Recent examples of continuing or emerging problems and allied foreign research programs include work on medflies, citrus blackflies, mole crickets, fire ants, sugarcane rust, citrus canker, and lethal yellowing of coconuts. We also have cooperative projects on insect-related livestock diseases; African swine fever, heartwater disease, blue tongue, and equine encephalitis have been of particular importance.

International programs also give us an opportunity to better manage our crops, develop new commodities, and open or expand markets. Increasingly populous and cosmopolitan societies of the Caribbean community (including Florida) demand a greater quantity, quality, and variety of food and fiber. Therefore, we have established cooperative efforts on various crops including winged bean, malanga, carambola, sugarcane and rice.

Specifically, the Government of Jamaica and the University of Florida have had cooperative projects in such diverse areas of mutual interest as: agricultural mechanization and dairy cooperatives with the Ministry of Agriculture; the Jamaica School of Agriculture through the Ministry of Education; Lethal Yellowing of coconut in conjunction with the Coconut Board; and, more recently, the Farming Systems Support Project and agricultural marketing with EXPO 21. We have also had individual scientists working on muck soils, sugarcane, root crops, aquaculture, and parasites to control insects and nematodes.

The Florida Entomological Society is to be commended for its decision to hold its 68th Annual Meeting in Jamaica, emphasizing the international dimension of its activities. It is a fitting recognition and a tribute to the very close bonds that exist among agricultural scientists and practitioners in the Caribbean Basin. Hopefully this is a precedent for future opportunities for the Society to be hosted by other countries in the region, to exchange information, promote friendship and further collegial relations.



IICA PLANT PROTECTION PROGRAMME
IN THE CARIBBEAN
A CASE OF TECHNICAL COOPERATION IN
AGRICULTURAL DEVELOPMENT ASSISTANCE

CHELSTON W. D. BRATHWAITE
Regional Plant Protection Specialist
IICA Office in Trinidad and Tobago

ABSTRACT

The IICA Plant Protection Programme for the Caribbean seeks to promote and support the efforts of the countries of the Caribbean to prevent and reduce crop losses caused by pests, diseases and weeds. The programme, which was started in 1981, has as a fundamental strategy reciprocal technical cooperation where the experiences and technical information of some countries are used in a transfer of technology to others utilising human resources, information exchange and mechanisms for communication. The establishment of a Society for Plant Protection in the Caribbean, the establishment of a Regional Plant Protection Newsletter and annual meetings of Heads of Plant Protection represent the major mechanisms in this technical cooperation package.

Attempts to harmonize pesticide legislation and the training and certification of Plant Quarantine Inspectors represent approaches to standardize the legislative aspects of Plant Protection in the region.

Initiatives have also been focused on survey and eradication studies and proposals are imminent to set up a data base of Plant Protection information for the Caribbean.

RESUMEN

El Programa de Protección de Plantas IICA para el Caribe busca promover y apoyar el esfuerzo de los países del Caribe para prevenir y reducir pérdidas, en los cultivos causadas por plagas, enfermedades y malezas. El programa que comenzó en 1981, tiene como estrategia fundamental la reciprocidad de cooperación técnica donde la experiencia e información técnica de algunos países son usadas en una transferencia de tecnología a otros utilizando fuentes humanas, intercambio de información, y mecanismos para la comunicación. El establecimiento de una Sociedad para la Protección de Plantas en el Caribe, el establecimiento de un Boletín Regional para la Protección de Plantas, y una reunión anual de los Directores de Protección de Plantas, representan los principales mecanismos en este paquete de cooperación técnica.

Intentos para armonizar legislación sobre pesticidas y el entrenamiento y certificación de Inspectores de Cuarentena de Plantas, representan acercamientos para hacer uniforme los aspectos de Protección de Plantas en la región.

Tabién se han concentrado iniciativas sobre estudios de encuesta y erradicación, y proposiciones para establecer una base de datos de información sobre Protección de Plantas para el Caribe son inminentes.

WHAT IS IICA

The Inter-American Institute for Cooperation on Agriculture—IICA—is an international, inter-governmental organization specialized in agriculture. It is governed by its own Convention and has been recognized as a specialized Inter-American Agency under the Charter of the Organization of American States.

The purposes of IICA are to “encourage, promote, and support the efforts of the Member States to achieve their agricultural development and rural well-being”.

The Institute was founded in 1942 as the Inter-American Institute of Agricultural Sciences. On December 8, 1980, a new Convention was ratified. Under this new Convention, the Institute changed its name to the Inter-American Institute for Cooperation on Agriculture, expanded its purposes and altered its institutional structure.

IICA has 29 Member States: Argentina, Barbados, Bolivia, Brazil, Canada, Chile, Colombia, Costa Rica, Dominica, Dominican Republic, Ecuador, El Salvador, Grenada, Guatemala, Guyana, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Peru, Saint Lucia, Suriname, Trinidad and Tobago, United States of America, Uruguay and Venezuela. Twelve Observer Countries contribute to Institute activities: Austria, Belgium, Egypt, France, Germany, Israel, Italy, Japan, Korea, the Netherlands, Portugal and Spain. IICA has a technical staff of 180 international professionals. Around 1,200 persons are working for the Institute throughout the hemisphere.

IICA's resources flow from annual quotas which the member countries commit themselves to pay each year. Funds also derive from agreements, contracts, contributions, and grants for which the Institute signs with other national and international organizations. For 1984, the Institute's highest governing body, the Inter-American Board of Agriculture, has approved a budget of 37 million dollars.

IICA's Director General is Venezuelan scientist and educator, Dr. Francisco Morillo Andrade. The Deputy Director is Dr. Quentin M. West of the United States.

WHAT IICA DOES

IICA concentrates its action in ten hemisphere-wide programs, which provide a framework for the annual performance of over a thousand activities. These activities are carried out through agreements reached with the Governments of the Member States, and are in the hands of decentralized technical teams covering the 29 Member Countries.

IICA's hemisphere-wide programs are: Formal agricultural education; Support of national institutions for the generation and transfer of agricultural technology; Conservation and management of renewable natural resources; Animal health; Plant protection; Stimulus for agricultural and forest production; Agricultural marketing and agro-industry; Integrated rural development; Planning and management for agricultural development and rural well-being; and Information for agricultural development and rural well-being.

The specific objectives over the medium term have been defined in accordance with the general objectives and overall strategy of IICA, and on the basis of the concepts of agricultural development and rural well-being that are put forth in the guidelines for the Institute's general policies. These specific objectives include cooperating with the Member States through:

a. Bringing about the growing, effective participation of rural dwellers, especially the low-income strata, in decision-making on projects affecting them, seeking to incorporate them fully into the benefits of economic and social progress.

b. Developing human resources by promoting formal and non-formal training, to improve productive efficiency and promote the participation of the rural population in processes for achieving rural well-being.

c. Developing and consolidating national systems for the generation and transfer of technology, in order to help each country fit itself into the regional and world technological framework. This would be done for the purpose of improving both agricultural and forest production and productivity, preventing and reducing losses to pests and diseases in crops and herds, and maximizing the use and conservation of renewable natural resources.

d. Developing policies, mechanisms and tools for stimulating the efficient production and marketing of inputs and of agricultural, livestock and forest products, domestically and internationally.

e. Reinforcing regional and integrated rural development institutions for planning and implementing integrated projects, so as to coordinate institutional action and provide for the effective participation of beneficiaries.

f. Reinforcing public and private institutional systems in the many facets of setting national goals, planning, and implementation at all levels, on the basis of the retrieval and analysis of information for better defining and implementing policies and programs of agricultural development and rural well-being, and for establishing IICA's own priorities for action.

THE PLANT PROTECTION PROGRAMME

The Ministers of Agriculture attending the VII Inter-American Conference of Agriculture held in Honduras in 1977 expressed their concern regarding the disease problems of plants and animals throughout the Western Hemisphere. Two of the ten recommendations made at this conference refer to this subject. The Special Committee of the Eighteenth Annual Meeting of IICA Board of Directors held in October, 1978 recommended that the Director General of IICA study a proposal aimed at the establishment of a mechanism for the coordination of efforts to fight pests and disease problems affecting animals and plants and which are the cause of significant losses in the Hemisphere.

As a result of these directives, IICA has established a Hemispheric Plant Protection Programme designed to prevent, control and if possible, eradicate diseases and pests which cause economic damage to crops in the Hemisphere and which threaten to spread to other regions. The programme is made up of a Programme Director stationed at IICA headquarters in San Jose, Costa Rica and four Plant Protection Specialists, one stationed in each of the four regions of the Hemisphere. The Plant Protection Specialist for the Caribbean is Chelston W. D. Brathwaite, Plant Pathologist stationed in the IICA Office in Trinidad and Tobago.

In accordance with IICA's basic strategy, this programme is directed towards strengthening national and regional efforts being carried out by other organizations. It is designed to support, coordinate and collaborate with other International, regional and subregional institutions working in this area and in no case will duplicate or replace existing institutions.

The programme recognises that the spread of pests, diseases, and weeds that affect basic food and export crops aggravate the food, foreign exchange and energy needs of the Latin American and Caribbean countries. Coordinated international action can contribute to reducing the spreading and incidence of these pests, weeds and diseases, since the individual capabilities of national plant protection institutions are usually limited by low levels of physical, human and financial resources with which to attain their objectives.

General Objective of the Programme—To promote and support the efforts of the countries to prevent and reduce crop losses caused by pests, diseases and weeds.

Specific Objectives of the Programme—To cooperate with the countries in expanding and improving their institutional capability to:

a. Update and standardize national and international legal provisions and regulations governing plant protection.

b. Identify, detect and estimate the damage caused by the main crops pests, diseases and weeds.

c. Plan, coordinate and implement programs for reducing the incidence and prevent-

ing the spread of the main crop pests, diseases and weeds.

d. Plan, coordinate and implement research and technical exchange programs on crop pests, diseases and weeds.

e. Generate mechanisms for upgrading the physical, human and financial resources of plant protect institutions, according to the levels of responsibility that have been assigned them.

Strategy of the Programme—To promote and support:

a. The updating and standardization of national and international legal provisions and regulations governing plant protection (quarantine and pesticides).

b. The formulation, implementation and evaluation of multinational projects that involve economically important pests and diseases of mutual interest to several countries.

c. The formulation, implementation and evaluation of high-priority projects at the national level.

d. The use of technical and human resources from other IICA programs, from CATIE, and from national and international institutions with experience in this field.

e. The operational and technical reinforcement of national and international institutions working in this field (OIRSA, FAO, CIP, NAPPO, CIAT, CIMMYT).

f. Coordination with other international agencies.

g. The organization and promotion of meetings, seminars and other events for consultation and orientation to establish working guidelines and priorities for action.

h. The organization of scientific associations for plant protection, that can provide a forum for studying plant health problems in the countries, the subregions and the hemisphere.

i. The participation of farmers' organizations, field workers and the rural population in campaigns to control pests and diseases, as well as in quarantine measures.

The Heads of Plant Protection of IICA Member States in the Caribbean met in San Jose, Costa Rica from 15-17th August, 1979, and again from July 27-29th, 1980 in Barbados. The objectives of these Meetings were to formulate a plan of action for the Caribbean within the Hemispheric Plant Protection Programme.

The Meeting in Barbados had as its objectives:

1. To analyse the programme objective to make them more precise, more limited in scope and more realistic in relation to the financial resources of IICA.

2. To establish lines of priority from among the various proposals made at the Meeting in Costa Rica.

3. To establish mechanisms for coordination with Regional and International Plant Protection Organizations.

The result of this Meeting formed the basis for the orientation of the Programme at the Regional level. The priorities identified included:

1. Training courses in Plant Quarantine and General Plant Protection.

2. Strengthening post entry Quarantine facilities.

3. Control and eradication of new pests and diseases.

4. Establishment of a Society for Plant Protection in the Caribbean.

5. Establishment of a Regional Newsletter.

The programme recognised the existence of several institutions concerned with plant protection in the Caribbean. These include:

—The Commonwealth Institute of Biological Control with its track record in the biological control of pests.

—The Caribbean Agricultural Research and Development Institute (CARDI) with its work in research and its outreach activities in several of the Islands.

—The Faculty of Agriculture of the University of the West Indies with its research and teaching capabilities.

—Plant Protection divisions of the various Ministries of Agriculture.

The programme, however, recognized that there was no agency that provided a formal mechanism for coordination and cooperation in plant protection and that reciprocal technical cooperation which is so vital in the region because of the lack of plant protection capability in some of the smaller territories and the limited human and financial resources available was not being fostered.

The programme also responded to the need for (1) information on pest and disease control and (2) lack of professional stimulation among professionals in Ministries of Agriculture, lack of access to Scientific journals and lack of trained sub-professionals in plant protection and plant quarantine.

In recognition of these challenges, the following are some of the achievements to date:

TRAINING—The programme recognises that the improvement of human resources represent one of the most important mechanism for the enhancement of agricultural development. Consequently, training was given high priority in the actions which were carried out. There were three types of training provided:

a. Plant Quarantine Training

Effective Plant Quarantine is necessary for the safe movement of agriculture produce in Regional and International trade. The Heads of Plant Protection in the Caribbean recognized that there is an urgent need for trained plant quarantine inspectors in the Region. Consequently, a Regional Plant Quarantine Training Course was established. The course was held in Trinidad and Tobago in 1982 and in Barbados in 1983.

The course objectives were as follows:

1. To develop and foster among Plant Quarantine Inspectors of the Region an awareness of their mutual responsibility to keep the Caribbean free from foreign pests and diseases.

2. To improve the skills of Plant Quarantine Inspectors in the detection and treatment of plant pests and diseases which pose a threat to Caribbean Agriculture from either Regional or extra-regional sources.

3. To improve communication between Plant Quarantine Inspectors of various territories of the Region.

4. To form the basis for the preparation of a Caribbean Plant Quarantine Training Manual.

The course was designed primarily for inexperienced Plant Quarantine Inspectors and dealt with the general principles of plant quarantine and the duties, responsibilities and requirements of Plant Quarantine Inspectors.

Twenty-one Plant Quarantine Inspectors have been trained so far. This include six from Barbados, two from Dominica, two from Grenada, two from Guyana, one from Haiti, two from Jamaica, one from St. Kitts, one from St. Lucia, two from Suriname and six from Trinidad and Tobago.

b. Integrated Pest Management

In collaboration with Caribbean Agricultural Research and Development Institute (CARDI), the University of the West Indies Faculty of Agriculture and the Consortium for International Crop Protection (CICP) a two week training programme on Integrated Pest Management was held at the Faculty of Agriculture, University of the West Indies, St. Augustine, Trinidad and Tobago 10th-21st, 1981. The seminar was attended by twenty-one participants from thirteen countries in the Region and together with participants from Trinidad and Tobago there was an average daily attendance of thirty-five persons. Lecturers were drawn from the Consortium for International Crop Protection, the University of the West Indies, Ministry of Agriculture of Trinidad and Tobago, the Commonwealth Institute of Biological Control, the Caribbean Agricultural Research and Development Institutes, Caroni Limited and IICA.

The course dealt with the basic concepts of integrated pest management and their application to the solution of pest and disease problems of crops grown in the Caribbean. While most participants expressed a high level of satisfaction with the training programme, it was the opinion of all that a more sustained effort and long-term training in this area was necessary. Certificates were presented at the end of the course.

c. Specialized Training

1. Training for the detection of pests in containerized cargo—Two officers of the Ministry of Agriculture, Lands and Food Production were training in this subject area.

2. Training in Acarology—An officer of the Ministry of Agriculture, Lands and Food Production was trained in Acarology.

3. Training in postharvest losses—Provided to an officer of a Research Institute in Trinidad and Tobago and in seed pathology for officers in Jamaica.

INFORMATION—In several of the Islands, access to current scientific literature is lacking; therefore, the programme introduced The Caribbean Plant Protection Newsletter in 1981. The Newsletter, which is distributed annually, collects relevant information from the scientific journals and from research in the region and makes it available in the form of abstracts to plant protection personnel throughout the region. It publishes information on the following:

1. New research findings in the Caribbean.
2. New research findings elsewhere which are relevant to the region.
3. Abstracts of relevant literature.
4. Information on conferences and meetings.
5. Activities of plant protection personnel and institutions in the Caribbean.
6. IICA's Regional Plant Protection Programme.
7. Information on new equipment, pesticides, etc.
8. Feature articles on regional plant protection matters.

A new feature has recently been introduced where readers of the newsletter can obtain photocopies of the original articles from the editor.

In addition to the newsletter the programme has published a document entitled "A Bibliography of Plant Disease Investigations in the Caribbean from 1880-1980". This publication, which contains references to cover 3,000 publications on plant disease work in the Caribbean, is intended to serve as a reference source for Plant Pathologists, Nematologists, Agronomists, Research students and other persons interested in Agriculture in the Caribbean.

The Bibliography covers all aspects of plant diseases and their control, including diseases caused by fungi, bacterial, viruses and nematodes. The geographic area covered by the references includes all the territories of the Commonwealth Caribbean. The material covered by the Bibliography dates from the 1880's to 1980. The entries were compiled mainly from primary sources, many of which have not been indexed previously. It would be impossible to list all the titles searched; however, the main sources of information were Agricultural News, Tropical Agriculture, West Indian Bulletin, the Journal of the Jamaica Agricultural Society, the Journal of Agricultural Society of Trinidad and Tobago, and the Annual Reports and Publications of the Departments and Ministries of Agriculture throughout the Region. The Secondary sources included Regional bibliographies on agriculture and related topics and computerised literature searches of the Commonwealth Agricultural Bureau data bases. Copies of this bibliography have been sent to all plant protection personnel in the Caribbean.

A book on Plant Disease Diagnosis was prepared by the Specialist to provide plant protection personnel with an introductory handbook for the practical study of plant diseases. The book outlines the basic steps, facilities and procedures which are necessary for the accurate diagnosis of plant diseases. This publication is especially valuable

to laboratory assistants who are being introduced to Plant Pathology for the first time, to give them the rudimentary principles and techniques which are required for plant disease diagnosis.

THE ESTABLISHMENT OF A MECHANISM FOR PROFESSIONAL STIMULATION—The establishment of a society for plant protection in the Caribbean in 1981 responded to the needs of the region for a professional body to give professional stimulation and also to act as a mechanism for communication and coordination of plant protection activities. The society which now has some 121 members throughout the region has as its objectives the following:

—to strengthen inter-governmental and inter-institutional cooperation in plant protection in the Caribbean;

—to establish a forum for the discussion of plant protection issues affecting Caribbean Agriculture;

—to act as a forum for the exchange of ideas and information among plant protection personnel in the Caribbean;

—to promote and stimulate research and teaching in plant protection subjects, viz., Entomology, Plant Pathology, Weed Science, etc. and to ensure that these are integrated into the discipline of plant protection;

—to stimulate discussion and actions to ensure that the Caribbean environment remains free from contamination by pesticides;

—to carry out all other activities which may be associated with preserving the plant genetic resources of the Caribbean from destruction by pests and diseases as may be defined by the Executive Committee.

IICA assisted in the establishment of the Society for Plant Protection in the Caribbean at the Second Regional Meeting of Plant Protection in Latin America and the Caribbean held in Mexico City in October 1980.

The Society has held two meetings so far. In 1981, it met in Jamaica and discussed urgent plant pests and disease problems in the Caribbean. In 1983, it met in Trinidad and Tobago and discussed the harmonization of pesticides legislation in the Caribbean. A document describing the Society has been prepared and is available.

TECHNICAL SUPPORT—This involves the direct use of the Specialist's expertise in the assistance to the Member States. It involves the answers given to questions of a plant protection nature and it provisions a resource person to assist in the solution of Regional problems. Examples of this would be the assistance given to the Barbados Ministry of Agriculture in the preparation of a Plant Quarantine facility for Cocoa; the advice given to Jamaica on the re-organization of the Plant Quarantine System, and on the design and analysis of plant protection experiments; suggestions for strengthening Plant Quarantine in Guyana; diagnosis of diseases of sugarcane in Haiti and; suggestions for studies on yellow spot disease of sugarcane, Caroni Limited Trinidad and Tobago.

In addition to these specific areas of work a number of studies have been carried out in collaboration with regional and extra-regional institutions. The following are examples of studies carried out:

a. An analysis of Plant Quarantine Systems in the Caribbean in collaboration with Animal and Plant Health Inspection Services (APHIS).

b. Training and Research needs in seed pathology in the Caribbean in collaboration with the Danish Institute for Seed Pathology in developing countries located in Copenhagen, Denmark.

c. Study of the pest risks associated with the movement of agricultural produce between St. Vincent, Grenada and Trinidad and Tobago, (in collaboration with Dr. G. V. Pollard of the University of the West Indies).

d. Study on the economic impact of Moko disease on the economy of Grenada, (in collaboration with Dr. G. V. Pollard of the University of the West Indies).

These studies were designed to generate new information necessary for the implementation of plans within the programme.

RECIPROCAL TECHNICAL COOPERATION—RTC means using the technical skills available in some countries to benefit others through IICA's action as a means of reciprocal transfer of know-how, and the exchange of technical personnel and useful experience. The International Agency acts only to facilitate and finance in the relationship. This was used successfully during the programme in the following activities:

1. Assistance to Grenada in the Control of Thrips of Cocoa—Thrips have been recognized as a severe problem in cocoa production in Grenada. The Government sought the assistance of IICA and Dr. Eslie Alleyne, Entomologist, Ministry of Agriculture, Barbados was contracted by IICA to provide technical assistance in Grenada. Dr. Alleyne's recommendations for the control of thrips in Grenada have been taken seriously by the Ministry of Agriculture authorities and the Chief Plant Protection Officer has now been seconded to Grenada Cocoa Association to manage the thrips problem on a full-time basis.

2. Assistance to the Food and Agriculture Corporation of Trinidad and Tobago in the Assessment of Pest Problems of Banana at Orange Grove—The Food and Agriculture Corporation of Trinidad and Tobago, an Agency set up for corporate action in the agricultural sector under the aegis of the Ministry of Finance and Planning is cooperating with the Orange Grove National Sugar Company of Trinidad and Tobago in the development of a banana enterprise geared to the production of green bananas either for fruit market or use as a basic carbohydrate food item to partially displace rice and other wheat-derived staples. Based on discussions with the Inter-American Institute for Cooperation on Agriculture (IICA) for close cooperation on technical matters, the Corporation sought the assistance of IICA through its national office in Trinidad and Tobago to evaluate the incidence of pest and diseases in the existing plantings of banana at the estate and to develop a strategy for management of these pests and diseases in the future. The study was carried out during the month of May, 1983. Mr. Frank McDonald, Ministry of Agriculture, Guyana, was contracted to look at the Moko disease aspects of the problem.

HARMONIZATION OF PESTICIDES LEGISLATION IN THE REGION—There has been a dramatic increase in pesticide usage in the Caribbean during the last decade and like many parts of the world there is concern with respect to the potential human and environmental hazards of pesticide use. The concept of the harmonization of pesticide legislation and registration requirements in the region stemmed from the initiatives developed by the FAO in 1977 to seek to harmonize the legislative aspects of pesticide use throughout the world. A meeting to consider the harmonization of pesticide legislation and the registration process in the region was held in Trinidad and Tobago under the auspices of IICA and with financial assistance from the National Agricultural Chemical Association (NACA) and GIFAP.

The meeting considered the status of pesticide legislation in the region and established guidelines for harmonization. The meeting had as its objectives:

- to examine and analyse the status of pesticide legislation in the Caribbean;
- to become familiar with measures currently in operation and to recommend others for standardizing the diverse requirements for pesticide use;
- to provide guidelines to those countries that need to enact legislation to regulate the use of guidelines, norms and technical procedures (chemical, analytical, biological, toxicological);
- to examine the status of establishment or acceptance of the maximum residue levels of pesticide (tolerance) in food in each country;
- to analyse the environmental impact of the large scale application of pesticides in the Caribbean;

—to stimulate training in pesticide registration procedures and in the safe and efficient use of pesticides.

Forty-five delegates from throughout the Caribbean and from Regional and International Organizations attended the meeting.

The meeting recommended, among other things, that the Pesticide and Toxic Chemicals Act of Trinidad and Tobago should be used as a model in the formulation of regional pesticide legislative actions. Follow-up action to this is now being taken in the development of a Regional Training Programme in pesticide safety in collaboration with the World Bank and the University of Miami, School of Medicine. A 263 page document has been prepared as a result of the meeting.

A MECHANISM FOR COORDINATION AND COOPERATION—THE HEADS OF PLANT PROTECTION MEETING—The Heads of Plant Protection Meeting which has been held annually since 1981 provided an excellent mechanism for consultation, cooperation and communication in plant protection in the region.

The meetings which are held in a different country each year provide opportunities for the Heads of Plant Protection to visit the countries of the region and to observe the programmes and facilities which exist in the region. The meetings contribute to:

1. Reduction in the possibilities for duplication of efforts.
2. Establishment of bilateral cooperative programme in the region.
3. Establishment of a fraternity of plant protection which can be a very important asset in problem solving.
4. It give guidance to the region programme.
5. Provides a forum for coordination of all technical assistance programmes in the region.

DEEPENING OF THE SCOPE OF THE PROGRAMME BY DIRECT ASSISTANCE TO NATIONAL SYSTEMS—The scope of the programme has now been deepened by the establishment of national professionals in plant protection in the IICA offices in Dominica, St. Lucia and Grenada. In addition, in collaboration with USAID and USDA/APHIS there are proposals to set up a pest management unit in Grenada. This initiative responds to the need for an effective plant protection capability in the small island states of the region which are embarking on a major thrust in the development of fruits and vegetables for the export markets of North America and Europe. The initiative also responds to the following situation and I quote from a recent document “Although chemical pesticides—particularly insecticides and herbicides—are being utilized in increasing levels, the pest problems actually seem to be worsening. Annual pest losses in cocoa now approach an estimated \$1 million (U.S.). Leaf spot disease, Moko disease, and root knot nematodes cause crippling losses in banana if expensive chemical treatments are not applied. GCA and GBCS together annually spend \$450,000—about 25 percent of their total budget—for control of cocoa and banana pest”. It also responds to need to have in place a point of contact for the delivery of technical cooperation in plant protection from International agencies.

In Suriname, a specialist in coconut pests and diseases has been located in the IICA Office in that country to attend to the pressing problems of coconut mainly “Hart Rot disease” and *Castnia* spp. It is hoped that with assistance from other agencies and friendly governments that these initiatives will result in the development of a regional centre for investigations on coconut and oil-palms.

FUTURE INITIATIVES

1. Preparation of project proposals for a survey of fruitflies in the Caribbean.
2. Preparation of field guides to plant pests and diseases of importance in the Caribbean and bibliography of pests.

3. Development of Third Regional Plant Quarantine Training Course.
4. Survey of the incidence of mango seed weevil in the Caribbean.
5. Workshop on the detection of pests and diseases of fruits in the Caribbean.
6. Establishment of Regional Training Programme in Pesticide Safety.
7. Establishment of a Data Base in Plant Protection for the Caribbean.

BACKGROUND REFERENCES

- ALLEYNE, E. A Report on a visit to Grenada to advise on the control of cocoa thrips (*Solenothrips rubrocinctus*) on cocoa. 1981. Mimeo 16 pp.
- ANON. An Investigation of the Incidence of Pest and Disease at Orange Grove National Sugar Company, Port-of-Spain, Trinidad and Tobago, IICA Office, 1983. 13 p.
- ANON. The Society for Plant Protection in the Caribbean. Its origin, Constitution and Current Membership. Port-of-Spain, IICA Office, 1982. 19 pp.
- BRATHWAITE, C. W. D. An Introduction to the Diagnosis of Plant Disease. Inter-American Institute for Cooperation on Agriculture. Series Book and Education Materials No. 47, 1981. 49 p.
- BRATHWAITE, C. W. D. Perspectives for Plant Protection in the Caribbean. Port-of-Spain, Trinidad & Tobago, IICA Office, 1981.
- BRATHWAITE, C. W. D., ALCOCK, M. AND SOODEEN, R. A bibliography of Plant Disease Investigations in the Commonwealth 1880-1980. Inter-American Institute for Cooperation on Agriculture Miscellaneous Publication No. 328. 1981. 280 p. (ISSN-0534-5391).
- BRATHWAITE, C. W. D. and POLLARD, G. V. The essential role of pest and disease control in crop production in the Caribbean. *Agricultural Extension Newsletter* (Trinidad & Tobago). 12: 32. 1981.
- BRATHWAITE, C. W. D. The challenge for Plant Protection in the Caribbean in the 1980's and beyond. In Meeting of the Society for Plant Protection in the Caribbean. 1st, Kingston, Jamaica, 1981. Urgent Plant Pest and Disease problems in the Caribbean. Edited by Chelston Brathwaite and Gene Pollard. Inter-American Institute for Cooperation on Agriculture Miscellaneous Publication No. 378. 1982. pp. 7-19.
- BRATHWAITE, C. W. D. Crop Protection in the 1980's—an analysis of present alternative technologies. In *New Technologies in Food Production*. Port-of-Spain, (Trinidad & Tobago). 12: 32-36. 1981.
- BRATHWAITE, C. W. D. IICA'S activities in the Caribbean. Port-of-Spain, (Trinidad and Tobago), IICA Office, 1983 6 p.
- BRATHWAITE, C. W. D. Pest and Diseases of Onion. In Workshop on Onion Production and Research for the Eighties, Bridgetown, Barbados, 1983. Proceedings. Inter-American Institute for Cooperation on Agriculture Miscellaneous Publication No. 378. 1982. 260 p.
- CARIBBEAN PLANT PROTECTION NEWSLETTER. Vol. 1 Nos. 1-4, 1981-1984. Edited by Chelston W. D. Brathwaite. Port-of-Spain, (Trinidad and Tobago), IICA Office.
- Meeting of the Society for Plant Protection in the Caribbean, 1st Kingston, Jamaica, 1981. Urgent Plant Pest and Disease problems in the Caribbean. Edited by Chelston W. D. Brathwaite and Gene V. Pollard. Inter-American Institute for Cooperation on Agriculture Miscellaneous Publication No. 328. 1982. 260 p.
- Meeting on the Harmonization of Pesticide Legislation in the Caribbean, Port-of-Spain, (Trinidad and Tobago), 1983. Proceedings. Edited by Chelston W. D. Brathwaite. Inter-American Institute for Cooperation on Agriculture Miscellaneous Publication No. 379. 1984. 253 p.
- POLLARD, G. V. The Economic Impact of Moko Disease on the Economy of Grenada. Port-of-Spain, (Trinidad and Tobago), IICA Office, 1983. 14 p.
- POLLARD, G. V. 1983. Report on a Visit to Grenada, St. Vincent and St. Lucia to investigate the Potential Pest Risks Associated with the Movement of Agricul-

tural Produce via the Inter-island schooner trade. Report to IICA, Port-of-Spain, Trinidad, November 1983. 23 pp.

SMALL, L. W. The legal framework of plant quarantine systems in the Caribbean.

AN ENVIRONMENTAL TOXICOLOGY PROGRAM FOR FLORIDA

D. L. SHANKLAND

Department of Entomology & Nematology
University of Florida
Gainesville, Florida 32611

AND

H. N. NIGG

Citrus Research and Education Center
700 Experiment Station Road
Lake Alfred, Florida 33850

ABSTRACT

The total burden of hazardous waste and pesticides in Florida does not appear excessive when compared with national figures. However, Florida is particularly vulnerable to these materials because it relies heavily on ground water for drinking water.

Florida has enacted an elaborate set of laws on water quality, hazardous waste management and disposal, pesticide usage, fuel storage, landfill management, and related matters that bear upon water and general environmental quality. In many cases, however, there are no cost effective technologies available that have been approved by the responsible agencies to permit compliance with these laws. This obvious need for strong research and delivery programs is being met by the Institute of Food and Agricultural Sciences at the University of Florida, the Center for Biomedical and Toxicological Research at Florida State University, and the Florida Toxicological Research Center at the University of South Florida. These agencies coordinate their efforts through the Center for Environmental Toxicology. The Toxicological Research Coordinating Committee ensures maximal contribution of these programs to the state through annual assessment and reports to the Governor and the Legislature.

A basis for research and development, thus, has been established in law and in program development. Fruitful results and real benefit to the state will come only with realistic support. To date funding has been inadequate for supporting the expanded research mandated by law.

RESUMEN

La carga total de desperdicios peligrosos y de pesticidas en la Florida no parece ser excesiva cuando se comparan con los datos nacionales. Sin embargo, la Florida es particularmente vulnerable a estos materiales porque depende mucho del agua debajo de la superficie de la tierra para beber.

La Florida ha enactado una serie de elaboradas leyes sobre la calidad del agua, la administración y disposición de desperdicios peligrosos, uso de pesticidas, almacenamiento de combustible, administración de rellenos de tierra, y materias relacionadas que tienen que ver con la calidad general del agua y del medio ambiente. Sin embargo, en muchos casos no hay tecnología disponible que su costo sea efectivo y que haya sido aprobado por agencias responsables que permita obedecer esas leyes. La

tural Produce via the Inter-island schooner trade. Report to IICA, Port-of-Spain, Trinidad, November 1983. 23 pp.

SMALL, L. W. The legal framework of plant quarantine systems in the Caribbean.

AN ENVIRONMENTAL TOXICOLOGY PROGRAM FOR FLORIDA

D. L. SHANKLAND

Department of Entomology & Nematology
University of Florida
Gainesville, Florida 32611

AND

H. N. NIGG

Citrus Research and Education Center
700 Experiment Station Road
Lake Alfred, Florida 33850

ABSTRACT

The total burden of hazardous waste and pesticides in Florida does not appear excessive when compared with national figures. However, Florida is particularly vulnerable to these materials because it relies heavily on ground water for drinking water.

Florida has enacted an elaborate set of laws on water quality, hazardous waste management and disposal, pesticide usage, fuel storage, landfill management, and related matters that bear upon water and general environmental quality. In many cases, however, there are no cost effective technologies available that have been approved by the responsible agencies to permit compliance with these laws. This obvious need for strong research and delivery programs is being met by the Institute of Food and Agricultural Sciences at the University of Florida, the Center for Biomedical and Toxicological Research at Florida State University, and the Florida Toxicological Research Center at the University of South Florida. These agencies coordinate their efforts through the Center for Environmental Toxicology. The Toxicological Research Coordinating Committee ensures maximal contribution of these programs to the state through annual assessment and reports to the Governor and the Legislature.

A basis for research and development, thus, has been established in law and in program development. Fruitful results and real benefit to the state will come only with realistic support. To date funding has been inadequate for supporting the expanded research mandated by law.

RESUMEN

La carga total de desperdicios peligrosos y de pesticidas en la Florida no parece ser excesiva cuando se comparan con los datos nacionales. Sin embargo, la Florida es particularmente vulnerable a estos materiales porque depende mucho del agua debajo de la superficie de la tierra para beber.

La Florida ha enactado una serie de elaboradas leyes sobre la calidad del agua, la administración y disposición de desperdicios peligrosos, uso de pesticidas, almacenamiento de combustible, administración de rellenos de tierra, y materias relacionadas que tienen que ver con la calidad general del agua y del medio ambiente. Sin embargo, en muchos casos no hay tecnología disponible que su costo sea efectivo y que haya sido aprobado por agencias responsables que permita obedecer esas leyes. La

obvia necesidad de programas de investigación y de rendición, está siendo llenada por el Instituto de Alimentos y Ciencias Agrícolas de la Universidad de la Florida, el Centro de Investigación Biomédico y Toxicológico de la Universidad del Estado de la Florida, y el Centro de Investigación Toxicológico de la Florida en la Universidad del Sur de la Florida. Estas agencias coordinan sus esfuerzos a través del Centro de Toxicología Ambiental. El Comité Coordinador de Investigaciones Toxicológicas aseguran la máxima contribución de estos programas al estado a través de evaluaciones anuales y reportes al Gobernador y a la Legislatura.

De aquí que se ha establecido en ley y en desarrollo de programa una base de investigación y desarrollo. Resultados fructíferos y beneficios reales para el estado vendrán solo con apoyo realístico. Hasta ahora, apoyo monetario ha sido inadecuado para mantener y expandir las investigaciones mandadas por la ley.

Under the Resource Conservation Recovery Act of 1976 (RCRA-Public Law 94-580), the United States Environmental Protection Agency (EPA) is required to institute a national program to control hazardous wastes. It was the intent of Congress in passing RCRA that states assume responsibility for controlling hazardous waste within their borders. In 1980 the Florida legislature passed a comprehensive Florida hazardous waste management act which codified into state statutes the federal requirements established by EPA and RCRA.

There are in the world approximately five million known chemical compounds of which about 70,000 are in commercial use (Fishbein 1980). EPA has named 654 of these chemicals as hazardous materials that pose special problems if disposed of into the environment (CFR 40, Chapter 1, Part 261.33). They are classified as hazardous because of toxicity, reactivity, ignitability, or corrosivity. Two hundred and sixty of these compounds are listed for their acute toxicity and many of the pesticides in the list are among this latter group. According to the law, these materials become hazardous wastes when they are intended for disposal or acutally disposed of.

EPA estimates that approximately 581 billion pounds of hazardous waste are generated in the U.S. annually (Ney 1984). On the average, this amounts to almost 158 thousand pounds for every square mile of land and water in the U.S. Furthermore, it is estimated that about one billion pounds of pesticides are used annually in the U.S. (Pimentel 1979). These pesticides, on the average, enter the U.S. environment at the rate of about 270 pounds per square mile, and account for about 0.17% of the total annual burden of hazardous materials on the environment.

This burden is, of course, not uniformly distributed. Florida is a smaller than average generator of hazardous waste, but larger than average user of pesticides. In a 1977 study of hazardous waste generators in Florida (Carter 1977), 320 organizations, including industrial firms and universities, were surveyed; and it was estimated that they generated approximately 638 thousand tons of waste per year or about 22 thousand pounds for every square mile of land and water in the state. Accurate figures on pesticide use in Florida are not available, but the state is generally considered to be second only to California in that regard. Thus, Florida is burdened with only about one-seventh the national average of hazardous waste per square mile but more than the national average of pesticides.

The total burden of hazardous waste and pesticides in Florida does not appear excessive when compared with national figures. However, Florida is particularly prone to serious problems from these materials because of the nature of its water supply (FDACS 1984). Over 90% of Florida's population relies on ground water for drinking water. Ground water is easily recharged by rain and surface runoff in much of the state and is easily contaminated by chemicals from spills, surface discharges, dumps, landfills,

and pesticide applications. Florida also shares the national concerns over atmospheric pollution, acid deposition, mycotoxins in food, and other kinds of environmental pollution. However, during the past three years the discovery of ground water and well field contamination by pesticides and other chemicals, the legislative action on hazardous waste management, and enforcement programs by the Florida Department of Environmental Regulation make it clear that the most urgent concern in Florida is point and nonpoint source pollution of ground water by toxic organic chemicals. The importance of this issue was emphasized in the summary of the Report of the Speaker's Task Force on Water Issues, Florida House of Representatives. This March, 1983, report cited contamination of ground and surface waters with hazardous wastes, sewage, industrial wastes, pesticides, and other chemical products as the most serious threat to Florida's supplies of clean water and its fragile ecosystem. The report further cited the absence in Florida of systematic programs to either assess the extent of, or minimize or remove the threats posed by these different classes of pollutants.

These circumstances led to an elaborate set of laws on water quality, hazardous waste management and disposal, pesticide usage, fuel storage, land fill management, and numerous other matters that bear upon contamination of water and other parts of the environment by chemicals. Enforcement agencies, like the Florida Department of Environmental Regulation and U.S. EPA, are mandated to enforce these laws. In many cases, however, there are no cost effective technologies available that have been approved by the agencies to permit compliance with the laws. The only approved method of disposal of some hazardous waste, including for example large areas of pesticide contaminated land, is to put the material in sealed drums and ship it to an approved dump in Alabama. This is not only prohibitively expensive, but it cannot be a permanent solution. Alabama cannot serve as an infinite sink for wastes from the southeastern states.

An obvious need for strong research and delivery programs to address these matters was recognized by the Institute of Food and Agricultural Sciences (IFAS) at the University of Florida, Florida State University, and the University of South Florida some years ago, before the intrusion of aldicarb and ethylene dibromide into ground water became public issues, and before other cases of ground water contamination received public notoriety. We need to develop environmentally sound, cost effective technologies to dispose of hazardous chemicals, and to decontaminate soil and water that have already been contaminated by them. We need sound data bases for determining human health risk posed by chemical pollutants in our water. We need to understand how chemicals behave in the environment, and we need to know the toxicological implications of these events. We must have the ability to identify and determine the concentrations of these chemicals in soil, water, food, and other parts of the environment. Finally, the state needs experts in epidemiology to assess the effects of environmental pollutants on public health. Toward meeting these needs, the University of Florida, Florida State University, and the University of South Florida independently organized centers of environmental toxicology.

The University of Florida researches analytical methods for pesticides, fate and transport of chemicals in the environment, human exposure to pesticides, water treatment, and many other relevant environmental subjects. These were not, however, coordinated and funded to address the urgent environmental toxicology needs of the state. In an effort to provide coordination and funding mechanisms, the Center for Environmental Toxicology was formed in 1982. The center has missions in research, extension, and instruction. At the present, the research mission deals mainly with the development of analytical methods for chemical pollutants, the fate and transport of those chemicals in the environment, and their toxicology. The extension component serves as an authoritative source of information on the issues for the public, state

agencies, legislators, or other interested parties. The mission in instruction is primarily graduate education and training to prepare scientists to work in this important aspect of environmental science.

At Florida State University, the Center for Biomedical and Toxicological Research forms the administrative hub for interdisciplinary research on ecological effects of marine pollutants, effects of toxic organic substances in the environment, effects of heavy metals, pesticides, and other pollutants on aquatic systems, etc. The center has provided the Florida Departments of Health and Rehabilitative Services and Environmental Regulation with health risk assessments of carcinogenic and toxic chemicals in ground water. That center also has a mission in graduate education.

At the University of South Florida there is a large and growing Medical Center, a newly established College of Public Health, and a close working relation with the VA Hospital all of which form a strong base for their Florida Toxicological Research Center. The missions of that center are basic research into the toxic chemicals present in Florida and investigation into alternative chemicals and processes to presently used hazardous chemicals, and to provide technical support for Florida state agencies with analytical expertise and scientific consultation.

In recognition of the serious nature of the threat by chemical pollutants to Florida's water supply and to the welfare of the citizens of the state, the legislature in 1984 provided a statutory basis for a systematic state-wide research program on those matters.

The Law of Florida, Chapter 84-338, Section 72 charges the Center for Biomedical and Toxicological Research at Florida State University, the Institute of Food and Agricultural Sciences (IFAS) at the University of Florida, and the Florida Toxicological Research Center at the University of South Florida to increase their research on chemicals that may adversely affect human health and the environment, and to do so without unnecessary duplication of effort.

To ensure maximal contribution of these programs to the state, Section 73 of the law established the Toxicological Research Coordinating Committee (TRCC) made up of representatives of the three universities, and representatives from other appropriate universities as recommended by the Board of Regents. The Committee is chaired by the representative of the Center for Environmental Toxicology. The Committee is charged to ensure efficient use of the state's resources, and toward that end, to meet at least once a year to review research, develop activities, and establish priorities as determined by state needs. The Committee is to submit annual reports concerning the activities of each participating university and short- and long-range plans of each for protecting human health and Florida's environment. The report shall be submitted on March 15 to the Governor, the President of the Senate, and the Speaker of the House of Representatives.

Section 74 of the law calls for submission of reports from participating universities to the Toxicological Research Coordinating Committee on:

- 1) Chemicals that may affect human health and welfare, including epidemiological studies.
- 2) Analytical methods, environmental fate and transport, and toxicology.
- 3) Environmentally safe methods to control pests other than through the use of chemicals.

The Committee in turn is to provide risk assessment analysis to the Department of Agriculture and Consumer Services, the Department of Health and Rehabilitative Services, the Department of Environmental Regulation, and Pesticide Review Council. It must recommend standards of safety for chemicals in the environment, and perform other functions necessary to carry out the provisions of the law. Section 75 of the law mandates the creation of a data bank on environmental toxicology research results in

the Center for Environmental Toxicology in IFAS. Each participating university is to provide results of completed research on environmental fate and transport and toxicology to the data bank. Although not specified in Section 75, the provisions of Section 74 imply that reports should also include results on environmentally safe methods to control pests other than through the use of chemicals. On September 30 of each year, IFAS is to publish a listing of publically available studies in the data bank. The list must also be issued to the Department of Agriculture and Consumer Services, the Department of Health and Rehabilitative Services, the Department of Environmental Regulation, and the Pesticide Review Council.

Unfortunately, the legislature was guilty of an oversight. The law was enacted without funding. Research relevant to the law has been funded by limited amounts of general review and by extramural funds of various kinds. In all cases, these funds are inadequate for, or contractually restricted from supporting the expanded research mandated by the law.

During the 1985 legislative session the oversight of last year was corrected by the provision of \$750,000 from the Water Quality Trust Fund to support this state-wide program. That funding is not assured for next year, however. In spite of that, the Toxicological Research Coordinating Committee is proceeding with plans for the development of the Data Bank and with specific research projects selected from a list of high priority issues developed by the Department of Environmental Regulation, the Department of Agriculture and Consumer Services, and the Pesticide Review Council. Requests for support from general revenue for continuation of this support will be coordinated next year during the legislative session.

It cannot be argued that a ground water contamination crisis exists in the state of Florida as a whole. The citizens of Fairbanks, Florida, however, whose well field was made unusable as a source of drinking water by contamination with toxic chemicals from a mismanaged chemical dump, have already lived through a crisis. That problem is being solved by extending the Gainesville water system to Fairbanks at a cost in excess of two million dollars.

The Florida Department of Health and Rehabilitative Services has been analyzing well water, mainly from drinking water wells, for the presence of ethylene dibromide (EDB) in areas where that chemical has been used for nematode control. As of June of this year, 9,208 wells had been analyzed and 1,019 (11%) of them were contaminated with ethylene dibromide in excess of the 0.02 parts per billion action level established by EPA. In fact some wells contained 600 to 700 parts per billion of EDB and the average among contaminated wells was 6.5 parts per billion. The owners of those wells face reduced property values and the inordinate inconvenience of relying on bottled water for household use. The state of Florida has assumed responsibility for some of these contaminated wells, and it was estimated in 1984 (DER, 1984b) that it would cost the state \$4.9 million to meet that responsibility. At the time of that estimate, however, solutions to the problem were in terms of possibilities only and included carbon filters, new wells, and connection to community water supplies. It is probable that the ultimate cost to the state will be much greater than that estimated.

Data is still being collected by state agencies and Union Carbide Corporation on the extent to which aldicarb (Temik) has intruded into ground water in areas where it has been used.

The Florida Department of Environmental Regulation is monitoring 402 sites at which hazardous wastes are being generated (DER, 1984a). Ground water contamination in excess of adopted standards, or in some cases by specific contaminants for which standards have not been adopted, has been confirmed at 119 (30%) of those sites. Furthermore, according to DER all 654 of the chemicals on the EPA hazardous materials list are to be found among hazardous wastes produced in Florida.

Within the constraints of presently available technology, the contamination of wells with ethylene dibromide is for practical purposes irreversible in situ. That is true also of wells or aquifers that have become contaminated with gasoline, as happened recently in a small community southwest of Gainesville, or with other toxic organic chemicals. Except for activated carbon filtration there are no other proven cost effective technologies for the homeowner or community to purify water that has become contaminated with these chemicals.

Much of the ground water contamination that has occurred in Florida has been due to mismanagement and irresponsibility. However, the unavailability of cost effective technologies to dispose of hazardous waste means the accumulation of large amounts of these materials in storage and increases the probability of accidental or purposeful illegal disposal of them.

In any event, the need for research and development in these and related matters, as mentioned earlier, is obvious. A basis for that research has been established in law and in program development at the universities. Fruitful results and real benefit to the state will come only with realistic support for those programs. That support will be sought from various sources; but, in the interest of continuity and to assure that urgent matters in the state will be addressed, a significant portion of it should come from the state. Whether or not there is serious intent by the legislature in that regard should be apparent by this time next year.

REFERENCES CITED

- CARTER, C. E. 1977. Hazardous Waste Survey for the State of Florida. Prepared for the Florida Department of Environmental Regulation.
- DER. 1984a. The Sites List. Summary Status Report, July 1, 1984-December 31, 1984. Florida Department of Environmental Regulation, Bureau of Operations, Tallahassee, Florida
- DER. 1984b. Florida's Environmental News. Vol. 6, No. 9. Florida Department of Environmental Regulation.
- FDACS. 1984. Summary of soil, hydrogeological and other environmental conditions in the state of Florida related to pesticide use. Report submitted to the U.S. Environmental Protection Agency by Florida Department of Agriculture and Consumer Services, Bureau of Product Evaluation, May, 1984.
- FISHBEIN, L. 1980. Potential industrial carcinogenic and mutagenic alkylating agents. Pages 329-363 in D. B. Walters, ed. Safe Handling of Chemical Carcinogens, Mutagens, Teratogens, and Highly Toxic Substances, Vol I. Ann Arbor Science, Ann Arbor, Mich.
- NEY, R. E., JR. 1984. Report at National Workshop on Pesticide Disposal, Jan. 28-29, Clarion Hotel, Denver.
- PIMENTEL, D. 1979. A cost-benefit analysis of pesticide use in U.S. food production. Pages 97-149 in T. J. Sheets and D. Pimentel, eds. Pesticides: Contemporary Roles in Agriculture, Health, and Environment. Humana Press, Clifton, N.J.

COOPERATIVE INDUSTRY EFFORTS WITH DEVELOPING COUNTRIES TO IMPROVE AGROCHEMICAL REGISTRATION, LABELING AND EDUCATION AND TRAINING PROGRAMS

WILLIAM L. HOLLIS
Director of International Affairs
National Agricultural Chemicals Association
1155 Fifteenth Street, NW
Washington, D.C. 20005

ABSTRACT

The agrochemical industry is cooperatively engaged in carrying out education and training activities to eliminate misuse and achieve safety in the use of their products throughout the world. Meaningful and lasting success of these activities will come only after a sound regulatory foundation for the registration, labeling, and use of agrochemicals is established by local governments. This goal is being pursued in Latin America and the Caribbean as a cooperative effort of governments and industry utilizing a consultative process.

The International Group of National Associations of Agrochemical Manufacturers, in 1979, began an intense process of consultations with some Latin American governments. Formal governmental consultations, under the sponsorship of IICA, followed in 1982-83 which included all governments of Latin America and the Caribbean. As a result recommendations were agreed upon among governments for registration requirements, labeling, toxicity categories, and other safety and training considerations. As of 1984, 11 Latin American nations had accepted the recommendations and 7 others were in various stages of the legislative process.

Most Caribbean nations are legally unable to accommodate the recommendations until they establish the prerequisite legislation. IICA is preparing a working document for the governments of the Caribbean to use to establish their own regulations.

An informal consultation between industry and environmental groups to resolve problems associated with the safe use of agrochemicals and the status of the Food and Agriculture Organization (FAO) Draft Code of Conduct on the Distribution and Use of Pesticides are also mentioned.

RESUMEN

La industria agroquímica está cooperativamente envuelta en llevar a cabo actividades de educación y entrenamiento para eliminar el mal uso y obtener seguridad en el uso de sus productos a través del mundo. El éxito duradero y que signifique algo de estas actividades, vendrá solo después de una sólida fundación de regulaciones para la registración, marcar, y el uso de agroquímicos sean establecidas por los gobiernos locales. Esta meta se está tratando de llevar a cabo en latinoamérica y en el Caribe como un esfuerzo de cooperación de gobiernos e industrias utilizando un proceso consultativo.

En 1979, el Grupo Internacional de las Asociaciones Nacionales de Fabricantes Agroquímicos, comenzó un intensivo proceso de consultas informales con algunos gobiernos latinoamericanos. Durante 1982-83, consultas formales con los gobiernos fueron auspiciadas por IICA que incluyeron todos los gobiernos de latinoamérica y del Caribe. Como resultado, se acordó entre los gobiernos recomendaciones de requisitos de registración, marcas, categorías de toxicidad, y otras consideraciones de seguridad y entrenamiento. A partir de 1984, 11 naciones han aceptado las recomendaciones y otras 7 están en varias etapas del proceso legislativo.

La mayoría de las naciones del Caribe no pueden legalmente acomodar las recomendaciones hasta que ellas establezcan las pre-requeridas leyes. IICA esta preparando un

documento con el cual los gobiernos del Caribe puedan usar para trabajar y establecer sus propias regulaciones.

Se menciona también una consulta informal entre la industria y grupos interesados en el medio ambiente para resolver problemas asociados con el uso seguro de los agroquímicos y el estado de la Version del Código de Conducta Sobre la Distribución y Uso de Pesticidas de la Food and Agriculture Organization (FAO)

An international movement to harmonize pesticide registration requirements according to FAO recommendations (FAO 1982) is being successfully implemented in Latin America and the Caribbean as a cooperative effort of governments and industry using the consultative process (GIFAP/WICEM 1984).

As a focal point there are a few premise statements of obvious facts on plant protection and some lesser known facts about the agro-chemical industry.

- (1) Agricultural food and fiber production is the primary industry of man. It serves his basic health and economic needs.
- (2) There are no major agricultural crops grown anywhere in the world that are free from pest destruction.
- (3) Agrochemicals are the most widely used means of providing immediate and economic plant protection.
- (4) All plant protection schemes and materials, natural and synthetic, have inherent limitations for pest control that ultimately determine the extent and nature of their practical use.

In essence, because plant protection is essential to assure food and fiber production worldwide, and since control options are not infinite, any inherent limitations in efficacy, safety, or efficiency for whatever controls are being used (Hollis 1977) must be overcome by correct management in use.

Regarding the agrochemical industry, one of its lesser known features is its size. It is quite small in the United States as well as internationally. In the U.S. it accounts for approximately two percent of the gross sales of the U.S. chemical industry (Hollis 1983). Its total worldwide value in sales in 1984 was 13.8 billion U.S. dollars. Even with recent increases, the total sales value of the worldwide agrochemical industry would still be less than the documented gross sales of some of our U.S. corporations. For instance, the EXXON Corporation reported gross sales for 1984 of 97.3 billion U.S. dollars.

According to Milton Russell (1984), Assistant Administrator for Policy, Planning and Evaluation, EPA, the number of major U.S. pesticide producers declined from approximately 80 companies to 30 companies between 1970-81. The number of compounds screened in relation to the number successfully registered went from 6500/10 in 1967-70 to 82600/11 in 1979. The time from discovery to full registration went from 68 months to 94 months for the same period.

Frawley (1961) cited National Academy of Science figures for 1956 as being three thousand chemicals screened per one marketable product. He approximated the developmental cost, in the 1950's, at almost two million dollars per product. The approximate developmental cost per product reported by some industry members today is in the vicinity of forty million dollars and only one of every 20,000 compounds screened has a possibility of reaching the marketplace. The research and development cost excludes the millions needed to build a plant to produce the product.

The global industrial resource of innovative research and development in plant protection chemistry is shrinking and is considered to be limited now to some 30-40 remaining companies worldwide who still have the financial resources and scientific capabilities

to continue. The evolution of newer plant protection products and their establishment in plant protection field practices takes longer and occurs at a reduced frequency from fewer sources than in the past. If the agrochemical options available for dependable plant protection slowly diminish in light of the need for enhanced productivity and crop diversity to meet the demographer's predictions for the world population in the next 20-30 years, then the potential for a future crisis in plant protection becomes substantive.

It is prerequisite to their continual availability that measures be taken to control the limitations of present and future plant protection products. These limitations are basically safety and misuse. Measures to overcome such limitations are underway within the National Agricultural Chemicals Association (NACA) and through our international organization, The International Group of National Associations of Agrochemical Manufacturers (GIFAP). The strategy followed is the orderly procedure depicted in Figure 1; the Circle of Safety.

For cooperation, there is first the question, how does a regulated industry, regulated more or less in every country, establish a cooperative effort with Government regulators and with non-governmental organizations (NGO). To do this, there are certain conditions that must evolve; the demonstration by the established industry of its scientific

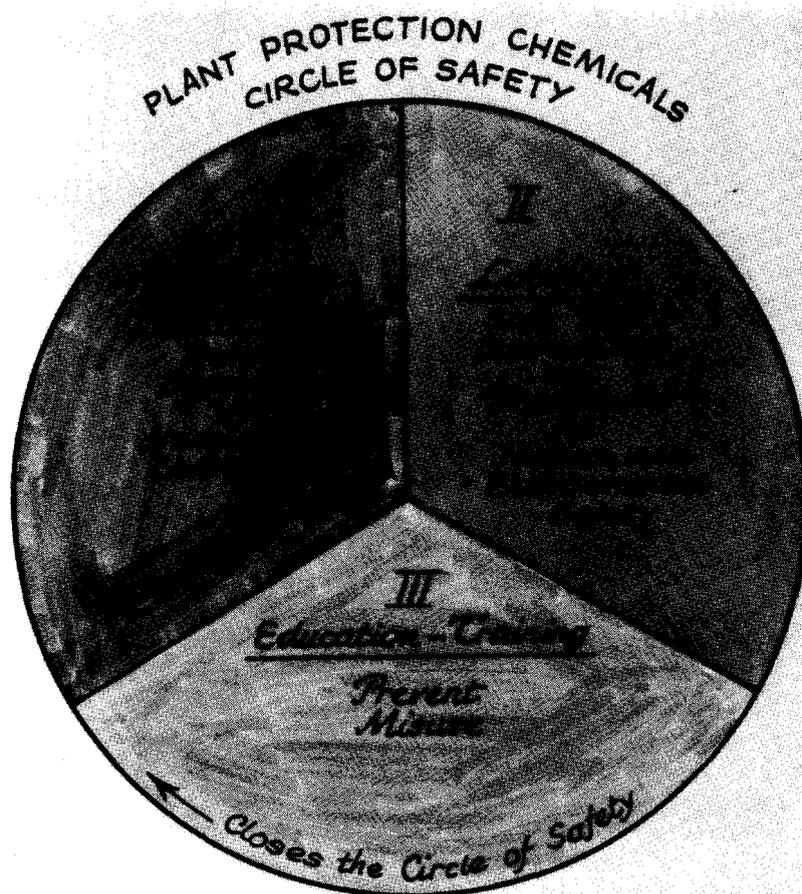


Fig. 1. Plant Protection Chemicals—Circle of Safety

competence and credibility, and the willingness to take the initiative to meet with NGOs, international organizations, and governments in uncompromising forums. Having met these conditions, the agrochemical industry can now announce some of their accomplishments.

Within the framework of NACA, the Association has joined in a forum, the Agricultural Chemicals Dialogue Group (ACDG) with a consortium of environmental and church organizations moderated by the Conservation Foundation. In the past few years, the ACDG has mutually agreed upon and issued voluntary guidelines for industry on advertising (ACDG 1983) and labeling (ACDG 1985) in developing countries.

The NACA International Registration Committee has given industry support through the U.S. Department of State to the FAO Draft Code of Conduct on the Distribution and Use of Pesticides (FAO 1985). The Code had its genesis as a recommendation in the Report of the FAO Consultation on the International Harmonization of Pesticide Registration Requirements held in Rome, Italy (FAO 1982). NACA was present as a member of the GIFAP delegation to the Consultation which supported the Report. GIFAP has since issued position papers indicating support and cooperation on principles reflected in the Code pertaining to hazardous substances export (GIFAP 1983b), good marketing practices in pesticide export (GIFAP 1985a), and options for ensuring quality in stored pesticide products (GIFAP 1985b).

The basic attributes of the Code are that it is voluntary; it is to be observed in countries that are without national laws in regulating pesticide safety or without registration controls prior to marketing; and it involves consideration for shared responsibility for safety measures among government officials, industry, importers and distributors, and users. The Code consists of twelve articles that comprehensively cover the essential regulatory requirements and safety measures set forth in the Report of the October 1982 FAO Consultation (FAO 1982).

The Draft Code was approved by the FAO Committee on Agriculture, comprised of some 94 delegations, in March 1985 and by the FAO Council in June 1985. The Code will be considered by the FAO Commission in November 1985 at which time it will be formally adopted (GIFAP 1985c).

There may be some jurisdiction conflicts and difficulties depending on how some governments conduct their business in agrochemicals. Nevertheless, the potential success of the Code depends most importantly on participating countries and local importers and distributors remaining attentive along with the industry, to carrying out their respective responsibilities as identified in the Code (GIFAP 1985c).

The agrochemical industry demands reasonable and responsible regulation. Industry prefers not to see the Code become a substitute for duly established regulations, but rather that it serve as an interim measure for safety pursuant to the institution of appropriate legislation and regulations in those countries to which the Code is relevant. The GIFAP Latin American Working Group is working cooperatively with the Inter-American Institute for Cooperation in Agriculture (IICA) to bring this about in the Caribbean Region.

Industry's cooperative efforts with international bodies and the governments they represent is accomplished through participation in GIFAP. The agrochemical industry is one of the few industries that has an international association. It is needed because national associations have no standing outside their borders. GIFAP is recognized as the worldwide representative of the agrochemical industry and is accepted by international bodies such as United Nations organizations and IICA. GIFAP has for some time had official status with FAO. Earlier this year, the Director General of the WHO confirmed the approval of the establishment of official relations between the WHO and GIFAP (GIFAP 1985d). Such industry recognition must be earned over time by the demonstration of competence and credibility.

Figure 2 : World pesticide market
(US \$13,000 million end-user sales value in 1981)
excluding non-crop outlets

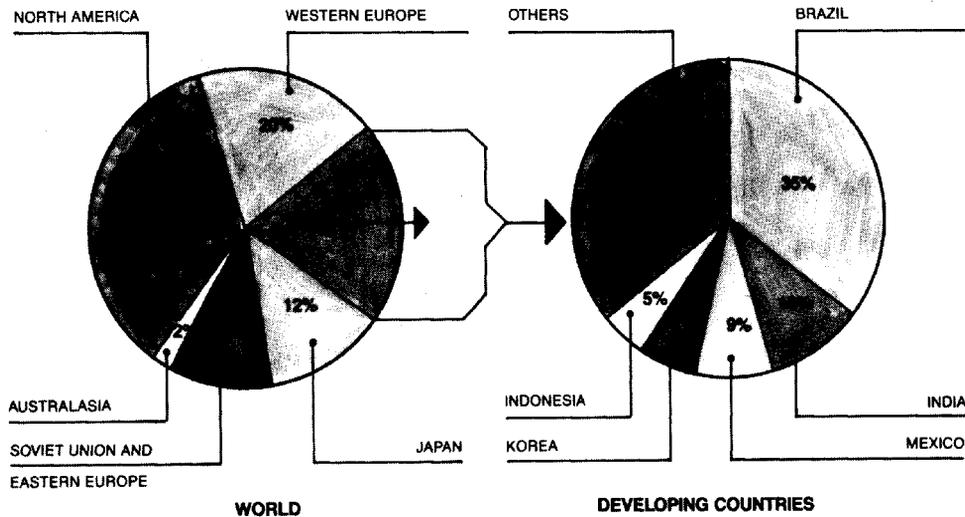


Fig. 2. World Pesticide Market

GIFAP's membership includes over 30 national agrochemical associations which together comprise more than 950 companies. This membership represents, at the international level, more than 90 percent of the world production of agrochemicals. The world distribution of agrochemicals according to end-user sales value in 1981 is shown in Figure 2. This data was presented (GIFAP 1983b), at a UN interagency meeting in the spirit of cooperation, to describe the economic and the health and environmental safety considerations that governments of developing countries should consider before deciding to set up plants to formulate or manufacture agrochemicals.

The member associations of GIFAP have common objectives—to promote crop protection by appropriate use of agrochemicals worldwide and to ensure that the properties and application of these products are in conformity with the needs of agriculture and society; i.e., optimal food and fiber production with minimal hazards for man, animal and environment.

To achieve this, some of GIFAP's aims are:

- To promote the safe and sensible manufacture, handling, packing and transport of agrochemicals by setting, and recommending high standards in conformity with internationally acceptable rules.
- To promote the safe and sensible application of agrochemicals, in conformity with national and international standards and regulations for the protection of the user, the environment, and the consumer.
- To promote harmonization of national and international legislation and regulations concerning control, testing and approval of agrochemicals.

These aims are in consort with the all-inclusive registration and safety guides initiated at the first such FAO Consultation in 1977 and reported final at the 1982 Consultation (FAO 1982). An examination of the Report (FAO 1982) shows, without question, that there are benefits for governments, farmers, consumers, and industry by the institution of the FAO proposals. Meanwhile, the benefits of the FAO proposals remain

latent in the absence of government initiative to implement them. GIFAP recognized this and further recognized that industry is the common denominator in this equation and the party best able to provide the initiative.

Consequently, GIFAP entered into a unique experiment in 1979 whereby discussions on regulatory matters with some governments of Latin America, as a group, were made possible through an informal consultative forum managed and directed by a neutral non-profit organization, the Policy Sciences Center, Inc. (PSC) interested in public policy issues. Public funds from the Charles F. Kettering Foundation, the Rockefeller Brothers Fund, The United Nations Environment Program, and the U.S. Agency for International Development supported the project.

The Consultative Process (GIFAP 1984a), is a strategy for bringing together parties of different persuasions, voluntarily, in a neutral forum so as to: a) encourage communication; b) achieve a better level of mutual understanding of a problem(s) than existed before; and c) reach nonbinding consensus agreements that may lead to the resolution of the problem(s). As such, the Consultative Process is a means of legitimizing essential communications between the regulated industry with its scientific and technological expertise and governments who need information and cooperation.

The PSC project included an on-site evaluation of the status of considerations given to labeling, application, and formulation by governments-in eight Latin American countries. The Review Team, lead by Professor Harvey Cromroy, University of Florida, issued a Report (Cromroy et. al. 1981) that was reviewed by all participants. Recommendations were presented and when assembled by PSC (GIFAP 1984a), served as the substance for a final meeting of the Consultation in Key Biscayne, Florida, in 1981. This experiment in the Consultative Process resulted in:

- candid and respectful dialogue on major concerns to both parties;
- provisions for safety information;
- emphasis on product use and application training;
- clear identification, definition, and organization of main issues and problems; and,
- impetus to undertake formal government consultations.

The industry, in complying with a voluntary commitment to the Forum to provide safety information, published guides for the safe handling of pesticides in formulating, etc. (GIFAP 1982), and guides for safe use of pesticides (GIFAP 1983a). Guides pertaining to first aid (GIFAP 1984b) were recently published. All these have been given wide distribution throughout the hemisphere.

The Consultative Process next shifted from unofficial to official government status when the Mexican Government, in applauding the efforts of the Key Biscayne Consultation, took the initiative to hold a "Consultation on the Proper Use of Pesticides in America and the Caribbean" in Mexico City, 1982. The Mexico City Hemispheric Consultation issued proceedings (Direcion 1982) and an official report (GIFAP 1984a) attesting to the essentiality of agrochemicals in food production and recognized problems that need attention. It identified the benefits that would accrue from the harmonization of requirements for registration, labeling, and use. The Report (GIFAP 1984a) recommended that IICA conduct Consultations to harmonize pesticide registration requirements, recognizing the guidelines set forth by the FAO (FAO 1982), in each of the four IICA regions; i.e., the Andean Region; the Central Region including Mexico, Panama, and the Dominican Republic; the Caribbean Region; and the Southern Cone, thus encompassing essentially all the nations of Latin America and the Caribbean. Consultations were held in Cartagena, Colombia, August 1982; San Jose, Costa Rica, April 1983; Port-of-Spain, Trinidad, August 1983; and Santiago, Chile, August 1983. Reports (IICA 1982, 1983a, b, c) were respectively issued and each included recommendations for registration requirements, labeling, toxicity categories, and other safety and training considerations that are universally needed. These were officially approved and signed

by all the government delegates.

An open session was held at the beginning of each Consultation to permit a small GIFAP delegation of experts to present papers (IICA 1982, 1983a, b, c) on registration, labeling, and toxicology requirements. The registration requirements presented included, among other items, suggestions to include information on worker reentry intervals, pre-harvest intervals, and container disposal.

Suggestions for a uniform label format were presented along with the safety idea of adding a precautionary color band commensurate with the toxicity category of a product. The colors, in decreasing order of hazard are: red, yellow, blue, and green. The colors would be standard according to an international color code and would appear at the bottom of the label as a band fifteen percent the height of the label. Toxicology requirements were presented including the suggestion that the WHO classification for toxicity be used. The suggestions of the GIFAP expert delegation were given favorable consideration.

Following completion of all four Consultations, the Director General of IICA prepared a summary report (GIFAP 1984a) of these events for the Inter-American Board of Agriculture. A Resolution (GIFAP 1984a) to accept the regional recommendations and implement them "quickly" was subsequently adopted by all the Ministers and Secretaries of Agriculture in Latin America, the U.S., Canada, and the Caribbean at the October 1983 meeting of the Board in Jamaica.

The status of implementation of the recommendations among the nations of the hemisphere, as of 1984, includes eleven nations in Latin America who have given full acceptance and are implementing the recommendations. Seven remaining nations in Latin America are in various stages of moving through the legislative and regulatory processes to full acceptance and implementation. Most of the Caribbean nations are legally unable to accommodate the recommendations until they establish the prerequisite laws. IICA is translating the now established regulations for the Central Region to serve as a working document for the governments of the Caribbean nations to use to establish their own regulations.

We are closing in on what was thought to be the impossible—the harmonization of the regulations of agrochemicals throughout the hemisphere. GIFAP and its member associations are sincerely encouraged by these progressive and enlightened moves by the governments of this hemisphere toward the orderly regulation of agrochemicals. The benefits to be derived from having responsible and reasonable national laws and regulations for the proper control and safe use of agrochemicals accrue to all concerned parties: governments, farmers, the public, and the established industry. The benefits include:

- label information and consistent format to meet local needs for correct use and human and environmental safety;
- quality assurance of the product for safety and efficacy reasons;
- proper toxicological considerations for safety of all concerned;
- user education and training for personal and environmental safety reasons; and
- incentives to industry to continue to improve services to local agriculture.

It is not too obvious, but the issue of misuse is addressed throughout these proceedings. Misuse and its attending human and environmental effects does occur and especially in situations of inadequate registration requirements and procedures as they may limit regulatory control. Misuse and its effects are always a matter of concern to the industry and is the main reason we are proponents of sound and enforceable regulations. The legitimate availability of agrochemicals is a main consideration of the FAO Code of Conduct (FAO 1985) and of U.S. requirements as evaluated in Congressional testimony by NACA (NACA 1983).

Meanwhile, developing countries who must import plant protection chemicals and

who do not have a regulatory system and basic registration requirements in place are vulnerable to foreign counterfeiters who fabricate look-a-like agrochemicals which, without quality control, may be contaminated with unknown toxic by-products and perhaps labeled without precautions. There may be no evidence of efficacy. These products may be marketed at attractive cut-rate prices directly or through some exporter who may or may not be interested in following recognized channels of commerce. It is possible that labels as well as containers may be counterfeits of those of an established company. That these activities do occur is verified (Deuse 1984). Developing countries must have the means to evaluate the source and quality of the agrochemicals they import as one primary means of overcoming inadvertent misuse.

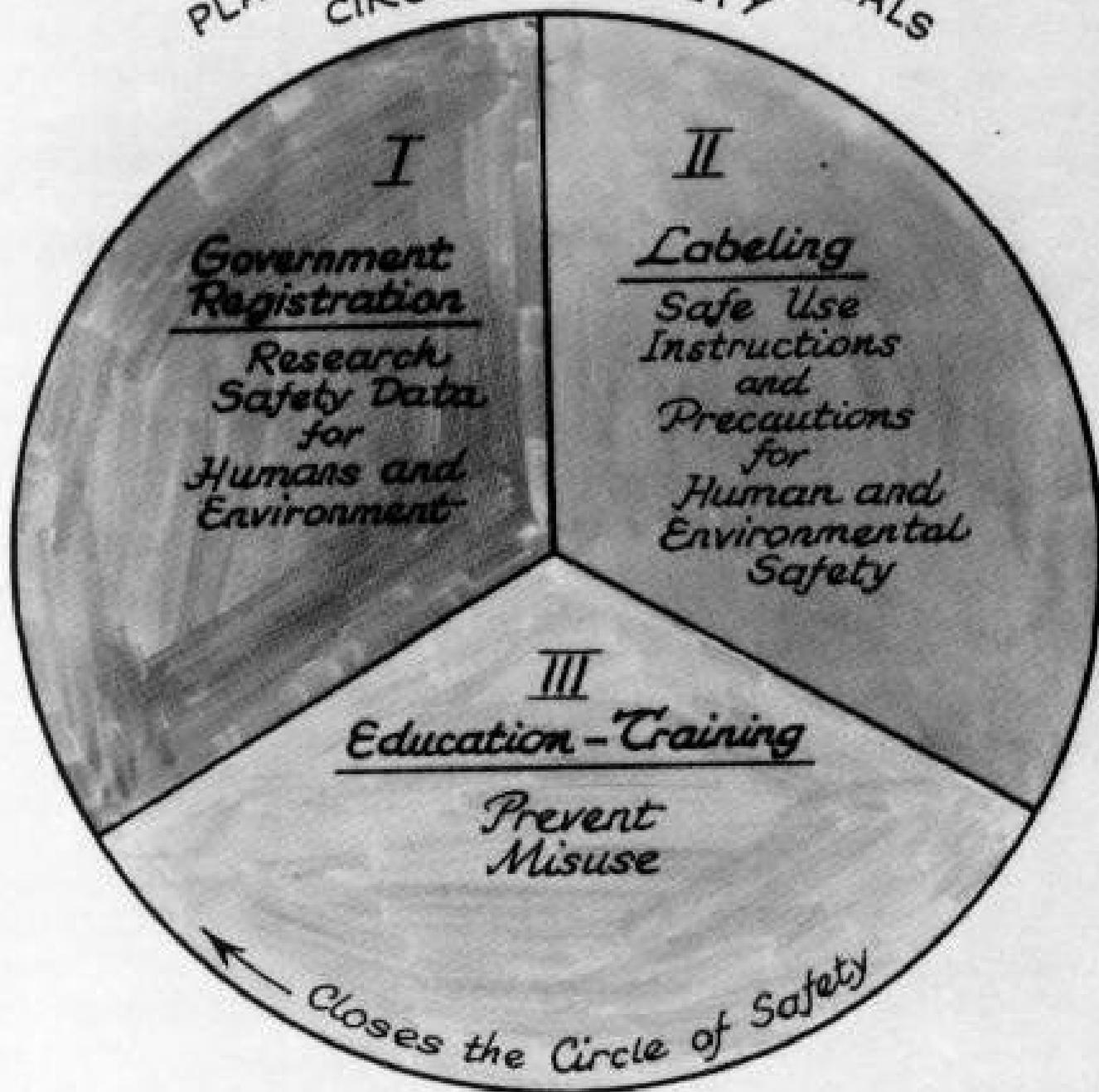
The agrochemical industry continues to be cooperatively engaged in carrying out education and training activities. It believes that, while these activities are the mainstays of eliminating misuse and achieving safety, meaningful and lasting success of these activities will come only after a sound regulatory foundation for the registration, labeling, and use of agrochemicals is established by local governments (Figure 1).

REFERENCES CITED

- ACDG. 1983. Guidelines for Advertising Practices in the Promotion of Pesticide Products in Developing Areas of the World. Conservation Foundation, 1717 Mass. Ave., N.W. Wash., D.C. 20006.
- ACDG. 1985. Guidelines on Labeling Practices for Pesticide Products in Developing Areas of the World. *Ibid.*
- CROMROY, H. L., L. O. ROTH, AND K. J. MOY. 1981. Improving the Safe Use of Agricultural Chemicals in Latin America. A Research Report on Labeling, Application, and Formulation. The Policy Sciences Center, Inc., 270 Broadway Room 1001, New York, N.Y. 10007.
- DEUSE, J. P. L. 1984. Imitation and Adulteration of Plant Health Products: A Plague in Developing Countries. Presented at the Phytopharmacology Seminar, Faculte des Sciences Agronomiques de l'Etat de Gembloux, Belgium. GIFAP Bulletin Vol. 11, No. 3, May/June 1985. GIFAP, Avenue Hamoir 12, 1180 Brussels, Belgium.
- DIRECCION GENERAL de SANIDAD VEGETOL. S.A.R.H. MEXICO CITY. 1982. III Consultation Meeting on Proper Use of Pesticides in America and the Caribbean. Proceedings.
- DIRECTORY. 1982-83. International Group of National Associations of Agrochemical Manufacturers. P. 11. (Available GIFAP, Avenue Hamoir 12, 1180 Brussels, Belgium.)
- FAO. 1982. Report of the Second Government Consultation on International Harmonization of Pesticide Registration Requirements. AGP: 1982/M/5.
- FAO. 1985. International Code of Conduct on the Distribution and Use of Pesticides. CL87/9-Sup. 1. May 1985.
- FRAWLEY, J. P. 1961-62. Process of Discovering and Developing A Marketable Pesticide. *Entoma*.
- GIFAP. 1982. Guidelines for the Safe Handling of Pesticides During Their Formulation, Packing, Storage, and Transport. GIFAP, Avenue Hamoir 12, 1180 Brussels, Belgium.
- GIFAP. 1983a. Guidelines for the Safe Handling and Effective Use of Pesticides. *Ibid.*
- GIFAP. 1983b. Hazardous Substances Export Policy Position Paper. *Ibid.*
- GIFAP. 1983c. The Manufacture and Formulation of Pesticides in Developing Countries. Technical Monograph No. 10. *Ibid.*
- GIFAP. 1984a. Agrochemical Industry Briefing Book for the UNEP World Industry Conference on Environmental Management. Papers with full references on: The Consultation Process: A Key to Communications, Understanding, Harmonization Between Governments and Industry; Constraints to Environmental Investment

- by Agrochemical Industry From Inadequate Propriety Protection; The Role of Product Stewardship and Co-Shared Responsibility in the Agrochemical Industry. Prepared at the invitation of the WICEM Agenda Committee, 1983. Ibid.
- GIFAP. 1984b. Guidelines for Emergency Measures in Cases of Pesticide Poisoning. Ibid.
- GIFAP. 1985a. GIFAP Principles and Objectives of Product Stewardship and Good Marketing Practices in the Export of Pesticides Position Paper. Ibid.
- GIFAP. 1985b. Options for Ensuring Quality in Stored Pesticide Products. Technical Monograph No. 10. Ibid.
- GIFAP. 1985c. International Code of Conduct on the Distribution and Use of Pesticides. Article. GIFAP Bulletin V. 11, N3, May/June 1985. Ibid.
- GIFAP. 1985d. Official Relations Between GIFAP and WHO. Article. GIFAP Bulletin Vol. 11, N2, March/April 1985. Ibid.
- HOLLIS, W. L. 1977. The Realism of IPM as a Concept and in Practice - With Social Overtones. Presented at the Annual Meeting of the Ent. Soc. of Am. Symp. IPM Relative to Fed. Agencies, Academia, and Ind. pp. 12-17. (Available Author, NACA, 1155 15th Street, N.W. Washington, D.C. 20005).
- HOLLIS, W. L. 1983. Agrichemical Residues in Perspective to Agriculture and Food Risks and Hazards. Assoc. Food & Drug Officials Quarterly Bulletin, Vol. 47, No. 2, p. 112.
- IICA. 1982. Reunion de Consulta Sobre la Armonizacion de Etiquetado Y Registro de Plaguicidas Para Los Paises Del Area Andina. Proceedings in Spanish. (Available IICA, Apartado Postal 55 - 2000 Coronado, San Jose, Costa Rica.)
- IICA. 1983a. II Reunion de Consulta Para La Armonizacion de Criterios en Registro Y Etiquetado de Plaguicidas Para Los Paises Del Area Central. Proceedings in Spanish. Ibid.
- IICA. 1983b. Pesticide Legislation and the Registration Process in the Caribbean. Proceedings. Ibid.
- IICA. 1983c. Reunion de Consulta Para la Armonizacion de Criterios en Registro Y Etiquetado de Plaguicidas Para Los Paises Del Area Sud. Proceedings in Spanish. Ibid.
- NACA. 1983. NACA Position on Pesticide Exports and U.S. Export Regulations. Testimony before the Subcommittee on Department Operations, Research, and Foreign Agriculture of the Committee on Agriculture, U.S. House of Rep. June 9. (Available Author, NACA, 1155 15th Street, N.W. Washington, D.C. 20005).
- RUSSEL, M. 1984. A Look at EPA's Regulatory Policy. UNEP Industry and Environment, July/Aug./Sept. 84 ed.

PLANT PROTECTION CHEMICALS
CIRCLE OF SAFETY



LATIN AMERICAN ENTOMOLOGICAL SERIALS

ANN H. KING
Hume Library
Institute of Food and Agricultural Sciences
University of Florida
Gainesville, FL 32611

ABSTRACT

This list of nearly 300 serial titles covers the Latin American literature of entomology comprehensively. Titles in the areas of general zoology plus plant and animal pathology are also included when they are substantially entomological in content. Serials included are published by governmental agencies at various levels, as well as commercial firms and scientific societies.

Latin America has always been an area of great interest to scientists at the University of Florida; consequently, the acquisition of scientific publications from this area has always had a high priority. This list of entomological serials has been produced as a means of identifying publications for possible acquisition.

In 1970, a significant list entitled *The Serial Literature of Entomology: A Descriptive Study* by Gloria M. Hammack, was published under the sponsorship of the Entomological Society of America and the National Science Foundation. It contained a substantial number of Latin American titles. In 1968, a similar unpublished list was produced locally by Jane Rayborn of the Florida Department of Agriculture and Consumer Services Division of Plant Industry Library (DPI Library). The present list was prompted by the need to combine the relevant sections of both the Rayborn and Hammack lists and to incorporate titles begun since 1970.

This list includes titles published by governmental agencies at various levels, as well as commercial publishing firms and scientific societies. Grouping is by major geographic area (Caribbean, Central America, South America) and then by country of origin. Entry is under the title, except when the publication is produced by a society, government agency, or university, in which case the sponsoring agency is generally used. This type of entry is similar to those normally found in library records. Recent changes in the cataloging rules will cause some discrepancies between headings used here and those used in libraries. There are no "see" or "see also" references since each country's list is relatively short.

Entomology is of major importance in almost every field of agriculture. Since it is not possible to list all serial publications of interest to the entomologist, the titles included have been largely limited to those concerned directly with entomology as evidenced by words in the title or agency name. The few exceptions are serials which deal with the related topics of general zoology, plus animal and plant pathology.

Since 1966 there has been a cooperative acquisition arrangement between the University of Florida Hume Agricultural Library and the Florida Department of Agriculture and Consumer Services Division of Plant Industry Library (DPI Library). Materials relating to entomological taxonomy are acquired by the DPI Library, while all other publications in entomology normally are acquired by Hume Library. Many serial titles have been acquired for Hume Library and for the DPI Library through the assistance of the Florida Entomological Society as exchanges for their publication, *Florida Entomologist*. This practice should be continued, and additional titles on this list should be acquired in this fashion for the appropriate area libraries. Titles in this list marked

by a dot are presently held by one or both of these libraries.

Many people have assisted in the compilation of this list. In order to enlarge and correct this list, the Florida Entomological Society sponsored a mailout of the draft to 104 scientists and research agencies throughout Latin America. There were fourteen responses. Several were extensive lists compiled locally, and they have contributed immeasurably to this list. We appreciate the opinions expressed as well as the additional titles suggested. Special thanks are due to Dr. Nelson Papavero of Brasil and Dr. Marion Elgueta of Chile for their contributions.

June Jacobson, as Librarian of the DPI Library, has verified holdings for her collection and added specialized titles not otherwise located. The University of Florida Latin American Collection has been a source of much information. Its Head Librarian, Rosa Q. Mesa, as author of *Latin American Serial Documents*, has furnished many relevant titles. Many thanks go to those who have translated and corrected in both Spanish and Portuguese. I would personally like to thank the Florida Entomological Society and its officers for their encouragement and for their financial support of the survey of Latin American scientists. I wish to thank the SHARE Office, Institute of Food and Agricultural Sciences, University of Florida, for financial support and to express my thanks to Tomás Zoebish for searching these references. Any omissions and errors are entirely my own.

Most important, thanks are due to Dr. Thomas J. Walker, University of Florida Department of Entomology. This list was initiated as a direct result of his strong interest in the literature of Latin America. We hope this final list will be of use to other scientists and librarians who have an interest in the entomology of Latin America.

Florida Agricultural Experiment Station Journal Series No. 6925.

July 31, 1985

Ann H. King

RESUMEN

Esta lista de casi 300 obras cubre, comprensivamente, la literatura entomológica de latinoamérica. También se incluyen títulos en las áreas de zoología general y en patología vegetal y animal cuando éstos, por su contenido, son esencialmente entomológicos. Las obras incluidas han sido publicadas por agencias gubernamentales a varios niveles, al igual que por compañías privadas y sociedades científicas.

América Latina ha sido siempre un área de gran interés para los científicos en la Universidad de Florida. Consecuentemente, la adquisición de publicaciones científicas de esta área ha tenido siempre alta prioridad. Esta lista de publicaciones en entomología se ha compilado con el propósito de poder identificar títulos para su posible adquisición.

En 1970, una lista significativa titulada *The Serial Literature of Entomology: A Descriptive Study*, fue compilada por Gloria M. Hammack, y publicada bajo los auspicios de la Sociedad Entomológica de América y la National Science Foundation. En 1968, una lista similar mas no publicada fue compilada localmente por Jane Rayborn de la División de Industria Agrícola de Florida. La presente lista fue iniciada con el propósito de combinar ambas secciones, la de Rayborn y la de Hammack, y a su vez incorporar títulos aparecidos a partir de 1970.

Esta lista incluye títulos publicados por agencias gubernamentales a varios niveles al igual que aquéllos publicados por compañías comerciales y sociedades científicas. La agrupación de estos títulos se ha hecho primero por áreas geográficas (Cariba, América Central) y luego por países de origen. La cita bibliográfica se encuentra

generalmente bajo el título, excepto cuando la publicación es producida por una sociedad, agencia de gobierno o universidad, en cuyo caso generalmente se usa el nombre de dicha agencia. Este tipo de cita es similar al normalmente encontrado en los catálogos de las bibliotecas. Los cambios recientes en las reglas de catalogación podrán causar discrepancias entre las citas aquí listadas y aquellas usadas en las bibliotecas. No se ha hecho referencia a "véase" o "véase también," ya que cada país tiene una lista relativamente corta.

La entomología es de gran importancia en casi todos los campos de la agricultura. Ya que no es posible compilar una lista de todas las obras que puedan ser de interés para el entomólogo, los títulos aquí incluidos se han limitado a aquéllos que evidentemente, palabras en el título o nombre de la agencia son relevantes para entomólogos. Como excepción se han incluido publicaciones que tratan con tópicos relacionados, esto es, zoología, y patología animal y vegetal.

Desde 1966 ha existido un acuerdo de adquisición cooperativa entre la Biblioteca Agrícola (Hume) de la Universidad de la Florida y la Biblioteca de la División de la Industria Agrícola de Florida (DPI Library). Todo material relacionado con taxonomía entomológica es adquirido por la DPI Library, mientras que otras publicaciones entomológicas son normalmente adquiridas por Hume. Muchas obras han sido adquiridas para Hume y para DPI Library a través de la Sociedad Entomológica de la Florida, a cambio de su publicación, *Florida Entomologist*. Esta práctica debe de continuarse, y las obras adicionales en esta lista deberán ser adquiridas y designadas de este modo a la biblioteca apropiada. Los títulos en esta lista que están marcados con un "dot" se encuentran presentemente en una o ambas bibliotecas.

Muchas personas han asistido en la compilación de esta lista. Con el propósito de expandir y corregir esta lista, la Sociedad Entomológica de la Florida envió un formulario por correo a 104 científicos y agencias de investigación en latinoamérica. Recibieron catorce respuestas. Algunas fueron listas extensas compiladas localmente, y las cuales contribuyeron inmensamente a esta lista. Estamos muy agradecidos por las sugerencias dadas al igual que por las obras propuestas. Estamos especialmente agradecidos al Dr. Nelson Papavero del Brasil y al Dr. Marion Elqueta de Chile por sus contribuciones.

La señora June Jacobson, en su capacidad como bibliotecaria del DPI Library, verificó las posesiones en su colección y asistió en la adición de obras especializadas, las cuales no se hubieran podido localizar de otra manera. La Colección LatinoAmericana de la Universidad de la Florida ha sido una fuente de mucha información. Su Bibliotecaria, la Sra. Rosa Q. Mesa, autora de *Latin American Serial Documents*, ha proveído muchos títulos relevantes. Muchas gracias les damos a todos los que ayudaron en las traducciones y correcciones en ambos español y portugués. Personalmente le quiero dar las gracias a la Sociedad Entomológica de la Florida y a sus dirigentes por el estímulo y las asistencias económicas en reconocimiento de los científicos Latinoamericanos. Yo quisiera agradecer a la oficina SHARE, del IFAS, Universidad de Florida, por la ayuda financiera otorgada para esta investigación. También quisiera dar las gracias a Tomás Zoebish por la investigación de estas referencias. Cualquier error u omisión son completamente míos.

Un agradecimiento muy especial se le debe al Dr. Thomas J. Walker del Departamento de Entomología de la Universidad de la Florida. Esta lista fue iniciada como resultado por su gran interés en la literatura de latinoamérica. Esperamos que esta lista sea útil para otros científicos y bibliotecarios interesados en la entomología de latinoamerica.

31 de julio 1985

Ann H. King

SUMARIO

Esta lista de aproximadamente 300 revistas científicas cobre de completamente a literatura entomológica da América Latina. Inclui igualmente revistas nas áreas de zoologia geral, patologia animal e vegetal, quando têm substancial conteúdo entomológico. As revistas incluídas são publicadas quer por agências governamentais a vários níveis, quer por firmas comerciais e sociedades científicas.

A América Latina, tem sido sempre uma área de grande interesse para os cientistas da Universidade da Flórida. Consequentemente, a aquisição de publicações desta área tem recebido, sempre, alta prioridade. A presente lista de periódicos entomológicos está sendo publicada como um meio de identificar publicações para possível aquisição.

Em 1970, Gloria M. Hammack compilou uma significativa relação relevante intitulada *The Serial Literature of Entomology: a Descriptive Study*, sob o patrocínio da Sociedade Entomológica da América e da National Science Foundation. Esta relação continha um número substancial de títulos oriundos da América Latina. Em 1968, uma listagem semelhante (não publicada) foi produzida localmente por Jane Rayborn, da Biblioteca do Departamento de Agricultura e Serviço para Consumidores da Flórida, Divisão de Indústria Agrícola (DPI Library). Esta lista foi feita pela necessidade de combinar as secções relevantes das listas de Hammack e Rayborn, e incorporar publicações iniciadas desde 1970.

A presente lista inclui títulos publicados por agências governamentais a vários níveis, bem como por editoras comerciais e sociedades científicas. O seu arranjo foi feito por áreas geográficas principais (i.e. América Central), e, seguidamente, por país de origem. A ordem de entrada é feita por título, excepto quando a publicação é editada por uma associação, agência, ou universidade, caso em que se usa geralmente a agência patrocinadora. Este tipo de citação é idêntico ao normalmente utilizado nos catálogos de bibliotecas. Alterações recentes das normas de catalogação poderão causar algumas discrepâncias entre os títulos usados aqui e os usados nas bibliotecas. Uma vez que a lista referente a cada país é relativamente curta, referências tais como "veja" ou "veja também" são omitidas.

A entomologia é de importância primordial em quase todos os campos da agricultura. Não sendo possível listar todas as revistas de interesse para os entomologistas, incluímos aqui apenas os títulos directamente ligados à entomologia, usando como critério o nome da revista ou da agência editora. Incluem-se, também publicações nas áreas relacionadas de zoologia geral e patologia animal ou vegetal.

Desde 1966, existe um acordo de aquisição cooperativo entre a Biblioteca Agrícola (Hume) da Universidade da Flórida e a Biblioteca da Divisão de Indústria Agrícola (DPI Library). Materiais relacionados com a sistemática entomológica são adquiridos pela DPI Library, sendo todas as outras publicações normalmente adquiridas pela Hume Library. Muitas das publicações têm sido adquiridas pela Hume Library e para DPI Library por permuta com a *Florida Entomologist*, publicação oficial da Sociedade Entomológica da América. Esta forma de actuação é desejável e novos títulos constantes desta lista deveriam ser adquiridos do mesmo modo para as bibliotecas das respectivas áreas. Títulos que nesta lista vão marcados com um "dot" existem presentemente numa ou em ambas as bibliotecas.

Muitas pessoas participaram na compilação desta lista. Para aumentar e corrigir esta lista, a Sociedade de Entomologia de Flórida financiou o envio de cópias preliminares a 104 cientistas ou instituições selecionadas em toda a América Latina. Foram obtidas catorze respostas. Várias delas eram listas exaustivas, compiladas localmente, que con-

tribuíram imensamente para a presente lista. Aqui agradecemos as opiniões expressas e as sugestões adicionais. Agradecemos especialmente ao Dr. Nelson Papavero do Brasil e ao Dr. Marion Elqueta do Chile pelas suas contribuições.

June Jacobson, como Bibliotecária da DPI Library, verificou as existências na respectiva coleção e acrescentou títulos da especialidade que não haviam sido previamente localizados. A Coleção Latinoamericana da Universidade de Flórida, foi igualmente uma fonte valiosa de informação. A sua bibliotecária chefe, Rosa Q. Mesa, autora dos *Latin American Serial Documents*, forneceu muitos títulos relevantes. Muitos agradecimentos são dirigidos aos tradutores para o espanhol e português. Gostaria de pessoalmente, agradecer à Sociedade de Entomológica de Flórida e respectiva direcção pelo seu encorajamento e suporte financeiro no levantamento dos cientistas latino-americanos. Gostaria de agradecer ao departamento SHARE, do IFAS, Universidade da Flórida, por apoio financeiro a esta investigação. Os meus agradecimentos vão também para Tomás Zoebish, pela pesquisa bibliográfica realizada. Por quaisquer omissões e enganos sou inteiramente responsável.

Agradecimentos especiais são devidos a Dr. Thomas J. Walker do Departamento de Entomológica da Universidade de Flórida. Esta lista foi iniciada como resultado directo do seu grande interesse pela literatura da América Latina. Esperamos que esta lista final seja útil a outros cientistas e bibliotecários que também tenham interesse na entomologia da América Latina.

31 julio 1985

Ann H. King

LIST OF BIBLIOGRAPHIES SEARCHED

- Aliaga de Vizcarra, Irma. Guía de Publicaciones Periodicas Agrícolas y Conexas de Bolivia. Sociedad de Ingenieros Agronomos de Bolivia. Boletin Bibliográfico, no.8, 1968.
- Arboleda-Sepúlveda, Orlando. Directorio de las Publicaciones Periodicas de la Biblioteca Conmemorativa Orton. Instituto Interamericano de Ciencias Agrícolas. 1966-68. Volume with Suplo. 1-5.
- Badillo, V. M. and C. Bonfanti. Indice Bibliografico Agrícola de Venezuela. Fundación Eugenio Mendoza, 1957.
- Bibliografía Brasileira de Zoología, v. 5, 1970; v. 6-7, 1971-72; v. 11, 1975-77; v. 12, 1977-78; v. 13, 1978-79.
- Catalogue of the Imperial College of Tropical Agriculture, University of the West Indies, Trinidad. Periodicals Section, p. 631-725. G. K. Hall, 1975.
- Gropp, Arthur E. A Bibliography of Latin American Bibliographies Published in Periodicals. Scarecrow, 1976.
- Hammack, Gloria M. The Serial Literature of Entomology: a Descriptive Study. Entomological Society of America, 1970.
- Hernández de Caldas, Angela. Publicaciones Periodicas Bioagricolas Latinoamericanas: un Directorio. Universidad de Nariño, Instituto Tecnológico Agrícola, 1966.
- Irregular Serials and Annuals. R. R. Bowker, 5th ed., 1978-79, 6th ed. 1980-81.
- Levi, Nadia. Guía de Publicaciones Periódicas de Universidades Latinoamericanas. Universidad Nacional Autónoma de México, 1967.
- Márquez, Orfila and Belkys Gutiérrez. Guía de Publicaciones Periodicas Agrícolas de Venezuela. República de Venezuela, Ministerio de Agricultura y Cría, Oficina de Comunicaciones Agrícolas, 1972.
- Mesa, Rosa Q. Latin American Serial Documents. R. R. Bowker.
 v. 1, Colombia, 1968
 v. 2, Brasil, 1968
 v. 10, Peru, 1973
 v. 11, Uruguay, 1973

- v. 3, Cuba, 1969
v. 4, Mexico, 1970
v. 5, Argentina, 1971
v. 6, Bolívia, 1972
v. 7, Chile, 1973
v. 8, Ecuador, 1973
v. 9, Paraguay, 1973
- v. 12, Venezuela, 1977
Costa Rica, unpublished
El Salvador, unpublished
Guatemala, unpublished
Haiti, unpublished
Nicaragua, unpublished
Panama, unpublished
- New Serial Titles 1950-70: Subject Guide. R. R. Bowker, 1975.
New Serial Titles 1971-80: Subject Guide. R. R. Bowker, 1971-80.
Pan American Union. Index to Latin American Periodical Literature. G. K. Hall.
Periódicos Brasileiros de Cultura. Edição Preliminar. Instituto Brasileiro de Bibliografia e Documentação. 1956.
Periódicos Brasileiros de Cultura. Instituto Brasileiro de Bibliografia e Documentação. 1968.
Rayborn, Jane. World List of Entomological Literature. Florida Division of Plant Industry, unpublished, 1968.
Shelby, Charmion, ed. Latin American Periodicals Currently Received in the Library of Congress and in the Library of the Department of Agriculture. The Library of Congress, 1944.
Ulrich's International Periodicals Directory. 18th ed., 1979-80, 19th ed., 1980, and 20th ed., 1981.
Velasquez, Pablo and Ramon Nadurille. Catálogo Colectivo de Publicaciones Periódicas Existentes en Bibliotecas de la Republica Mexicana. v. 1-2. Instituto Nacional de Investigaciones Agrícolas, 1968.

CARIBBEAN

CUBA

- Academia de Ciencias de Cuba. Instituto de Zoología. Informe Científico-Técnico. (Habana. Dirección de Publicaciones de la A.C.C.) no. 1, 1977-
- Academia de Ciencias de Cuba. Instituto de Zoología. Miscelánea Zoológica. (Habana) no. 1, 1975-
- Catálogo de la Fauna Cubana. Serie 4: Ciencias Biológicas. (Habana. Centro de Información Científica y Técnica, Universidad de la Habana) no. 35, 1975-
- Control de Plagas. (Habana) v. 13, no. 1, 1950-
- Cuba. Secretaría de Agricultura, Industria y Trabajo. Sección de Sanidad Vegetal. Anuario. (Habana) 1926/27-
- Cuba. Secretaría de Agricultura, Industria y Trabajo. Sección de Sanidad Vegetal. Boletín. (Habana) no. 1, 1917-no.4, 1923?
- Cuba. Secretaría de Agricultura, Industria y Trabajo. Sección de Sanidad Vegetal. Bulletin. [In English] (Habana) no. 1, 1917.
- Cuba. Secretaría de Agricultura, Industria y Trabajo. Sección de Sanidad Vegetal. Circular. (Habana) no. 1, 1916-no.6, 19?
- Cuba. Secretaría de Agricultura, Industria y Trabajo. Sección de Sanidad Vegetal. Informe de los trabajos. (Habana) 1924/25?
- Poeyana. Serie A. no. 1, 1964-
 - Poeyana. Serie B. no. 1, 1964-
- Revista Kuba de Medicina Tropical y Parasitología. (Habana) 1947- [Was: Revista de Parasitología, Clínica y Laboratorio. (Habana) 1935-36; Revista de Medicina Tropical y Parasitología, Bacteriología, Clínica y Laboratorio. (Habana) 1936-46; Revista de Medicina Tropical y Parasitología. (Habana) 1945-46.]

DOMINICAN REPUBLIC

- Moca. Estación Nacional Agronómica. Publicación. Serie E. Entomología y Zoología. (Santo Domingo) v. 1, 1927-
 [no. 1 as Laboratorio de Entomología. Boletín. (Santo Domingo) no. 2 as
 Laboratorio de Entomología. Circular. (Santo Domingo)]
- Moca. Estación Nacional Agronómica. Laboratorio de Entomología. Informe de la Sección de Entomología.

GUADELOUPE

- Attini.
 Nouvelles Agronomiques. (Antilles-Guyane)
 Revue Agricole: Organe du Service de l'Agriculture de la Guadeloupe et Dependances. (Basse-Terre) v. 1-3, 1926-28?

JAMAICA

- Jamaica. Department of Agriculture. Entomological Bulletin. (Kingston) 1921-32.
 Jamaica. Department of Agriculture. Entomology Circular. (Kingston) 1921-34.

PUERTO RICO

- Journal of Agriculture of the University of Puerto Rico. (Rio Piedras) v.1, 1917-
 School of Tropical Medicine of Puerto Rico. Report. (San Juan) 1943-47?
- University of Puerto Rico. Estación Experimental Agrícola. Boletín.

TRINIDAD AND TOBAGO

- Caribbean Plant Protection Commission. Quarterly Report (Port of Spain, Food and
 Agriculture Organization of the U.N.)
 Commonwealth Institute of Biological Control. Quarterly Report. (Trinidad)
- Tropical Agriculture. (University of the West Indies) v.1, 1924-

CENTRAL AMERICA

COSTA RICA

- El Agricultor Costarricense. (San José) 1943-
- Brenesia. (San José, Museo Nacional de Costa Rica) v.1, 1972-
 Ciencias Veterinarias. (Heredia, Universidad Nacional) v.1, 1980-
 Revista de Biología. (San José, Universidad de Costa Rica) v.1, 1953-
 - Turrialba. (San José) v.1, 1953-

EL SALVADOR

- El Salvador. Centro Nacional de Tecnología Agropecuaria. Boletín Técnico. no.1, 1970?-
 El Salvador. Centro Nacional de Tecnología Agropecuaria. Publicaciones. Varias v.1,
 1977-
- El Salvador. Dirección General de Investigaciones Agronómicas. Sección de Entomología. Boletín Técnico. (San Salvador) v.1, 1960-

HONDURAS

- Entomología Económica Hondureña. Boletín Técnico. no.6, 1958-

MEXICO

- Abejas y miel. Boletín. (México, D.F. Dirección General de Avicultura y Otras Especies Menores) v.1, 1964-
- Chapingo, México. Escuela Nacional de Agricultura. Departamento de Parasitología. Memoria del Día del Parasitólogo. v.1, 1963-
- Enciclopedia Apícola. (México, D.F. Editorial Agrícola Mexicana) v.1, 1953-

- Fitófilo. (San Jacinto) año 1, 1942-
- Fitopatología Mexicana. (Chapingo, Escuela Nacional de Agricultura, Laboratorio de Fitopatología, Sociedad Mexicana de Fitopatología. v.1, 1962-?)
- Folia Entomológica Mexicana. (México, D.F., Sociedad Mexicana de Entomología) no.1, 1961-
- El Informador Apícola. (Mérida) 1964-
- Instituto de Salubridad y Enfermedades Tropicales. Revista. 1939-65.
- México (City). Universidad Nacional. Instituto de Biología. Serie Zoología. (México, D.F.) v.39, 1967- [Supercedes, in part, and continues v. nos. of its Anales.]
- México. Comisión de Parasitología Agrícola. Boletín. no.1, 1900-no.4, 1908.
- México. Comisión de Parasitología Agrícola. Circular. no.1, 1903-no.75, 1908.
- México. Comisión de Parasitología Agrícola. Las Plagas de la Agricultura. Entrega no.1, 1902-no.12?, 1903.
- México. Comisión Nacional para la Erradicación del Paludismo. CNEP Boletín. (México, D.F.) no.1, 1957-
- México. Consejo Superior de Salubridad. Boletín Extraordinario. Documentos Oficiales Relativos a la Epidemia de la Peste Bubónica. no.1, 1902-no.4, 1903.
- México. Instituto de Higiene. Sección de Parasitología. Monografías. no.1, 1923-no.4, 1926.
- México. Instituto Nacional de Investigaciones Agrícolas. Reporte Entomológico del Noroeste. (Hermosillo) v.1, 1965-
- México. Instituto Pecuario. Laboratorio de Parasitología. Folleto de Divulgación. no.1, 1942-
- México. Instituto Politécnico Nacional. Escuela Nacional de Ciencias Biológicas. Anales de la Escuela nacional de ciencias biológicas. v.1, 1938-
- México. Junta Nacional Directora de la Campaña contra la Langosta. Consejos Sencillos para Destruir la Langosta. Boletín. no.1, 1926?- no.4, 1926?.
- México. Oficina para Defensa Agrícola. Boletín de Divulgación. (Tacubaya, D.F.) no.1, 1929-
- México. Oficina para Defensa Agrícola. Boletín Mensual. (San Jacinto, D.F.) no.1, 1927-?, 1929.
- México. Secretaría de Agricultura y Ganadería. Boletín Sanitario. v.1, 1929-
- Revista de Paludismo y Medicina Tropical. (México) 1949?-
- Revista Latinoamericana de Microbiología y Parasitología (México, D.F.) v.1, 1958- and Suplemento, 1958-
- Sociedad Mexicana de Entomología. Revista. (México, D.F.) v.1, nos.1-2, 1955.
- Sociedad Mexicana de Lepidopterología. Boletín Informativo. (México, D.F.) v.1, 1974-?
- Sociedad Mexicana de Lepidopterología. Revista. (México, D.F.) v.1, 1975-

NICARAGUA

Nicaragua. Departamento de Entomología. Servicio Técnico Agrícola. Circular Entomológica. (Managua) v.1, 1952-

PANAMA

Panamá. Ministerio de Agricultura, Comercio, e Industria. Departamento de Sanidad Vegetal. Boletín. no.1, 1959-

SOUTH AMERICA

ARGENTINA

- Acta Scientific. Serie Entomología. (Buenos Aires, Instituto Entomológico San Miguel) no.1, 1955-no.14, 1980.
- Acta Zoológica Lilloana. (Tucumán. Universidad Nacional de Tucumán) v.1, 1943-
 - Agro. (La Plata. Ministerio de Asuntos Agrarios) 1959-
 - Apicultura Argentina. (Buenos Aires) v.1, 1953-

- Archivo de Ciencias Biológicas y Naturales, Teóricas y Aplicadas. (Buenos Aires, Librart) 1956-
- Argentine Republic. Comisión Central de Investigaciones sobre la Langosta. Memoria de la Comisión Central de Investigaciones sobre la Langosta Correspondiente . . . (Buenos Aires) 1934-37?
- Argentine Republic. Comisión de Parasitología. Memoria. (Buenos Aires) 1932/33-
- Argentine Republic. Dirección General de Agricultura y Defensa Agrícola. Boletín. (Buenos Aires) 1907-1911.
- Argentine Republic. Dirección General de Agricultura y Defensa Agrícola. Circular. (Buenos Aires) no.1, 1911-no.6, 1914?
- Argentine Republic. Dirección General de Agricultura y Defensa Agrícola. Memoria Ministerial. (Buenos Aires) 1912?
- Argentine Republic. Dirección General de Agricultura y Defensa Agrícola. Publicaciones. (Buenos Aires) 1915, 1917?
- Argentine Republic. Dirección General de Paludismo, Tucumán. Boletín. (Tucumán) no.1, 193?-
- Argentine Republic. Dirección General de Paludismo, Tucumán. Memoria. (Tucumán) 1937?-
- Argentine Republic. Dirección General de Paludismo. Tucumán. Biblioteca. Boletín Bibliográfico. (Tucumán) no.1, 1942-no.44, 1948?
- Argentine Republic. Instituto de Sanidad Vegetal. Boletín. (Buenos Aires).
- Argentine Republic. Instituto de Sanidad Vegetal. Departamento de Zoología Agrícola. Circular. (Buenos Aires) no.1, 1944-
- Argentine Republic. Instituto de Sanidad Vegetal. Laboratorio Central de Fitopatología. Circular. (Buenos Aires) no.1, 1945-
- Argentine Republic. Instituto Regional de Entomología Sanitaria. Publicaciones. (Buenos Aires) 1/8, 1948-50-
- Argentine Republic. Ministerio de Agricultura. Anales. Sección de zootecnia, bacteriología, veterinaria y zoología. (Buenos Aires) no.1, 1902-no.3, 1907.
- Arthropoda. (Buenos Aires, Asociación Argentina de Artropodología) v.1, 1950-?
- Bibliografía Entomológica Argentina. Suplemento. (Augusto A. Piran) 1961-
- Boletín Epizootiológico. (Buenos Aires?) 1967?-
- Boletín Fitosanitario. (Buenos Aires, Secretaría de Estado de Agricultura y Ganadería de la Nación, Dirección General de Sanidad Vegetal) no.1, 1962-
- Buenos Aires. Dirección de Lucha contra las Plagas. Circular D. 1957-
- Buenos Aires. Instituto Científico de Medicina Veterinaria. Boletín Técnico. 1957-
- Buenos Aires. Instituto de Entomología Sanitaria. Publicaciones del Instituto Regional de Entomología Sanitaria. (Buenos Aires) v.1, 1948-v.8, 1950.
- Buenos Aires. Instituto de Patología Vegetal. Hoja Informativa. 1966?-
- Buenos Aires. Instituto de Patología Vegetal. Publicaciones. Serie A. 1945-54.
- Buenos Aires. Instituto de Patología Vegetal. Publicaciones. Serie B. 1945-52.
- Buenos Aires. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Anales. v.1, 1864-v.?, 1947.
- Buenos Aires. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Comunicaciones. Entomología. v.1, 1964-v.1, no.7, 1981.
- Buenos Aires. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Publicaciones. Entomología. no. 1, 1883-no.162, 1947. [became: Revista. Entomología.]
- Buenos Aires. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Revista. Entomología. v.1, 1964-v.5 no.11, 1979.
- Buenos Aires. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Revista. Parasitología. vol.1, 1968-v.2 no.5, 1980.

- Ciencia y Abejas. (Asociación Cooperadora de la Cabaña Apiario el Salado) v.1, 1972-
Comité Interamericano Permanente Antiacridiano. Memoria y Balance. (Buenos Aires)
[Title varies: Memoria.]
- Comité Interamericano Permanente Antiacridiano. Reunión Anual. (Buenos Aires)
Entomología. Catálogo y Periódico. (Buenos Aires) v.1, 1953-
Fitosanitarias. (La Plata) v.1, 1962-
Genera et Species Animalium Argentinorum (Tucumán) v.1, 1948- v.11, 1950?.
- Idia. (Buenos Aires. Instituto Nacional de Tecnología Agropecuaria) no.1, 1948-
Instituto de Patología Vegetal. Publicación Técnica. (Castelar) 1957?-
 - Neotrópica: Notas Zoológicas Americanas. (Buenos Aires) v.1, 1964-
Opera Lilloana. (Tucumán, Instituto Miguel Lillo) v.1, 1957-
Physis. (Buenos Aires, Asociación Argentina de Ciencias Naturales.) v.1, 1912-
 - Revista Argentina de Entomología. (Buenos Aires) v.1, 1935-v.2, 1944.
 - Revista de Investigaciones Agropecuarias. Serie 4: Patología Animal. (Buenos Aires)
no.1, 1964-
 - Revista de Investigaciones Agropecuarias. Serie 5: Patología Vegetal. (Buenos
Aires). no.1, 1964-
- Revista de la Cátedra de Microbiología y Parasitología. (Universidad de Buenos Aires.
Facultad de Ciencias Medicas.) 1930-
- Revista Industrial y Agrícola de Tucumán. (San Miguel, Estación Experimental Agr-
rícola) v.1, 1910-
- Revista Sudamericana de Entomología Aplicada. Serie A. Entomología Agrícola. 1946-
Sociedad Entomológica Argentina. Periódico Zoológico. (Buenos Aires) v.1, 1874-
v.3,1878. [Became: Sociedad Zoológica Argentina. Periódico Zoológico with
1974.]
- Sociedad Entomológica Argentina. Boletín. (Buenos Aires) v.1, 1925?-
- Sociedad Entomológica Argentina. Revista. (Buenos Aires) v.1, 1926-v.40, 1981.
 - Universidad de Buenos Aires. Facultad de Agronomía y Veterinaria. Boletín.
(Buenos Aires) no.1, 19-
 - Universidad de Buenos Aires. Facultad de Agronomía y Veterinaria. Revista de la
Facultad de Agronomía y Veterinaria. (Buenos Aires) v.1, 1917-v.19 no.3, 1971.
- Universidad Nacional. Facultad de Agronomía y Veterinaria. Instituto de Parasitología
y Enfermedades Parasitarias. Publicación. v.1, 1938/40-
- Universidad Nacional. Museo. Anales. Sección Zoológica. (La Plata) no.1, 1893-no.3,
1895.
- Universidad Nacional. Museo. Anales. Nueva Serie. Zoología. (La Plata) no.1, 1953-
Universidad Nacional. Museo. Notas. Zoología. (La Plata) no.1, 1935-no.213, 1963?.

BOLIVIA

- Bolivia. Departamento de Sanidad Vegetal. Boletín Entomológico. (La Paz) no.1, 1951-
Bolivia. Departamento de Sanidad Vegetal. Hoja Divulgativa de la Sección Ent-
tomología. (La Paz) no.1, 1947-
- Cooperativa Apícola Cruaña. Hoja informativa. (Santa Cruz de la Sierra) no.1, 1953-
no.12, 1958.
- Universidad Mayor de San Simón. Facultad de Ciencias Agronómicas. Cuadernos de
Entomología. (Cochabamba) no.1, 1948-

BRASIL

- Abelhas. (Leça do Bálío) v.15, 1972-
- Acta Amazônica. (Manaus, Instituto Nacional de Pesquisas da Amazonia) v.1, 1971-
Acta Biológica Paranaense. (Curitiba, Universidade Federal do Paraná) v.1, 1972- [was
Universidade Federal do Paraná. Boletim. Zoologia.]

- Apicultor. (Niteroi, Associação Fluminense de Apicultores) v.1, 1961-
- Apicultor. (Porto Alegre, Associação Gaucha de Apicultores "AGA") v.1, 1965-
- Apicultor. (Confederação Brasileira de Apicultura) v.1, 1968?-
- Arquivos de Entomologia. Série A. (Pelotas, Instituto Agronômico do Sul, Escola de Agronomia "Eliseu Maciel") v.1, 1958-
- Arquivos de Entomologia. Série B. (Pelotas, Instituto Agronômico do Sul, Escola de Agronomia "Eliseu Maciel") v.1, 1959- [was: Instituto Biológico de Defesa Agrícola e Animal. Arquivos. (São Paulo.)]
- Arquivos de Zoologia. (Universidade de São Paulo, Museu de Zoologia) v.1, 1940-
 - Biológico. (São Paulo, Instituto Biológico) v.1, 1935-
- Boletim Apícola. (Limeira, Associação dos Apicultores do Brasil) v.1, 1957-
- Boletim Biológico. (São Paulo, Clube Zoológico do Brasil e da Sociedade Brasileira de Entomologia.) v.1, 1926-v.21, 1932. ns. v.1, 1933-
- Boletim Fitossanitário. (Rio de Janeiro. Dept. Nacional da Produção Vegetal) v.1, 1944-
- Brasil Apícola. (São Paulo) v.1, 1951-
- Ciência e Cultura. (São Paulo, Sociedade Brasileira para o Progresso da Ciência) v.1, 1949-
- Colmeia. (Canãos) v.1, 1971-
- DIPAN. (Rio Grande do Sul. Secretária de Agricultura) v.1, 1948-
- Dusenja: Publicação Periodica de Scientia Naturali. (Curitiba) 1950-
- Entomologia Médica. (São Paulo) v.1, 1962-v.3, 1965.
- Entomologista Brasileiro. (São Paulo) Ano 1, 1908-ano 3, 1910. [was: Entomologo]
- Entomologo, O. (São Paulo) v.1, 1908. [became: Entomologista Brasileira]
- Escola Nacional de Agronomia. Boletim. (Rio de Janeiro) v.1, 1938-v.3, 1942. [was: Escola Superior de Agricultura e Medicina Veterinária. Archivos]
- Escola Superior de Agricultura e Medicina Veterinária. Archivos. (Rio de Janeiro) no.1, 1917-v.10, 1933. [became: Escola Nacional de Agronomia. Boletim.]
- Fertilizantes, insecticidas e rações. F.I.R. (São Paulo) v.1, 1959?-
- Fitopatologia Brasileira. (Brasília, Sociedade Brasileira de Fitopatologia) v.1, 1976-
- Fitossanidade. (Fortaleza. Grafica Recol.) no.1, 1974-
- Fólia Clínica et Biologia. (São Paulo, Universidade de São Paulo. Faculdade de Medicina) 1929-
- Iheringia Zoológica. (Rio Grande do Sul, Museu Rio-Grandense de Ciência Naturais. Departamento de Ciência e Cultura da Sec.) 1957-
- Instituto Biológico da Bahia. Boletim. (Bahia) 1954-
- Instituto Biológico de Defesa Agrícola e Animal. Arquivos. (São Paulo) 1928-31.
 - Instituto Butantan. Memórias. (São Paulo) v.1, 1921-
- Instituto de Biológico e Pesquisas Tecnológicas. Boletim. (Curitiba) v.1, 1941-
- Instituto de Medicina Tropical de São Paulo. Revista. 1958-
- Lima, Angelo Moreira da Costa. Insetos (sic) do Brasil da Costa Lima. (Rio de Janeiro, Escola Nacional de Pesquisas da Amazônia Zoológica.) v.1, 1939-
 - Museu Nacional. Arquivos. v.1, 1876-
- Museu Nacional. Publicações Avulsas. (Rio de Janeiro) v.1, 1945-
- Museu Nacional. Boletim. Nova série Zoológica. Boletim. no.1, 1942-
 - Museu Paraense Emílio Goeldi. Boletim. Nova série. Zoologia. Instituto Nacional de Pesquisas da Amazônia Zoológica. (Bélem) v.1, 1957-
 - Museu Paranaense. Publicações Avulsas. (Curitiba) v.1, 1944-
- Natura. (Bahia, Universidade Federal da Bahia. Instituto de Biologia) 1975-
- Nossas Colmeias.
- Resúmenes de Malariologia. (Rio de Janeiro) 1942-46?
- Resumos de Malariologia e Doenças Tropicais. (Rio de Janeiro) 1948-

- Reunião de fitossanitaristas do Brasil. Anais. 1st, 1956? -
Revista Brasileira de Apicultura. (Rio de Janeiro) v.1, 1922-v.1, 1923.
- Revista Brasileira de Biologia. (Rio de Janeiro, Academic Brasileira de Ciências) v.1, 1941-
- Revista Brasileira de Entomologia. (São Paulo, Sociedade Brasileira de Entomologia) v.1, 1954-
- Revista Brasileira de Malariologia. (Rio de Janeiro, Serviço Nacional de Malária) v.1, 1949?
- Revista Brasileira de Malariologia e Doenças Tropicais. (Rio de Janeiro. Dept. Nacional de Endemias Rurais) v.1, 1949-
- Revista Brasileira de Pesquisas Médicas Biológicas/Brazilian Journal of Medical and Biological Research. (São Paulo, Editora Médico) v.1, 1968-
- Revista de Agricultura (Piracicaba) v.1, 1926-
- Revista de Entomologia. (Rio de Janeiro. Thomaz Borgmeier, O.F.M.) v.1, 1931-no.22, 1951. Suplemento, no.1, 1941.
- Rio de Janeiro. Instituto Biológico de Defesa Agrícola. Boletim. No.1, 1921-no.9, 1939. [became: Studia Entomológica]
- Rio Grande do Sul, Brasil (State) Secretária da Agricultura, Indústria, e Comércio. Informes e Comunicados: Defesa Sanitária Vegetal. (Porto Alegre) no.1, 1960-
- Rio Grande do Sul, Brasil (State) Serviço de Entomologia. Boletim. (Porto Alegre?) v.1, 1955-
- São Paulo. Brasil (State) Departamento da Produção Animal. Serie de Vulgarização. Apicultura. v.1, 1961?-
- Seminário Brasileiro de Herbicidas e Ervas Daninhas. Anais. (Rio de Janeiro) 1956-
- Sociedade Brasileira de Agronomia. Revista. (Rio de Janeiro) v.1, 1937- [title varies: known as Boletim, v.3, 1940-v.11, 1948.]
- Sociedade Brasileira de Entomologia. Anais de Reunião Anual. (São Paulo. Escola Superior de Agricultura "Luiz de Queiroz." v.1, 1968-
- Sociedade Brasileira de Entomologia. Boletim. (São Paulo) v.1, 1948- v.9, 1958.
- Sociedade Brasileira de Nematologia. Publicação. (Piracicaba, Escola Superior de Agricultura "Luiz de Queiroz") v.1, 1974-
- Sociedade de Biologia de Pernambuco. Anais. (Recife, Universidade do Recife. Instituto de Antibióticos) 1941-
- Sociedade Entomológica do Brasil. Anais. (Rio de Janeiro) v.1, 1972-
- Sociedade Entomológica do Brasil. Boletim. (Rio de Janeiro) No.1, 1922-no.6, 1923.
- Studia Entomologica, Revista Internacional de Entomologia. First Series. (Rio de Janeiro) No.1, 1952-no.3, 1955.
- Studia Entomologica, Revista Internacional de Entomologia. New Series. (Rio de Janeiro) v.1, 1958-v.20, 1978.
- Summa Phytopathológica. (São Paulo. Grupo Paulista de Fitopatologia, Sociedade Brasileira de Fitopatologia) v.1, 1975- [was: Revista de Entomologia]
- Universidade de Minas Gerais. Museu de Historia Natural. Boletim. Zoologia. (Belo Horizonte) no.1, 1968-
- Universidade Federal do Paraná. Boletim. Zoologia. (Curitiba) v.2, 1965-v.5, 1972. [became: Acta Biológica Paranaense]

CHILE

- Anales de Zoología Aplicada. (Santiago) v.1, 1914-v.9, 1922.
Boletín Agrícola Shell. (Santiago)
- Boletín chileno de parasitología. (Santiago) v.1, 1946-
 - Boletín de Sanidad Vegetal. (Santiago de Chile) v.1, 1941-v.3, 1943.
 - Chile. Comisión de Parasitología Agrícola. Circular. (Santiago de Chile) 1903-1908.

- Chile. Departamento de Sanidad Vegetal. Boletín Técnico. (Santiago de Chile) no.1, 1942-
- Chile. Departamento de Sanidad Vegetal. Circular. (Santiago de Chile) no.1, 1941-
- Chile. Estación de Patología Vegetal. Publicaciones. (Santiago de Chile?) no.1, 1900-no.17, 1905?
- Chile. Estación Nacional Agronómica. Laboratorio de Entomología. Boletín. (Santo Domingo)
- Chile. Estación Nacional Agronómica. Laboratorio de Entomología. Circular. (Santo Domingo)
- Chile. Servicio Nacional de Salubridad. Departamento de Parasitología. Memoria anual. (Santiago de Chile) 1952?-
- Colección insectos portadores de enfermedades. (Santiago de Chile. Sub. Depto. de Educación Sanitaria) 1956-
- Instituto de la Patagonia. Anales. (Punta Arenas) v., 1970-
- Investigaciones Zoológicas Chilenas. (Santiago, Centro de Investigaciones Zoológicas) 1950-
 - Revista Chilena de Entomología. (Santiago, Sociedad Chilena de Entomología, Universidad de Chile) v.1, 1951-
- Revista Chilena de Historia Natural Pura y Aplicada. (Valparaíso, Museo de Historia Natural) v.1, 1897-v.55, 1960/63. [title varies: Revista Chilena de Historia Natural, Valparaíso]
- Santiago de Chile. Museo Nacional de Historia Natural. Boletín. t.1, 1908-
- Sociedad Entomológica de Chile. Boletín. (Santiago) no.1, 1928-no.2, 1929.
- Sociedad Entomológica de Chile. Boletín Semestral. (Santiago) no.1, 1973-no.2, 1975.
- Universidad de Chile. Biblioteca Técnica de Parasitología. Contribución a la Bibliografía Chilena de Parasitología. (Santiago) v.1, 1954-
- Universidad de Chile. Centro de Estudios Entomológicos. (Santiago) Publicaciones. no.1, 1960-no.10, 1970. [became: Universidad de Chile. Departamento de Biología. Publicaciones Entomológicas]
- Universidad de Chile. Departamento de Biología. Publicaciones Entomológicas. (Santiago) v.11, 1974- [was: Universidad de Chile. Centro de Estudios Entomológicos. Publicaciones Entomológicas.]
- Universidad de Chile. Departamento de Parasitología. Boletín de Información Técnica. (Santiago) v.1, 1945?- v.7, 1952. [title varies: Boletín de Informaciones Parasitarias Chilenas; Boletín chileno de parasitología?]
- Universidad de Chile. Departamento de Parasitología. Boletín de Informaciones Parasitarias Chilenas. (Santiago) v.4, 1949-v.8, 1953. [title varies: Boletín de Información Técnica]
- Universidad de Chile. Departamento de Parasitología. Memoria. (Santiago) no.1, 1952-
- Universidad de Chile. Departamento de Parasitología. Publicaciones Instructivas de Carácter Sanitario. (Santiago)
- Universidad de Chile. Departamento de Parasitología y Servicio Nacional de Salud. Índice Bibliográfico Parasitológico de Artículos de Revistas. (Santiago) 1952-
- Universidad de Chile. Facultad de Agronomía. Estación Experimental Agronómica. Boletín Técnico. (Santiago) v.1, -

COLOMBIA

- Actualidades Biológicas. (Medellín, Universidad de Antioquia) 1972-
- Agricultura Tropical. (Bogotá, Asociación Colombiana de Ingenieros Agrónomos) v.1, 1945-
 - Caldesia. (Bogotá, Instituto de Ciencias Naturales) v.1, 1940-
- Colombia. Comisión Central para la Extinción de la Langosta. Boletín de los trabajos.

no.1, 1912-no.20, 1913?.

- Revista Colombiana de Entomología. (Sociedad Colombiana de Entomología) v.1, 1975-
- Sociedad Biológica de Bogotá. Anales. (Bogotá) v.1, 1945-
Sociedad Colombiana de Entomología. Memorias. 1976?-
Sociedad Colombiana de Entomología. Resúmenes. 1976?-
Universidad Nacional de Colombia. Facultad de Medicina Veterinaria y de Zootecnia.
Revista. (Bogotá) 1928-

ECUADOR

- Revista Ecuatoriana de Entomología y Parasitología. (Quito. Centro Ecuatoriano de Investigaciones Entomológicas) v.1, 1953-
Sanidad Vegetal. (Quito, Ministerio de Economía) no.1, ?

GUYANA

British Guiana. Department of Agriculture. Entomological Bulletin. (Georgetown) 1930-
British Guiana. Mosquito Control Service. Report. (Georgetown) 1947-

PARAGUAY

Asunción. Instituto Nacional de Parasitología. Anales. no.1, 1928-no.5, 1932? [Name varies: 1905-1907? as Instituto Nacional de Bacteriología.]
Paraguay. Ministerio de Agricultura. Servicio de Extensión Agrícola y Ganadería. Boletín de Divulgación.
Senepa. (Asunción, Servicio Nacional de Erradicación del Paludismo.) no.1, 1961?-
Sociedad Científica del Paraguay. Revista.
Universidad Nacional. Instituto de Ciencias Básicas. Informes Científicos. (Asunción)

PERU

Archivos de Biología Andina. (Lima, Universidad Nacional Mayor de San Marcos. Instituto de Biología Andina. Centro de Investigaciones) 1965-
Canete. Estación Experimental. Departamento de Entomología. Circular.
Convención Nacional de Entomología. Anales. (Chiclayo) v.1, 1955-
Fitopatología. (Lima, Asociación Latinoamericana de Fitopatología) v.1, 1966-
Huacho, Perú. Estación Experimental Agrícola. Departamento de Entomología. Informe General de la Campaña Perú. 1964/65?-
Lima, Peru. Estación Experimental Agrícola. Informe Mensual. 1927-
Perú. Departamento de Malaria. Publicaciones. (Lima, Dirección General de Salud Pública.)
● Perú. Servicio de Investigación y Promoción Agraria. Informe especial. no.1, 1962-
Perú. Servicio Nacional de Erradicación de la Malaria. Boletín. (Lima) no.1, 1960-
Perú. Servicio Nacional de Erradicación de la Malaria. Informe de Actividades. (Lima) no.1, 195?- [Title varies: Informe Anual de Actividades.]
● Revista Peruana de Entomología Agrícola. (Lima, Sociedad Entomológica Agrícola del Perú) v.1, 1958-v.2, 1959.
Sociedad Entomológica Agrícola del Perú. Boletín. (Lima) v.1, 1959-
Universidad Agraria. Departamento de Entomología. Boletín Técnico. (La Molina)

SURINAM

Centrum voor Landbouwkundig Onderzoek in Surinam.
Landbouwproefstation in Surinam. Bulletin
● De Surinam Landbouw. v.1, 1953-

URUGUAY

Apicultor Americano. (Montevideo) v.1, 1954-v.2, 1958.

Láminas Entomológicas. (Montevideo)

- Museo Nacional de Historia Natural. Comunicaciones Zoológicas. (Montevideo) v.1, 1943-

Sociedad Uruguaya de Biología. Revista.

- Sociedad Uruguaya de Entomología. Revista. v.1, 1956-

Uruguay. Comisión Central de Defensa Agrícola. Defensa Agrícola. Boletín Mensual. (Montevideo) no.1, 1920-no.5, 1924.

Uruguay. Comisión Central de Defensa Agrícola. Defensa Agrícola. Memoria. (Montevideo) 1914/15-1917/18.

Uruguay. Comisión Central de Defensa Agrícola. Defensa Agrícola. Publicación. no.1, 1912-no.12, 1918?

Uruguay. Comisión Especial de la Lucha contra la Mosca. Publicación. no.1, 1919-

VENEZUELA

Agricultura Tropical. (Maracay) v.1, 1951-

Apicultura Venezolana. (La Victoria. Asociación Nacional de Apicultores) v.1, 1966-

Archivos Venezolanos de Medicina Tropical y Parasitología Médica. (Universidad Central. Facultad de Medicina. Instituto de Medicina Tropical.) no.1, 1948-no. , 1954.

Boletín de Entomología Venezolana. (Caracas, Ministerio de Sanidad y Asistencia Social) v.1, 1941-v. , 1955?

- Caracas. Museo de Ciencias Naturales. Boletín. t.1, 1955-

Insectos cuarentenarios para Venezuela. (Caracas, Ministeria de Agricultura y Cria) no.1, 1982 -

Maracay, Venezuela. (State) Instituto Nacional de Agricultura. Boletín Técnico. (Maracay) v.1, 1956-v.6, 1951.

Maracay, Venezuela. (State) Instituto Nacional de Agricultura. División de Entomología y Zoología. Circulares.

Maracay, Venezuela. (State) Instituto Nacional de Agricultura. División de Fitopatología. Noticias Fitopatológicas Venezolanas. 1948-?

Medicina Veterinaria y Parasitología. (Caracas)

Revista de Medicina Veterinaria y Parasitología. (Maracay. Facultad de Medicina Veterinaria, Universidad Central de Venezuela) v.1, 1939-

Sociedad de Ciencias Naturales. Memoria. (La Salle, Caracas) v.9, 1949?-

Sociedad Venezolana de Ciencias Naturales. Boletín. (Caracas) v.1, 1931-

Tijeretazos sobre Malaria. (Caracas, División de Malariología) v.1, 1938-?

Universidad Central. Facultad de Agronomía. Revista. (Maracay) v.1, 1952-

- Universidad de Zulia. Facultad de Agronomía. Revista. (Maracaibo) v.1, 1960?-

Venezuela. Dirección de Agricultura. División de Entomología y Zoología. Boletín Técnico. (Caracas) no.1, 1949?-

Venezuela. Dirección de Agricultura. División de Fitopatología. Boletín. (Caracas) no.1, 1950-?

Venezuela. Dirección de Agricultura. División de Sanidad Vegetal. Boletines. (Caracas)

Venezuela. Dirección de Agricultura. División de Sanidad Vegetal. Circulares. (Caracas)

Venezuela. Dirección de Ganadería. Compañía de Sanidad Animal.

Venezuela. Dirección de Malariología y Saneamiento Ambiental. Boletín Informativo. (Maracay) v.1, 1961-

Venezuela. Dirección de Malariología y Saneamiento Ambiental. Informe anual. (Caracas)

Venezuela. Dirección de Malariología y Saneamiento Ambiental. Reuniones Quin-

- cenales: Informe. (Caracas) 1961?-
Venezuela. Dirección de Malariología y Saneamiento Ambiental. Reuniones Quincenales: Minuta. (Caracas) 1961?-
Venezuela. División de Malariología. Boletín Informativo. (Maracay) no.1, 1959-?; 2 serie. v.1, no.1; 1961-
Venezuela. División de Malariología. Publicaciones. (Caracas) no.1, 1938-
Venezuela. Instituto Nacional de Agricultura. División de Entomología y Zoología. Circulares.
Venezuela. Instituto Nacional de Agricultura. División de Fitopatología. Boletín.
Venezuela. Instituto Nacional de Agricultura. División de Fitopatología. Noticias Fitopatológicas.

STOCHASTIC POLYPHENISM: COPING WITH UNCERTAINTY

THOMAS J. WALKER*

"A potentially important source of individual phenotypic variation is examined which has heretofore received little recognition as a general and probably widespread phenomenon." (Cooper and Kaplan 1982, p. 135)

SYNOPSIS

Polyphenism (i.e., polymorphism in which non-genetic differences cause the development of the contrasting forms) can be *conditional* or *stochastic*. In conditional polyphenism, a genotype responds to different current environments that predict different future environments by producing different, appropriate phenotypes. For example, short days may cause the development of the diapause phenotype, appropriate to winter, and long days may cause the development of the nondiapause phenotype, appropriate to summer. In stochastic polyphenism, a genotype responds to differences in its environment that occur with probabilities approximating the probabilities of different future environments. For example, if 30% of winters are severe enough to require diapause and the other 70% yield a corresponding advantage to nondiapausing morphs, a genotype would produce the diapause phenotype 30% of the time and the nondiapause phenotype the other 70%. Modeling and empirical evidence support the concept of stochastic polyphenism.

In a constant environment natural selection should lead to genotypes that develop into individuals adapted to that environment. In a predictably varying environment natural selection should operate to yield genotypes that cause the development of individuals appropriate to whatever environment is coming next. In fact, genotypes that anticipate the deterioration of a local habitat or the progression of the seasons are commonplace in insects. Such genotypes switch development into one path or another in response to present conditions that predict the future.

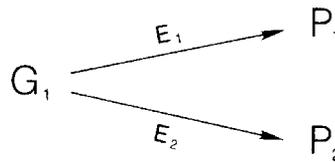
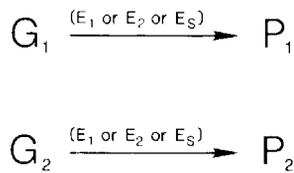
In environments that vary unpredictably—i.e., in truly uncertain environments—the outcome of evolution is hard to predict. The thesis of this paper is that genotypes which have probabilistic or stochastic output should prosper in uncertain environments and that such genotypes exist in insects.

Although I arrived at the notion of stochastic genes independently, the concept is not original. D. A. Roff (1975) investigated models in which the *probability* of dispersal was a function of genotype. W. S. Cooper and R. H. Kaplan (1982, p. 136; also, Kaplan and Cooper 1984) made a strong case for "intra-genotypic strategy-mixing or, less formally, adaptive coin flipping."

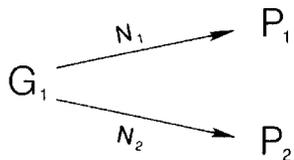
If genotypes have stochastic outputs, outputs of a single genotype could vary continuously (e.g., intensity of diapause, minimum duration of flight in a dispersing individual) or discontinuously (e.g., diapause vs. nondiapause; winged vs. apterous). Stochastic outputs of both types are indicated, but only discontinuous variation will be discussed here because it is more striking and easier to treat.

*Thomas J. Walker is a Professor of Entomology in the Department of Entomology and Nematology, University of Florida. His research deals mostly with the systematics, acoustic behavior, and ecology of crickets and katydids, but he also studies butterfly migration. Current address: Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611.

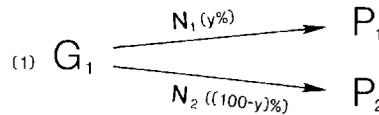
A GENETIC POLYMORPHISM C CONDITIONAL POLYPHENISM



B POLYPHENISM



D STOCHASTIC POLYPHENISM



(2) $E_s = y \% N_1 + (100 - y) \% N_2$

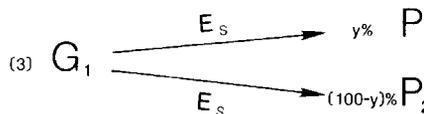


Fig. 1. Diagrams illustrating different types of polymorphism. (A) In *genetic polymorphism*, different phenotypes (P_1 and P_2) develop as a result of differences in genotype (G_1 and G_2). (B) In *polyphenism*, different phenotypes develop as a result of nongenetic differences (N_1 and N_2). (C) In *conditional polyphenism*, the nongenetic differences are environmental circumstances (E_1 and E_2) that predict different future environments to which the different phenotypes are adapted. (D) In *stochastic polyphenism*, (1) the nongenetic differences occur at probabilities that correlate with the probabilities of future environments to which the different phenotypes are adapted; (2) these stochastically occurring alternatives can be considered to comprise an "environment" (E_s), and (3) this environment causes the two phenotypes to be produced in the proportions of N_1 and N_2 .

POLYMORPHISM

Discontinuous variation occurring within a deme between individuals of the same ontogenetic stage is called *polymorphism* (see Kennedy 1961). Polymorphism can be divided into *genetic polymorphism* and *polyphenism* depending on what sort of differences lead to the development of the distinctive phenotypes. In genetic polymorphism the distinctive phenotypes result from differences in genotype, whereas in polyphenism nongenetic differences are responsible (Fig. 1a,b). It should be noted that polyphenism depends on a *genotype* that can be switched by the environment from one path of development to another.

Two modes of selection may lead to polyphenism. First, and most obvious, is that natural selection will increase genotypes that respond to different environments by producing different, appropriate phenotypes.¹ Such genotypes are responsible for *conditional polyphenism* (Fig. 1c). The defining aspect of this type of polyphenism is that

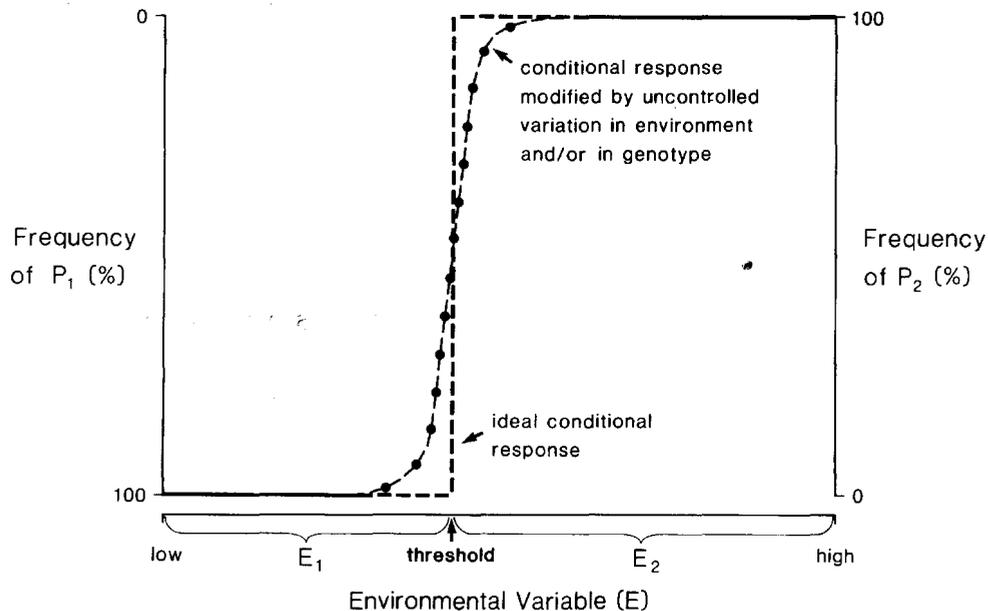


Fig. 2. The concept of *threshold* as applied to conditional polyphenism. An environmental variable ("E", abscissa) that varies continuously is divided into two regimes (E_1 and E_2) by a threshold. The transition from 100% of one phenotype (P_1) to 100% of the other (P_2) is likely to be sigmoid rather than rectilinear, and the best estimate of threshold becomes the value of E at which 50% of the exposed population develop into P_1 and 50% into P_2 .

development of a phenotype adapted to a specific future environment is conditional upon a particular present environment that is correlated with the future one. Examples include development of seasonally appropriate diapausing or nondiapausing individuals (Beck 1980) or flight-worthy or flightless individuals (Harrison 1980) in response to photoperiod. Conditional polyphenism depends on a genotype responding to one environmental condition by developing one phenotype and to an alternative condition by developing another. The transition between these two conditions is a threshold that delimits the production of 100% of one phenotype from the production of 100% of the other (Fig. 2). Ideally the threshold is sharp, but in practice it is likely to be blurred, because individuals in the responding population are not genetically identical (and therefore vary in their thresholds) and because individuals in a population do not experience identical environments even under carefully controlled circumstances (Fig. 2).

The second mode of selection is that a genotype may increase because it produces alternative phenotypes in proportions that approximate the probabilities of future environments that favor the respective phenotypes. Such selection would lead to *stochastic polyphenism* (Fig. 1d).

If stochastic polyphenism occurs, (1) genes must be able to effect a stochastic output and (2) such genes must be able to increase at the expense of genes that have a deterministic output. If these two conditions are met, (3) one would expect to find examples of stochastic polyphenism in insects living in environments exhibiting important, short- to medium-term, unpredictable variation. The next three sections of this paper deal with these subjects.

CAN GENES GAMBLE?

For genes to produce a stochastic output they must make use of environmental differences that occur in the right proportions without pattern. To use the metaphor of Cooper and Kaplan (1982), they must flip coins (properly biased to produce the needed proportions of heads and tails).

Recent advances in genetics suggest a variety of ways that genes might, in effect, gamble with the phenotype of their carrier. Transposable genetic elements ("jumping genes"), identified by Barbara McClintock in maize and now known to be commonplace in other plants and in animals (Fedoroff 1984), offer one such possibility. The developmental effect of a mobile element depends on its position in the genome. For instance, if it attaches to site "A" 40% of the time and to site "B" 60% of the time, the outcome would be 40% of one phenotype and 60% of another. The genomes would be the same except for the positions of their components, but the phenotypes produced would be determined stochastically.² Another possibility was suggested by Spudich and Koshland (1976), who demonstrated individual variation in genetically identical bacterial cells grown in a homogeneous environment. In trying to account for the variations, they noted that certain molecules occur in such small numbers in cells that their numbers are subject to "Poissonian variation" when cells divide and that this could lead to significant random variation in phenotype.

A final example is from immunology. The ability to produce millions of different antibodies is passed from generation to generation in a limited number of genes. These genes specify a "kit of [genetic] components," which are "shuffled" in the developing *B* lymphocytes leading "to a different result in each of millions of lines of cells" (Leder 1982, p. 102). Even millions of different phenotypes can be produced stochastically by a single genotype.

CAN STOCHASTIC GENES COMPETE?

If stochastic genes can arise by mutation from deterministic forebears, how well will they compete. Simulation modeling is a suitable way to investigate this question. Using a microcomputer, I developed two models that test stochastic genes in uncertain environments.³ In each model, the environment was made to vary without pattern between two states.⁴

The first model concerned insects that sometimes benefit from diapause and sometimes benefit by continuing development. One environmental state (e.g., mild winter), occurring $p\%$ of the time, was more favorable to the nondiapause phenotype. The other state (e.g., severe winter), occurring $(100-p)\%$ of the time, was more favorable to the diapause phenotype. Diapause was determined by three alleles at one locus: D_D , producing the diapause phenotype; D_N , nondiapause phenotype; and D_S , $y\%$ diapause phenotype and $(100-y)\%$ nondiapause phenotype.⁵ The following conditions were specified to start the model: dominance relations of the alleles, initial frequencies of alleles, proportion of generations that environment favors diapause phenotype (i.e., p), proportion of diapause phenotypes produced by D_S (i.e., y), relative fitness of diapause phenotype when the environment is less favorable to it, relative fitness of nondiapause phenotype when the environment is less favorable to it, number of generations per run of model, and number of runs.

Table 1 gives representative results for the first model. When allele D_S was recessive to the other two alleles, it quickly replaced them under a variety of scenarios—even if the probability of the diapause phenotype deviated greatly from the probability of the diapause-favoring environment (e.g., Table 1, A and B). When the other alleles were recessive, they persisted more than 400 generation under a wide range of assumptions,

TABLE 1. REPRESENTATIVE RESULTS OF A SIMULATION MODEL IN WHICH AN ALLELE WITH MIXED OUTPUT (D_S) COMPETED WITH ALLELES FOR DIAPAUSE (D_D) AND NONDIAPAUSE (D_N). ENVIRONMENT VARIED WITHOUT PATTERN BETWEEN FAVORING DIAPAUSE AND NONDIAPAUSE PHENOTYPES.^a RESULTS OF SIMULATIONS MADE WITH SIMILAR ASSUMPTIONS ARE GROUPED (A-D).

Dominance	Prob. diapause enviro. ^b (p)	Prob. diapause phenotype ^c (y)	Relative fitness when not favored ^d		Allele frequencies ^e		
			diapause phenotype	nondiap. phenotype	D_D	D_N	D_S
A) $D_D > D_N > D_S$	0.50	0.50	0.01	0.01	0.00	0.00	1.00
$D_D > D_S > D_N$	"	"	"	"	0.00	0.04	0.96
$D_S > D_D > D_N$	"	"	"	"	0.01	0.05	0.94
B) $D_D > D_N > D_S$	0.50	0.01	0.01	0.01	0.00	0.00	1.00
"	"	0.99	"	"	0.00	0.00	1.00
C) $D_S > D_D > D_N$	0.70	0.70	0.01	0.01	0.04	0.04	0.92
"	"	0.50	"	"	0.30	0.19	0.51
"	"	0.90	"	"	0.00	0.33	0.67
D) $D_S > D_D > D_N$	0.50	0.50	0.50	0.01	0.95	0.05	0.00
"	"	0.70	"	"	0.95	0.05	0.00
"	"	0.90	"	"	0.76	0.04	0.20
"	"	0.99	"	"	0.49	0.04	0.47

^aModel assumed discrete generations, random mating, and continuously large population. Initial frequencies of alleles were 0.33 (but results are independent of starting frequencies).

^bProbability that environment favoring diapause over nondiapause will occur. (1.00-p = probability of environment favoring nondiapause.)

^cProportion of D_S - controlled individuals having the diapause phenotype. (1.00-y = proportion having nondiapause phenotype.)

^dFavored phenotype has fitness of 1.00.

^eMean allele frequencies after 400 generations in 100 runs of the model. Standard errors are <0.005 for A and B and <10% of the mean for C and D. No consistent change in frequencies occurred when these allele frequencies were used to initialize the model and the model was run an additional 100 generations. However, when the model was run 1000 generations or more, further changes occurred.

TABLE 2. REPRESENTATIVE RESULTS OF A SIMULATION MODEL IN WHICH AN ALLELE FOR MIXED OUTPUT (P_S) COMPETED WITH ALLELES FOR ONE (P_O) OR TWO (P_T) WINTERS OF DIAPAUSE. ENVIRONMENT VARIED WITHOUT PATTERN BETWEEN GROWING SEASONS THAT FAVORED INDIVIDUALS THAT BROKE DIAPAUSE AND THOSE THAT DISFAVORED THEM.^a A) EFFECT OF DOMINANCE. B) EFFECTS OF PROBABILITY OF UNFAVORABLE GROWING SEASON, w , AND a . C) EFFECT OF MAKING UNFAVORABLE GROWING SEASONS LESS UNFAVORABLE.

Dominance	Prob. unfav. growing season	Maximum winters for P_S^b (w)	Annual attrition of p.d.'s ^c (a)	Fitness in unfav. growing season ^d	Allele frequencies ^e		
					P_O	P_T	P_S
A) $P_O > P_T > P_S$	0.50	2	0.10	0.01	0.00	0.00	1.00
$P_S > P_T > P_O$	"	"	"	"	0.08	0.18	0.74
B) $P_O > P_T > P_S$	0.50	6	0.10	0.01	0.00	0.00	1.00
"	0.10	"	"	"	0.00	0.00	1.00
"	0.01	"	"	"	0.75	0.08	0.17
"	"	"	0.01	"	0.10	0.01	0.89
"	"	2	0.10	"	0.55	0.00	0.45
C) $P_O > P_T > P_S$	0.50	2	0.10	0.10	0.00	0.00	1.00
"	"	"	"	0.50	0.71	0.09	0.20

^aModel assumed that individuals entered diapause no more than once, that only diapausing individuals survived winter, that mating was random among those breaking diapause each spring, that the number of their descendants entering diapause that fall depended only on the quality of the growing season, and that breeding populations were always large.

^b P_S allele causes geometrically decreasing proportions of individuals to remain in diapause for 1 to w winters ($0.5/2^{w-1}$ for winters 1 to $(w-1)$).

^cAnnual attrition of prolonged diapausers. Survival each winter beyond first was $(1.00-a)$.

^dProportion of favorable-season number that enter diapause when growing season is unfavorable.

^eMean allele frequencies after 120 generations in 100 runs of the model. Initial allele frequencies were based on pilot runs and did not differ by more than 10% from mean final frequencies. Standard errors <0.01 for A and C; <0.03 for B.

and the average frequency of D_S after 400 generations depended on the assumptions. For example, when y was made to deviate from p and the fitnesses of the disfavored phenotypes were kept equal, the frequency attained by D_S decreased (Table 1, C, lines 2 and 3). On the other hand, if the fitnesses of the disfavored phenotypes were made unequal, the frequency realized by D_S was increased by changing its "setpoint" (i.e., y) toward a higher proportion of the less disfavored phenotype (Table 1, D).

The second model concerned insects in which a portion of diapausing individuals remains dormant for more than a year (e.g., Prebble 1941, Powell 1974, Ushatinskaya 1976). In the wheat-blossom midge (*Sitodiplosis mosellana*), for example, diapause may last as long as 12 years; the emergence from year to year is irregular, but the trend is for a smaller percentage of a cohort to emerge each succeeding year (Barnes 1952). A presumed advantage of prolonged diapause is that the individual may skip a poor or disastrous annual growing season and emerge in a favorable one. If bad seasons cannot be foretold by the time diapause is broken⁶, the *individual* should, on average, benefit by breaking diapause the first year—because the probability of happening on a good year is the same each year but the mortality associated with staying in diapause accumulates year after year. On the other hand, a *gene* that caused most carriers to emerge the first year and lesser numbers to emerge subsequent years should be superior to any single-output gene. The model to test the superiority of genes with mixed outputs made certain assumptions⁷; and, again, initial conditions had to be set.⁸

Table 2 gives representative results. When recessive, the allele with mixed output (P_S) sometimes quickly replaced the other alleles (Table 2, A-C). When unfavorable growing seasons were rare relative to the annual attrition rate, P_S was less successful (Table 2, B). Similarly, when unfavorable growing seasons were less severely unfavorable, P_S attained at lower frequencies (Table 2, C).

The results from these two models suggest that alleles producing a stochastic output can increase in frequency at the expense of competing deterministic alleles and sometimes completely replace them.

Other workers have tested models of stochastic alleles. Roff (1975) created a variety of complex models in which genes controlled the probability of dispersal among subpopulations that varied independently and randomly in their finite rates of increase (generally between 0 and 2.8). In his simplest version, he assumed the population was fixed for an allele that determined a stated dispersal probability, and he showed that populations with probabilities intermediate between 0 and 1.0 would persist. In another version, dispersal was controlled by a single locus with two alleles—a non-dispersal allele and a dispersal allele that produced dispersal and non-dispersal phenotypes in a specified ratio. The probability that dispersers would survive was also specified. Roff found that when the stochastic allele was recessive it either reached 100% and the population survived or, in cases where low survival of dispersers had been specified, the non-dispersal allele reached 100% and extinction ensued. When he made the stochastic allele partially dominant, the model reached an enduring genetic polymorphism under a wide range of assumptions about the probabilities that the two genotypes permitting dispersal would produce dispersal phenotypes.

Cooper and Kaplan (1982) were first to focus directly upon the fitness of genotypes with stochastic output. They used "decision trees" to compare the fitnesses of genotypes with deterministic and stochastic outputs in uncertain environments and concluded that genotypes with mixed output would win over deterministic genotypes under a variety of conditions and even if their output did not match exactly the probabilities of the alternative environments.

All efforts at simulation modeling of genotypes with mixed and pure outputs in uncertain environments have yielded similar results: stochastic alleles can replace or reach a lasting genetic polymorphism with alleles that have a single output.

EXAMPLES

Because stochastic polyphenism is expected to coexist with conditional polyphenism and genetic polymorphism, with all three affecting the same traits, clearcut examples may be difficult to identify even if the phenomenon is frequent. Some examples from insects are instructive.

APHIDS

Aphids are remarkably adapted to the study of polyphenism. All species are polymorphic and produce several to many generations of viviparous parthenogenetic females each year (Dixon 1985a). Parthenogenetic reproduction in aphids apparently includes no recombination, making all parthenogenetically produced females genetically identical to their mothers, except for new mutations (Blackman 1979, Tomiuk and Wöhrmann 1982, Dixon 1985b).⁹ In other words, the asexual descendants of any parthenogenetic female (and there may be millions) constitute a clone. The abundant polymorphism within parthenogenetic aphid lineages is thus entirely polyphenism (Lees 1961, Dixon 1985b).

Much of aphid polyphenism is clearly conditional. For example, the production of sexual females, which lay winter-hardy eggs, is cued variously by short photoperiods, cool temperatures, and season-related changes in host plants (Dixon 1985a). Winter is predictable.

More relevant to possible stochastic determination of morphs is the production of winged and wingless midseason morphs (alatae and apterae). The relative fitnesses of these morphs depend on the future suitability of the home host plant and the quantity and quality of other host plants, reachable only by flight. Host quality and availability are less easily predicted than is winter. In most cases that have been studied, production of alatae is only to a degree conditional to environment correlates of decreasing home host quality (e.g., crowded conditions and decline in nutritional quality of the host) (Dixon 1985a). An important aspect of the response to these correlates is that rarely is it 100%; the response is ordinarily 20 to 95% alatae (and 80 to 5% apterae). The switch is thus generally between development of one phenotype (apterae) and development of two phenotypes (apterae and alatae) rather than between one phenotype and another.

Shaw's (1970a) studies of the bean aphid (*Aphis fabae*) are representative. When he reared offspring of apterae under the crowded conditions of 200/bean stipule, about 40% developed into alatae (65%, if the mothers had been crowded too). This degree of crowding could be construed to be the approximate threshold for the switch from 100% apterae to 100% alatae (see Fig. 2), except that densities nearly half as great and densities twice as great still produced a mixture of phenotypes (Fig. 3).

Most other studies have yielded similar results. Lees (1967) found that crowding caused most apterous female vetch aphids (*Megoura viciae*) to produce mixtures of alatae and apterae, generally 70 to 95% alatae. Sutherland (1969) reported that crowding pea aphids (*Acyrtosiphon pisum*) resulted in a maximum of 80 to 85% alatae (in green and pink strains, respectively). Lamb and MacKay (1979) tested ca. 500 clones of pea aphids taken from alfalfa fields in southern Ontario and found that crowding increased production of alatae to an average of 66% (but never to 100%). On the other hand, Watt and Dixon (1981) reported 100% alatae when one strain of the English grain aphid (*Sitobion avenae*) was crowded—though another strain of the same species gave rise to few alatae when treated the same way.

The general lack of a 100% response in production of alatae suggests that selection has favored genotypes that produce a mixture of alatae and apterae under conditions signaling a decline of the home host. The proportions of the mix can be influenced by genotype, as indicated by consistent interclone variability in proportions of alate and

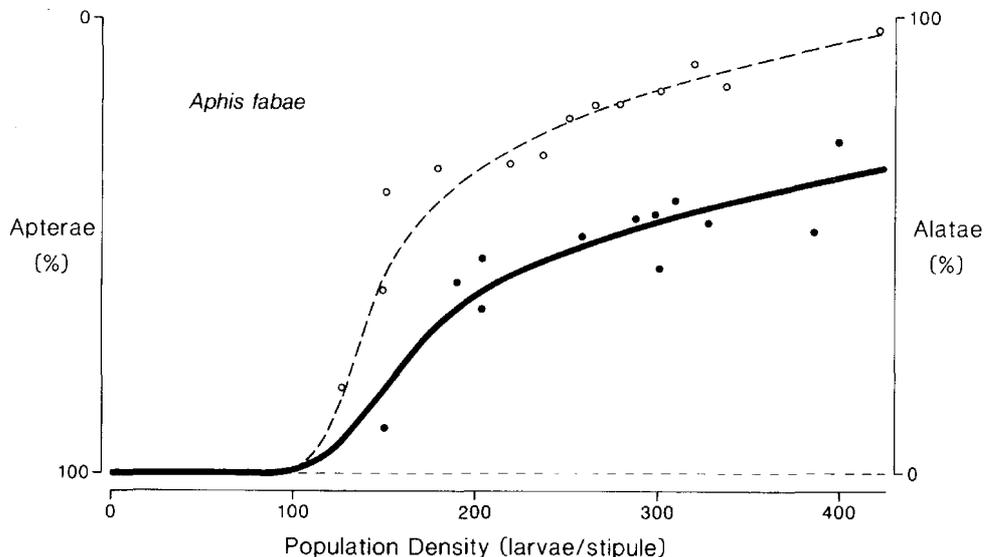


Fig. 3. Response of bean aphids to crowding (data from Shaw 1970a). Filled points and solid line are for the crowded progeny of uncrowded apterae. Open points and upper dashed line are for crowded progeny of apterae that were themselves crowded 100-400 per stipule. No alatae are produced at densities below 100 larvae/stipule. The difference between the two data sets shows that the environment of the mother influences the likelihood of her offspring being alatae. (The lower dashed line is for crowded offspring of alatae. Offspring of alatae are never alate, again demonstrating a maternal influence.) (Lines are eye-fitted.)

apterous pea aphids (Lamb and MacKay 1979). Mixed-output genotypes and genetic differences, as well as conditional responses, apparently contribute to wing dimorphism in midseason aphids.

CRICKETS

Dispersal polymorphisms in sexually reproducing insects are common, and they seldom are attributable to simple genetic differences, although the proportions of the morphs can be altered by selection (Harrison 1980). A case in point is wing dimorphism in field crickets (*Gryllus* spp.).

Field crickets are either long-winged or short-winged (Walker and Sivinski 1986). The short-winged morph, like the apterous aphid, never flies. The long-winged morph, characterized by the metathoracic wings extending well beyond the tegmina, has, like an alate aphid, the external equipment for flight. (And again like the alate aphid, it does not necessarily fly—Shaw 1970b; Walker, unpublished data.)

Collections of *Gryllus rubens* the most abundant field cricket in southeastern United States, vary greatly in the proportions of long- and short-winged morphs (Veazey et al. 1976). When progeny of field-collected females are reared under controlled conditions or in outdoor cages, they are generally 5-95% long-winged (Walker, unpublished data). Walker (unpublished data), starting with field-collected stock, selected for long and short wings under controlled temperature and photoperiod ($25 \pm 1^\circ\text{C}$, 16L:8D). The two strains diverged until one was ca. 95% long-winged and the other was ca. 95% short-winged. Even though selection was 100%, in neither strain was the rejected phenotype eliminated in seven generations (Fig. 4). The change in propor-

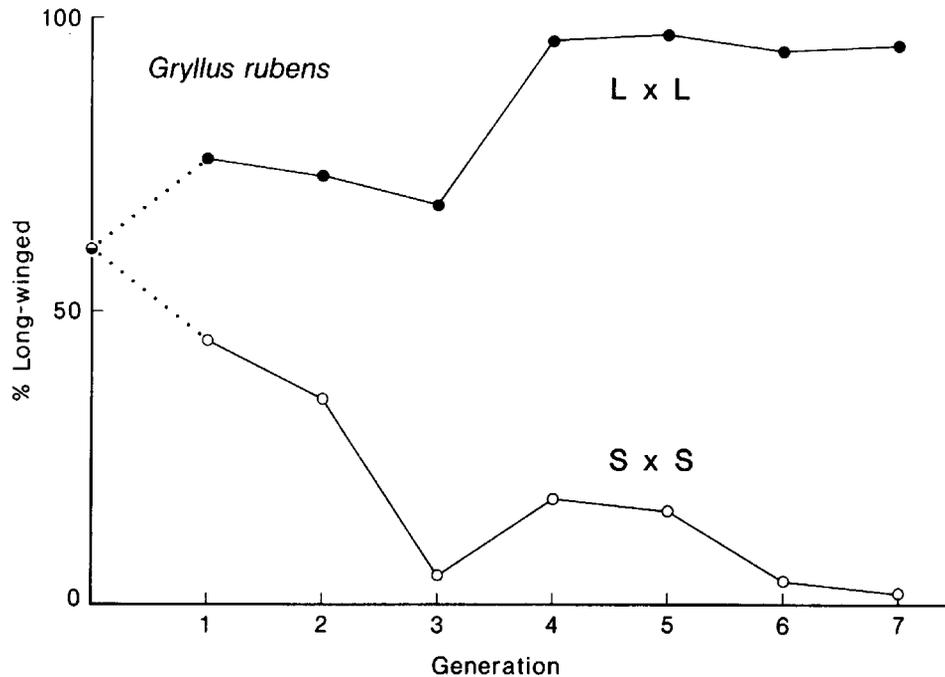


Fig. 4. Results of 100% selection for the long- and short-winged morphs of a field cricket (*Gryllus rubens*) for seven generations. Long- and short-winged parents were collected in Gainesville, Fla., March 1983, and all subsequent rearing and selection was at $25 \pm 1^\circ\text{C}$, 16L:8D. Only long-winged morphs were used as parents in the L x L line and only short-winged morphs were used in the S x S line.

tions of morphs showed that some of the original polymorphism was attributable to genetic differences (as in other *Gryllus*: Harrison 1979, Roff 1984). Conditional polyphenism is also part of the explanation, as shown by a variety of studies of related species by others (see Alexander 1968) and as shown by exposing the F_6 generation of the selected *G. rubens* lines to three rearing conditions (Fig. 5). However, the persistent dimorphism, in the face of selection and under the almost constant environment of a controlled temperature room, suggests that *G. rubens* genotypes have been selected to maintain a mixed output—i.e., that stochastic polyphenism is also involved in the polymorphism.

MOSQUITOES

The pitcher-plant mosquito *Wyeomyia smithii* is dimorphic in its warm season larval development. Some third instars enter diapause and others continue development. Using standardized rearing conditions, including a 15-h photoperiod, C. A. Istock and co-workers studied environmental and genetic determinants of this dimorphism. In one series of experiments, Istock et al. (1975), varied the amount of food per larva. Diapause incidence dropped to as low as 15% with ample food and increased to 100% (among survivors) when food was deficient. In another series of experiments, Istock et al. (1976) maintained conditions that gave 56% diapause in the unselected stock and selected for diapause and nondiapause strains. The course of selection resembled that in Fig. 4 in that progress was irregular and at the end of the study both strains were still producing both phenotypes. After 15 generations of selection for fast, nondiapause development, diapause incidence was 4%. After 7 generations of selection for diapause,

Rearing Conditions	L x L (F6)	S x S (F6)
16L:8D VBC diet 1/cup	G_{LW} → 98% LW → 2% SW	G_{SW} → 6% LW → 94% SW
16L:8D Cricket Chow 50/jar	G_{LW} → 89% LW → 11% SW	G_{SW} → 3% LW → 97% SW
11L:13D Cricket Chow 50/jar	G_{LW} → 47% LW → 53% SW	G_{SW} → 1% LW → 99% SW

Fig. 5. Response of two strains of *Gryllus rubens* to three sets of rearing conditions at $25 \pm 1^\circ\text{C}$. Each strain was in its sixth generation of 100% selection for long or for short wings (see Fig. 4). G_{LW} = genotype(s) of the L x L strain; G_{SW} = genotype(s) of the S x S strain; LW = long-winged phenotype; SW = short-winged phenotype. Rearing conditions differed in photoperiod, diet, type of container, and number of crickets per container. (In the language of Fig. 1, each set of rearing conditions is an "E_S".) (For treatments of L x L, n = 47, 165, and 97; for S x S, n = 63, 170, 86; the proportion of LW from G_{LW} is significantly lower for the short-day treatment than for the two long-day treatments.)

incidence was 88%. In contrast to these results at a 15-h photoperiod, under fall photoperiods (14 h or less) all third instars diapause. Diapause dimorphism in *W. smithii*, like wing dimorphism in *G. rubens*, includes genetic polymorphism and conditional polyphenism as well as what seems to be stochastic polyphenism.

MOTHS

J. G. Sternburg and G. P. Waldbauer (see Waldbauer 1978) found that the silk moth *Hyalophora cecropia* has two modes of emergence in central Illinois. About 10% of the moths emerge in late May (Group I) and the other 90% in late June (Group II). The adult moths are too short-lived to survive the gap between modes, suggesting reproductively isolated populations. However, the majority of the progeny of Group I moths emerge the following year in Group II and a minority of the progeny of Group II emerge in Group I the following year—proving that Group I and Group II emergers belong to the same Mendelian population. Four generations of selection for Group I emergence changed the proportion emerging in Group I to ca. 80% (Waldbauer 1978). The proportion of the wild population that emerged in Group I during the years of selection varied between 4.7% and 10.0%. That genotypic differences are partly responsible for the bimodal emergence is demonstrated by the pronounced increase in proportion of Group I emergers in the selected lineage. That conditional polyphenism is slightly involved is implied by the year to year fluctuation in the proportion of Group I emergers in the wild population (but that fluctuation could also result from changes in genotype frequen-

cies from one year's generation to the next). Finally, the failure of four generations of selection to establish a pure line of Group I emergers shows that mixed emergence is entrenched in *H. cecropia* genotypes, as expected in stochastic polyphenism.

DISCUSSION

If stochastic polyphenism should be a frequent evolutionary response to uncertainty, why might it go generally unrecognized? One reason is that it occurs in combination with other types of polymorphism, and a researcher who proves that one of the other types occurs is likely to emphasize what is explained by accepted principles rather than what is not. A related reason is that chance seems unsatisfactory as a scientific explanation. This misses the point that selection may favor events that are stochastic in effect even though deterministic in means (a flipped coin obeys the laws of physics, but the effect is close enough to 0.50 probability that football games are started with one). A third reason is that in stochastic polyphenism individual fitness is subordinate to fitness at another level. Those who have been trained that selection at the individual level is the only safe way to view evolution may be reluctant to accept as an adaptation a phenomenon that causes some individuals to have reduced fitness for the long term advantage of stochastic genes. However, as Dawkins (1982) has emphasized, selection is as much (or more) the differential survival of genes as the differential reproduction of individuals.

How have those who eschewed stochastic polyphenism explained the type of data used here to support it? Most have ignored the issue. Some have cited maternal influence. A mother aphid that can make her offspring be $y\%$ one phenotype and $(100-y)\%$ another phenotype may, on average, have more grandprogeny than one that produces 100% of what is, on average, the fittest phenotype. Maternal influence seems unlikely when the development of phenotypic differences occurs long after maternal contact has ceased (e.g., wings in field crickets). More to the point, maternal influence is not actually an alternative to stochastic polyphenism. The mother's genotype (rather than the progeny's) simply becomes the one that flips the coin that determines the progeny's phenotype. Furthermore, in aphids, the mother's and progeny's genotypes are generally the same! For sexually reproducing insects, a more credible alternative to stochastic polyphenism is a form of genetic polymorphism—viz., polygenic inheritance with threshold effect (Fig. 6) (see Falconer 1981, Chap. 18).¹⁰ In the case of *Gryllus rubens* or *Wyeomyia smithii*, the production of both phenotypes after 7-15 generations of 100% selection could be attributed to a polygenic complex's normally slow response to selection (Falconer 1981, Chap. 12).¹¹ Finally, frequency dependent selection should be mentioned. Although it is a common cause of genetic polymorphisms (Clarke 1979, Rausher 1986), it cannot account for polymorphism within aphid clones or for the difficulty in artificially selecting for pure breeding strains of long-winged crickets, warm-season diapausing mosquitoes, or early emerging moths.¹²

When consequences of maladaptation are unequal, what should be the effect on the setpoint of stochastic polyphenism? In most of Table 1 the disadvantage of diapause in a nondiapause environment was made equal to the disadvantage of nondiapause in a diapause environment (A, B, C). If the disadvantages are made unequal (as in Table 1, D), stochastic alleles that produce more of the least disadvantaged phenotype achieve higher frequencies.¹³ If one disadvantage is eliminated, then the optimal setpoint becomes 100% of the phenotype that is never disadvantaged—i.e., the polymorphism should cease.

What more general evolutionary principles is stochastic polyphenism a subset of? One is that natural selection does not always favor genotypes that produce higher average numbers of offspring. Gillespie (1977) showed that genotypes with lesser vari-

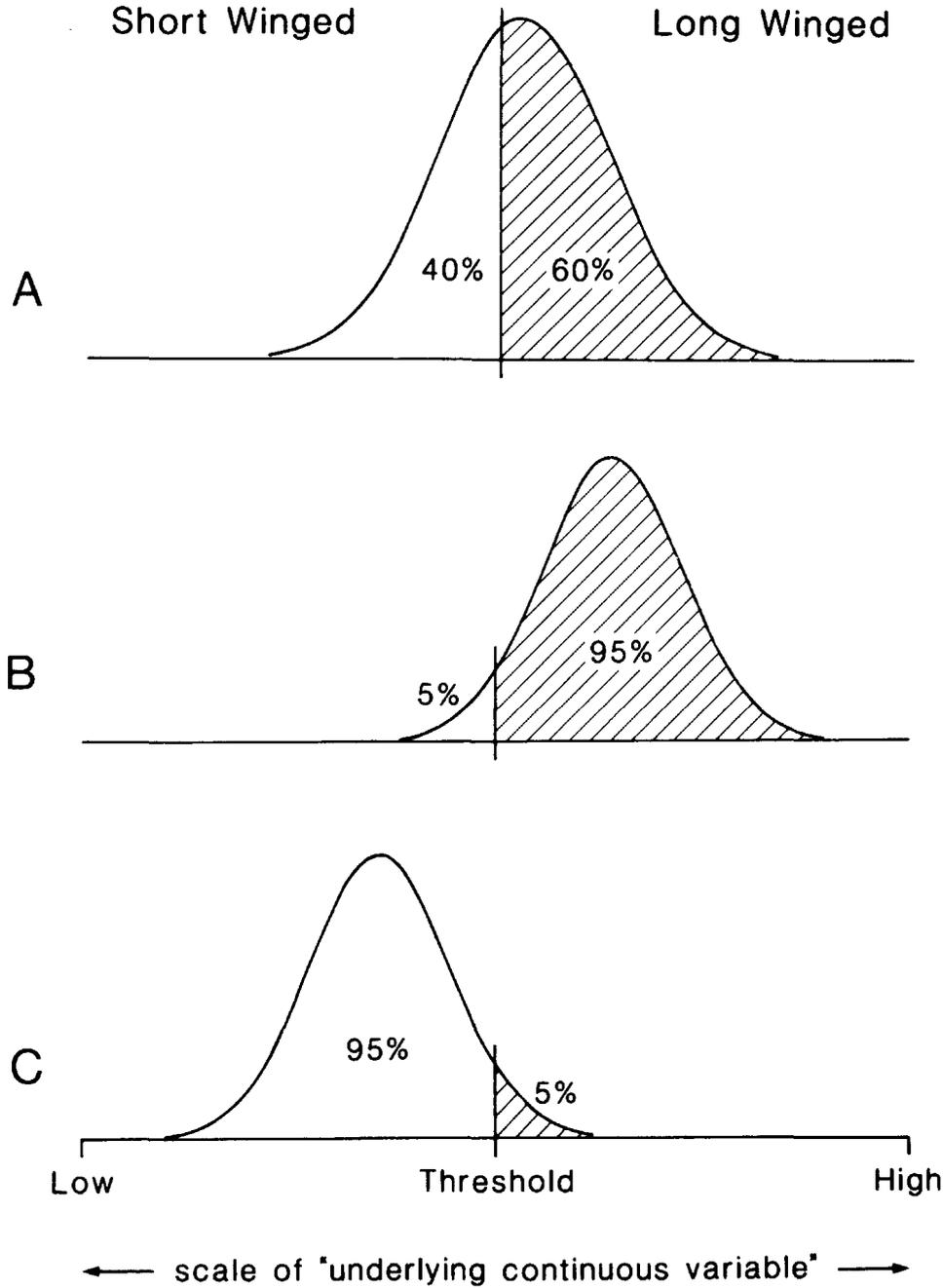


Fig. 6. Diagram illustrating polygenic inheritance with threshold effect as an alternative explanation of wing dimorphism in *G. rubens* (Fig. 4). An underlying continuous variable controls the dimorphism (e.g., the concentration of a wing-promoting substance). This variable is controlled by genes at many loci with additive effects, producing a normal distribution of levels. Some of the loci are linked in opposite phase, prolonging the time required to develop a pure breeding short- or long-winged strain. A. Unselected. B. After 6-8 generations of 100% selection for long-winged morph. C. After 6-8 generations of 100% selection for short-winged morph. (Diagrams modified from Falconer 1981).

ances in offspring numbers can increase at the expense of those with higher average numbers of offspring. In the case of stochastic temporal fluctuations of the environment, he found the best measure of fitness to be the geometric mean of offspring number, averaged over time (the procedure used by Cooper and Kaplan, 1982, in their decision tree analyses). Another principle is that evolution is more easily understood when analyzed at the level of the replicator (Dawkins 1982). As Cooper and Kaplan (1982, p. 145) explained, a strategy-mixing genotype causes some individuals to be stuck with an inferior phenotype—"for the sake of the long term advantage of the genotype."

What terms should be used for the types of polyphenism? Dawkins (1980), writing of evolutionarily stable strategies, distinguished *conditional* from *mixed* or *stochastic* strategies in individual behavior. This distinction aided my theorizing about polyphenism. Cooper and Kaplan (1982; also, Kaplan and Cooper 1984) used *predictive* and *coin-flipping* to name the same distinction and were first to apply it to "adaptive phenotypic plasticity," which includes polyphenism. Both sets of terms are appealing and nearly self-defining. I chose Dawkins' because they are more likely to be familiar to behavioral ecologists. Less this choice be viewed as deemphasizing Cooper and Kaplan's priority in applying the distinction to polyphenism, I end as I began by quoting from their synopsis (1982, p. 135): "The variation is a product of the action of genetically controlled stochastic processes; metaphorically, it is produced because individuals are genetically programmed to 'flip coins' to decide what characteristics to adopt. Thus it is not the variable phenotypic traits themselves that are genetically specified, but only the nature of the coin-flipping process that will ultimately determine them. . . . coin-flipping strategies of this kind are robust and can evolve under a variety of conditions."

ACKNOWLEDGEMENTS

I thank James B. Kring for help with the aphid literature, Chai-Lin Tan for a summary of the literature on prolonged diapause, and H. M. Wallbrunn for guiding me to Wright's studies of inbred guinea pigs; I am grateful to J. E. Lloyd, Todd Pickard, John Sivinski, Frank Slansky, Sue Wineriter, and Tony Zera for constructive criticism of the manuscript. The study of wing polymorphism in *G. rubens* was aided by NSF grant BNS 81-03554. Florida Agricultural Journal Series No. 7065.

APPENDIX

¹In sexually reproducing animals, natural selection increases genotypes indirectly—by altering frequencies of alleles that in turn alter the probability of particular genotypes forming in the next generation and by altering linkage relationships.

²The effect of a transposable element is that of a mutation and its back mutation being exceedingly frequent, making the occurrence of the phenotypes they produce unpredictable except on a probabilistic basis. That a mobile element can actually control a polymorphism has been demonstrated in the bacterium *Salmonella* (Simon et al. 1980, p. 1370), in which the inversion of a 970-base-pair DNA sequence "behaves like a flip-flop switch activating and inactivating *H2* gene transcription. Depending on the frequency of switching, a fraction of the population expresses one flagellar antigen while the rest of the cells express the other flagellar antigen."

³These models were written in BASICA for an IBM PC. They are menu-driven and suitable for classroom use. I will make copies for anyone sending me two blank diskettes (one of which I will return with the programs).

⁴This was accomplished through the random-number generating function of BASICA.

⁵Phenotypes were assigned individuals in the proportions $y:(100-y)$. For large populations this procedure should not differ in effect from true stochastic assignment with probabilities y and $(100-y)$.

⁶In some instances, circumstances in one growing season foretell circumstances the following year, making possible control of prolonged diapause by conditional polyphenism. For example, a dense population (as in an outbreak) can predict scarce resources or high parasitoid populations for the next year.

⁷The assumptions were: (1) Bad years occur at random. (2) Three alleles control duration of diapause— P_0 , which causes emergence after one winter; P_T emergence after two winters; and P_S , 50% emergence after one winter, 25% emergence after two winters, 12.5% emergence after three winters, etc. up to w winters, with all remaining individuals emerging after the w^{th} winter (e.g., for $w=4$, 12.5% emerged the last winter). (3) The annual mortality caused by remaining in diapause is a constant proportion of survivors. (4) Each year's cohort (i.e., those entering their initial winter of diapause) is numerically independent of the number that had broken diapause earlier that year to produce it but dependent on whether the growing season had been good or bad.

⁸In running the prolonged-diapause model these values were set: dominance relations of alleles, initial frequencies of alleles, maximum number of winters in diapause for individuals controlled by P_S , probability of a bad growing season, number going into diapause after a bad growing season (as a proportion of the number for a good growing season), number of generations per run, number of runs.

⁹Mutation-caused morphs should be easily separable from polyphenism because such morphs would occur rarely and, once present, the responsible allele should be passed to all parthenogenetically produced descendants of the original mutant individual.

¹⁰A way to refute the hypothesis of polygenic inheritance with threshold effect as an alternative explanation (for data that suggest stochastic polyphenism in sexually reproducing insects) is the establishment of homozygous strains through inbreeding. As strains become more and more homozygous through generations of inbreeding, the polymorphism may be maintained if it is stochastic polyphenism and should be reduced and then eliminated if it is dependent on genetic difference. As an example of this approach, Wright and Chase (1936) (see also, Festing 1976) studied white spotting in inbred and outbred lines of guinea pigs and found that in inbred lines the degree of spotting was almost entirely under nongenetic control. Individuals ranging from nearly white to nearly "self colored" (i.e., 5-95% white spotted) occurred in the same litter. In one inbred line the environment controlled 97% of the variance, and less than 10% of this environmental component was attributable to age of mother and other factors common to litter mates—89% of the variance was random. Even in an outbred line, 52% of the variance in degree of spotting was random.

¹¹One of the causes of slow response is linkage of polygenes of opposite sign. If such linkage is tight, the group of linked loci can act as a "supergene" for stochastic polyphenism—by keeping the level of the "underlying continuous variable" close enough to the threshold of response for individuals of both phenotypes to occur.

¹²Frequency dependent selection occurs, by definition, whenever fitness of a genotype is an inverse function of its frequency. Wing dimorphism in crickets is partly a result of genetic differences among individuals, and the frequency of alleles for long- and short-winged morphs may depend in part on long-winged and short-winged morphs becoming more fit on average as they (respectively) become rarer. On the other hand the relative success of long- and short-winged morphs must depend in part on uncertain meteorological events. Frequency dependent selection may occur as a result of unpredictable environmental changes but it is not an adaptation to them.

¹³Cooper and Kaplan (1982) derived this formula for calculating the optimal setpoint for a stochastic genotype:

$$q_0 = \frac{\lambda_{1,0}}{\lambda_{1,0} - \lambda_{0,0}} P_1 + \frac{\lambda_{1,1}}{\lambda_{1,1} - \lambda_{0,1}} P_0$$

where q_0 = proportion of phenotype 0

$\lambda_{1,0}$ = finite rate of increase, in environment favoring phenotype 1, of phenotype 0
 $\lambda_{0,0}$ = finite rate of increase, in environment favoring phenotype 0, of phenotype 0
 P_1 = probability of environment favoring phenotype 1
 etc.

If $0 < q_0 < 1$, then a mixed strategy is superior to either pure strategy and the optimal proportions of phenotypes 0 and 1 are q_0 and $1 - q_0$.

Applying this formula to the circumstances in Table 1,C, yields an optimal y of 0.704; to the circumstances in Table 1,D, an optimal y of 0.995.

REFERENCES CITED

- ALEXANDER, R. D. 1968. Life cycle origins, speciation, and related phenomena in crickets. *Q. Rev. Biol.* 43: 1-41.
- BARNES, H. F. 1952. Studies of fluctuations in insect populations. XII. Further evidence of prolonged larval life in the wheat-blossom midges. *Ann. Appl. Biol.* 39: 370-73.
- BECK, S. D. 1980. *Insect photoperiodism*, 2nd ed. Academic Press, New York.
- BLACKMAN, R. L. 1979. Stability and variation in aphid clonal lineages. *Biol. J. Linn. Soc.* 11: 259-77.
- CLARKE, B. C. 1979. The evolution of genetic diversity. *Proc. R. Soc. London B* 205: 453-74.
- COOPER, W. S., AND R. H. KAPLAN. 1982. Adaptive "coin-flipping": a decision-theoretic examination of natural selection for random individual variation. *J. Theor. Biol.* 94: 135-51.
- DAWKINS, R. 1980. Good strategy or evolutionarily stable strategy? Pages 331-67 in G. W. Barlow and J. Silverberg, eds. *Sociobiology: beyond nature/nuture*. Westview Press, Boulder, Colo.
- DAWKINS, R. 1982. *The extended phenotype*. W. H. Freeman, San Francisco.
- DIXON, A. F. G. 1985a. *Aphid ecology*. Blackie and Sons, Glasgow.
- DIXON, A. F. G. 1985b. Structure of aphid populations. *Annu. Rev. Ent.* 30: 155-74.
- FALCONER, D. S. 1981. *Introduction to quantitative genetics*, 2nd ed. Longman, London.
- FEDOROFF, N. V. 1984. Transposable genetic elements in maize. *Sci. American* 250(6): 84-98.
- FESTING, M. F. W. 1976. Genetics. Pages 99-120 in J. E. Wagner and P. J. Manning, eds. *The biology of the guinea pig*. Academic Press, New York.
- GILLESPIE, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. *American Nat.* 111: 1010-14.
- HARRISON, R. G. 1979. Flight polymorphism in the field cricket *Gryllus pennsylvanicus*. *Oecologia* 40: 125-32.
- HARRISON, R. G. 1980. Dispersal polymorphisms in insects. *Annu. Rev. Ecol. Syst.* 11: 95-118.
- ISTOCK, C. A., S. S. WASSERMAN, AND H. ZIMMER. 1975. Ecology and evolution of the pitcher-plant mosquito: 1. Population dynamics and laboratory responses to food and population density. *Evolution* 29: 296-312.
- ISTOCK, C. A., J. ZISFEIN, AND K. J. VAVRA. 1976. Ecology and evolution of the pitcher-plant mosquito. 2. The substructure of fitness. *Evolution* 30: 535-47.
- KAPLAN, R. H., AND W. S. COOPER. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. *American Nat.* 123: 393-410.
- KENNEDY, J. S. 1961. Insect polymorphism. *Symp. R. Ent. Soc. London*, No. 1.
- LAMB, R. J., AND P. A. MACKAY. 1979. Variability in migratory tendency within and among natural populations of the pea aphid, *Acyrtosiphon pisum*. *Oecologia* 39: 289-99.
- LEDER, P. 1982. The genetics of antibody diversity. *Sci. American* 246(5): 102-15.

- LEES, A. D. 1961. Clonal polymorphism in aphids. Symp. R. Ent. Soc. London 1: 68-79.
- LEES, A. D. 1967. The production of the apterous and alate forms in the aphid *Megoura viciae* Buckton, with special reference to the role of crowding. J. Insect Physiol. 13: 289-318.
- POWELL, J. A. 1974. Occurrence of prolonged diapause in ethmiid moths (Lepidoptera: Gelechioidea). Pan-Pac Ent. 50: 220-25.
- PREBBLE, M. L. 1941. The diapause and related phenomena in *Gilpinia polytoma* (Hartig). V. Diapause in relation to epidemiology. Canadian J. Res. D. 19: 437-54.
- RAUSHER, M. D. 1986. Competition, frequency-dependent selection, and diapause in *Battus philenor* butterflies. Florida Ent. 69: 000-000.
- ROFF, D. A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia 19: 217-37.
- ROFF, D. A. 1984. The cost of being able to fly: a study of wing polymorphism in two species of crickets. Oecologia 63: 30-37.
- SHAW, M. J. P. 1970a. Effects of population density on alienicolae of *Aphis fabae* Scop. I. The effect of crowding on the production of alatae in the laboratory. Ann. Appl. Biol. 65: 191-96.
- SHAW, M. J. P. 1970b. Effects of population density on alienicolae of *Aphis fabae* Scop. II. The effects of crowding on the expression of migratory urge among alatae in the laboratory. Ann. Appl. Biol. 65: 197-203.
- SIMON, M., J. ZIEG, M. SILVERMAN, G. MANDEL, AND R. DOOLITTLE. 1980. Genes whose mission is to jump. Phase variation: evolution of a controlling element. Science 209: 1370-74.
- SPUDICH, J. L., AND D. E. KOSHLAND, JR. 1976. Non-genetic individuality: chance in the single cell. Nature 262: 467-71.
- SUTHERLAND, O. R. W. 1969. The role of the host plant in the production of winged forms by two strains of the pea aphid, *Acyrtosiphon pisum*. J. Insect Physiol. 15: 2179-201.
- TOMIUK, J., AND K. WÖHRMANN. 1982. Comments on the genetic stability of aphid clones. Experientia 38: 320-21.
- USHATINSKAYA, R. S. 1976. Prolonged diapause in Colorado beetle and conditions of its formation. Pages 168-200 in K. V. Arnoldi, ed. Ecology and physiology of diapause in the Colorado beetle. Academic Press, New York.
- VEAZEY, J. N., C. A. R. KAY, T. J. WALKER, AND W. H. WHITCOMB. 1976. Seasonal abundance, sex ratio, and macroptery of field crickets in northern Florida. Ann. Ent. Soc. America 69: 374-80.
- WALDBAUER, G. P. 1978. Phenological adaptation and the polymodal emergence patterns of insects. Pages 127-44 in H. Dingle, ed. Evolution of insect migration and diapause. Springer-Verlag, New York.
- WALKER, T. J., AND J. SIVINSKI. 1986. Wing dimorphism in southeastern field crickets (Orthoptera: *Gryllus*). Ann. Ent. Soc. America 79: 84-90.
- WATT, A. D., AND A. F. G. DIXON. 1981. The role of cereal growth stages and crowding in the induction of alatae in *Sitobion avenae* and its consequences for population growth. Ecol. Ent. 6: 441-47.
- WRIGHT, S., AND H. B. CHASE. 1936. On the genetics of the spotted pattern of the guinea pig. Genetics 21: 758-87.

COMPETITION, FREQUENCY-DEPENDENT SELECTION,
AND DIAPAUSE IN *BATTUS PHILENOR* BUTTERFLIES

MARK D. RAUSHER*

SYNOPSIS

The pipevine swallowtail butterfly, *Battus philenor*, exhibits a diapause polymorphism in east Texas. Approximately half the offspring of first-brood females enter and remain in pupal diapause until the following year. The other half ecloses to form a second brood. Evidence is presented to indicate that second-brood females compete for oviposition sites. It is deduced that this competition causes the fitness of non-diapausers to be frequency dependent: as the proportion of non-diapausers in the population increases, their fitness decreases. A single-locus model showing that this type of frequency dependence can maintain a stable diapause polymorphism is presented.

INTRODUCTION

It is generally agreed that the availability of food plants greatly influences the voltinism patterns of herbivorous insects (Opler and Langston 1968, Slansky 1974, Gilbert and Singer 1975, Shapiro 1975). In northern temperate communities, trees and shrubs often produce a brief burst of high-quality, nutrient-rich foliage that rapidly becomes a poor substrate for larval growth as nutrient levels decline and growth inhibitors increase in concentration (Feeny 1970, Raup and Denno 1983). In response to this brief period of availability of high-quality larval food, many insects have evolved to be univoltine and avoid having to use mature foliage. Other species, which feed on mature foliage, may have a univoltine life cycle imposed upon them because slow growth rates on low-quality foliage do not permit two generations to be completed during a single growing season (Feeny 1970). By contrast, many forb-feeding insects, whose food plants remain nutritious for much of the growing season, are multivoltine (Slansky 1974). Similarly, in areas of summer drought, where larval food plants rapidly senesce with the onset of dry conditions, herbivorous insects tend to be univoltine. Multivoltine species in these communities normally feed on host plants that remain green, such as those growing along streams (Opler and Langston 1968, Shapiro 1975, Gilbert and Singer 1975).

Many, if not most, populations of herbivorous insects are uniformly either single-brooded (univoltine) or multiple-brooded (multivoltine). All individuals enter diapause at approximately the same time of year and remain dormant for approximately the same period of time (Danilevsky 1965, Danilevsky *et al.* 1970, Waldbauer 1978). This monomorphic pattern is expected in species whose food supply remains constant through much of the season (multivoltine species) or is present for a short pulse and then disappears completely (univoltine species). Recently, however, it has become clear that some species are polymorphic within a single population for the number of broods that occur within a season (Helle 1968, Geyspitz 1968, Slansky 1974, Shapiro 1975, Istock *et al.* 1975, 1976, Istock 1978, Waldbauer 1978).

While diapause polymorphisms have been well-documented, little is known about

*Mark D. Rausher is an Associate Professor in the Department of Zoology and the University Program in Genetics at Duke University. In 1979 he received his Ph.D. under Paul Feeny at Cornell University. He has been studying the behavioral ecology of *Battus philenor* butterflies since 1974. Other current research concerns the ecological genetics of plant-insect interactions and modelling the evolution of searching behavior in herbivorous insects. Department of Zoology, Duke University, Durham, North Carolina 27706.

the selective forces that preserve them in populations. Here I present evidence suggesting that frequency-dependent selection, apparently mediated through competition for oviposition sites, acts to maintain a diapause polymorphism in an east Texas population of the pipevine swallowtail butterfly, *Battus philenor*.

PHENOLOGY AND DIAPAUSE IN *B. philenor*

In east Texas, populations of *B. philenor* overwinter in pupal diapause. In mid-March, adults eclose to form the first brood (brood 1) and mated females begin laying eggs on larval food plants. At this time of the year, most females search preferentially for and oviposit on a small, perennial herb, *Aristolochia reticulata* (Aristolochiaceae). In mid-May, some offspring of brood-1 adults eclose to form a second brood (brood 2). Most females of this brood search preferentially for and oviposit on a closely related host, *Aristolochia serpentaria*, because the foliage of *A. reticulata* has by this time become tough and nutrient-poor (Rausher 1978, 1980, 1981, Rausher and Papaj 1983a).

Larval rearing experiments were performed in 1976 and 1977 to determine the proportions of offspring of brood-1 and brood-2 adults that entered diapause.¹ In these experiments, approximately half of the offspring of brood-1 individuals entered diapause in both years (Table 1). There is thus clearly a polymorphism for diapause in the population examined, but it is not known whether this phenotypic polymorphism is the result of an underlying genetic polymorphism or whether the decision to diapause is based on perception of a particular environmental cue². Regardless of whether diapause is genetically or environmentally determined, however, it seems reasonable to hypothesize that natural selection actively maintains both diapausing and non-diapausing morphs within the population studied.

In the remainder of this work I provide evidence that is consistent with this hypothesis. In particular, I first document the existence of competition for oviposition sites among brood-2 *B. philenor* females. I then describe why it is reasonable to infer that the existence of such competition means that the fitness of the non-diapausing morph, measured as representation in the next generation, depends on the frequency of that morph in the population. Finally, I present a genetic model that shows how this type of frequency-dependence can maintain the observed diapause polymorphism in east Texas populations of *B. philenor*.

COMPETITION FOR OVIPOSITION SITES

By following female butterflies in the field, it is possible to determine the rate at which they alight on (discover) host plants, the rate at which eggs are laid on host plants, and the proportion of host plants alighted on that already bear eggs (Rausher 1979, 1983). Examination of temporal trends in these rates for brood-1 and brood-2 females in 1977 (the only year for which brood-2 data are available) provides the evi-

TABLE 1. FRACTION OF EXPERIMENTALLY-REARED PUPAE THAT DIAPAUSE.

Year	Offspring of	
	Brood 1	Brood 2
1976	.41 (59) ¹	.79 (24)
1977	.55 (60)	—

¹Numbers in parentheses are sample sizes for diapausing and non-diapausing pupae.

dence that competition for oviposition sites occurs during the second brood.

During the first brood, oviposition rate shows no trend over time (Fig. 1a), probably because females actively maintain a constant rate of oviposition (Rausher 1983). By contrast, during the second brood, oviposition rate declines steadily (Fig. 1b). There are

EGGS LAID/10 MIN

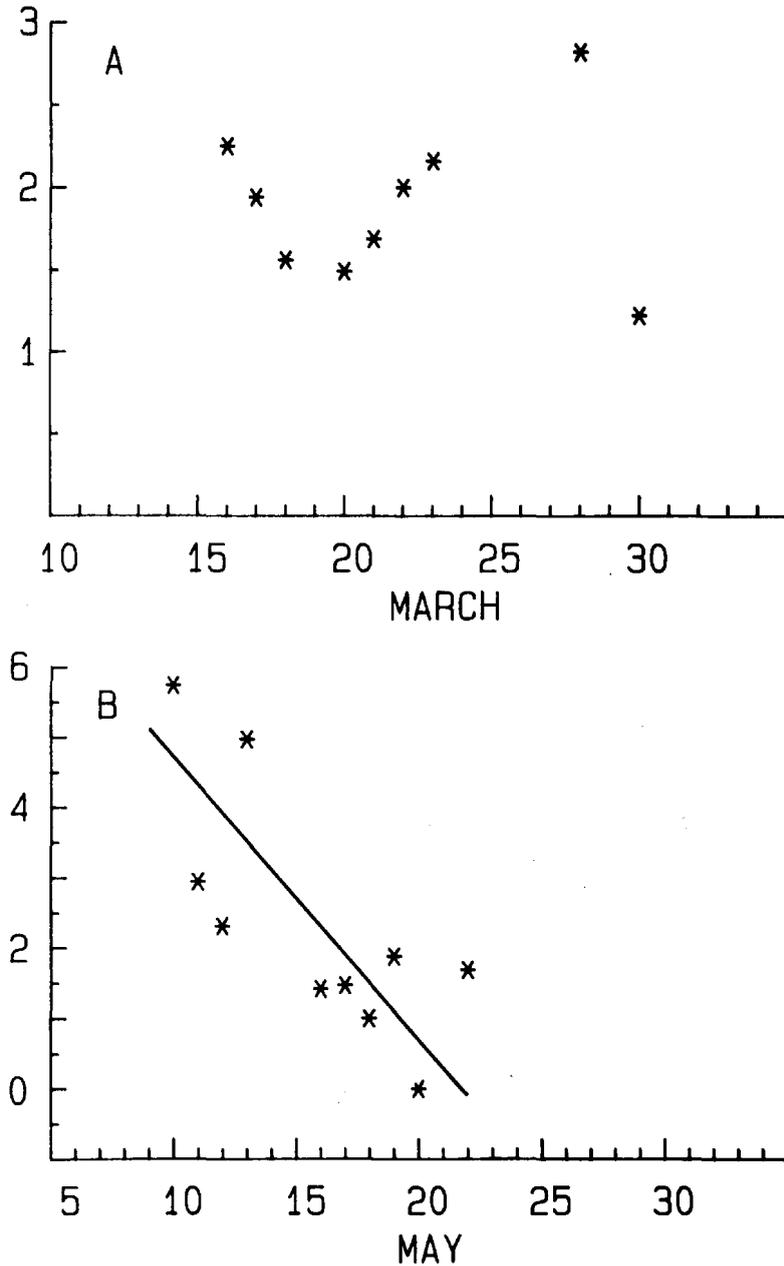


Fig. 1 Temporal trend in oviposition rate (No. eggs laid/10 min.) over the course of a brood. Each point represents pooled data for all individuals on the corresponding day. Data based on a total of 1095 observation minutes for brood 1, 784 observation minutes for brood 2. A. Brood 1. Spearman correlation coefficient (on pooled data), $r_s = .39$, NS. B. Brood 2. $r_s = -.72$, $P = .01$.

three plausible explanations for this decline: (1) oviposition rate declines with female age³, (2) alighting rates decline over time⁴, or (3) the number of acceptable host plants decreases over time due to preemption by other females.⁵

It is unlikely that explanation 1 is correct. If aging of individuals were responsible for the decline in oviposition rate during brood 2, then such a decline should also have been observed in brood 1, which serves as a control for the observations made during brood 2. Because a decline was not observed during brood 1 (Fig. 1a), the cause of the decline during brood 2 is most likely due to some factor or process, unlike aging, that was not operative during brood 1.

Analysis of alighting rates indicates that explanation 2 is also probably not correct. Alighting rates do not decline over time during brood 2 (Fig. 2b; the increase in alighting rates during brood 1 (Fig. 2a) is for reasons explained in Rausher 1983), as would be expected if this explanation were true. Instead, they remain more or less constant, and the decline in oviposition rate occurs in spite of this constancy. While doubtless some host plants were consumed by larvae during brood 2, the number is expected to be small, since larval feeding activity in the habitat is minimal at this time (Rausher and Feeny 1980). Evidently, so few were eaten that there was a negligible effect on host abundances, and hence alighting rates.

By elimination, it would appear that explanation 3 is most likely the correct one. Moreover, observed trends in proportion of alightings that are on host plants that already bear eggs are precisely what are expected under this explanation. During the second brood, there is a steady increase in the proportion of hosts that have previously-laid eggs, from 0 at the beginning of the brood to approximately .85 by the end of the brood (Fig. 3b)⁶. Consequently, the rate of alighting on potentially acceptable host plants (plants without eggs) decreases markedly over the brood (Fig. 4b). Females seem to be able to counteract this decrease in rate of alighting on plants without eggs to some extent by increasing the probability of ovipositing as the brood progresses and alighting rate falls (Fig. 5b). However, because even at the beginning of the brood the probability of oviposition is high (*i.e.*, approximately .6), the scope for such compensation is limited. The decline over time in rate of alighting on plants without previously laid eggs is thus necessarily accompanied by a decline in oviposition rate.

The picture that emerges from this analysis, then, is as follows: females emerging at the beginning of the second brood find that virtually all suitable host plants (primarily *A. serpentaria*) are free of eggs. Oviposition rates at the beginning of the brood are presumably limited by the rate at which host plants are discovered. Over time, as more eggs are laid by females, a larger fraction of the host plants bear eggs or larvae. These plants have been, in effect, preempted. By the end of brood 2, most host plants alighted on have been preempted and only rarely does a female encounter a plant without eggs or larvae. Consequently, oviposition rate, which is limited to a large extent by alighting rate, has fallen to only about one quarter what it was at the beginning of the brood. It is thus apparent that competition for oviposition sites is intense during the second brood, even when only about half the offspring of brood-1 individuals emerge to form the second brood.

FREQUENCY-DEPENDENT FITNESS

Because it is technically impossible to manipulate with adequate controls the proportions of the progeny of brood-1 individuals that eclose or enter diapause, it is not possible to ascertain directly whether changing the frequency of individuals would affect the mean fitness of non-diapausers. However, the data reported in the last section imply that mean representational fitness of non-diapausers, defined as the number of offspring represented in the next generation of adults (*i.e.*, number of eggs laid times the average

PLANTS ALIGHTED ON/10 MIN

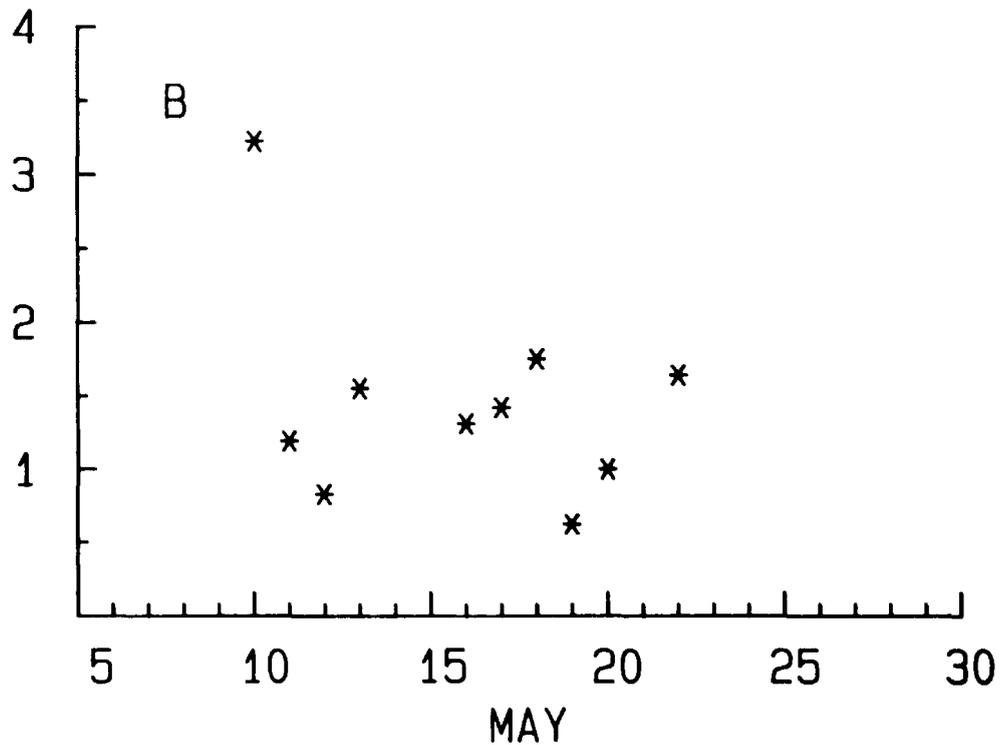
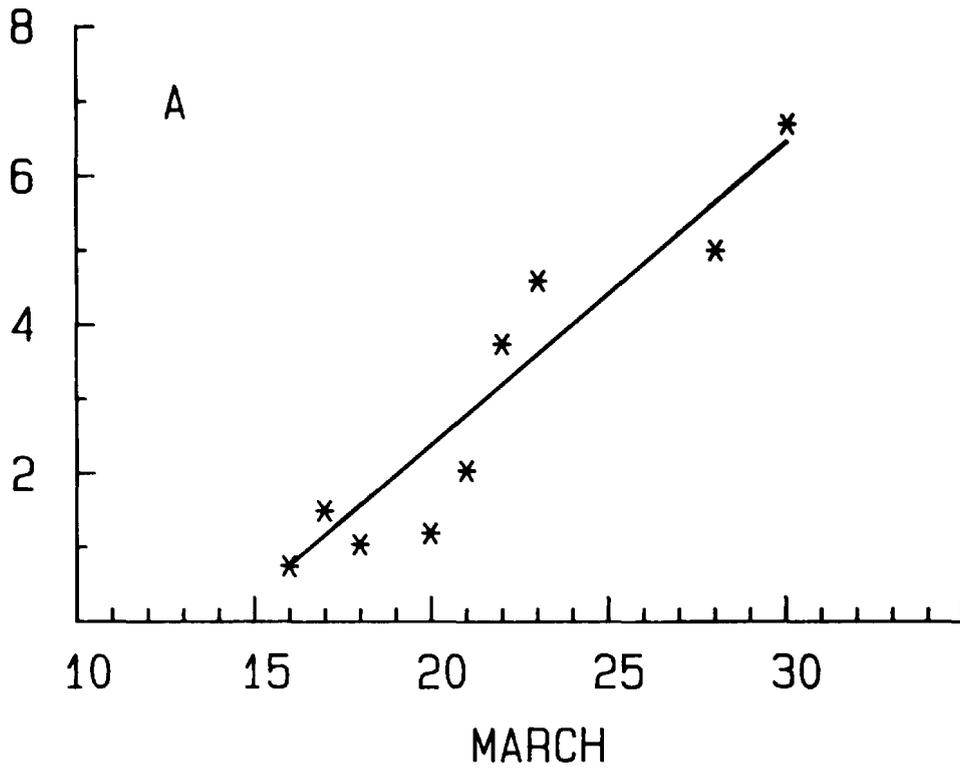


Fig. 2 Temporal trend in alighting rate (No. host plants alighted on/10 min.) over the course of a brood. A. Brood 1. $r_s = .98$, $P < .001$. B. Brood 2. $r_s = .14$, NS.

FRACTION OF PLANTS WITH EGGS

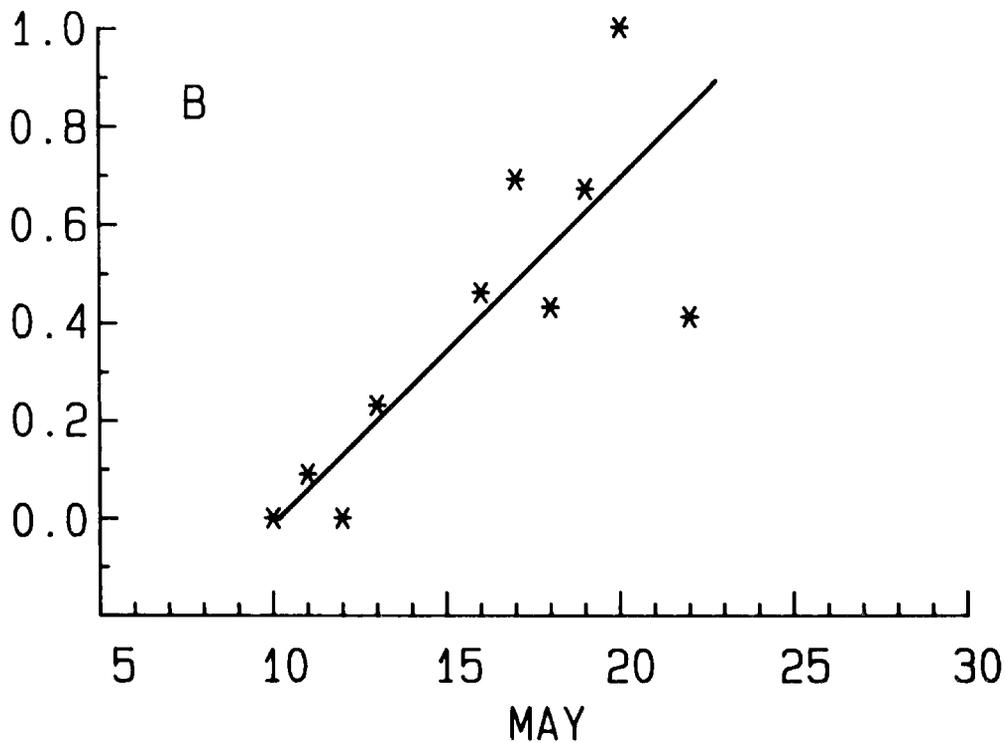
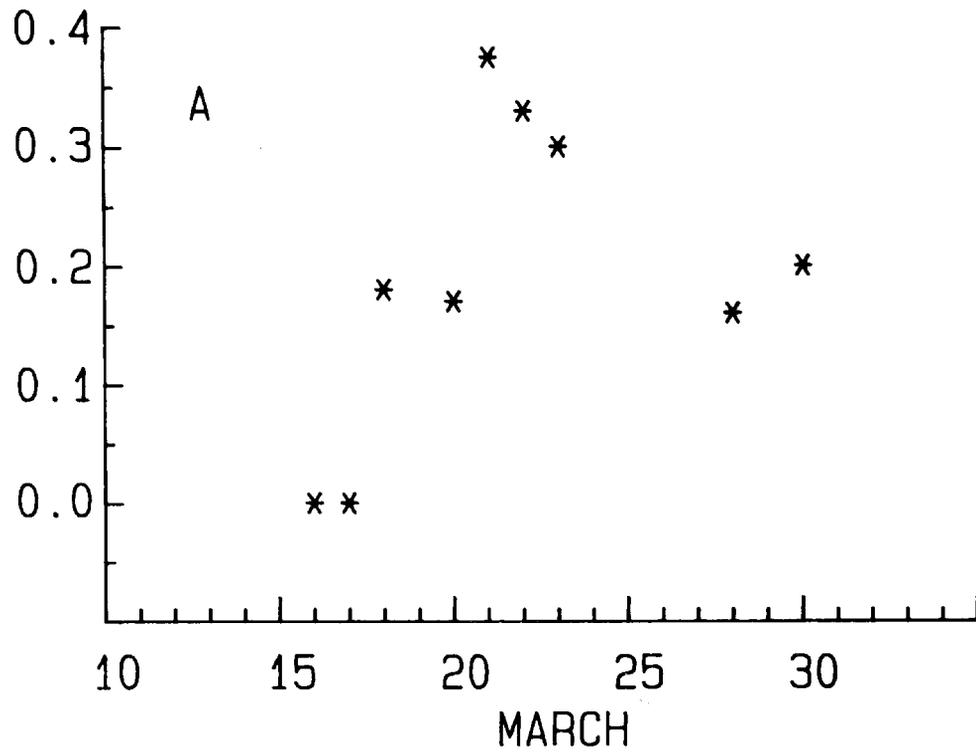


Fig. 3 Temporal trend in proportion of host plants alighted on that bear previously-laid eggs. A. Brood 1. $r_s = .51$, NS. B. Brood 2. $r_s = .74$, $P < .01$.

PLANTS W/O EGGS/10 MIN

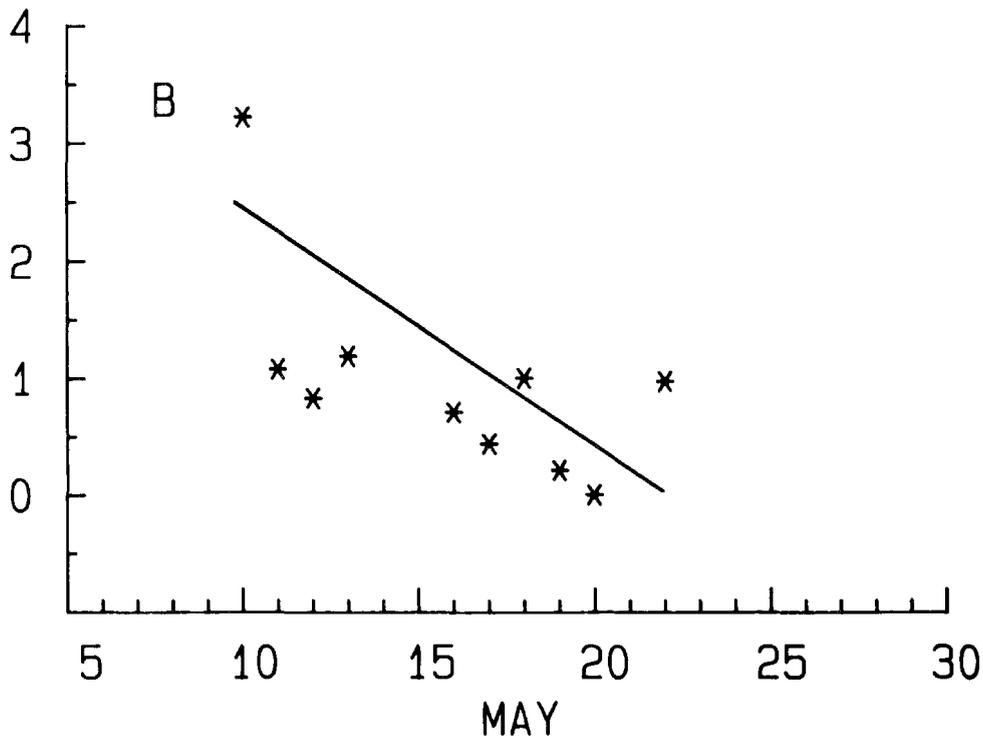
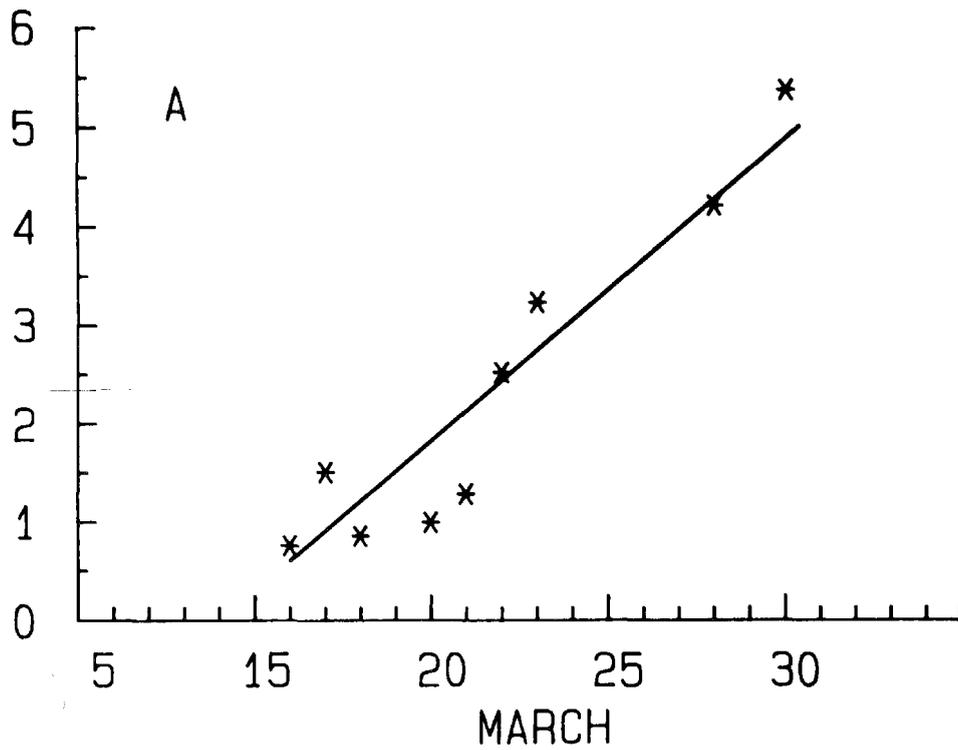


Fig. 4 Temporal trend in rate of alighting on plants without previously laid eggs. A. Brood 1. $r_s = .95$, $P < .01$. B. Brood 2. $r_s = -.71$, $P < .05$.

FRACTION OF PLANTS ACCEPTED

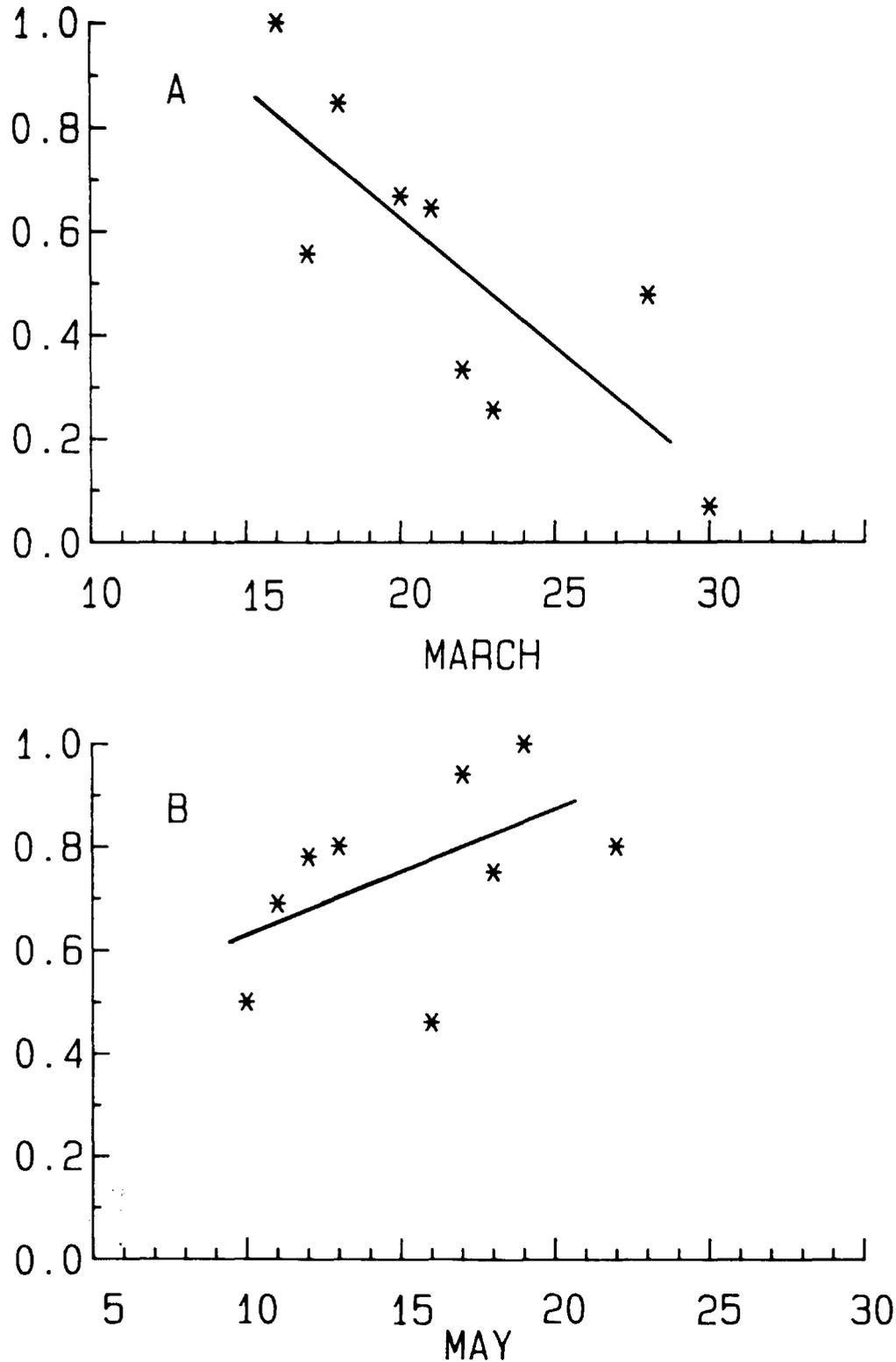


Fig. 5 Temporal trend in probability of ovipositing, once alighting occurs, on host plants without eggs. A. Brood 1. $r_s = -.85$, $P < .01$. B. Brood 2. $r_s = .63$, $P < .05$.

probability of survivorship of offspring (Rausher 1985)), does in fact depend on their frequency in the population.

Consider what would happen if all progeny of first-brood individuals emerged to form the second brood. There would be approximately twice as many females competing for the same limited number of oviposition sites. The 15% of the host plants that are not typically preempted by the end of the second brood is not nearly sufficient to allow twice as many females to lay the same mean number of eggs per capita with the same average number of eggs laid per plant. One or more of several changes would therefore occur: (1) Females might decrease the mean number of eggs laid per individual; (2) Females might maintain the same mean fecundity by laying more of their eggs on plants that already bear eggs and larvae; (3) Females might maintain the same mean fecundity by laying more eggs per plant on plants lacking previously laid eggs or larvae; and/or (4) Females might maintain the same mean fecundity by increasing the amount of time spent searching for and ovipositing on *A. reticulata*. Each of these possible changes would result in a decline in representational fitness, because of either a decline in fecundity (1) or in offspring survivorship (2-4).⁷ Consequently, the fitness of non-diapausers should decline as their frequency increases.

MAINTENANCE OF DIAPAUSE POLYMORPHISM

With the plausibility of frequency-dependence of representational fitness of non-diapausers established, it is now possible to suggest how the diapause polymorphism may be maintained in east Texas populations of *Battus philenor*. In this section I present a simple genetic model of the evolution of diapause which shows that frequency-dependence of the type seen in *B. philenor* can be sufficient to maintain a polymorphism.

The model assumes that whether an offspring of a first-brood female enters pupal diapause or emerges to participate in the second brood is controlled by a single Mendelian locus with two alleles, A_1 and A_2 . Individuals homozygous for A_1 are non-diapausers, whereas individuals homozygous for A_2 enter diapause. For simplicity, I treat in detail the case in which heterozygotes also are non-diapausers (*i.e.*, complete dominance of allele A_1), though it will be seen later that the properties of the model do not differ in the case of complete recessiveness of A_1 , and hence, by inference, for cases of intermediate dominance. I assume that genotype at the A locus affects only tendency to diapause. In particular, I assume that the A-locus genotype does not affect mating success, fecundity, or larval or pupal survivorship.

Let p_1 be the gene frequency of allele A_1 , and let G_1 be the genotype frequency of A_{11} , G_2 the genotype frequency of A_{12} , and G_3 the genotype frequency of A_{22} in overwintering pupae. Assuming that random mating occurs among brood-1 individuals that emerge from these pupae, the genotype frequencies among the offspring of brood-1 individuals are given by

$$\begin{aligned} G_1 &= p_1^2 && \text{(proportion of population that is homozygous, non-diapausing)} \\ G_2 &= 2p_1p_2 && \text{(proportion of population that is heterozygous, non-diapausing)} \\ G_3 &= p_2^2 && \text{(proportion of population that is diapausing).} \end{aligned}$$

In particular, these are the genotype frequencies at the time of pupation when the decision to diapause or not is presumably made. Consequently, a fraction p_2^2 of the individuals (those that are A_{22}) enter diapause and the remainder, $1 - p_2^2$, emerge to form the second brood.

The gene frequencies, q_i , among the non-diapausing portion of the population are

$$q_1 = (p_1^2 + p_1p_2)/(p_1^2 + 2p_1p_2) = 1/(1 + p_2) \text{ (see appendix footnote 8)}$$

$$q_2 = p_1p_2/(p_1^2 + 2p_1p_2) = p_2/(1 + p_2).$$

Again, assuming random mating among non-diapausing individuals, the genotype frequencies, G_i' , among the offspring of second-brood individuals are

$$\begin{aligned} G_1' &= q_1^2 = 1/(1 + p_2)^2 \\ G_2' &= 2q_1q_2 = 2p_2/(1 + p_2)^2 \\ G_3' &= q_2^2 = p_2^2/(1 + p_2)^2. \end{aligned}$$

Next, let m be the mean number of eggs laid by brood-2 females and l be the mean probability of survival of those eggs to the pupal stage. Then $W_{nd} = lm$ is the representational fitness of non-diapausing females, as defined previously. Finally, let W_d be the probability that a diapausing pupa will survive from the time brood-2 adults emerge until their offspring pupate. The genotype frequencies among all overwintering pupae, G_i'' , are then the weighted average of the frequencies among offspring of the first and second broods, where the weightings are given by W_{nd} and W_d :

$$TG_1'' = (1 - p_2^2)W_{nd}/(1 + p_2)^2 \quad (1a)$$

$$TG_2'' = 2p_2(1 - p_2^2)W_{nd}/(1 + p_2)^2 \quad (1b)$$

$$TG_3'' = p_2^2(1 - p_2^2)W_{nd}/(1 + p_2)^2 + p_2^2W_d \quad (1c)$$

and where T is the sum of the right-hand sides of the equations⁹, and is given by

$$T = (1 - p_2^2)W_{nd} + p_2^2W_d \quad (2).$$

Eqs. (1) are in fact the recursion equations¹⁰ for the system, since $G_3 + 1/2 G_2$ could be substituted for p_2 . The recursion equation for the frequency of allele A_2 , obtained by summing (1c) and 1/2 of (1b), is

$$Tp_2'' = p_2(1 - p_2)W_{nd} + p_2^2W_d \quad (3).$$

In the previous sections, I have argued that the representational fitness of brood-2 females is frequency-dependent. In particular, W_{nd} is an increasing function of p_2^2 , the proportion of diapausers. For simplicity, let this relationship be represented by $W_{nd} = kp_2^2 + c$, where k and c are constants. By contrast, there is little reason to suspect that the survivorship of pupae is density-dependent and I therefore assume W_d is constant.¹¹

I now show that if there is some value of p_2 at which $W_{nd} = W_d$, then a stable polymorphism will be maintained in the population. First note that if $W_{nd} = W_d = W$, then $T = W$. This is shown by summing Eqs.(1a)-(1c) and combining terms, recognizing that the sum of the G_i is 1. When this is done, (3) reduces to

$$p_2'' = p_2(1 - p_2) + p_2^2 = p_2,$$

which says that there is no change in gene frequency when $W_{nd} = W_d$. Because genotype frequencies are functions of the gene frequencies, once gene frequencies reach equilibrium, so do genotype frequencies. The equilibrium gene frequency, \hat{p}_2 , obtained by solving

$$W_d = k\hat{p}_2^2 + c,$$

is

$$\hat{p}_2 = \sqrt{(W_d - c)/k}.$$

Next, I show that when $W_{nd} < W_d$, the frequency of the diapause allele, A_2 , will increase, whereas if $W_{nd} > W_d$, that frequency will decrease. There will be an increase in p_2 (the frequency of allele A_2 in one time period) if p_2'' (the frequency of allele A_2 in the next time period) - $p_2 > 0$, or, equivalently, if

$$Tp_2'' - Tp_2 > 0 \quad (4).$$

Substituting (2) and (3) into (4) and simplifying yields $W_d > W_{nd}$. In similar fashion, it can be shown that p_2 decreases whenever $W_d < W_{nd}$.

In Fig.6 are portrayed the assumed relationships between W_d and the frequency of diapausers, p_2^2 , and between W_{nd} and p_2^2 . The point at which these two curves intersect represents an equilibrium, \hat{p}_2^2 . That equilibrium is stable because for values of p_2^2 less than \hat{p}_2^2 , $W_{nd} < W_d$, so p_2^2 , and hence the frequency of A_2 , will increase toward the equilibrium. By contrast, when p_2^2 is greater than \hat{p}_2^2 , $W_{nd} > W_d$ and p_2^2 will decrease toward \hat{p}_2^2 .

This analysis shows that the frequency-dependent effect of competition for oviposition sites on representational fitness can maintain a stable diapause polymorphism. The only requirements are that (1) when the diapause allele is rare (*i.e.*, when few individu-

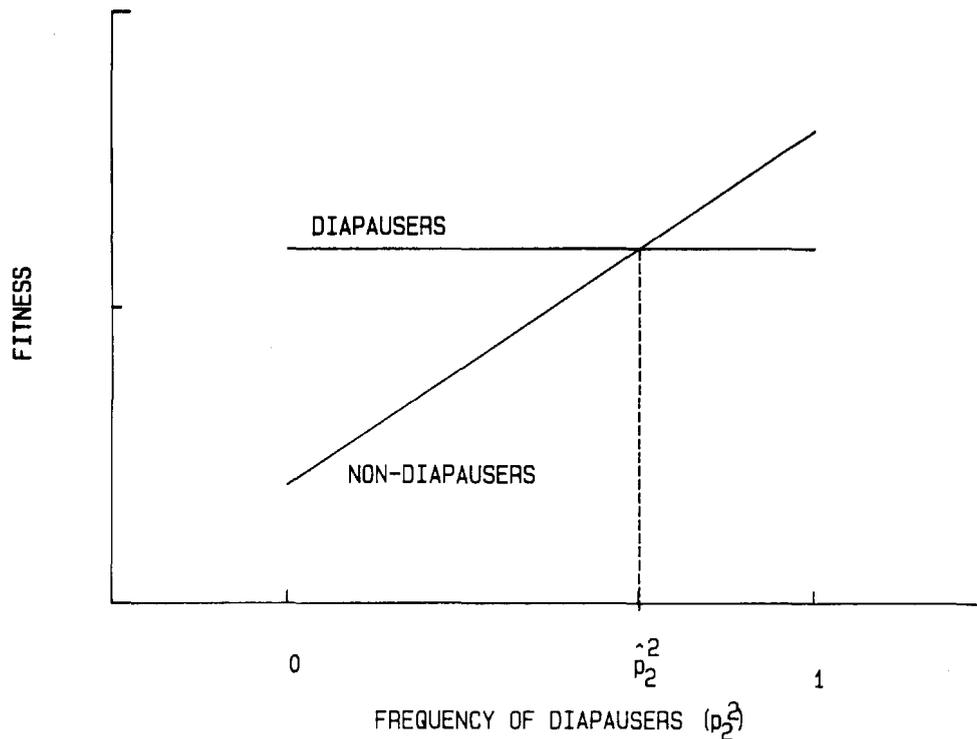


Fig. 6 Assumed relationship between frequency of diapausers, p_2^2 , and fitness for diapausers and non-diapausers. The broken line indicates the equilibrium frequency of diapausers

als diapause and competition for oviposition sites is intense), pupal survivorship during the period when brood-2 adults are flying and their offspring are developing as larvae is greater than the representational fitness of second-brood females (*i.e.*, $W_d > W_{nd}$), and (2) when the diapause allele is common (*i.e.*, most individuals diapause and competition for oviposition sites is lax), pupal survivorship is less than the representational fitness of second-brood females (*i.e.*, $W_d < W_{nd}$). These two conditions ensure that the two curves in Fig. 6 intersect and hence ensure the existence of a stable diapause polymorphism.

As presented, the analysis may seem restricted in its applicability because of the assumption that A_1 is dominant to A_2 . If one performs a completely analogous analysis under the assumption of A_2 being dominant to A_1 , one still finds that requirements (1) and (2) above guarantee the existence of a stable polymorphism.¹² This and the previous case represent the extremes in degree of dominance of one allele over the other, ignoring cases of overdominance. Because in both cases requirements (1) and (2) above are necessary and sufficient conditions for the existence of a stable diapause polymorphism, this should also be true for intermediate degrees of dominance.

DISCUSSION

The existence of competition for oviposition sites among second-brood *Battus philenor* females provides an explanation for the evolution and maintenance of a diapause polymorphism in east Texas populations of this butterfly species. Because oviposition sites are limited, an individual's expected genetic representation in the next generation is inversely proportional to the number of females that compete for those sites.

A larva that pupates in mid- to late April in east Texas can be thought of as having an option to either enter diapause and remain in that state until the following spring or emerge two weeks later to participate in the second brood. Which option natural selection will favor depends crucially on what option other individuals in the population elect. Consider first a situation in which all individuals in the population are genetically programmed to enter diapause. A mutant female that fails to enter diapause will then emerge in early May and find an unexploited supply of *Aristolochia serpentaria* plants on which to oviposit and on which its offspring may develop (provided, of course, a mutant non-diapausing male is available for mating). Since there is no competition from other females, the number of offspring of the mutant individual pupating successfully should be high. In particular, as long as the expected number of offspring pupating is greater than the expected survivorship of diapausing pupae, the mutant type will increase its genetic representation in the population as a whole, and the mutant will be favored by selection.

As selection increases the frequency of the mutant type, however, the number of females competing during the second brood will also increase, and consequently the expected number of offspring per female reaching the pupal stage will decrease. This decrease will continue until the expected number of offspring pupating per female exactly equals the probability of survival of diapausing pupae. At this point, the genetic contribution of a non-diapausing individual is exactly equal to that of a diapausing individual and there will be no selective forces acting to increase or decrease the frequency of non-diapausers. A similar argument holds for a mutant diapauser, which would increase in a population of non-diapausers.

The model presented in the previous section is a formal representation of this scenario. It assumes, of course, that diapause is controlled by a single Mendelian locus with two alleles. Because nothing is currently known about the genetic control of diapause in *B. philenor*, however, a polygenic mode of inheritance of diapause tendency in *B. philenor* can not be ruled out; nor can the possibility be eliminated that the decision to enter diapause is primarily environmentally controlled in *B. philenor*. In many insects, a photoperiod threshold controls diapause. If individuals pupate when daylength is below a certain threshold, a state of diapause is (or is not) entered. By contrast, if pupation occurs with daylength above the threshold, diapause is not (is) entered (Danilevsky *et al.* 1970, Tauber and Tauber 1976). Because there is at least a 2-3 week range of pupation dates for offspring of brood-1 *B. philenor* females in east Texas (personal observation) during a time when daylength is rapidly increasing, it is conceivable that the threshold daylength falls within that period. If so, individuals pupating early will emerge to form a second brood while those pupating late will enter diapause.

Although the one-locus model presented above would not be relevant to a situation in which diapause tendency were controlled either polygenically or environmentally, in either case the basic verbal argument given above would still pertain. In fact, Slatkin (1978) has shown that when the proportion of individuals in either of two phenotypic classes is controlled polygenically, the genetic equilibrium is characterized by equilibration of the fitnesses of the two phenotypic classes. Thus, Fig. 6 schematically portrays the equilibrium for polygenic control of diapause, with the proviso that the x-axis is taken to be the proportion of individuals in the population that enter diapause.

Environmental control of diapause is just a special case of polygenic control of diapause, because the threshold daylength is likely to be genetically variable to some degree and hence can presumably evolve (Hoy 1978). Increasing or decreasing the threshold simply increases or decreases the proportion of the population that pupates before daylength passes the threshold, and hence adjusts the proportions of individuals that are in each phenotypic class (*i.e.*, diapause or non-diapause). Slatkin's results are

then applicable and an equilibrium occurs when the fitness of non-diapausers (W_{nd}) equals that of diapausers (W_d).

The explanation proposed here for the maintenance of a diapause polymorphism in *B. philenor* is of course not the only one possible. In particular, it is conceivable that this polymorphism is maintained by simple heterosis (Roughgarden 1979), by temporally fluctuating selection pressures (Felsenstein 1976), or even represents an example of "adaptive coin flipping" (Cooper and Kaplan 1982, Walker 1986). None of these possibilities, or even some combination of them, can be ruled out at this point. However, demonstration of the existence of competition for oviposition sites and the reasonable inference of frequency-dependence of the fitness of non-diapausers is positive evidence arguing in favor of the explanation offered here. Closer scrutiny of the genetics and ecology of diapause in *Battus philenor* will be needed to determine conclusively whether that explanation is correct.

APPENDIX

¹Larvae fed a mixture of excised leaves of *A. reticulata* and *A. serpentaria* were reared under natural temperature and photoperiod conditions on the porch of a cabin in east Texas. Upon pupation, each larva was placed in its own container. If eclosion occurred within three weeks of pupation, a butterfly was considered not to have entered diapause. Individuals that failed to eclose within this period still had not eclosed within six months, indicating that they were either in diapause or had died. These butterflies emerged over the course of several months beginning in late December and early January in the laboratory. Only individuals that actually emerged were included in the counts.

²Genetic variation for diapause tendency has been found in the papilionid *Papilio zelicaon*. Simms (1983) argues that this variation is polygenic in nature, but his data are also consistent with single-locus, Mendelian inheritance. Simms and Shapiro (1983) show that environmental conditions can influence tendency to diapause in California populations of *Battus philenor*, but they did not rule out the possibility that variation in diapause tendency may also be explained partly by underlying genetic variation.

³In many insects, the rate at which females mature eggs, and hence the rate at which eggs may be laid, declines as females age (Wigglesworth 1972, Price 1984). Because the average age of females increases over the course of a brood (Odendaal, Lederhouse, and Rausher, unpublished data), one might then expect to see a gradual decline in average oviposition rate.

⁴In *B. Philenor*, the rate at which females alight on host plants is directly proportional to the abundance of host plants in the habitat (Rausher 1983). If host plant abundance decreases over time, then alighting rates will do likewise; and if the probability of oviposition is not influenced by alighting rate, then oviposition rate will also decline. In east Texas, the number of host plants available to ovipositing females may be expected to decline during brood 2 because they are consumed by dispersing larvae that are the slowly growing offspring of brood-1 and the early-laid offspring of brood-2 individuals.

⁵Because females tend to avoid ovipositing on plants that already bear eggs (Rausher 1979), the number of plants acceptable to females (*i.e.*, that lack previously laid eggs) is expected to decline over time. If oviposition probability, once a plant is alighted on, remains constant, then oviposition rate will decline.

⁶During brood 1, there is no significant trend in the proportion of plants alighted on that already bear eggs (Fig. 3a). This constancy is probably due to the variation in host-plant leafing phenology, which causes the number of plants available to females to increase steadily during the first brood (Rausher 1980, 1983). This increase in host-plant numbers, along with the constancy in proportion of plants that bear eggs, is also responsible for the steady increase in the number of host plants alighted on during the first brood that do not bear eggs (Fig. 4a). Because there is an internally-regulated maximum oviposition rate (Fig. 1a and Rausher 1983), while the number of host plants alighted

on rises steadily, the proportion of host plants alighted on that are accepted declines steadily during the first brood (Fig. 5a; see also Rausher 1983).

⁷This conclusion is obvious for change (1). Since it is less obvious for the other possible changes, I briefly provide here justification for why changes (2)-(4) would also lower the representational fitness of non-diapausers. Rausher (1979) has shown that offspring placed on plants that already harbor eggs or larvae have a lower survivorship than eggs placed on unoccupied plants. Consequently, increasing the proportion of eggs that are laid on occupied plants will decrease mean offspring survivorship, and hence mean representational fitness.

Although we have no direct experimental evidence, it is also almost certain that increasing the number of eggs laid per plant by a single female will also decrease offspring survivorship. This conclusion is based on the results of several experiments and observations. First, no single host plant is large enough to support the complete development of one *B. philenor* larva. A larva, after feeding on all edible foliage on the plant on which it hatches, must disperse to find other host plants (Rausher 1980, 1981, Rausher and Papaj 1983b). The size of a larva when it disperses from its initial host plant is directly proportional to the amount of edible foliage that was present on that plant (Pilson and Rausher, unpublished). Presumably, the more larvae that are placed on a plant, the less each obtains of the fixed amount of edible foliage, and the smaller they are when they disperse from their first host. Because the probability of finding another plant, and hence of surviving to the adult stage, decreases with decreasing size at dispersal (Rausher 1979), an increase in the number of eggs a female lays on a host plant will presumably decrease mean offspring survivorship, and hence decrease mean representational fitness.

Finally, an increase in the proportion of offspring placed on *A. reticulata* during the second brood will also lower mean representational fitness. Because the leaves of *A. reticulata* become sclerophyllous by the time of the second brood, whereas those of *A. serpentaria* do not, the foliage of the latter host is much more suitable for larval development than that of the former. Larvae that hatch on *A. serpentaria* are therefore much larger when they disperse to find new hosts than larvae that hatch on *A. reticulata*, resulting in greater overall survivorship for offspring placed on *A. serpentaria* (Rausher 1980, 1981). A shifting of eggs from *A. serpentaria* to *A. reticulata* in response to increased competition for oviposition sites would therefore lead to a decrease in mean offspring survival and in representational fitness.

⁸This identity may be derived as follows:

$$\begin{aligned} (p_1^2 + p_1p_2)/(p_1^2 + 2p_1p_2) &= p_1(p_1 + p_2)/p_1(p_1 + 2p_2) \\ &= (p_1 + p_2)/(p_1 + p_2 + p_2) \end{aligned}$$

and since $p_1 + p_2 = 1$,

$$= 1/(1 + p_2).$$

⁹T is a normalizing factor that, when divided into the right-hand side of Eqs. (1) makes their sum equal to 1. By multiplying each side of these equations by T, one obtains the form shown in the text.

¹⁰A set of recursion equations provides the mathematical rule that transforms gene or genotype frequencies in one time period into the frequencies in the next time period.

¹¹The inferences derived from the model remain valid even if density-dependence exists, as long as the slope of the relationship between pupal survival and p_2^2 is less than k , i.e., as long as the curves relating gene frequency to fitness for diapausers and non-diapausers intersect and to the right of the intersection (high values of p_2) the curve for non-diapausers is above that for diapausers.

¹²In this case the relationship between gene frequency and representational fitness is assumed to be

$$W_{nd} = k(1 - p_1^2) + c$$

and the equilibrium gene frequency is

$$\hat{p}_2 = 1 - \sqrt{(k + c - W_d)/k}.$$

ACKNOWLEDGMENTS

I wish to thank Jim Lloyd for organizing the symposium at which this paper was presented. I also wish to thank Frank Slansky, Thomas Walker, and an anonymous reviewer for suggested improvements to the manuscript. Anne Lacey contributed invaluable moral support throughout the writing of this manuscript. This work was supported in part by NSF grant BSR-8406870.

REFERENCES CITED

- COOPER, W. S. AND R. H. KAPLAN. 1982. Adaptive "coin-flipping": a decision-theoretic examination of natural selection for random individual variation. *J. Theor. Biol.* 94: 135-51.
- DANILEVSKY, A. S. 1965. Photoperiodism and seasonal development of insects. Oliver and Boyd, London.
- DANILEVSKY, A. S., N. I. GORYSHIN AND V. P. TYSCHENKO. 1970. Biological rhythms in terrestrial arthropods. *Annu. Rev. Ent.* 15: 201-44.
- FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-81.
- FELSENSTEIN, J. 1976. The theoretical population genetics of variable selection and migration. *Annu. Rev. Genet.* 10: 253-80.
- GEYSPITZ, K. F. 1968. Genetic aspects of variation of photoperiodic adaptations, Pages 52-79 *In* A. S. Danilevsky, Ed. Photoperiodic adaptations in insects and acari. Leningrad. Leningrad State Univ. Press.
- GILBERT, L. E. AND M. C. SINGER. 1975. Butterfly ecology. *Annu. Rev. Ecol. Syst.* 6: 365-97.
- HELLE, W. 1968. Genetic variability of photoperiodic response in an arrhenotokous mite (*Tetranychus urticae*). *Ent. Exp. Appl.* 11: 101-13.
- HOY, M. A. 1978. Variability in diapause attributes of insects and mites: some evolutionary and practical implications. Pages 101-26 *In* H. Dingle, Ed. Evolution of insect migration and diapause. Springer-Verlag, New York.
- ISTOCK, C. A. 1978. Fitness variation in a natural population. Pages 171-90 *In* H. Dingle, Ed. Evolution of insect migration and diapause. Springer-Verlag, New York.
- , S. S. WASSERMAN AND H. ZIMMER. 1975. Ecology and evolution of the pitcher-plant mosquito. 1. Population dynamics and laboratory responses to food and population density. *Evolution* 29: 296-312.
- , J. ZISFEIN AND K. J. VAVRA. 1976. Ecology and evolution of the pitcher-plant mosquito. 2. The substructure of fitness. *Evolution* 30: 535-47.
- OPLER, P. P. AND R. L. LANGSTON. 1968. A distributional analysis of the butterflies of Contra Costa County, California. *J. Lepid. Soc.* 22: 89-107.
- PRICE, P. W. 1984. Insect ecology, 2nd Edition. John Wiley, New York.
- RAUP, M. J. AND R. F. DENNO. 1983. Leaf age as a predictor of herbivore distribution and abundance. Pages 91-124 *In* R. F. Denno and M. S. McClure, Eds. Variable plants and herbivores in natural and managed systems. Academic Press, New York.
- RAUSHER, M. D. 1978. Search image for leaf shape in a butterfly. *Science* 200: 1071-3.
- . 1979. Egg recognition: its advantage to a butterfly. *Anim. Beh.* 27: 1034-40.
- . 1980. Host abundance, juvenile survival, and oviposition preference in *Battus philenor*. *Evolution* 34: 342-55.
- . 1981. Host plant selection by *Battus philenor* butterflies: the roles of predation, nutrition, and plant chemistry. *Ecol. Monogr.* 51: 1-20.
- . 1983. Alteration of oviposition behavior by *Battus philenor* butterflies in response to variation in host plant density. *Ecology* 64: 1028-34.
- . 1985. Variability for host preference in insect populations: mechanistic and evolutionary models. *J. Insect Physiol.* 31: 873-89.
- AND P. FEENY. 1980. Herbivory, plant density and plant reproductive success:

- the effect of *Battus philenor* on *Aristolochia reticulata*. Ecology 61: 905-17.
- AND D. R. PAPAJ. 1983a. Host plant selection by *Battus philenor* butterflies: evidence for individual differences in foraging behaviour. Anim. Beh. 31: 341-7.
- . 1983b. Demographic consequences of host discrimination by *Battus philenor* butterflies. Ecology 64: 1402-10.
- ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology. Macmillan, New York.
- SHAPIRO, A. M. 1975. The temporal component of butterfly species diversity. Pages 181-95 In M. L. Cody and J. M. Diamond, Eds. Ecology and evolution of communities. Belknap Press, Cambridge.
- SIMMS, S. R. 1983. Inheritance of diapause induction and intensity in *Papilio zelicaon*. Heredity 51: 495-500.
- SIMMS, S. R. AND A. M. SHAPIRO. 1983. Pupal diapause in *Battus philenor* (Lepidoptera: Papilionidae). Ann. Ent. Soc. Am. 76: 407-12.
- SLANSKY, F. 1974. Relationship of larval food plants and voltinism patterns in temperate butterflies. Psyche 81: 243-53.
- SLATKIN, M. 1978. On the equilibration of fitnesses by natural selection. Am. Nat. 112: 845-59.
- TAUBER, M. J., AND C. A. TAUBER. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Annu. Rev. Ent. 21: 81-107.
- WALDBAUER, G. P. 1978. Phenological adaptation and phenological emergence patterns in insects. Pages 127-44 In H. Dingle, Ed. Evolution of insect migration and diapause. Springer-Verlag, New York.
- WALKER, T. J. 1986. Stochastic polyphenism: coping with uncertainty. Fla. Ent. (this symposium).
- WIGGLESWORTH, V. B. 1972. The principles of insect physiology, 7th Edition. Chapman and Hall, London.

CALLING BEHAVIOR: CAN IT BE USED TO IDENTIFY MIGRATORY SPECIES OF MOTHS?

JEREMY N. McNEIL*
 Departement de Biologie
 Universite Laval
 Ste. Foy, P.Q., G1K 7P4
 Canada

SYNOPSIS

There is considerable debate concerning the fate of populations of noctuid moths, founded during the summer, by migrants moving considerable distances northward of areas where permanent populations persist. This paper compares the female calling behavior of moth species that maintain permanent populations in Canada with those that are known immigrants. Residents initiate calling soon after emergence, regardless of climatic conditions, while the mean age of calling for immigrant species is variable, even under favorable conditions. Furthermore the onset of calling by immigrants is

*Jeremy McNeil is a full professor in the Biology Department at Laval University. His main interests are the ecological and behavioral aspects of pheromone mediated systems in insects, especially Lepidoptera. Current address: Departement de biologie, Universite Laval, Ste. Foy, P.Q., G1K 7P4, Canada. (Contribution 470, Departement de biologie).

- the effect of *Battus philenor* on *Aristolochia reticulata*. Ecology 61: 905-17.
- AND D. R. PAPAJ. 1983a. Host plant selection by *Battus philenor* butterflies: evidence for individual differences in foraging behaviour. Anim. Beh. 31: 341-7.
- . 1983b. Demographic consequences of host discrimination by *Battus philenor* butterflies. Ecology 64: 1402-10.
- ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology. Macmillan, New York.
- SHAPIRO, A. M. 1975. The temporal component of butterfly species diversity. Pages 181-95 In M. L. Cody and J. M. Diamond, Eds. Ecology and evolution of communities. Belknap Press, Cambridge.
- SIMMS, S. R. 1983. Inheritance of diapause induction and intensity in *Papilio zelicaon*. Heredity 51: 495-500.
- SIMMS, S. R. AND A. M. SHAPIRO. 1983. Pupal diapause in *Battus philenor* (Lepidoptera: Papilionidae). Ann. Ent. Soc. Am. 76: 407-12.
- SLANSKY, F. 1974. Relationship of larval food plants and voltinism patterns in temperate butterflies. Psyche 81: 243-53.
- SLATKIN, M. 1978. On the equilibration of fitnesses by natural selection. Am. Nat. 112: 845-59.
- TAUBER, M. J., AND C. A. TAUBER. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. Annu. Rev. Ent. 21: 81-107.
- WALDBAUER, G. P. 1978. Phenological adaptation and phenological emergence patterns in insects. Pages 127-44 In H. Dingle, Ed. Evolution of insect migration and diapause. Springer-Verlag, New York.
- WALKER, T. J. 1986. Stochastic polyphenism: coping with uncertainty. Fla. Ent. (this symposium).
- WIGGLESWORTH, V. B. 1972. The principles of insect physiology, 7th Edition. Chapman and Hall, London.

CALLING BEHAVIOR: CAN IT BE USED TO IDENTIFY MIGRATORY SPECIES OF MOTHS?

JEREMY N. McNEIL*
 Departement de Biologie
 Universite Laval
 Ste. Foy, P.Q., G1K 7P4
 Canada

SYNOPSIS

There is considerable debate concerning the fate of populations of noctuid moths, founded during the summer, by migrants moving considerable distances northward of areas where permanent populations persist. This paper compares the female calling behavior of moth species that maintain permanent populations in Canada with those that are known immigrants. Residents initiate calling soon after emergence, regardless of climatic conditions, while the mean age of calling for immigrant species is variable, even under favorable conditions. Furthermore the onset of calling by immigrants is

*Jeremy McNeil is a full professor in the Biology Department at Laval University. His main interests are the ecological and behavioral aspects of pheromone mediated systems in insects, especially Lepidoptera. Current address: Departement de biologie, Universite Laval, Ste. Foy, P.Q., G1K 7P4, Canada. (Contribution 470, Departement de biologie).

strongly influenced by prevailing temperature and photoperiodic conditions during adult life. These differences may only be of importance for the northward spring dispersal, but as fall conditions induce a delay in the onset of calling of known immigrants it is proposed that this could potentially permit a southerly, upper air migration to suitable overwintering sites.

INTRODUCTION

A number of noctuid moths of major economic importance in North America (see Rabb and Kennedy 1979) are known to be highly mobile and, during the summer months, expand their geographic distribution into northerly areas where they are unable to establish permanent populations. These temporary populations have often been considered as dead end ones that are killed off at the onset of adverse weather conditions in the fall. Rabb and Stinner (1978) referred to this type of movement as the "Pied Piper" phenomenon, suggesting that man's agricultural practices temporarily increase suitable and available habitats and that "this [the Pied Piper effect] seems to "pervert" the survival strategies of the species involved. . . .". However, Walker (1980) proposed that if there is a genetic basis for this repeated seasonal dispersal, the demise of individuals exploiting these temporally available habitats would create an evolutionary dilemma as such suicidal dispersal would be strongly selected against. Stinner et al. (1983) provided a counter argument on this point, but agreed that the testable predictions proposed by Walker (1980) would help elucidate whether or not noctuids have a return fall migration.

There is considerable concrete evidence that some butterfly species have unidirectional spring and fall migrations, generally occurring within the boundary layer (Walker 1980; Baker 1984 and references therein). On the other hand there is little data for night flying moths, one obvious reason being the difficulty with which direct observations can be made. Two well documented cases for noctuids do exist: the bogong moth in Australia (Common 1954) and the army cutworm in North America (Pruess 1967; Kendall 1981) migrate, as adults in reproductive diapause, to the mountains for the summer before returning in the fall to the plains where they reproduce. Dingle (1982) pointed out that migration associated with adult reproductive diapause is quite common, and the derived advantages of such a system are evident for Lepidoptera that migrate to aestivation (the army cutworm) or overwintering sites (the monarch) and return before the onset of reproduction. However, temperate species that expand their range into temporarily available habitats during the summer months, if capable of a return fall migration, would benefit from pre-reproductive strategies permitting the optimal utilisation of both summer and winter resources. Based on data pertaining to the calling behavior of several temperate species of Lepidoptera, I propose that certain insects undertaking long distance, upper air, northward migrations (i) possess pre-reproductive traits that differ considerably from resident species and (ii) that these traits, which fit within the context of the diapause syndrome (Tauber et al. 1984), would facilitate a return southward migration to suitable overwintering sites in the fall.

SUBJECT SPECIES

The true armyworm, *Pseudaletia unipuncta* is a noctuid that is found annually throughout much of eastern Canada but does not establish permanent populations due to the inability to overwinter in these areas (Ayre 1985; Fields and McNeil 1984). The closely synchronized appearance of adults over a wide area, having very different local climatic conditions, strongly supports the hypothesis that moths immigrate on prevail-

ing weather fronts, as suggested for other Lepidoptera (Arthur and Bauer 1981; Domino et al. 1983). Studies investigating the nocturnal calling behavior of true armyworm virgin females has shown that even under favorable summer conditions (25°C, 16L:8D) individuals initiate calling for the first time from 2 to 12 days following emergence; the mean age for the onset of calling varying from 4 to 6 days (Turgeon and McNeil 1982; Delisle and McNeil 1986). The mean calling age of *P. unipuncta* is also significantly influenced by ambient temperature conditions during adult life (Turgeon and McNeil 1983); the lower the temperature, the older females are when they start calling, e.g. at 10°C the mean age of calling is 17.9 days. Furthermore there is a photoperiodic effect, with females at 25°C calling significantly later under 12L:12D (\bar{X} =7.9 days) than at 16L:8D (\bar{X} =6.0 days) (Delisle and McNeil 1986). The combined effect of 10°C, 12L:12D, during adult life resulted in a mean calling age of approximately 21 days, and when females were transferred to 25°C, 16L:8D, at 5, 10, or 15 days following emergence, calling was initiated within six days (Delisle and McNeil, unpublished). The observed delays in the onset of calling fit the "oogenesis-flight syndrome" (Johnson 1969), being initiated by short days and low temperatures, conditions responsible for the initiation of diapause of many temperate species (Beck 1980). I believe the responses observed in the true armyworm reflect one extreme within the spectrum of adult reproductive diapause associated with the migration of Lepidoptera as (i) ovarian development does occur, albeit slowly, under short day/low temperature conditions and, (ii) females initiate calling rapidly when transferred to long day/high temperature conditions. As previously stated this strategy would benefit species that reproduce in both the summer and winter limits of the distribution. This contrasts with the other extreme reported in other noctuids, such as the army cutworm and the bogong moth (Common 1954; Pruess 1967), where reproductive diapause persists for several months. In these cases, little or no reproductive activity occurs before the adults that immigrated to the mountains initiate their return migration.

A markedly different situation is seen with the Bertha armyworm, *Mamestra con-figurata*, a species that does overwinter in Canada. For this moth temperature and photoperiodic conditions have very little effect on the age at which calling starts. At 25°C, 16L:8D, all females initiated calling by the fourth night following emergence, with a mean age of first calling of 2.2 days (Howlander 1985; J. Haley, unpublished data), while at 10°C, 16L:8D, it is 5.2 days (Howlander 1985). In addition, 100% of all females held at 25°, 12L:12D, were calling by the second night following emergence (Howlander 1985).

While the data base relative to calling behavior under different abiotic conditions is less substantial, there is evidence that differences similar to those observed between the true armyworm and the Bertha armyworm may exist for other resident and immigrant noctuids. Greater than 83% of virgin females of the potato stem borer, *Hydraecia micacea*, an introduced European species that is now an established resident in Canada, called the first night following emergence at 23°C, 14L:10D, in the laboratory, while 100% did so under field conditions (West et al. 1984). On the other hand Swier et al. (1976) reported that at 24-27°C under 16L:8D, the black cutworm, *Agrotis ipsilon*, a suspected spring immigrant (Domino et al. 1983; Kaster and Showers 1982), had an average precopulatory period of 4.4 days, and that it took at least three nights following emergence for more than 33% of the virgin females to initiate calling under a 18L:6D photoperiod at 24°C (Swier et al. 1977). A high incidence of unmated females in fall light trap catches, together with low male catches in pheromone traps, was interpreted as evidence of a reproductive diapause that might facilitate a return fall migration of the black cutworm (Kaster and Showers 1982). Similar results have been collected since 1979 for the true armyworm in our Quebec trapping program (McNeil, unpublished), and the delay in the onset of reproductive activity has been proposed as potentially

facilitating a return migration of this species to suitable overwintering sites (McNeil 1986). Consequently, I suggest that the black cutworm responds to fall conditions in the same way as the true armyworm, with only a short delay in the onset of reproduction. Examination of the calling behavior of *A. ipsilon* under a range of different climatic conditions would test this hypothesis.

In an effort to determine whether the proposed differences between resident and migrant species have any wider application within the Lepidoptera my students and I have recently started comparative work on the calling behavior of pyralids, because members of this Family, like noctuids, are capable of upper air migration (Drake 1985). The sunflower moth, *Homoeosoma electellum*, which migrates annually into Canada (Arthur and Bauer 1981), was chosen as the migrant species as it has a number of biological attributes that differ considerably from the true armyworm. The sunflower moth calls during the photophase (Arthur 1978) rather than the scotophase, even though for most other activities this species is nocturnal, and has the ability to enter diapause as a last instar larva (Chippendale and Kikukawa 1983; Kikukawa and Chippendale 1983; Teetes et al. 1969). However, in Canada non-diapausing larvae leave the host in August and give rise to adults in September. At this time climatic conditions do not permit the completion of another generation, making it highly unlikely that *H. electellum* successfully overwinters this far north (Arthur 1978). If this is the case then these adults, like those of the true armyworm, would have to migrate southward if their offspring are to survive. The resident species chosen for this study was the European corn borer, *Ostrinia nubilalis*, which like the sunflower moth overwinters as a last instar larva. While studies have only recently been initiated, the data obtained to date support the hypothesis that the pre-reproductive behavior of migrant and resident temperate Lepidoptera vary considerably. Females of both univoltine and bivoltine races of the European corn borer call within two days of emergence at 25°C, 16L:8D (L. Royer and McNeil, unpublished), while under the same conditions sunflower moth females have a mean age of calling of 9.7 days (McNeil and Delisle, unpublished). The longevity of our *H. electellum* adults, established from immigrants collected in Saskatoon, while similar to that of the Missouri strain (Kikukawa and Chippendale 1983), was considerably longer than the 8.5 days reported for adults from Texas (Randolph et al. 1972). Temperature and photoperiodic conditions were similar in the laboratory rearings, although other aspects such as relative humidity, available food, and adult densities could explain the observed differences in adult longevity. However, an alternate explanation that merits further investigation within the context of the migration of this species is the possible existence of polymorphism in the population, where life statistics of migrants exploiting temporarily available habitats differ from those that remain in the area of permanent occupation.

DISCUSSION

The evidence presented above strongly supports the hypothesis that pre-reproductive strategies of resident and migrant moth species differ markedly. Indigenous species mate soon after emergence, which would permit rapid exploitation of the resources available in the immediate habitat. On the other hand, species that have significant northward expansions in their summer distribution show considerable variability in the time required for the onset of reproduction, even under optimal summer conditions. At least in the case of the true armyworm, and most probably in the case of the black cutworm, fall conditions induce a further delay in reproductive activity. This could provide the time necessary for a southerly migration to favorable overwintering sites if dispersal occurred in upper air masses, where it has been shown that moths may be carried for at least 90 km in 24 h (Rose et al. 1985). Furthermore, the rapidity with which sexual activity is resumed when females are transferred to favorable conditions

would permit successful emigrants to maximize their reproductive potential upon arrival in acceptable overwintering habitats. However, whether or not seasonal variability in pre-reproductive behavior is uniquely associated with emigration from sites where permanent populations occur or, as suggested by McNeil (1986), is a life history trait permitting a return migration remains to be elucidated. There is one encouraging point for those of us who believe that the answer to Walker's question, "are butterflies better than moths?" (Walker 1980), is no. The oriental armyworm, *P. separata*, the only noctuid species where clear evidence for both north and south migration has been obtained by means of a massive adult mark-recapture program (Li et al. 1964, reference from Baker 1978), has at least a 3 day delay in the onset of calling after emergence at 25°C, 16L:8D (Hirai 1984), similar to *P. unipuncta*.

ACKNOWLEDGMENTS

I would like to thank Jim Lloyd for the kind invitation to participate in the 1985 Behavioral Ecology Symposium. Thanks are also due to M. Cusson, J. Delisle, S. Fitzpatrick and J. Richardson for their comments on an earlier version of this manuscript, as well as to T. J. Walker for valuable editorial suggestions.

LITERATURE CITED

- ARTHUR, A. P. 1978. The occurrence, life history, courtship, and mating behaviour of the sunflower moth, *Homoeosoma electellum* (Lepidoptera: Phycitidae) in the Canadian prairie provinces. Canadian Ent. 110: 913-16.
- ARTHUR, A. P., AND D. J. BAUER. 1981. Evidence of the northerly dispersal of the sunflower moth by warm winds. Environ. Ent. 10: 528-33.
- AYRE, G. L. 1985. Cold tolerance of *Pseudeletia unipuncta* and *Peridroma saucia* (Lepidoptera: Noctuidae). Canadian Ent. 117: 1055-60.
- BAKER, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York.
- . 1984. The dilemma: When and how to go or stay. Pages 279-296 In R. I. Vane-Wright and P. R. Ackery, Eds. The biology of butterflies. Academic Press, New York.
- BECK, S. D. 1980. Insect photoperiodism. 2nd Edition. Academic Press, New York.
- CHIPPENDALE, G. M., AND S. KIKUKAWA. 1983. The effect of daylength and temperature on the larval diapause of the sunflower moth, *Homoeosoma electellum*. J. Insect Physiol. 29: 643-49
- COMMON, I. F. B. 1954. A study of the ecology of the adult bogong moth, *Agrostis infusa* (Boesd.) (Lepidoptera: Noctuidae), with special reference to its behaviour during migration and aestivation. Australian J. Zool. 2: 223-63.
- DELISLE, J., AND J. N. MCNEIL. 1986. The effect of photoperiod on the calling behaviour of virgin females of the true armyworm, *Pseudalitia unipuncta*. J. Insect Physiol. (In press).
- DINGLE, H. 1982. Function of migration in the seasonal synchronization of insects. Ent. Expt. Appl. 31: 36-48.
- DOMINO, R. P., W. B. SHOWERS, S. ELWYNN TAYLOR, AND R. H. SHAW. 1983. Spring weather pattern associated with suspected black cutworm moth (Lepidoptera: Noctuidae) introduction to Iowa. Environ. Ent. 12: 1863-72.
- DRAKE, V. A. 1985. Radar observations of moths migrating in a nocturnal low-level jet. Ecol. Ent. 10: 259-65.
- FIELDS, P. G., AND J. N. MCNEIL. 1984. The overwintering potential of the true

- armyworm, *Pseudaletia unipuncta* (Lepidoptera: Noctuidae), populations in Quebec. Canadian Ent. 116: 1647-52.
- HIRAI, K. 1984. Migration of *Pseudaletia separata* Walker (Lepidoptera: Noctuidae). Considerations of factors affecting time of taking-off and flight period. Ann. Ent. Zool. 19: 422-29.
- HOWLANDER, M. M. A. 1985. The biology of calling behaviour in the Bertha armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae). Ph.D. Thesis, University of Manitoba.
- JOHNSON, C. G. 1969. Migration and dispersal of insects by flight. Methuen, London.
- KASTER, L. V., AND W. B. SHOWERS. 1982. Evidence of spring immigration and autumn reproductive diapause of the adult black cutworm in Iowa. Environ. Ent. 11: 306-12.
- KENDALL, D. M. 1981. Bionomics of *Euxoa auxiliaris* Grote (Lepidoptera: Noctuidae) in the Rocky Mountains and comparison with two resident species of alpine moths. M. Sc. Thesis, University of Colorado.
- KIKUKAWA, S., AND G. M. CHIPPENDALE. 1983. Seasonal adaptations of different geographic populations of the sunflower moth, *Homoeosoma electellum*. J. Insect Physiol. 30: 451-55.
- MCNEIL, J. N. 1986. The true armyworm *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae). A possible migrant species. In D. R. MacKenzie, C. S. Barfield, G. G. Kennedy and R. D. Berger, Eds. The movement and dispersal of agriculturally important biotic agents. Claitor's Publishing Division, Baton Rouge (in press).
- PRUESS, K. P. 1967. Migration of the army cutworm, *Chorizogrotis auxiliaris* (Lepidoptera: Noctuidae). I. Evidence of a migration. Ann. Ent. Soc. America 60: 910-20.
- RABB, R. L., AND G. G. KENNEDY, Eds. 1979. Movement of highly mobile insects: Concepts and methodology in research. North Carolina State University, Raleigh.
- RABB, R. L., AND R. E. STINNER. 1978. The role of insect dispersal in population processes. Pages 3-16 In C. R. Vaughn, W. Wolf and W. Klassen, Eds. Radar, insect population ecology and pest management. NASA Conf. Publ. No. 2070, NASA Wallops Flight Center, Wallops Island, VA.
- RANDOLPH, N. M., G. L. TEETES, AND M. C. BAXTER. 1972. Life cycle of the sunflower moth under laboratory and field conditions. Ann. Ent. Soc. America 65: 1161-64.
- ROSE, D. J. W., W. W. PAGE, C. F. DEWHURST, J. R. RILEY, D. R. REYNOLDS, D. E. PEDGLEY, AND M. R. TUCKER. 1985. Downwind migration of the African armyworm moth, *Spodoptera exempta*, studied by mark-and-capture and by radar. Ecol. Ent. 10: 299-313.
- STINNER, R. E., C. S. BARFIELD, J. L. STIMAC, AND L. DOHSE. 1983. Dispersal and movement of insect pests. Annu. Rev. Ent. 28: 319-35.
- SWIER, R. W. RINGS, AND G. J. MUSICK. 1976. Reproductive behavior of the black cutworm, *Agrotis ipsilon*. Ann. Ent. Soc. America 69: 546-50.
- . 1977. Age-related calling behavior of the black cutworm, *Agrotis ipsilon*. Ann. Ent. Soc. America 70: 919-24.
- TAUBER, M. J., C. A. TAUBER, AND S. MASAKI. 1984. Adaptations to hazardous seasonal conditions: Dormancy, migration and polyphenism. Pages 149-83. In C. B. Huffaker and R. L. Rabb, Eds. Ecological entomology. John Wiley and Sons, New York.
- TEETES, G. L., P. L. ADKISSON, AND N. M. RANDOLPH. 1969. Photoperiod and temperature as factors controlling the diapause of the sunflower moth,

- Homoeosoma electellum*. J. Insect Physiol. 15: 755-61.
- TURGEON, J. J., AND J. N. MCNEIL. 1982. Calling behaviour of the armyworm, *Pseudaletia unipuncta*. Ent. Expt. Appl. 31: 402-8.
- . 1983. Modifications in the calling behaviour of *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae), induced by temperature conditions during pupal and adult development. Canadian Ent. 115: 1015-22.
- WALKER, T. J. 1980. Migrating Lepidoptera: Are butterflies better than moths? Florida Ent. 63: 79-98.
- WEST, R. J., P. E. A. TEAL, J. E. LAING, AND G. M. GRANT. 1984. Calling behavior of the potato stem borer, *Hydraecia micacea* Esper (Lepidoptera: Noctuidae) in the laboratory and the field. Environ. Ent. 13: 1399-1404.

PREZYGOTIC MALE REPRODUCTIVE EFFORT IN INSECTS: WHY DO MALES PROVIDE MORE THAN SPERM?

JAMES S. QUINN* AND SCOTT K. SAKALUK*

SYNOPSIS

Males' incentives for providing benefits to females and/or their offspring are ambiguous during the period prior to zygote formation. The benefits may function to increase the number of available eggs fertilized by a male and/or enhance the production and survival of his offspring. In some cases, male prezygotic investment may be an adaptation to secure fertilizations despite the fact that it incidentally benefits the female or her offspring. More often, the benefits to offspring production and survival are not simply incidental and probably account, in part, for the magnitude of the male investment. Regardless of the adaptive significance of male provided benefits, they typically reduce the females' costs of producing surviving offspring while raising the males' costs. The extent to which provisioning of benefits increases males' costs and decreases females' costs will affect the degree to which females limit male reproduction (or *vice versa*). If male-provided benefits (prezygotic or otherwise) are more costly than female costs of offspring production, reproductively-ready males will act as resources limiting female reproduction. From an evolutionary perspective it is important to consider the effect of male-provided benefits. The primary function of the investment (e.g., to maximize sperm transfer) is irrelevant in terms of the degree to which one sex limits the other's reproduction.

"Women and men move back and forth in between effect and cause. Just beyond the range of normal sight, this glittering joker was dancing in the dragon's jaws"

(B. Cockburn)

During the past two decades there has been considerable interest in Darwin's (1871)

*James S. Quinn is a Ph.D. student at the University of Oklahoma with research interest in behavioral ecology and is currently studying the causes and consequences of sexual size dimorphism in Black Skimmers (*Rynchops niger*) compared with Caspian Terns (*Sterna caspia*). Scott K. Sakaluk is a postdoctoral fellow at the University of Arizona with research interests in insect reproductive behavior and especially the evolution of cricket mating systems. Current addresses: Quinn, Department of Zoology, University of Oklahoma, Norman, OK 73019; Sakaluk, Department of Entomology, University of Arizona, Tucson, AZ 85721.

- Homoeosoma electellum*. J. Insect Physiol. 15: 755-61.
- TURGEON, J. J., AND J. N. MCNEIL. 1982. Calling behaviour of the armyworm, *Pseudaletia unipuncta*. Ent. Expt. Appl. 31: 402-8.
- . 1983. Modifications in the calling behaviour of *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae), induced by temperature conditions during pupal and adult development. Canadian Ent. 115: 1015-22.
- WALKER, T. J. 1980. Migrating Lepidoptera: Are butterflies better than moths? Florida Ent. 63: 79-98.
- WEST, R. J., P. E. A. TEAL, J. E. LAING, AND G. M. GRANT. 1984. Calling behavior of the potato stem borer, *Hydraecia micacea* Esper (Lepidoptera: Noctuidae) in the laboratory and the field. Environ. Ent. 13: 1399-1404.

PREZYGOTIC MALE REPRODUCTIVE EFFORT IN INSECTS: WHY DO MALES PROVIDE MORE THAN SPERM?

JAMES S. QUINN* AND SCOTT K. SAKALUK*

SYNOPSIS

Males' incentives for providing benefits to females and/or their offspring are ambiguous during the period prior to zygote formation. The benefits may function to increase the number of available eggs fertilized by a male and/or enhance the production and survival of his offspring. In some cases, male prezygotic investment may be an adaptation to secure fertilizations despite the fact that it incidentally benefits the female or her offspring. More often, the benefits to offspring production and survival are not simply incidental and probably account, in part, for the magnitude of the male investment. Regardless of the adaptive significance of male provided benefits, they typically reduce the females' costs of producing surviving offspring while raising the males' costs. The extent to which provisioning of benefits increases males' costs and decreases females' costs will affect the degree to which females limit male reproduction (or *vice versa*). If male-provided benefits (prezygotic or otherwise) are more costly than female costs of offspring production, reproductively-ready males will act as resources limiting female reproduction. From an evolutionary perspective it is important to consider the effect of male-provided benefits. The primary function of the investment (e.g., to maximize sperm transfer) is irrelevant in terms of the degree to which one sex limits the other's reproduction.

"Women and men move back and forth in between effect and cause. Just beyond the range of normal sight, this glittering joker was dancing in the dragon's jaws"

(B. Cockburn)

During the past two decades there has been considerable interest in Darwin's (1871)

*James S. Quinn is a Ph.D. student at the University of Oklahoma with research interest in behavioral ecology and is currently studying the causes and consequences of sexual size dimorphism in Black Skimmers (*Rynchops niger*) compared with Caspian Terns (*Sterna caspia*). Scott K. Sakaluk is a postdoctoral fellow at the University of Arizona with research interests in insect reproductive behavior and especially the evolution of cricket mating systems. Current addresses: Quinn, Department of Zoology, University of Oklahoma, Norman, OK 73019; Sakaluk, Department of Entomology, University of Arizona, Tucson, AZ 85721.

theory of sexual selection. In various theoretical discussions, authors have attempted to identify the key variables affecting the operation and intensity of sexual selection (Trivers 1972, Emlen and Oring 1977, Wade and Arnold 1980, Gwynne 1984a, Thornhill in press. At the same time, other studies have investigated the mechanisms through which sexual selection is mediated, specifically, intrasexual competition and mate choice (for a review of these processes in insects see Thornhill and Alcock 1983). These two approaches ask very different questions—what causes sexual selection? *and* what is the function of adaptations that arise through selection processes? In this paper we will adopt Williams' (1966) use of "function" to mean that the characteristic being considered was fashioned by natural selection for the goal attributed to it. When such a relationship is not intended we will use the term "effect" to imply that certain consequences of the characteristic may not necessarily be the goal fashioned by natural selection (see Williams 1966).

Relative parental contribution by the sexes has long been considered a key variable influencing the operation of sexual selection. Bateman (1948) proposed that the unequal energetic expenses of gamete production led to the typical pattern of courtship in animals. He found that in *Drosophila melanogaster*, female reproduction was limited by the number of eggs laid while male reproduction was limited by the number of females inseminated. Thus, females could be viewed as a limiting resource for which males were expected to compete. Females are selected to be more discriminating in their choice of mates because they have more to lose (their initial gametic investment) from mating with a genetically incompatible or otherwise unsuitable mate.

Trivers (1972) provided a more general hypothesis to explain interspecific differences in the operation of sexual selection, proposing that the amount of parental investment by the sexes was the key variable influencing the operation of sexual selection. He defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Trivers concluded that parental investment, measured as a cost to other parenting efforts, ultimately explained sexual differences in such life history variables as age of first breeding, differential mortality, and adult sex ratio, as well as the differences in sex roles during mating.

Insect females typically provide almost all parental investment in their production of eggs. However, in some species parental investment is shared. An example of parental investment by a male insect comes from the work of R. L. Smith (1979a, 1979b, 1980) in his studies of the giant waterbug *Abedus herberti*, and other Belostomatidae. These males provide oviposition sites (on their backs) for the eggs of their mates and provide care for those eggs. Paternal care involves aeration of eggs and brood pumping, a behavior that expedites the escape of young from the egg. This paternal care involves a cost to the male's ability to invest in other offspring because back space is limited. The extra drag associated with swimming while encumbered, as well as brooding behaviors, may increase risks of predation and decrease success at capturing prey (Smith 1979b, 1980). This increased time and risk associated with paternal care excludes encumbered males from mating and apparently affects the operational sex ratio (Emlen and Oring 1977), as well as the courtship roles.

In this paper, we consider costly investments by male insects *before* they fertilize the eggs of females. We investigate the adaptive significance of such prezygotic investments, and examine the impact of these benefits on the operation of sexual selection. We consider the contention that prezygotic male investment is best considered mating effort (Low 1978) and not parental investment. We conclude that from an evolutionary perspective, the effects of the investment, and not the primary function, are the critical factors.

CATEGORIES OF MALE PREZYGOTIC INVESTMENT

Males often minimize their investment in offspring. This is because males produce many energetically inexpensive sperm compared with few expensive eggs produced by females (Bateman 1948). Male reproduction is typically limited by the number of females inseminated, a potentially great number. By providing parental effort rather than seeking other copulations, males potentially experience greater losses of other reproductive opportunities than would females who make additional investments in offspring. Additionally, males may not be certain of the paternity of their mate's offspring and therefore risk investing in the offspring of other males (Thornhill and Alcock 1983). Despite the substantial costs, males of many insect species often provide benefits to females before the females's eggs are fertilized. Such prezygotic investments include:

1. nuptial prey items consumed by the female (Downes 1970, Thornhill 1976a, 1980, 1983 and references).
2. spermatophores and/or accessory gland secretions
 - a. ingested orally by the female (Boldyrev 1927, Alexander and Otte 1967a, Mullins and Keil 1980, Sakaluk and Cade 1980, Gwynne 1981, 1983, 1984b, Bowen *et al.* 1984, Sakaluk 1984, 1985)
 - b. absorbed in the female's reproductive tract (Friedel and Gillott 1977, Boggs and Gilbert 1979, Sivinski 1980a, Boggs 1981, Greenfield 1982, Marshall 1982, Rutowski 1982, Schal and Bell 1982, Markow and Ankney 1984, Pivnick and McNeil ms)
3. secretions from glands other than the accessory glands (Fulton 1915, Mays 1971, Walker 1978, Bell 1980a,b, Bidochka and Snedden 1985)
4. portions of the male's body (Alexander and Otte 1967b, Dodson *et al.* 1983, Hubbell 1985)
5. protection of the female from predators (Sivinski 1980b, 1983)
6. reduction of harassment of the female by other conspecific males (Waage 1979, 1983, Borgia 1981, Wilcox 1984)
7. assistance in the collection of suitable oviposition substrate such as dung or carrion (Klemperer 1983, Tyndale-Biscoe 1984, Wilson and Fudge 1984)
8. provisioning of a burrow in which the female can rear her offspring (Walker 1980, 1983).

Trivers specifically excluded effort spent finding or subduing a mate from his concept of parental investment, except in those cases where such effort affects the survival chances of the offspring. For example, defense of a territory that benefits offspring survival, providing nuptial gifts, and other behaviors providing "incidental" benefits to offspring were included as parental investment. Low (1978) proposed that reproductive effort be divided into two components, mating effort and parental effort. The division and attendant definitions have resulted in a roundabout redefinition of parental investment that stresses the primary function of the investment rather than any effects it might have on offspring survival or production costs.¹

Alexander and Borgia (1979) and Gwynne (1984a) continued to stress the primary function of the components of reproductive effort (Low 1978). The former argued that because males have little control over the fate of their gametes or their mates' uses of prezygotic paternal contributions, such investments would be best considered mating effort. Gwynne (1984a) similarly identified prezygotic reproductive effort by males as mating effort² and suggested a further subdivision to distinguish effort influencing the operation of sexual selection. His "non-promiscuous mating effort" refers to effort providing benefits to offspring or mates at a cost of lost reproductive opportunities, while "promiscuous mating effort" provides no such benefits (Gwynne 1984a). Non-promiscuous mating effort, as defined, is similar to parental investment in its effect on sexual

selection. However, in species where males offer no more than sperm to females, substantial male investment in courtship, guarding, or fighting (promiscuous mating effort) also can influence the operation of sexual selection and lead to male mate choice or even sex role reversal in courtship behavior (Hatzios and Caldwell 1983, Johnson and Hubbell 1984 and references). Furthermore, as mentioned earlier, the classification of such effort as a type of mating effort is based on the primary function of the effort or the "intention" of the male.

These different treatments of prezygotic male reproductive effort can result in the identification of an effort that benefits offspring as either a parental investment (Trivers 1972, Thornhill 1976b, Boggs and Gilbert 1979, Morris 1979, Mullins and Keil 1980, Zeh and Smith 1985) or a mating effort (Alexander and Borgia 1979, Gwynne 1984a, Thornhill *in press*). The basis for this difference is whether male-provided benefits are viewed according to the effect on offspring production or according to the primary function of the investment.

ADAPTIVE SIGNIFICANCE: WHY DO MALES PROVIDE MORE THAN SPERM?

The selective advantages to males providing benefits to mates and offspring include two main categories. First, such investments may increase the number of eggs fertilized by the male's sperm by: a) increased sperm transfer to the female; b) increased utilization of that male's sperm by the female; and/or c) increased number of females inseminated. Second, male-provided benefits may increase the production and survival of offspring. Male-derived selective advantages in the second category would be devalued if some or all of the benefited offspring were fathered by other males².

The evolution of beneficial prezygotic investments by males is more likely in species in which males can provide useful services (e.g., protection from predators) or collect and/or defend resources that potentially limit reproduction. In species where reproduction is limited by protein or nutrients that are contained within the sperm or sperm transfer device, females are expected to digest any materials as long as this does not result in costly infertility of eggs. Thus, particularly in species engaging in multiple mating, females may make use of sperm as a nutritional resource.

Many of the examples of male prezygotic investment provide both increased fertilizations and increased survival or production of offspring. For example, mate guarding by male damselflies and dragonflies increases the male's likelihood of fertilizing eggs, diminishes predation on the mate (and hence her offspring) and increases oviposition by the female by reducing harassment by other males (Waage 1979, 1983). Detailed examples from crickets (Orthoptera: Gryllidae) and katydids (Orthoptera: Tettigoniidae) will help illustrate the functions and effects of male prezygotic contributions.

First consider the adaptive significance of the spermatophylax produced by male decorated crickets. *Grylloides supplicans* (Sakaluk 1984, 1985). In crickets, copulation ends when a male transfers the sperm-containing vessel (spermatophore) to the female. The spermatophore of most cricket species consists of a small sperm-containing ampulla that remains outside the female's body after mating. This ampulla is drained as the sperm enter the female genital tract. Later the female often eats the evacuated spermatophore (Alexander and Otte 1967a, Loher and Rence 1978, Sakaluk and Cade 1980, 1983), but premature removal is prevented by the male who remains with and antennates his mate (Loher and Rence 1978). Interestingly, *G. supplicans* males produce a bipartite spermatophore consisting of the ampulla plus a spermatophylax, a larger gelatinous portion devoid of sperm (Alexander and Otte 1967a, Sakaluk 1984, Sakaluk and O'Day 1984). Immediately after mating, the female removes the easily detached spermatophylax from the ampulla with her mouthparts and begins to feed on it. The time required for a female to consume this nuptial 'meal' completely, increases with

spermatophore weight (Sakaluk 1985). Within several minutes of eating the spermatophylax, the female removes and eats the sperm ampulla and the remaining contents. Thus a male that provides a small spermatophylax will have his ampulla removed sooner than a male providing a larger one. Because the ampulla must be attached for a minimum of about 50 min to be emptied completely of sperm (Sakaluk 1984), males providing under-sized spermatophylaxes will not transfer a full complement of sperm. However, the average time at which females removed sperm ampullae was 52 min, which matches the time required for complete sperm transfer (Sakaluk 1984). Therefore males, on the average, provide females with a nuptial meal no larger than that required to prevent the premature removal of the ampulla. The ease with which the spermatophylax breaks off is important to fulfilling the function of preventing premature removal of the ampulla. Furthermore, male *G. supplicans* are definitely less intense in their post-copulatory interaction with the female than other crickets, which are known to rely on direct contact and antennation for prevention of premature ampulla-removal by females (Loher and Rence 1978). This suggests that the spermatophylax "replaces" contact guarding and that the function of the bipartite spermatophore is to maximize sperm transfer (Alexander and Otte 1967a).

The largest possible sperm transfer is expected to be particularly important in species where sperm from a number of males are mixed in the spermatheca and fertilization success is essentially by lottery (Parker 1970, Sakaluk in press). It appears that the function of the spermatophylax, or more specifically the bipartite nature of the spermatophore, is to ensure the maximum transfer of a male's sperm. There are other possible beneficial *effects* of this nuptial offering, such as increasing production and survival of offspring or inducing a female refractory period (i.e., a period when the female refrains from mating). However, the bipartite spermatophore of *G. supplicans* was not likely designed by natural selection to provide these other possible benefits. There may be additions to the spermatophore that serve those other functions, such as substances included in the spermatophore that promote a female refractory period or that provide nutrition for the young. It appears likely that the evolution of the spermatophylax itself did not require males to reap these extra benefits. Thus, some of these benefits may be incidental to the evolution of the spermatophylax.

The *size* of a spermatophylax represents a continuous variable. Costs of producing a spermatophore are not trivial; in *G. supplicans*, the spermatophore can assume up to about 6% of the male's body weight and males require 3.3 ± 0.1 h for spermatophore replenishment before they can remate (Sakaluk 1985). This may be a considerable cost if mating opportunities are lost during this period of replenishment. In other crickets, males transfer small unipartite spermatophores consisting of a sperm ampulla alone and remate within as little as 15 min (Alexander and Otte 1967a). The costs can be viewed as time or energy, but ultimately as lost reproductive opportunity. These costs are weighed against the benefits—increased likelihood of fertilizing available eggs and increased number of surviving offspring. In *G. supplicans*, secondary benefits to increased spermatophylax size, such as potentially increased production of surviving offspring, may be small. Nevertheless, the determination of the optimal spermatophylax *size* by natural selection involved the balancing of all benefits against all costs.

Research by D. T. Gwynne and colleagues (Gwynne 1984b, Gwynne *et al.* 1984, Bowen *et al.* 1984) on the katydid *Requena verticalis* serves to illustrate the impact of secondary benefits on optimal investment in a continuous character. The bipartite spermatophores produced by males of this species are huge, representing about 20% of male body weight (derived from Table 2 in Bowen *et al.* 1984). Again, females consume the spermatophylax fully before removing and eating the sperm ampulla. However, the spermatophylax in this species is almost twice as large as necessary to protect the ejaculate (Gwynne *et al.* 1984). Protein from the spermatophylax is incorporated into

the batch of eggs produced after the mating (Bowen *et al.* 1984). This suggests that one function of the large spermatophylax is the production of surviving offspring because it is likely that the male providing the spermatophylax fathers those young. Gwynne (1984b) allowed female *R. verticalis* raised on a low protein diet to eat 0, 1, 3 or 7 spermatophylaxes, then recorded numbers and weights of eggs produced. Volumes of sperm and other contents of the ejaculate were held constant between treatments. He found significant increases in both egg weight and egg number produced as a function of increased numbers of spermatophylaxes eaten. While other benefits to males providing large spermatophylaxes might exist, the production of surviving offspring may be important to males. Gwynne (1982) found that when given the choice between two singing male katydids (*Conocephalus nigropleurum*), females always mated with the larger individual. This may represent an adaptive choice since spermatophore size correlated positively with male body weight. The potential role that female choice or the inducement of a refractory period could have played in the evolution of large spermatophylaxes remains to be investigated. Indeed, multiple benefits to male reproduction, some promoting fertilization of eggs and others favoring production of surviving offspring, appear to be responsible for the large spermatophylax produced by *R. verticalis*.

The adaptive significance of benefits provided by males during the prezygotic period may include increases in both fertilization of eggs and production of surviving offspring. The male's cost of providing such benefits is the loss of reproductive opportunity. The arguments by Alexander and Borgia (1979) identifying such investments as mating effort ignore the contributions to offspring production.

PREZYGOTIC BENEFITS AND THEIR INFLUENCE ON SEXUAL SELECTION

Under some conditions the benefits to offspring production and survival provided by males are probably incidental to their attempts to fertilize eggs. For example, mate-guarding from copulation until oviposition by some odonates presumably evolved to protect the male's genetic interests by reducing the competition among his sperm and that of other males. Assuming that benefits of increased fertilization by the male guarding exceed the costs of guarding, the benefits obtained by the female (a period free of harassment by other males during which she can choose a suitable oviposition site; Waage 1983) are probably incidental or secondary from the male's perspective, although this remains to be demonstrated. Because carefully chosen oviposition sites may lead to increased survivorship of young and because male guarding may enable the female to take significantly greater care in selecting her site, the effect of this effort by males could include increased survival of his offspring and reduced female costs for producing surviving young. In some odonates the method of guarding precludes investment by males in other mating attempts, and so limits a male's ability to invest in other offspring. A similar case can be made for mate-guarding that incidentally reduces female predation risk prior to oviposition, as in the stick insect *Diaperomera veliei* (Sivinski 1980b, 1983). Assuming the simultaneous existence of other reproductive opportunities for males, investments of this sort alter the degree to which females limit reproduction, and thus decrease the competition for mates by males.

The distinction in classification of reproductive effort between the prezygotic and postzygotic periods suggested by Alexander and Borgia (1979) is misleading when reproductive effort is viewed in terms of its effect on the degree to which one sex *versus* the other limits reproduction (*sensu* Trivers 1972). Male contributions affecting the production of surviving young during the postzygotic period usually can be seen easily as parental effort (Low 1978). We suggest that the main reason postzygotic investments are easier to understand as parental investment is that in most cases the primary

function is unequivocally for the production and survival of offspring. The primary function of a prezygotic investment does not alter the investment's effect as limiting reproduction. Various types of prezygotic and postzygotic investments involving benefits provided by males reveal that irrespective of their primary functions, the impact on sexual selection's intensity is the same (see Gwynne 1984a). A similar conclusion was reached independently by Zeh and Smith (1985). Increases in male reproductive effort that enhance offspring survival may reduce female costs of producing independent offspring and increase the degree to which female reproduction is limited by the male's ability to provide that effort. This in turn should lead to reduced intensity of sexual selection on males.

Male contributions to offspring do, indeed, influence the operation of sexual selection and affect the courtship roles adopted by male and female insects. In the giant waterbug, *A. herberti*, females are aggressive in courtship, although male display is an essential element of the courtship (Smith 1979b). Sex roles in this species are not completely reversed, probably because the costs of egg production and paternal care are equivalent (Smith 1979b). When parental investments by males and females are equal, theory predicts that the sexes should be equally eager to mate (Trivers 1972). Gwynne's (1981) study of Mormon crickets, *Anabrus simplex*, showed that prezygotic male investments can have an equal or greater impact on sex roles in courtship. During mating, a male *A. simplex* transfers a very large spermatophore that accounts for up to 27% of a male's body weight to the female. Females consume the proteinaceous spermatophylax and then the ampulla after it has been emptied of sperm. Gwynne demonstrated that females compete for access to males whereas males exhibit mate preference, actively rejecting smaller, less fecund, females as potential mates.

CONCLUSION

In some species, males provide "gifts" or services that aid in the production of surviving offspring. These aids to reproduction can be provided before or after zygote formation. During the prezygotic period the function of such investments may be exclusively to increase male success at fertilizing eggs. This is more likely to be the case for discrete adaptations such as a bipartite spermatophore. Continuous traits such as the size of a spermatophore represent a compromise between the benefits (increased number of eggs fertilized and increased number of sired offspring surviving) and the costs (lost reproductive opportunities).

The primary *function*, or "intention", of male reproductive effort has no bearing on the operation of sexual selection (i.e., the direction and intensity of the selection). Instead, what matters is the *effect* of that effort on the degree to which males *versus* females limit reproduction. We suggest that the classification of components of reproductive effort according to the "intentions" of the investor, or the primary function of the investment, should be avoided. The identification of function is operationally difficult, and the exclusion of "incidental" effects may result in erroneous conclusions. Furthermore, we suggest that the original concept of parental investment (*sensu* Trivers 1972) is most suitable for understanding the relationship between parental investment and sexual selection.

ACKNOWLEDGMENTS

We thank James E. Lloyd for inviting us to participate in the Insect Behavioral Ecology Symposium. The Florida Entomological Society and the University of Oklahoma Zoology Department and Graduate College provided travel funds so that one of us (JSQ) could present the oral version of this paper. We are grateful to Todd A. Crowl,

Katherine D. Graham, Douglas W. Mock, Patricia L. Schwagmeyer, and John Sivinski for helpful comments on the manuscript. Randy Thornhill and David Zeh and Robert L. Smith graciously provided copies of manuscripts that were *in press*. J. S. Q. was supported by a Welder Wildlife Foundation Fellowship during the writing of this paper. Page charges were met, in part, by a NSERC operating grant (4946) to Glenn K. Morris.

APPENDIX

1. The concept of parental investment has become obfuscated. Low (1978) divided reproductive effort into two components, mating effort and parental effort. She defined mating effort as "any expenditure of nutrient or effort or taking of risks to secure matings." Parental effort was defined as "any expenditure of nutrient or effort or taking of risks in the production and raising of offspring or other kin." This divides reproductive effort according to the function of the effort (for mating or for production and raising of offspring) and removes the emphasis from the effect of the investment on production and survival of offspring. Furthermore, effort with multiple functions would be classified according to the primary function alone. In this scheme, incidental benefits to offspring production and survival are neglected. Despite the apparent inconsistency of this classification with that of Trivers (1972), Low considered parental investment to be that portion of parental effort received by an individual offspring.
2. Gwynne (1984a) also suggested that postzygotic investment by males could function as mating effort. Regarding the egg-brooding of male waterbugs, he stated "As long as there is space available for eggs on a male's back (there is some evidence that male backs are a limiting resource for females; Smith 1979a), the investment can be considered ME involved in advertising the male's parental abilities that may aid in the acquisition of matings with other egg-laden females." There are two problems with this interpretation. First, if the possession of eggs functions as a signal attracting other mates, "unattractive" males lacking eggs might be expected to accept eggs without requiring copulations. Males apparently do not allow oviposition on their backs unless they have just copulated with the ovipositing female (Smith 1979a, b). Furthermore, a partially egg-laden male must have been able to obtain at least one mating without having any eggs on his back. If egg-brooding functioned as a signal of a male's quality, it is not clear why a male would employ the signal if he were able to obtain matings without it, especially given its obvious costs. Second, that females exploit information made available to them by egg-brooding males, thereby allowing females to make optimal mate choices, could be an incidental effect of the behavior (see Otte's 1974 distinction between the evolved function and incidental effects of 'signals'). Gwynne (1984a) did concede that paternal care exhibited by *A. herberti* after the male is completely encumbered functions to increase the survival of the young.
3. Because females can store sperm and mate with more than one male, parentage is less certain for male than for female insects of many species. If benefit-providing males enjoy increased certainty of paternity over males that fail to provide benefits, then the degree of paternal certainty will affect the level of investment favored by natural selection. Whether or not males provide benefits is determined by natural selection according to the net benefits of available options (e.g., whether to provide benefits, and if so, to what extent). Males who provide benefits may experience enhanced offspring survival, and/or increased mate attraction and/or increased probability of fertilization of eggs, hence increased certainty of paternity (Zeh and Smith 1985). The cost of providing benefits may be the loss of other mating opportunities. Males that do not provide benefits may experience increased mating opportunities, but may have reduced offspring survival, and/or probability of mate attraction, and/or certainty of paternity.

LITERATURE CITED

- ALEXANDER, R. D. AND G. BORGIA. 1979. On the origin and basis of the male-female phenomenon. Pages 417-440 in M. S. Blum and N. A. Blum eds. Sexual selection and reproductive competition in insects. Academic Press, New York.
- , AND D. OTTE. 1967a. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Misc. Publ. Zool. Univ. Michigan. 133: 1-62.
- , AND ———. 1967b. Cannibalism during copulation in the brown bush cricket, *Hapithus agitator* (Gryllidae). Florida Ent. 50: 79-87.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2: 349-368.
- BELL, P. D. 1980a. Multimodal communication by the black-horned tree cricket, *Oecanthus nigricornis* (Walker) (Orthoptera: Gryllidae). Canadian J. Zool. 58: 1861-1868.
- . 1980b. Opportunistic feeding by the female tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae). Canadian Ent. 112: 431-432.
- BIDOCHKA, M. J., AND W. A. SNEDDEN. 1985. Effect of nuptial feeding on the mating behaviour of female ground crickets. Canadian J. Zool. 63: 207-208.
- BOGGS, C. L. 1981. Selection pressures affecting male nutrient investment at mating in heliconiine butterflies. Evolution 35: 931-940.
- , AND L. E. GILBERT. 1979. Male contribution to egg production in butterflies. Science 206: 83-84.
- BOLDYREV, B. T. 1927. Copulation and spermatophores of *Gryllomorpha dalmatina* (Oesk.) (Orth. Gryllidae). Eos 3: 279-288.
- BORGIA, G. 1981. Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. Anim. Behav. 29: 71-80.
- BOWEN, B. J., C. G. CODD AND D. T. GWYNNE. 1984. The katydid spermatophore (Orthoptera: Tettigoniidae): male nutritional investment and its fate in the mated female. Australian J. Zool. 32: 23-31.
- DARWIN, C. 1871. The descent of man and selection in relation to sex. John Murray, London.
- DODSON, G. N., G. K. MORRIS, AND D. T. GWYNNE. 1983. Mating behavior of the primitive Orthopteran genus *Cyphoderris* (Haglidae). In D. T. Gwynne and G. K. Morris, eds., Orthopteran mating systems: sexual competition in a diverse group of insects. Westview Press, Boulder, CO.
- DOWNES, J. A. 1970. The feeding and mating behaviour of the specialized Empidinae (Diptera): observations on four species of *Rhamphomyia* in the high arctic and a general discussion. Canadian Ent. 102: 769-791.
- EMLEN, S. T. AND L. W. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.
- FRIEDEL, T., AND C. GILLOTT. 1977. Contribution of male-produced proteins to vitellogenesis in *Melanoplus sanguinipes*. J. Insect Physiol. 23: 145-151.
- FULTON, B. B. 1915. The tree crickets of New York: life history and bionomics. Tech. Bull. New York Agric. Exp. Stn. 42. 47 pages.
- GREENFIELD, M. D. 1982. The question of paternal investment in Lepidoptera: male-contributed proteins in *Plodia interpunctella*. Int. J. Invert. Reprod. 5: 323-330.
- GWYNNE, D. T. 1981. Sexual difference theory: Mormon crickets show role reversal in mate choice. Science 213: 779-780.
- . 1982. Mate selection by female katydids (Orthoptera: Tettigoniidae), *Conocephalus nigropleurum*. Anim. Behav. 30: 734-738.
- . 1983. Male nutritional investment and the evolution of sexual differences in Tettigoniidae and other Orthoptera. In D. T. Gwynne and G. K. Morris, eds., Orthopteran mating systems: sexual competition in a diverse group of insects. Westview Press, Boulder, CO.
- . 1984a. Male mating effort, confidence of paternity and insect sperm competition. Pages 117-149 In R. L. Smith ed., Sperm competition and the evolution of animal mating systems. Academic Press, New York.

- . 1984b. Courtship feeding increases female reproductive success in bushcrickets. *Nature* 207: 361-363.
- , B. J. BOWEN, AND C. G. CODD. 1984. The function of the katydid spermatophore and its role in fecundity and insemination (Orthoptera: Tettigoniidae). *Australian J. Zool.* 32: 15-22.
- HATZIOLOS, M. E., AND R. L. CALDWELL. 1983. Role reversal in courtship in the stomatopod *Pseudoquilla Ciliata* (Crustacea). *Anim. Behav.* 31: 1077-1087.
- HUBBELL, T. H. 1985. Unfinished business and beckoning problems. *Florida Ent.* 68: 1-10.
- JOHNSON, L. K., AND S. P. HUBBELL. 1984. Male choice. Experimental demonstration in a brentid weevil. *Behav. Ecol. Sociobiol.* 15: 183-188.
- KLEMPERER, H. G. 1983. The evolution of parental behaviour in Scarabaeinae (Coleoptera, Scarabaeidae): an experimental approach. *Ecol. Ent.* 8: 49-59.
- LOHER, W., AND B. RENCE. 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. *Z. Tierpsychol.* 46: 225-259.
- LOW, B. S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. *American Natur.* 112: 197-213.
- MARKOW, T. A., AND P. F. ANKNEY. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. *Science* 224: 302-303.
- MARSHALL, L. D. 1982. Male nutrient investment in the Lepidoptera: what nutrients should males invest? *American Nat.* 120: 27-35.
- MAYS, D. L. 1971. Mating behavior of nemobiine crickets—*Hygronemobius*, *Nemobius* and *Pteronemobius* (Orthoptera: Gryllidae). *Florida Ent.* 54: 113-126.
- MORRIS, G. K. 1979. Mating systems, paternal investment and aggressive behavior of acoustic Orthoptera. *Florida Ent.* 62: 9-17.
- MULLINS, K. E. AND C. B. KEIL. 1980. Paternal investment of urates in cockroaches. *Nature* 283: 567-569.
- OTTE, D. 1974. Effects and functions in the evolution of signaling systems. *Ann. Rev. Ecol. & Syst.* 5: 385-417.
- PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525-567.
- PIVNICK, K. A., AND J. N. MCNEIL. manuscript. Puddling in butterflies: sodium affects *Thymelicus lineola* mating success.
- RUTOWSKI, R. L. 1982. Mate choice and lepidopteran mating behavior. *Florida Ent.* 62: 72-82.
- SAKALUK, S. K. 1984. Male crickets feed females to ensure complete sperm transfer. *Science* 223: 609-610.
- . 1985. Spermatophore size and its role in the reproductive behaviour of the cricket, *Grylloides supplicans* (Orthoptera: Gryllidae). *Canadian J. Zool.* 63: 1652-1656.
- . 1986. Sperm competition and the evolution of nuptial feeding behavior in the cricket, *Grylloides supplicans* (Walker) *Evolution* (in press).
- , AND W. H. CADE. 1980. Female mating frequency and progeny production in singly and doubly mated house and field crickets. *Canadian J. Zool.* 58: 404-411.
- , AND ———. 1983. The adaptive significance of female multiple matings in house and field crickets. *In* D. T. Gwynne and G. K. Morris, eds., *Orthopteran mating systems: sexual competition in a diverse group of insects*. Westview Press, Boulder, CO.
- , AND D. H. O'DAY. 1984. Hoechst staining and quantification of sperm in the spermatophore and spermatheca of the decorated cricket, *Grylloides supplicans* (Orthoptera: Gryllidae). *Canadian Ent.* 116: 1585-1589.
- SCHAL, C., AND W. J. BELL. 1982. Ecological correlates of paternal investment of urates in a tropical cockroach. *Science* 218: 170-172.
- SIVINSKI, J. 1980a. Sexual selection and insect sperm. *Florida Ent.* 63: 99-111.
- . 1980b. The effects of mating on predation in the stick insect *Diaperomera veliei* Walsh (Phasmatodea: Heteronemiidae). *Ann. Ent. Soc. America* 73: 553-556.

- . 1983. Predation and sperm competition in the evolution of coupling durations, particularly in the stick insect *Diaperomera veliei*. In D. T. Gwynne and G. K. Morris eds., Orthopteran mating systems: sexual competition in a diverse group of insects. Westview Press, Boulder, CO.
- SMITH, R. L. 1979a. Repeated copulation and sperm precedence: paternity assurance for a male brooding water bug. *Science* 205: 1029-1031.
- . 1979b. Paternity assurance and altered roles in the mating behaviour of a giant water bug, *Abedus herberti* (Heteroptera: Belostomatidae). *Anim. Behav.* 27: 716-725.
- . 1980. Evolution of exclusive postcopulatory paternal care in the insects. *Florida Ent.* 63: 65-78.
- THORNHILL, R. 1976a. Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *American Nat.* 110: 529-548.
- . 1976b. Sexual selection and paternal investment in insects. *American Nat.* 110: 153-163.
- . 1980. Competitive, charming males and choosy females: was Darwin correct? *Florida Ent.* 63: 5-30.
- . 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *American Nat.* 122: 765-788.
- . *in press*. Relative parental contribution of the sexes to their offspring and the operation of sexual selection. In M. Nitecki and J. Kitchell, eds., *Evolution of behavior*. University of Chicago Press, Chicago.
- , AND ALCOCK. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-179. In B. Campbell ed., *Sexual selection and the descent of man, 1871-1971*. Aldine-Atherton, Chicago.
- TYNDALE-BISCOE, M. 1984. Adaptive significance of brood care of *Copris diversus* Waterhouse (Coleoptera: Scarabaeidae). *Bull. Ent. Res.* 74: 453-461.
- WAAGE, J. K. 1979. Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.* 6: 147-154.
- . 1983. Sexual selection, ESS theory and insect behavior: some examples from damselflies (Odonata). *Florida Ent.* 66: 19-31.
- WADE, M. J., AND S. J. ARNOLD. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. *Anim. Behav.* 28: 446-461.
- WALKER, T. J. 1978. Post-copulatory behavior of the two-spotted tree cricket, *Neoxabea bipunctata*. *Florida Ent.* 61: 39-40.
- . 1980. Reproductive behavior and mating success of male short-tailed crickets: differences within and between demes. *Evol. Biol.* 13: 219-260.
- . 1983. Mating modes and female choice in short-tailed crickets (*Anurogryllus arboreus*). In D. T. Gwynne and G. K. Morris, eds., *Orthopteran mating systems: sexual competition in a diverse group of insects*. Westview Press, Boulder, CO.
- WILCOX, R. S. 1984. Male copulatory guarding enhances female foraging in a water strider. *Behav. Ecol. Sociobiol.* 15: 171-174.
- WILLIAMS, G. C. 1966. *Adaptation and natural selection*. Princeton Univ. Press, Princeton.
- WILSON, D. S., AND J. FUDGE. 1984. Burying beetles: intraspecific interactions and reproductive success in the field. *Ecol. Ent.* 9: 195-203.
- ZEH, D. W., AND R. L. SMITH. 1985. Paternal investment by terrestrial arthropods. *American Zool.* 25: 785-805.

A REVIEW OF TOOL USE IN INSECTS

JOHN D. PIERCE, JR.*

SYNOPSIS

The category of tool use, like many scientific concepts, is elusive and difficult to define precisely. This paper considers several major attempts to define tool use, discusses the problems associated with delineating this category, and advances a definition which classifies tool use as "the active external manipulation of a moveable or structurally modified inanimate environmental object, not internally manufactured for this use, which, when oriented effectively, alters more efficiently the form, position, or condition of another object, another organism, or the user itself." On the basis of this definition, eight instances of insect behavior are categorized as tool use and reviewed. Problems of definitional boundaries and the resulting differences in classification are discussed.

A REVIEW OF TOOL USE IN INSECTS

A consideration of tool-using behavior must necessarily begin with the problem of defining tool use in animals. Hall (1963), in one of the initial reviews of this behavior, viewed tool use as "the use by an animal of an object or of another living organism as a means of achieving an advantage . . . The mediating object is required by definition to be something extraneous to the bodily equipment of the animal, and its use allows the animal to extend the range of its movement or to increase their efficiency" (p. 479). van Lawick-Goodall (1970) defined tool use more narrowly: Tool use is "the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal" (p. 195). Alcock (1972) has provided a definition most commonly accepted: Tool use is "the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the form or position of some separate object" (p. 464).

These attempts at definitions raise a few key issues involved in determining what constitutes tool use. First, should the use of "another living organism" be classified as tool use? Hall's definition includes this behavior, while van Lawick-Goodall's and Alcock's do not. At issue here are such diverse behaviors as agonistic buffering in primates (Whiten & Rumsey 1973, Strum 1983), an ant crossing a streamlet over a bridge of linked fellow ants, or the use of conspecifics as "gluing mechanisms" by weaver ants (Beck 1980). Kummer (1982) has proposed the term "social tools" to account for the use of conspecifics as tools and this terminology provides a useful distinction between social tools and mechanical tools.

Another problem concerns the nature of these tools. Hall and van Lawick-Goodall both limit tool use to the use of an external object. Alcock does similarly with his requirement that the tool be "an inanimate object, not internally manufactured". This requisite excludes the use of attached parts of the user's body as tool use and rightly so. Morphological adaptations must necessarily be excluded to preserve the meaningfulness of the category of tool use. Otherwise, valid cases could be made for any manipulation of a body part as tool use. For instance, the use of a tail by an Old World monkey

*Author is a graduate student in psychology at the University of Florida. His research is under the guidance of Donald A. Dewsbury and focused on mammalian reproductive behavior. Address: Department of Psychology, University of Florida, Gainesville, Florida 32611. This paper is based on a term paper written for Insect Behavior (ENY 6451), a graduate level course at the Dept. of Entomology and Nematology, University of Florida, Florida Agric. Exp. Sta. J. Series No. 7067.

to obtain objects otherwise out of reach is not a bona fide instance of tool use, although attempts have been made to label this behavior as such (Karrer 1970, Erwin 1974). Likewise, web construction by a spider, repulsion of an attack by the spray of a skunk, and nuptial gifts by some male empidid flies (empty silken balls composed solely of bodily secretions—Thornhill and Alcock 1983) are excluded. Again, these are physiological adaptations whose inclusion in this category makes further exclusions seem arbitrary. If these adaptations are included, why not scent marking or pheromones or even salivation (as a tool for food use)? At this point, the category of tool use becomes meaningless.

However, there are instances in which the use of internally-manufactured objects may qualify as tool use. Harcourt (1981) has proposed that washing of the hands and feet with urine may facilitate grip in galago species. Chimpanzees and other primates throw feces in an attempt to repel intruders (Beck 1980). Loehrl (1983) reported "well-aimed" defecation in the fieldfare as an attack strategy against potential predators. Which of these behaviors, if any, should be classified as tool-using behaviors?

Beck (1980) has provided a rather tortuous, complex definition in an attempt to negotiate the above concerns. His definition of tool use is "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (p. 10). This definition allows for fine discriminations in categorizing tool-using behaviors. For instance, the definition includes the Egyptian vulture opening an egg by dropping stones on the egg, but excludes a herring gull opening a mussel by dropping the mussel on stones. Further, this definition allows for aimed throwing of feces as tool use, but not aimed defecation.

Beck's definition, like Hall's, categorizes social manipulation of others (such as agonistic buffering) as tool use, but this allows for other social behaviors which clearly do not comprise tool-using behavior. For example, a female water strider can forage effectively "only by carrying a copulating male who apparently repels copulatory attempts by other males" (Wilcox 1984, p. 171). Female water striders foraging singly recopulated within 10 minutes and continued to forage in 61% of trials. By Beck's definition, the copulating male constitutes tool use by the female. Further, in some insect species, females copulate with a second male to replace the sperm of a genetically inferior male (e.g., a mate that fails to guard). In these cases, copulation with the second male meets Beck's criterion for tool use, although this classification is questionable at best. This problem can only be satisfactorily resolved by elimination of social manipulations from the category of "tool use". In this respect, Kummer's (1982) classification of social tools is useful as a separate but complementary class of behaviors.

Components of the above definitions can be juxtaposed and modified to form a definition which, while retaining the discriminability of Beck (1980), also excludes problematical classifications of tool use, such as social tools. Tool use can thus be defined as follows:

Tool use is the active external manipulation of a moveable or structurally modified inanimate environmental object, not internally manufactured for this use, which, when oriented effectively, alters more efficiently the form, position, or condition of another object, another organism, or the user itself.

This definition is similar to Beck's criterion but differs in two important respects. First, this definition restricts tools to inanimate objects and excludes occurrences of social tool use. Second, this definition allows for the classification of nest and burrow building (but not web building) as instances of tool use, whereas Beck's definition excludes these behaviors. This inclusion is controversial but, I argue, necessary given the elaborate construction and crucial functions served by these structures (thermoregulation, de-

fense, raising of the young, etc.). McFarland (1981), among others, has provided an argument against this inclusion:

. . . to regard the nest material as a tool for making a nest would be like calling knitting-wool a tool for making a garment. Most biologists would distinguish between the material being manipulated and the means by which the material is manipulated. Knitting-needles are normally regarded as tools, but not knitting-wool. (p. 575).

In defense of including nest building as tool use, I argue that another distinction is necessary—the result of the material being manipulated. A human wearing the knitted sweater (or covering himself with the knitted blanket) is using this object as a tool. Likewise, an animal using the nest as a thermoregulatory device or a defense mechanism is also employing this object as a tool. Further, field evidence clearly establishes the efficacy and necessity of these structures to the survival of the organism via reduction of energy requirements, increased protection against predators, and so on. These constructions represent adaptations in response to strong selection pressures. Thus, the use of nests and burrows will be considered as tool-using behavior, when these structures serve a necessary function and improve the efficiency of the organism's behavior in some manner.

EXAMPLES OF TOOL USE IN INSECTS

Documented cases of tool use in insects are rare when evaluated by the strict requirements of the present definition. These cases can be divided into eight main categories.

1) FOOD TRANSPORTATION

This behavior has been reported for several species of ants. Morrill (1972), in the initial paper to report this behavior, noted that Florida harvester ants (*Pogonomyrma badius*) when confronted with a liquid food source dropped small pellets of sand into the food and then carried the food-absorbed sand back to the nest. Tanaka and Ono (1978) noted the same behavior in Japanese ants (*Aphaenogaster famelica*), and Fellers and Fellers (1976) described a similar behavior for four species of myrmicine ants (*Aphaenogaster rudis*, *A. treatae*, *A. tennesseensis*, and *A. fulva*).

When individuals of *A. rudis* reached a sample of bait, they would leave after 5 to 60 seconds and return with pieces of leaves which they then placed on the jelly. As leaf fragments accumulated, ants from the same colony tended them, adjusting the positions of the leaves or sometimes pulling the leaves off completely and repositioning them. By individually marking ants with small spots of paint, we were able to determine that a given individual may bring several leaves and that ants tend leaves brought by other ants.

After 30 to 60 minutes, ants began to remove leaves from the bait and carried them directly back to the colony, once as far as 152 cm. These leaves were visibly covered with jelly, and we suggest that the ants are using these leaves as tools to transport large quantities of food: (p. 70).

Ants in the study preferentially used mud chunks for food transportation, but also employed pine needles, small sections of dry decaying wood, and leaf fragments. Foods transported included not only jelly, but also rotten fruit pulp and body fluids of a dead spider and coleopteran larvae. An ant worker, by using tools, can transport "an amount of food approximately equaling its body weight back to the colony" (Fellers & Fellers 1976, p 72).

McDonald (1984) questioned the veracity of labelling this behavior as tool use by

arguing that throwing soil on a liquid substance may be solely a reflexive response to a potentially nest threatening liquid. Accordingly, he placed petri dishes of water and honey water at different distances from the nest. Within 2.13 m of the nest, ants placed soil in each liquid but returned only the honey water soil to the nest. Beyond 2.13 m, only honey water produced soil-soaking behavior and transportation back to the nest. These results argue against the nest protection hypothesis and for a tool-using explanation.

2) SOIL/STONE DROPPING

Two species of ants perform a similar behavior in response to potential competitors. Moglich and Alpert (1979) observed dolichoderine ants (*Conomyrma bicolor*) surround the nests of ant competitors and drop small pebbles and other objects down the entrances. This stone dropping behavior produced an almost complete cessation of foraging by the competing colony and thus was an effective interfering behavior by the dolichoderine ants.

Schultz (1982) observed a similar behavior in pavement ants (*Tetramorium caespitum*) in response to the ground-nesting alkali bee (*Nomia melanderi*). Schultz describes a typical sequence:

When the ant found an entrance to a bee nest, it usually went into the hole unless the entrance was blocked by a bee. . . . Upon discovering the bee, the ant normally paused several seconds at the rim of the nest, then wandered over the surrounding area, picked up a small piece of soil, or dislodged one from the crusted soil surface. After obtaining a piece of soil, the ant headed straight back to the nest entrance, held the soil over the entrance . . . , hesitated for about 1 second, and then dropped the soil. The ant then waited there for several seconds before going quickly for another piece of soil.

Other ants usually arrived at the nest entrance and joined the first ant in dropping soil. Occasionally the bee responded to these attacks by coming near the surface and lunging at the ants with its mandibles. However, a bee was never observed successfully grasping an ant. Instead these attacks only excited the ants and intensified their soil-dropping behavior. (p. 278).

This behavior was solely a function of the presence of the bee. Unoccupied holes were investigated but soil dropping behavior did not occur. Further, this behavior most frequently resulted in the death of the bee as it attempted to leave the hole. An attack ensued and typically led to the death of the bee. It is interesting to note that a different population of pavement ants used the same behavior in an attack on a halictid bee (*Lasioglossum zephyrum*) although the death of the bee was not a consequence (Lin 1964-1965).

3) SAND THROWING

The ant-lion, larvae of neuropteran flies, constructs a funnel-shaped pit to entrap prey (see STRUCTURE BUILDING below). Worm-lions, larvae of *Vermileo* and *Lampromyia* dipteran flies, do similarly. Prey captured in these pits are grasped, dragged beneath the soil, and consumed. Prey able to elude the initial grasp attempt to escape the pit by climbing the side, eliciting sand throwing by the ant-lion or worm-lion. Sand throwing is accomplished by quick dorsiflexion of the head and mandibles, resulting in a shower of sand aimed at the escaping prey which hinders its escape or knocks it back into the pit (Wheeler 1930). Worm-lions further throw sand at approaching prey, sometimes succeeding in knocking this prey into the pit.

4) NEST CLOSURE

Female sphecine wasps of the genera *Ammophila* and *Sphex* sometimes use tools in closing the burrow or nest in which eggs and a prey have been placed. The female selects pebbles or pellets with which to close the burrow, and then

. . . the major pellet is placed deep in the burrow and additional, smaller objects are placed above it. Sometimes these pellets are pulverized with blows of the head, and on some occasions the female uses a pebble in the manner of a hammer to pound the fill into a compact plug. (Evans & Eberhard 1970, p. 85)

The tool is typically held in the mandibles for pounding. In addition to pebbles, "clods of earth, bits of twig, bark, seeds, and the tarsus and tibia of what appeared to be a locust have been observed to be used for pounding" (Beck 1980, p. 17).

5) CAMOUFLAGE/BAIT AND CAPTURE

McMahan (1982, 1983a, 1983b) has furnished a fascinating account of tool use in the assassin bug *Salyavata variegata* of Costa Rica. *S. variegata* nymphs feed upon termites and use tools to aid in prey capture. This bug uses tools in two ways; to provide camouflage, and to "bait" termites for capture.

Termite nests are constructed from a hardened anal secretion called carton. The nymphal *S. variegata* coats itself with carton crumbs scraped from the termite nest and thus camouflages itself. "The crumbs are patted onto the body surface, which is covered with glue-secreting setae . . . The camouflage effectively conceals the bug from would-be predators that hunt visually, as well as preventing its detection during tactile and olfactory examination by its blind prey" (McMahan 1983b, p. 483). Use of this camouflage enables the bug to capture a termite prey, which is then killed by a paralytic toxin and consumed by a sucking behavior, leaving only a hollowed carcass. The hollowed carcass is then used to lure other termites closer, a tactic McMahan labeled as a "bait and capture" strategy:

The bug, still holding the carcass in front of its head with its forelegs, moves back to the breach which is being repaired. It slowly pushes the carcass into the opening, jiggling it slightly in a movement that may be described as "tantalizing", while remaining effectively insulated from the termites. Usually one or more of the workers will try to seize the carcass with their mandibles and pull it into the hole. Occasionally a worker succeeds in wresting the carcass from the bug and carries it into the nest interior. Usually, however, the bug pulls the grasping worker steadily backward, and draws it slowly from the nest. When the worker's head is in an accessible position, the bug grasps it quickly with its forelegs and continues to back away from the hole. Insertion of the beak and ingestion of the body fluids soon follow. The carcass that had been used in baiting is dropped as soon as the fresh prey has been seized. (McMahan 1982, p. 349).

In one episode, McMahan witnessed one nymph successfully bait and capture 31 worker termites within three hours, finally quitting with a distinctly distended abdomen!

6) DEFENSE BY A FECAL SHIELD

The larva of the *Cassida rubiginosa* beetle carries a "fecal shield" above its back and uses this tool in defense against potential predators (Eisner et al. 1967). This shield is a packet consisting of "the molted skins previously shed by the larva, together with the dried remains of its accumulated fecal wastes" (p. 1471) and held in a raised position above the back by a two-pronged fork projecting from the tip of the abdomen. Immediate defensive positioning of the shield was elicited by experimental prodding of the larva. In tests of larvae exposed to ant attacks, the shield was maneuvered in the

direction of the attacking ant and was successful in repelling the ant attack in all but one of "several dozen encounters" (p. 1473). The lone exception occurred when a larva was fatally bitten before the shield was mobilized. Experimental removal of the fecal shield left a defenseless larva, one highly vulnerable to attacking ants.

7) SOUND BAFFLE

Tree crickets of the *Oecanthus* species employ a calling song to attract mates. *O. burmeisteri* are able to increase the effectiveness of this behavior through the construction and use of a tool. *O. burmeisteri* males gnaw a small hole in a leaf, then orient so that the front of the body and the front legs rest on the upper surface of the leaf. Stridulation in this position results in a greater sound amplitude than stridulation without this tool (Prozesky-Schulze et al. 1975). The leaf acts as a baffle to prevent destructive interference of the signal (Forrest 1982) and, consequently, to increase the sound amplitude produced by stridulation. It should be noted that this behavior, the effective use of a tool, would not be so classified under Beck's (1980) definition because the leaf is neither "unattached" nor held or carried by the user. Yet this behavior is effective in attracting females through sound amplitude and used by virtually all male singers (Prozesky-Schulze et al. 1975).

8) STRUCTURE BUILDING

Many insect species fashion structures (burrows, nests, etc.) that serve a multiplicity of function. An exhaustive review of this behavior is beyond the scope of this paper, but a few examples merit mention. Evans and Eberhard (1970) classified wasps' nests into certain types and noted that nests of these species range from minor modifications of pre-existing cavities to constructions composed of mud or plant materials. Their use as a subterranean birth place for the young has already been noted. Eumenid wasps, in nest construction, often carry water to the nesting site which is used to soften the earth before digging (Evans & Eberhard 1970). Further, an Australian eumenid of the genus *Paralastor* builds a complex funnel as the opening to the nest. The funnel apparently functions to keep out parasitic wasps while the nest is constructed. The funnel is destroyed following nest closure (Barnett 1981).

Worm-lions and ant-lions, as discussed above, excavate a funnel-shaped pit in which prey are captured. Lucas (1982) performed a biophysical analysis of pit construction by ant-lion larvae (specifically *Myrmeleon crudelis*) and found that both the physical properties of the sand (the angle of repose and Stoke's drag force) and ant-lion behavior (trajectory angle of throw, regulation of particle velocity) increase the number of fine particles on the pit walls and therefore enhance the prey capture efficiency of the structure by making escape more difficult.

The hive of the honey bee (*Apis mellifera*), in addition to maintaining group cohesion and keeping out enemies, provides thermoregulatory aid as well. The honeybee hive retains heat and moisture and, during winter, can maintain a temperature differential as great as +59°C (Wilson 1975). This differential is maintained by the construction and position of the nest and the body heat and behavior of the workers (Wilson 1971). During the summer, bees cool and provide moisture in the hive by bringing in water in response to high temperatures.

The thermoregulatory properties of the insect nest is well illustrated by the mosaic nests of termites. The complexity of the nests of *Macrotermes* termites of Africa in particular attest to this function:

The labyrinthine internal structure of these termitaries has been designed in the course of evolution to guide a regular flow of air from the central fungus gardens, where it is heated and rises by convection, upward and outward to a flat,

peripheral system of capillarylike chambers, where it is cooled and freshened by proximity to the outside air. In *M. natolensis* the architecture is so efficient that the temperature within the fungus garden remains within one degree of 30°C and the carbon dioxide concentration varies only slightly, around 2.6 percent. (Wilson 1975, pp. 11-12).

The burrows of male mole crickets (*Gryllotalpa* species) serve a unique function: Their design increases the calling male's acoustical output (Bennet-Clark 1970). *G. vineae*, in particular, constructs a shallow two-exit burrow which acts like an acoustic horn, increasing the conversion of muscle action into sound by over 30%. The design also acts to provide directionality as well. The burrows of two *Scapteriscus* species of mole crickets perform a similar role with acoustical output increased as a result of calling from the entrance of the burrow (Nickerson et al. 1979).

DISCUSSION

At the onset of this paper, problems of defining tool-use behavior and attempts to satisfy these intricacies were presented and critiqued. I recognize that the definition put forth currently may not hurdle all obstacles to the satisfaction of every reader. Accordingly, Table 1 lists the behavioral examples presented in this paper and their classification based on other definitions. Readers are invited to judge for themselves which definition best encapsulates their view of tool-using behavior.

As Table 1 indicates, there is general agreement of the classification of tool-using

TABLE 1. CLASSIFICATION OF TOOL USE BY FOUR DEFINITIONS

Behavior	Van Lawick-Goodall(1970)	Alcock (1972)	Beck (1980)	Pierce (1986)
Weaver ants using conspecifics as gluing mechanisms	N	N	Y	N
Ants crossing a streamlet over a bridge of linked fellow ants	N	N	N	N
Nuptial gifts by male empidid flies (composed of bodily secretions)	N	N	Y	N
Foraging female water striders while copulating	N	N	Y	N
Use of sand/soil for food transportation by ant	Y	Y	Y	Y
Soil/stone dropping behavior by <i>Conomyrma</i> and <i>Tetramorium</i> ants	Y	Y	Y	Y
Sand throwing by ant-lion and worm-lion	Y	Y	Y	Y
Nest Closure by <i>Ammophila</i> and <i>Sphex</i> wasps	Y	Y	Y	Y
Camouflage/Bait and capture by the assassin bug	Y	Y	Y	Y
Fecal shield defense by <i>Cassida rubiginosa</i>	Y	Y	Y	Y
Sound baffle use by <i>Oecanthus</i> crickets	Y	Y	N	Y
Structure building by many species	N	N	N	Y

behavior with exceptions primarily resulting from subtleties of definition. Distinctions established may appear trivial at times, and boundaries of definition may be perceived as artificial. The claim of artificiality of boundaries may be true to a certain extent. However, it is also true that, as Mason undoubtedly said to Dixon, we've got to draw the line somewhere. Boundaries must be established to make the category a valid one; i.e., to restrict "tool use" to a meaningful subset of the behaviors performed by organisms. The restrictions placed by the current definition represent an endeavor to isolate tool use to a restricted set of behavioral adaptations. Social manipulations of others are excluded because these actions expand the range of the definition to an increasingly widening set of behaviors and produce fuzziness in the boundaries of this category. Likewise, adaptations such as the spider's web and the skunk's spray are excluded to preserve the requirement that tool use represent behavioral adaptations that compensate for the restrictions of morphology. In this respect, the classification of structure building as tool-using behavior fits well. Functionally, the behavior acts to compensate for morphological restrictions. Structurally, the behavioral components are comparable to the manipulations associated with other tool-using behaviors (selecting, carrying, orienting, etc.).

What does animal tool use have to do with intelligence? At one time, a strong relationship between tool use and intelligence was postulated, even assumed. Pioneers in this field often considered tool use the exclusive domain of man and some even took tool use (and later, tool making) as one of the defining characteristics of man (eg., Oakley 1964, Gruber 1969). However, Hall (1963) argued that tool use behavior is not an index of intelligence, but rather, indicative of behavioral adaptations to the environment. Alcock (1972) proposed that current instances of tool use originated by "the novel use of a pre-existing behavior pattern" (p. 466). Once established, selection acts on the new behavior pattern if this new pattern provides an adaptive advantage. Alcock's example for insects was the sand-throwing behavior performed by ant-lions and worm-lions. These larvae remove sand from their prey pits by the characteristic head dorsiflexion. According to Alcock,

All that would be required for the origin of sand throwing at prey is an individual with a low threshold for the performance of the action. A passing prey or a struggling one which dislodged some sand grains might trigger sand throwing, be struck by some particles, and be captured by the pioneer tool-users in ant-lion and worm-lion populations. (p. 466).

This pre-adaptation hypothesis is a plausible explanation for other instances of tool use. For instance, McDonald (1984—see above) demonstrated that soil dropping is a response elicited by liquids near the nest. Given that carrying foods back to the nest is an elicited response to a food stimulus, a liquid food source near the nest might have produced both behaviors as a response. Tool use then results from pre-existing behavior patterns. As another example, Moglich and Alpert (1979) noted that *C. bicolor*, like many different ant species, cover odor sources and other objects (like liquids—see above) with soil or other materials. This initial behavior pattern could have served as the preadaptation for the specific stone dropping behavior in response to competitor nests. As final examples, the two uses of tools to increase acoustical effectiveness (sound baffles in leaves and acoustical burrows) may have arisen from the simultaneous execution of two separate behavior patterns. In the case of acoustic burrows, an advantage would have arisen when a male called while constructing the burrow if this behavior produced a louder signal. As evidence for this point, males call from the front of the burrow while facing inward (Nickerson et al. 1979). In the case of sound baffling by use of a leaf, the fortuitous production of this effect could have arisen when a cricket stridulated while feeding. Prozesky-Schulze et al. (1975) noted that the pear-shaped hole used for baffling differs from the "irregularly shaped feeding holes" (p. 142), but this per se

does not rule out a preadaptation explanation. Thus, to answer the question posed earlier, tool use, at least in insects, has nothing to do with intelligence. Of the eight main categories of tool use described, each instance enables the animal to increase the efficiency or effectiveness with which it obtains a goal and thus gain a selective advantage over individuals who do not perform this behavior. Rather than indices of intelligence, tool-using behaviors are adaptations to compensate for morphological restrictions; adaptations which are shaped by selection pressures and guided by evolutionary processes.

POSTSCRIPT: A REQUEST

This review was intended to be an exhaustive survey of tool use by insects, but its comprehensiveness is limited to the scope of the reference tools used. I fully expect that I have missed some (few, I hope) examples of insect tool use. Readers aware of any references overlooked are invited to chastise me at the address given at the front of this article, so that a complete catalogue, if warranted, can be composed at a later date.

ACKNOWLEDGMENTS

The helpful comments and suggestions of James E. Lloyd, Donald A. Dewsbury, Bruce Ferguson, and D. Kim Sawrey are gratefully acknowledged. Also, thanks go to Thomas J. Walker and John H. Kaufmann for critical readings of earlier forms of this article.

LITERATURE CITED

- ALCOCK, J. 1972. The evolution of the use of tools by feeding animals. *Evolution* 26: 464-73.
- BARNETT, S. A. 1981. *Modern ethology: The science of animal behavior*. Oxford University Press, Oxford.
- BECK, B. 1980. *Animal tool behavior*. Garland STPM Press, New York.
- BENNET-CLARK, H. C. 1970. The mechanism and efficiency of sound production in mole crickets. *J. Exp. Biol.* 52: 619-52.
- EISNER, T., E. VAN TASSELL, AND J. E. CARREL. 1967. Defensive use of a "fecal shield" by a beetle larva. *Science* 158: 1471-3.
- ERWIN, J. 1974. Laboratory-reared rhesus monkeys can use their tails as tools. *Perc. Motor Skills* 39: 129-30.
- EVANS, H., AND M. EBERHARD. 1970. *The wasps*. University of Michigan Press, Ann Arbor.
- FELLERS, J., AND G. FELLERS. 1976. Tool use in a social insect and its implications for competitive interactions. *Science* 192: 70-2.
- FORREST, T. G. 1982. Acoustic communication and baffling behaviors of crickets. *Florida Ent.* 65(1): 33-44.
- GRUBER, A. 1969. A functional definition of primate tool-making. *Man* 4: 573-79.
- HALL, K. 1963. Tool-using performances as indicators of behavioral adaptability. *Curr. Anthropol.* 4: 479-94.
- HARCOURT, C. 1981. An examination of the function of urine washing in *Galago senegalensis*. *Z. Tierpsychol.* 55: 119-28.
- KARRER, R. 1970. The use of the tail by an Old World monkey. *Primates* 11: 171-75.
- KUMMER, H. 1982. Social knowledge in free-ranging primates. Pages 113-30 in D. R. Griffin ed., *Animal Mind-Human Mind*. Springer-Verlag, New York.
- LIN, N. 1964-1965. The use of sand grains by the pavement ant, *Tetramorium caespitum*, while attacking Halictine bees. *Bull. Brooklyn Ent. Soc.* 59-60: 30-4.

- LOEHL, H. 1983. Well-aimed defecation in the fieldfare (*Turdus pilaris*). J. Ornithol. 124(3): 271-9.
- LUCAS, J. R. 1982. The biophysics of pit construction by antlion larvae (*Myrmeleon*, Neuroptera). Anim. Behav. 30(3): 651-64.
- MCDONALD, P. 1984. Tool use by the ant, *Novomessor albisetosus* (Mayr). New York Ent. Soc. 92(2): 156-61.
- McFARLAND, D. ed. 1981. The Oxford companion to animal behaviour. Oxford University Press, Oxford.
- McMAHAN, E. A. 1982. Bait-and-capture strategy of a termite-eating assassin bug. Insectes Soc., Paris 29(2): 346-51.
- . 1983a. Bugs angle for termites. Nat. Hist. 92(5): 40-7.
- . 1983b. Adaptations, feeding preferences, and biometrics of a termite-baiting assassin bug (Hemiptera: Reduviidae). Ann. Ent. Soc. America 76(3): 483-6.
- MOGLICH, M., AND G. ALPERT. 1979. Stone dropping by *Conomyrma bicolor* (Hymenoptera: Formicidae): A new technique of interference competition. Behav. Ecol. Sociobiol. 6: 105-13.
- MORRILL, W. 1972. Tool-using behavior of *Pogonomyrma badius* (Hymenoptera: Formicidae). Florida Ent. 55: 59-60.
- NICKERSON, J. C., D. E. SNYDER, AND C. C. OLIVER. 1979. Acoustical burrows constructed by mole crickets. Ann. Ent. Soc. America 72: 438-40.
- OAKLEY, K. 1964. Man the tool-maker. University of Chicago Press, Chicago.
- PROZESKY-SCHULZE, L., O. PROZESKY, F. ANDERSON, AND G. VAN DER MERWE. 1975. Use of a self-made sound baffle by a tree cricket. Nature 255: 142-143.
- SCHULTZ, G. W. 1982. Soil-dropping behavior of the pavement ant, *Tetramorium caespitum* (L.) (Hymenoptera: Halictidae). J. Kansas Ent. Soc. 55(2): 277-82.
- STRUM, S. C. 1983. Use of females by male olive baboons (*Papio anubis*), American J. Primatol. 5: 93-109.
- TANAKA, T., AND Y. ONO. 1978. The tool use by foragers of *Aphaenogaster famelica*. Japanese J. Ecol. 28(1): 49-58.
- THORNHILL, R., AND J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts.
- VAN LAWICK-GOODALL, J. 1970. Tool-using in primates and other vertebrates. Pages 195-249 in D. Lehrman, R. Hinde, and E. Shaw eds. Advances in the study of behavior, Vol. 3. Academic Press, New York.
- WHEELER, W. 1930. Demons of the dust. Norton, New York.
- WHITEN, A., AND T. RUMSEY, 1973. "Agonistic buffering" in the wild Barbary macaque, *Macaca sylvana* L. Folia Primatol. 14: 421-5.
- WILCOX, R. S. 1984. Male copulatory guarding enhances female foraging in a water strider. Behav. Ecol. Sociobiol. 15: 171-4.
- WILSON, E. O. 1971. The insect societies. Belknap Press, Cambridge, Massachusetts.
- . 1975. Sociobiology: The new synthesis. Belknap Press, Cambridge, Massachusetts.

"FIREFLEAS" OF THE SEA: LUMINESCENT SIGNALING IN MARINE OSTRACODE CRUSTACEANS

JAMES G. MORIN*

SYNOPSIS

Caribbean ostracodes of the genus *Vargula* secrete luminescent emissions either as bright, long-lasting clouds or as complex trains of shorter, precisely spaced pulses. The large, bright clouds are generally produced during late twilight and have an effective antipredatory function. These emissions are similar among all species. Conversely, complex trains usually occur for a limited time just post-twilight in specific habitats within reef and seagrass systems. These trains are species specific displays produced by males and are presumably directed toward sexually receptive benthic [=bottom dwelling] females. In most species, luminescing males are accompanied by silent satellite males. These swarms have characteristics of both leks and sprints. There are three primary display patterns among the approximately 15 species observed: 1) about two thirds of the species produce trains that progressively shorten, 2) about one quarter produce evenly spaced trains, and 3) one species produces pulsed displays from multiple males. In most species, displaying males will usually synchronize their signals, by entrainment, with distantly signaling males. This synchronization produces a spectacular, reef-wide, sweeping luminescence that is reminiscent of a slow motion version of the flashing of synchronous fireflies from Southeast Asia. The reproductive patterns, life history, and biological activities of these ostracodes, along with their unusual signaling patterns, suggest that there is strong male-male competition and probably female choice involved in their mating systems. They show interesting parallels and differences to various insect mating aggregations including fireflies, chorusing insects and insect swarms.

INTRODUCTION

Luminescent organisms are diverse, abundant, and widespread in the sea (e.g. Herring 1978a). They show varied biochemical, morphological, and physiological mechanisms of light production (Herring 1978a, Hastings 1983). These features suggest that luminescence probably serves important adaptive functions in all such organisms (Morin 1983, Young 1983—and refs). However, except for a few well documented cases (e. g. Morin et al. 1975, Young and Roper 1977, Warner et al. 1979, Buskey and Swift 1985), most of these presumed functions are speculative and based solely on morphological and physiological data.

Ostracode crustaceans are a case in point. Much is known about the biochemical mechanisms of light production in cypridinid ostracodes (Shimomura 1982 and refs) and somewhat less about the morphology (Herring 1978b, 1985 and refs) and kinetics (e.g. Tsuji et al. 1970) of luminescence. However, until recently, little was known about how, when, and where luminescent ostracodes used this luminescent capacity. In 1980 I began a study of the spectacular luminescent displays produced by the ostracode *Vargula bullae* among reefs near the Caribbean island of St Croix (Morin and Bermingham 1980 [the species was incorrectly identified as *V. harveyi* in that report]). I have subsequently studied similar behaviors of at least 9 species among the reef systems along

*James G. Morin is Professor of Biology at the University of California at Los Angeles. His research focuses primarily on functions and mechanisms of light production in shallow water, marine organisms including ostracodes, ophiuroids, cnidarians, fishes, bacteria, and polychaetes. Mailing address: Department of Biology, University of California, Los Angeles, California 90024.

the San Blas region of the Caribbean coast of Panama and a comparable number in Jamaica.¹ These studies indicate that these tiny crustaceans, which are aptly called marine 'firefleas', produce exceedingly complicated mating and antipredatory luminescent signals that are as complex as any yet documented in the sea. The displays are probably as intricate as those known to occur among the luminescent insects and appear to have many characteristics in common with signaling fireflies, chorusing insects, and insect nuptial swarms.

BIOLOGY OF LUMINESCENT OSTRACODES

Bioluminescent ostracodes are known to occur in only two marine myodocopid families: the benthic [=bottom dwelling] cypridinids (in the genera *Vargula* and *Cypridina*) and the pelagic halocyprids (Herring 1978b, 1985 and refs). The most well known luminescent ostracodes are in the genus *Vargula*². There are 24 described species within the genus, and they have a worldwide marine distribution from tropical to polar seas, and from the surface to at least 3,400m (Kornicker 1984). Most appear to be benthic/demersal [=near bottom] species. Most species in the genus are luminescent.

Members of the genus *Vargula* have a number of biological characteristics that make them very interesting subjects for studying luminescent signaling, sexual selection, and mate choice. Since this is a group that is likely to be relatively unknown to my entomological colleagues, I will briefly delineate some of the salient features of their morphology, reproduction, and life history before discussing their luminescent patterns. Various features of myodocopids have been observed by a number of authors (e.g. Müller 1893, Cannon 1931, Elofson 1941, Okada and Kato 1949, Nakamura 1954, Hartmann 1967, Kornicker 1969, 1975, Cohen 1983, Cohen and Morin 1986 and unpublished).

MORPHOLOGY AND LIFE HISTORY PATTERNS

Structurally, *Vargula* (Figs. 1-3) is typical of most myodocopid ostracodes. Species of *Vargula* are generally less than 3mm in length, are sexually dimorphic (including body size, eye size and first antennae), possess a bivalved carapace that encloses the entire organism but has an anterior notch (incisur) through which the second antennae may be projected for swimming, have a single simple medial eye and a pair of large lateral compound eyes, have a total of 7 pairs of appendages, and have a terminal pair of furcal lamellae. The first pair of appendages, the first antennae (Figs. 1 and 2), are used as sensory structures and are also used by males for grasping the female during copulation. The second pair of appendages, the second antennae, are used primarily for locomotion (swimming, crawling, and burrowing). Swimming in the adult is rapid (averaging 8-12cm s⁻¹ in a 1.5 to 2.5mm individual [i. e. ca. 60 body lengths per sec]). The lateral compound eyes are a quarter to a third longer in males than females and can represent more than 15% of the body length (Fig. 1). Anterior to the mandibles and maxillae and just in front of the mouth is the upper lip, which possesses a pair of tusks. Luminescent secretions are produced from pores on the upper lip and/or the tusks; the luminescence is always external (see below).

Just anterior to the furcae are the genitalia (Fig. 1). The males have a paired copulatory apparatus (penis); the females have paired genital openings. Females, which are 15-20% longer than males (Fig. 1), brood 12 to 70 eggs within the carapace, but above and behind the posterior of the body in the marsupium (Fig. 1). Development is direct and the first instar hatches as a benthic, crawl-away (poor swimming) juvenile. At no time does there appear to be a long term planktonic stage. All stages appear to be both benthic (both on and within the substratum) and demersal [=near bottom].

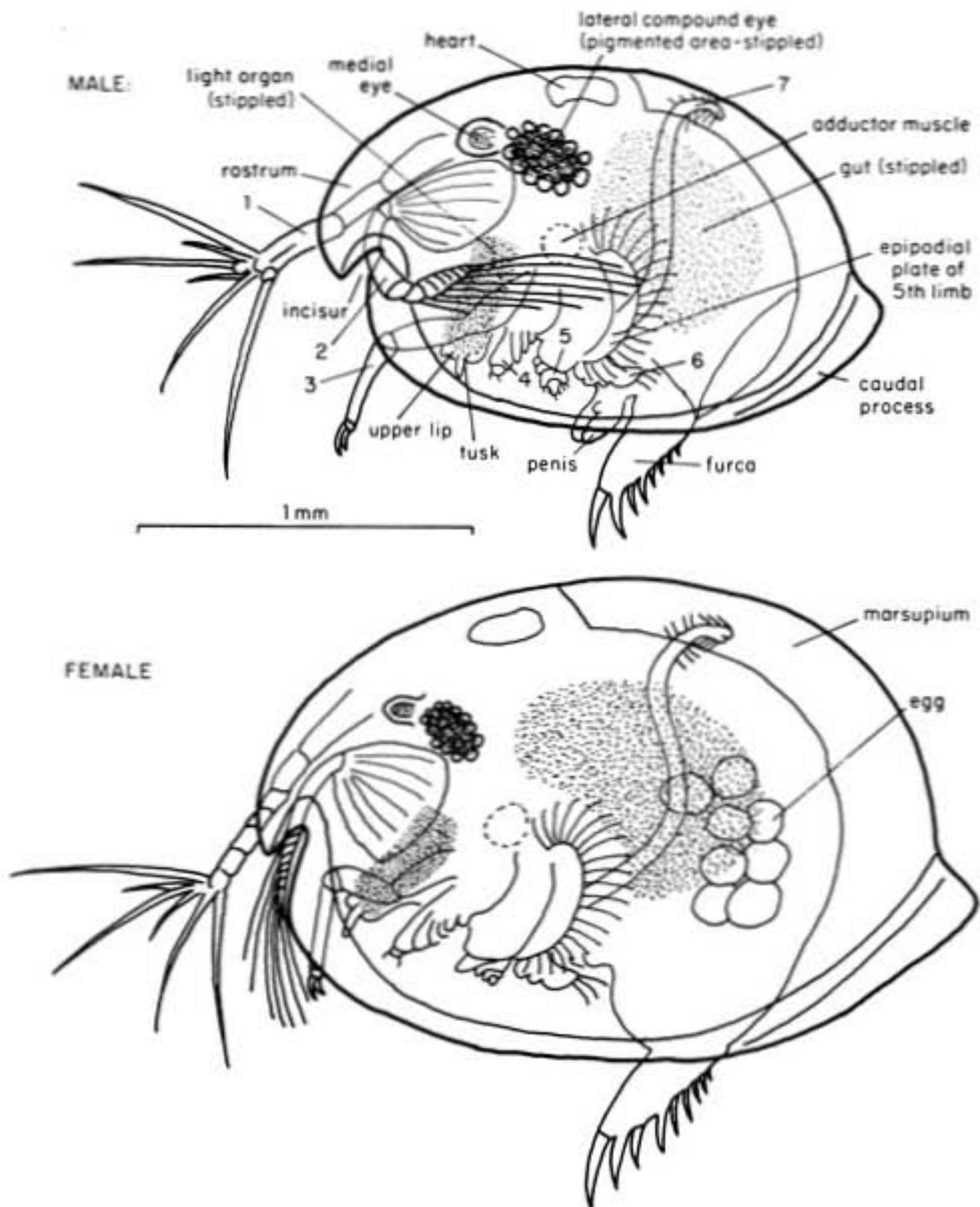


Fig. 1. Major morphological features and male-female comparisons in the ostracode genus *Vargula*. Numbers 1-7 indicate the sequential order of the paired limbs; see text for details.

During copulation, male myodocopid ostracodes deposit spermatophores on the genital opening of the female (Okada and Kato 1949). Mature eggs are fertilized by these stored sperm as they are extruded and deposited in the marsupium. The non-luminescent *Skogsbergia leneri*, which is closely related to *Vargula*, has been reared from egg to the adult (Cohen 1983) and I have partially reared it and *Vargula graminicola* (Morin unpublished). The combined observations show that these species brood their young for 2-4 weeks and then release them as first instars. These juveniles, over a period of 2-4 months, pass through 5 subadult instars. There is a single terminal adult molt. The

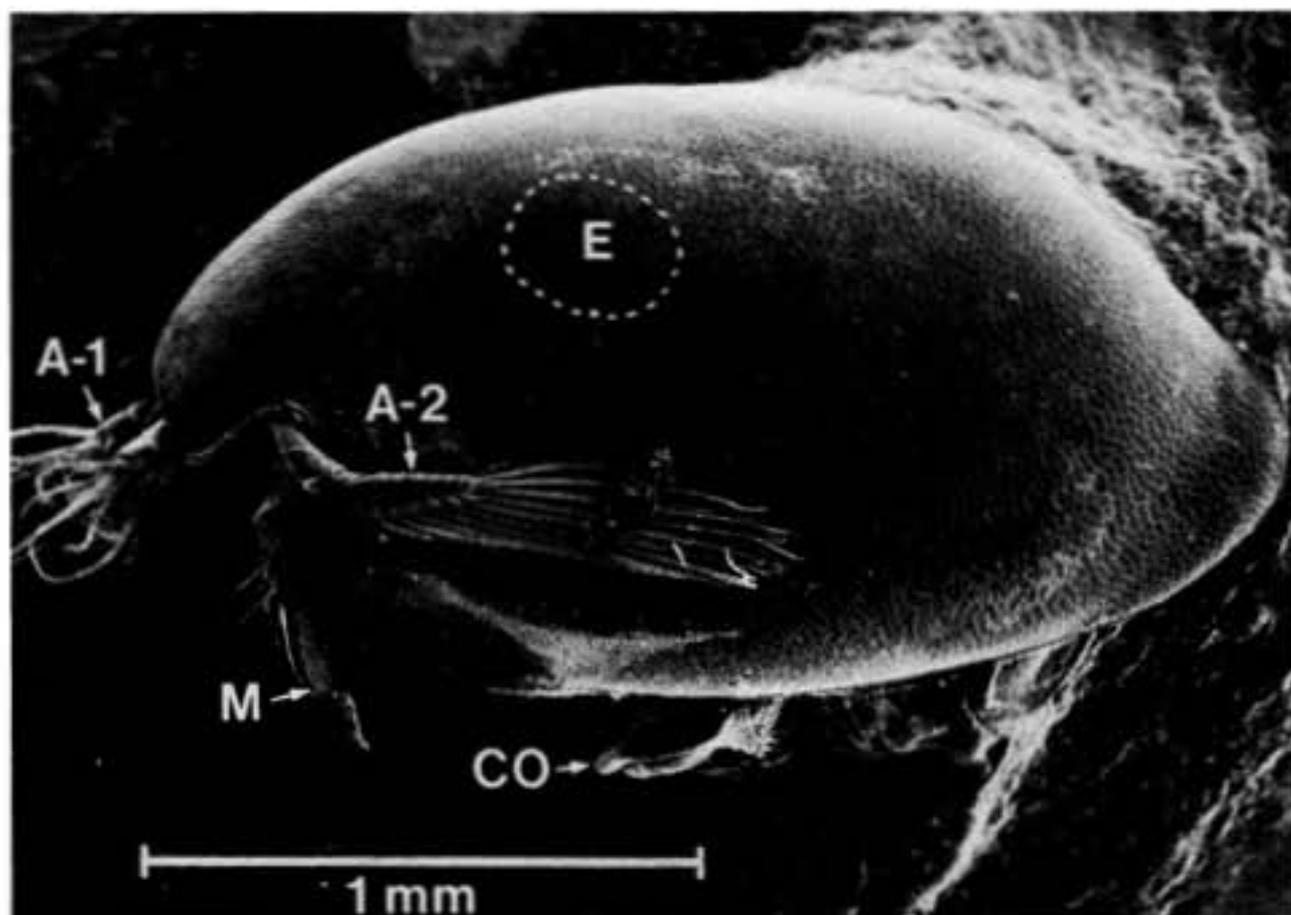


Fig. 2. Scanning electron micrograph of a male *Vargula contragula*: dotted line indicates the size and position of the lateral eye (E), A-1 = first antennae, A-2 = second antenna, M = mandible, CO = copulatory apparatus (penis); scale bar = 1mm.



Fig. 3. Scanning electron micrograph of a male *Vargula graminicola* with the left valve and left first antenna removed; scale bar = 1mm.

female first becomes sexually receptive shortly after this final molt (Morin unpublished). In *S. lernerii* one copulation with subsequent sperm storage suffices for at least three broods (Cohen 1983). New eggs form shortly after the first instars are released. Myodocopids have reported life spans that range from 3-4 months (Cohen 1983) to 3 years (Elofson 1941).

All known *Vargula* species are benthic and/or demersal (e.g. Kornicker 1975, Morin unpublished, Cohen and Morin 1986 and unpublished). Based on my own observations of the Panamanian species (Morin unpublished, Cohen and Morin 1986 and unpublished) and those of various other species (e.g. Stepien and Brusca 1985, Kornicker and Baker 1977, Tsuji et al. 1970), it is likely that most will prove to live on and in the substratum by day and to be planktonic, but near the substratum, at night.

MECHANISMS OF OSTRACODE LUMINESCENCE

The biochemical mechanisms of bioluminescence are well known for *Vargula* (usually incorrectly referred to as *Cypridina* in the biochemical literature²) and there is a large literature on the subject (e.g. Cormier 1978, Johnson and Shimomura 1978, Tsuji 1978, Shimomura 1982, Hastings 1983). The reaction requires a light emitting substrate molecule (ostracode luciferin), an enzyme (ostracode luciferase), oxygen and water. Ostracode luciferin is a tripeptide made up of arginine, isoleucine, and tryptophan such that their cores form an imidazopyrazine skeleton. This molecule also occurs in the fish *Porichthys* and some apogonid and pempherid fishes, probably by dietary transfer from ostracodes (e.g. Tsuji 1978, Herring and Morin 1978, Warner and Case 1980). However, this luminescent system is distinctly different chemically from other known light emitting systems, even within the arthropods [e.g. fireflies, shrimps, euphausiids] (reviewed in Shimomura 1982, Hastings 1983).

The luminescence produced by cypridinid ostracodes is always *extracellular*. Secretory glands (2 to 4 distinct types, depending on the author—e.g. Yatsu 1917, Takagi 1936) located on the upper lip and tusks apparently secrete the enzyme (ostracode luciferase) from one and the substrate (ostracode luciferin) from another; they mix in the sea water with oxygen to produce the light emitting reaction. There are conflicting data on the exact organization of these glands and the mechanisms of secretion, but all authors agree that the secretions occur from the upper lip glands (see Harvey 1952 and refs for details of the histological data). My observations corroborate these general observations. In living individuals the upper lip in both sexes is characterized by a rectangular or crescent-shaped pigmented region (the shape and color are somewhat species specific) which I call the light organ (Fig. 1); it is not present in non-luminous cypridinids such as *Skogsbergia*.

My field and laboratory observations indicate that the size (diameter), duration, frequency and position (outside or inside of the mantle cavity) of the emitted light can be precisely controlled by the ostracode. The duration can be varied by almost two orders of magnitude (msec to many sec). The mechanisms of kinetic control are unclear but most likely involve either variations in the luciferin-luciferase ratios and/or the addition of a mucus component that controls the diffusion characteristics of the reaction (this latter method could account for some authors finding more than two secretory glands on the upper lip).

FUNCTIONS OF OSTRACODE LUMINESCENCE

Until recently the functional aspects of the luminescence in ostracodes were unknown. Ostracodes had been known to secrete luminescent spots into the water column

in response to flashes of artificial illumination [i.e. light stimulated luminescence] (Haneda 1940, Tsuji et al. 1970, Morin and Bermingham 1980, and Morin unpublished). But until I began my studies of *Vargula*, spontaneous luminescent displays were undocumented. In fact little was known about the biology of *Vargula* in general (summarized in Sars 1922, Okada and Kato 1949, Harvey 1952, Nakamura 1954, Kornicker and King 1965, Tsuji et al. 1970, Kornicker 1975, Andersson 1977, Kornicker and Baker 1977, Lapota 1983, Felder 1982—and refs).

In 1980 I began an *in situ* underwater study of the nocturnal activity patterns of *V. bullae* among the shallow back reefs in St. Croix (Morin and Bermingham 1980). It quickly became apparent that they are using their secreted luminescence in complicated ways. Subsequent work in Panama on 9 *Vargula* species,¹ all distinguishable by their luminescent patterns, indicates that they have perhaps the most complex signaling patterns yet documented in the sea, and that these patterns are at least comparable to terrestrial fireflies (e.g. Lloyd 1983 and refs) and tropical flashlight fishes (Morin et al. 1975).

In most if not all light emitting organisms, bioluminescence provides a benefit to the emitter (Morin 1983, Young 1983—and refs). Luminescence can serve one or more of the following major functions: 1) evading predators, 2) obtaining prey, 3) intraspecific communication, and 4) mutualistic attractions (Morin 1983). My observations on *Vargula* species indicate that they use their luminescence for at least two of these major functions: *predator evasion* and *intraspecific communication* (as sexual signals). Signals functioning in intraspecific communication occur regularly each night as species specific displays while anti-predatory signals are rare, sporadic, and similar among all species.

PREDATOR DETERRENCE: LUMINESCENT BOMBS AND BURGLAR ALARMS

All *Vargula* species appear to behave identically when attacked by planktivorous fishes or crustaceans:² they invariably produce a brilliant and massive (several cm) bomb-like cloud of luminescence that persists for many seconds, often more than a minute, around and within the predator. It sometimes results in the predator regurgitating the ostracode and probably startles ('boo' effect) and temporarily blinds (flashbulb effect) the predator [see Morin 1983 for review]. Perhaps even more importantly the luminescent cloud sometimes results in attracting a second order predator,⁴ which then attacks and often consumes the initial predator (burglar alarm—Burkenroad 1943). During some of these attacks the ostracode, along with other gut contents, has been seen to be regurgitated by the initial predator, and thus survived the encounter. Preying on luminescent ostracodes would thus appear to subject these planktivores to increased predatory risk by making them conspicuous to their own predators. Furthermore, plankters similar in size and distribution to *Vargula*, might benefit from the presence of the ostracode since their predators might be wary of taking *Vargula*-sized prey.

Attacks on *Vargula* that trigger a luminescent cloud are rare and usually occur near the end of twilight but before the *Vargula* begin their regular nightly signaling. I have never observed such attacks on ostracodes to occur within the displays. These observations suggest that the planktivores that do attack *Vargula* have done so mistakenly while foraging by dim ambient light, but avoid attacking when the *Vargula* are identifiable, by their light cues, as being 'dangerous'. The net effect is that these ostracodes are probably consumed at very low frequencies relative to their nocturnal planktonic densities and the densities of other nocturnally active zooplankters.

LUMINESCENT TRAINS AS SEXUAL SIGNALS

The dominant and repeated luminescent pattern I have observed in most *Vargula*

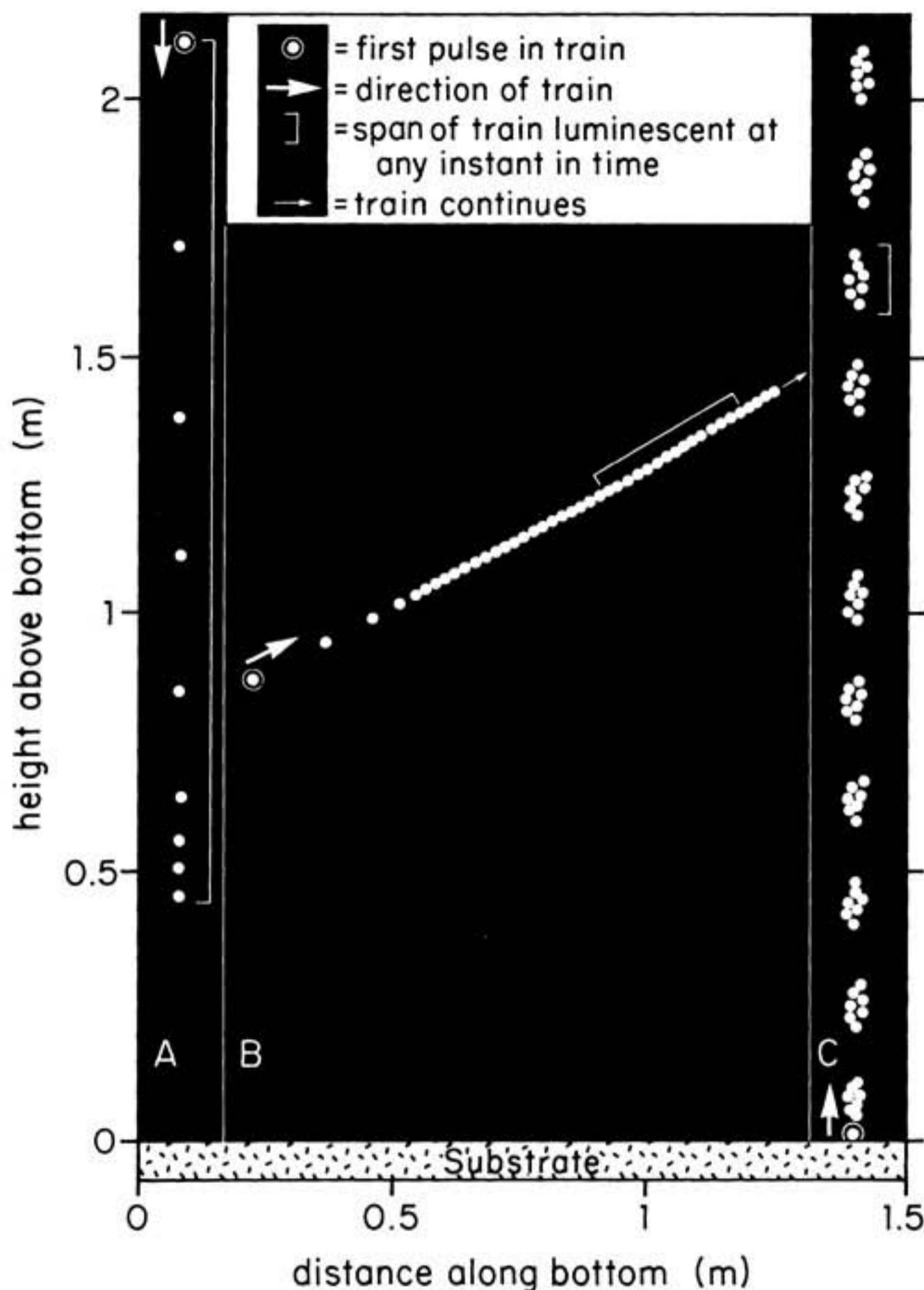


Fig. 4. Relative spatial relationships of the three main types of luminescent displays seen in Caribbean species of the ostracode genus *Vargula*: A. *V. shulmanae* showing a progressively shortening train; B. *V. contragula* showing an evenly spaced train; C. *V. graminicola* showing a group pulsing train.

species occurs as species specific trains of long-lasting luminescent pulses that are secreted into the water column (Fig. 4) by a rapidly swimming male ostracode. This signaling male is usually followed and surrounded by a swarm of non-signaling satellite males.

In general each luminescent train has two components: 1) It begins with several widely spaced luminescent pulses that are secreted progressively closer together as the male swims at a constant speed of about 8-12cm s⁻¹; each pulse lasts several seconds. 2) In the later portion of the train the pulses are evenly and closely spaced and have a shorter duration. The signal is apparently a calling signal to sexually receptive females. Females do not signal during this interaction. By cueing on and tracking the luminescent train, a female presumably swims to the males in the water column for copulation. More than 90% of the individuals caught within the luminescent displays are males.

In addition, luminescent trains will often synchronize, by entrainment (i.e. leader-follower),⁵ within an entire reef area so that numerous trains (spaced about 1/2m apart) turn on and off together. This entrained synchronization produces a spectacular reef-wide luminescent phase that alternates with a dark phase of comparable duration. It also produces an apparent sweeping synchrony along reefs in some areas. In most species the display period commences near the end of twilight (about 50min post-sunset) and lasts for about one hour.

DISPLAY VARIATIONS, HABITAT SPECIFICITY AND SPECIES DIVERSITY

While most of the luminescent trains produced as mating displays show the general features indicated above, each species shows its own unique variations. There are two major variants in these *train type* signals, and also a distinctly different *group pulsing type* signal: 1) The most common train type (which I call *shortening trains*), is exemplified by *Vargula shulmanae*⁶ (Fig. 4A) and *V. bullae*. In these displays the first part of the train, in which widely spaced pulses become progressively closer, dominates the display and the shorter, evenly spaced pulses toward the end are proportionally fewer. These displays are almost invariably produced by a vertically swimming male, either upward or downward, who is surrounded by non-luminescing ('silent') males. The entire trains, which are made up of long duration pulses (5-15s), are generally long in space (50-200cm) and time (10-30sec) About two-thirds of the fifteen species studied show this kind of a pattern. 2) The second train variant (which I call *even trains*), exemplified by *Vargula contragula*⁷ (Fig 4B) and *V. sp. 'n'* (noropsela), emphasizes the later part of the generalized display: relatively short duration pulses (1-2 sec) that are evenly spaced. Usually only the first one or two intervals of the train show progressive shortening. About one quarter of the species examined fall into this category. The displays are usually produced by a male swimming horizontally or obliquely upward or downward and accompanied by 'silent' males. While the short pulse duration and their close spacing produces a relatively short visible train (ca. 10-25cm), the trains may continue for long distances (many m) and appear somewhat like miniature glowing contrails of jet aircraft. Side by side signaling of 2 or more individuals sometimes increases complexity.⁷ 3) The most divergent pattern (which I call *group pulsing*) occurs in *V. graminicola*⁸, a species of the shallow grass beds (Fig. 4C). Male swarms of *V. graminicola* display vertically upward, but *each male* in the cluster produces very short (ca. 280msec), equally spaced pulses in entrained synchrony with all the other males. This is the only species of the 15 studied that produces this pulsating-swarm kind of a display. They show entrainment synchrony, not only within clusters, but also between luminescing clusters across many meters of the grass beds.

Although all species fall into one of these three major categories, each species also appears to obey the 'one habitat, one time, one signal, one species' rule found for fireflies (Lloyd 1981, p. 144). Variations between species, including those listed above, have been found to occur in: 1) habitat (and microhabitat), 2) train pattern (pulse intervals become progressively shorter or show equal spacing), 3) train direction (up, down,

oblique, horizontal), 4) train length and 5) duration, 6) time between subsequent trains, 7) entrained synchrony between adjacent trains, 8) number of pulses per train, 9) duration of each pulse in the train, 10) distance between pulses, 11) pulse intensity, 12) total number of individual males per train, 13) number of luminescing males per train, and 14) display period during the night (Morin unpublished). Even though species may occur together, the result of the many differences is a complex partitioning of the habitat in time and space so that each species is ecologically and behaviorally distinct from all others within a given reef system. These species specific bioluminescent behavioral characters are as distinct as any morphological features we have found (Cohen and Morin 1986 and unpublished, Morin unpublished). It is likely that these bioluminescent behavioral patterns are under strong selection and this, coupled with the apparent short dispersal capabilities of each species, may have been responsible for the remarkable species radiation apparent in this group within the Caribbean.

FIREFLEAS AND MATING AGGREGATIONS IN INSECTS

The remarkable reef-wide mating displays made by luminescent tropical marine ostracodes of the genus *Vargula* have many characteristics of leks (*sensu* Alexander 1975): they are non-resource based male aggregations, but without a permanent location, that females apparently visit only for copulation (see also Bradbury 1981, Thornhill and Alcock 1983, Bradbury and Gibson 1983—and refs). Many also show characteristics of sprees (*sensu* Walker 1983): *temporal* assemblies of sexually displaying males. Ostracode group activities show a number of similarities to the spatial and temporal clustering of mating activities in many insects.

'Firefleas' produce luminescent displays comparable in many ways to fireflies (Coleoptera: Lampyridae). For convenience, fireflies can be viewed as falling into two distinct mating patterns: solitary-searchers and sedentary-aggregators (Lloyd 1983, Case 1984—and refs). In searching fireflies such as most *Photinus*, *Photuris* and *Luciola* species, population densities tend to be low and dispersed and males patrol while emitting a repeated species-specific luminescent pattern. Stationary females respond with a specific luminescent signal at a precise latency after the male's signal. By reciprocal signaling, the male locates the female and mating usually follows. Receptive females appear to respond to all patrolling males, showing little or no choice of mates. Male-male signaling coordination is usually infrequent or absent. There are numerous variations to this basic pattern (e.g. Lloyd 1966, 1973b, 1983, Case 1984—and refs). The second type, aggregators, which are more similar to *Vargula*, has another level of complexity. In these primarily Old World species (e.g. most *Pteroptyx*) there appear to be two components to the signaling: a spectacular synchronous group male calling phase (which probably incidentally also calls competing males) and a less conspicuous interactive courtship phase (Buck and Buck 1966, 1978, Lloyd 1973b, 1983, Otte 1980, Case 1984—and refs). The males tend to be fairly stationary in prominent trees and may occur by the thousands. Each night as the males congregate they flash in simultaneous synchrony⁶ with each other. This pulsating beacon effect is a truly spectacular phenomenon in the forests of Southeast Asia. The display appears to act as a species specific attractant (call) to females as well as to other males. Once a female arrives in the tree the second phase involving small group interactions appears to commence between her and one or more males. This interaction is only partially understood but usually results in the male walking to the female. It occurs while the males still flash in synchrony. This second phase interaction may involve any or all of the following activities: reciprocal male-female signaling, perhaps with intensity modulations or ratios and aiming; complex tactile responses; and the use of pheromones (Lloyd 1973a, Buck and Buck 1978, Case 1980, 1984—and refs). Whatever the final courtship interactions are for a particular

species, it seems clear that, unlike searching fireflies, local densities are high, the operational sex ratio is male biased, male-male competition is significant, and females may be able to choose their mates.

Similarly, *Vargula* species have high local densities, seem to have operational sex ratios (i.e. the clusters) biased toward males, probably have male-male competition and perhaps female choice. As in aggregating fireflies, luminescence is also involved in the calling by males, but the ostracodes are motile, not sedentary while calling. Furthermore, females do not seem to reciprocate in the luminescent displays, but probably swim *to the males without signaling*. In this respect, these ostracodes are similar to chorusing insects or swarming dipterans in which females are attracted to the males but do not reciprocally signal their presence (Downes 1969, Walker 1969, Alexander 1975, Sullivan 1981, Greenfield and Shaw 1983—and refs). Presumably such a silent approach might have two benefits: it may give the female greater protection from potential predators and it may give her greater flexibility in choosing her mate (Thornhill and Alcock 1983). The details of the final courtship and copulation are as yet unknown in any of the luminescent ostracode species with mating displays. Thus it is unclear what direct male-male interactions occur, if the females exercise any mate choice, or even how mates couple (for instance it might well be that luminescence is used primarily to place the female in the vicinity of the signaling male but that another channel, such as pheromones, is used for the final approach—a similar switching of channels has been proposed for synchronizing fireflies [Lloyd 1973a]).

Recently Walker (1983) coined the term spree, a temporal mating aggregation, as a temporal analog to a lek, which is a spatial mating aggregation. Lekking and spreeing are not mutually inclusive or exclusive; a male mating system may involve neither, either, or both. The male aggregations in the majority of the *Vargula* species studied appear to be both leks and sprees. Most signal for only about an hour or two just post-twilight, the earliest part of the time period (darkness) within which the signal can operate. Such signaling patterns are sprees. Presumably the temporal crowding of the signal to just post-twilight is a consequence of males signaling (and competing) for females that have become sexually receptive during non-calling hours (daylight and twilight). Similarly, limited periods of calling occur widely among chorusing insects (Walker 1983 and refs). Both sprees and leks also occur among fireflies (Walker 1983). For instance many searching fireflies display for very short periods in and around twilight (i.e. they spree), while most synchronous fireflies congregate (i.e. lek) but signal for extended periods of time (all night). Some fireflies neither lek nor spree. No known fireflies do both. In contrast, most 'firefleas' simultaneously lek and spree, as swarms in the early evening. However a few, e.g. *V. graminicola* (a group pulser), signal throughout the night and hence only lek and do not spree.

Another difference between 'firefleas' and aggregating fireflies is that in ostracodes with train-type displays only one male signals and the rest follow as silent satellites. Among aggregating fireflies many nearby individuals signal at the same time. In insects where silent satellites occur along with signaling males, these two seem to represent alternative mating strategies with the satellite males acting as interlopers (Thornhill and Alcock 1983). For instance, the phenomenon of one signaler surrounded by silent satellites has been studied in chorusing crickets (Cade 1981). Cade has shown that there are some genetic differences between individuals employing each strategy. In ostracodes, however, relative mating success of signalers and silent satellites is unknown. Furthermore, it is unknown whether satellites and signalers ever switch roles. Satellite males can luminesce and there is no obvious morphological dimorphism between males. Thus switching may occur. The intriguing pattern found in *Vargula graminicola*, in which all the males flash in unison as they rise in the water column, may provide useful comparative insights into male-male competition within the genus. It appears that no

silent satellites exist in these clusters and thus each male may compete on a more nearly equal basis for females.

Not only would it appear that there is male-male competition *within* clusters of both train type signalers (e.g. *V. shulmanae* and *V. contragula*) and group pulsing type signalers (i.e. *V. graminicola*), but competition is almost certainly also occurring *between* clusters when they are entrained. As is hypothesized for synchronization in fireflies and chorusing insects, it is likely that by coordinating a display to coincide with that of the nearest neighbor, the species specific identifiers are maintained, thus improving chances of attracting a receptive female to the cluster (Lloyd 1983 and refs). Were this signaling male to display slightly earlier or later he might lose a potential mate since a female nearby might ascend toward a synchronizing cluster within her visual field.

The actual operational sex ratio of these ostracodes is unknown. However, given the following possible assumptions: that a female is impregnated only once and early in her adulthood, that she lives for about six months, and that males from her cohort live equally long and are ready to mate each evening throughout their adult lives, then the operational sex ratio in an actual 1:1 sex ratio population would become male skewed to about 180:1. If we assume about 18 males per cluster (actual numbers vary from 1 to 40), then the *per cluster* operational sex ratio drops to about 10:1. Even if these assumptions are off somewhat, they serve to indicate that it is highly likely that there is strong competition both between synchronizing clusters of males *and* between males within each cluster.

It is also possible that synchronizing fireflies are involved in two tiered competition similar to what may be occurring in the group pulser, *V. graminicola*. If each firefly tree, with its myriad of males distributed around the tree but territorially spaced slightly apart from one another, is actually made up of a large number of subgroups (e.g. all individuals within one branch of the tree), then the initial task of the female is to choose among groups she will fly to (i.e. the calling phase). This would be analogous to a female ostracode deciding between two or more neighboring clusters of displaying males. Once that decision has been achieved in either fireflies or 'firefleas', then the male-male interactions shifts from cooperation between groups to attract females, to competition within the group for the receptive female (i.e. the courtship phase in synchronous fireflies). While flashing in synchrony continues, selection of a firefly mate could be accomplished by the female assessing particular qualities of the synchronous flash, secondary signaling within the inter-flash interval, and/or through other channels. In ostracodes the female, following the line of luminescent pulses, may be assessing the light signal itself and/or signals from another channel (e.g. pheromones). During both the calling and the courtship phases of the mating procedure in either fireflies (Lloyd 1983, Otte 1980) or 'firefleas', it is individual selection that would be driving the synchronizations and subsequent exchanges.

Mating aggregations involving lek-like interactions have not previously been demonstrated in crustaceans; it is likely that such systems are widespread and important in marine crustaceans and in marine organisms in general. Understanding the intricate interactions involved in mate choice and sexual signaling in ostracodes is in its infancy. The first serious study of the phenomenon was only begun in 1980 so that knowledge of these unusual systems is over 25 years behind what is known of firefly systems. Once better understood, ostracode mating systems and their luminescent signals may provide insights into understanding mate choice and sexual selection, particularly in the marine environment where they have been less well studied.

ACKNOWLEDGEMENTS

I thank the Kuna Indians and the government of Panama for allowing me to work in the San Blas Islands of Panama; the Smithsonian Tropical Research Institute for the use of their facilities in the San Blas; the Discovery Bay Marine Laboratory, Jamaica, for the use of their facilities; and the numerous individuals who aided in my nocturnal diving pursuits, some by diving and some by delaying many dinners. I especially thank Anne Cohen, Michael Greenfield, Matthew Grober, James E. Lloyd, Myra Shulman, and Thomas J. Walker for comments on the manuscript. This work was supported in part by a National Geographic Society Grant, an American Philosophical Society Grant, and a University Research Grant from U.C.L.A.

APPENDIX

¹Prior to this current work only 4 species of *Vargula* had been described from the Caribbean and Gulf of Mexico and each appears to have a rather limited distribution: *Vargula bullae* from the Virgin Islands, *V. harveyi* from Jamaica, the southern Bahamas and Puerto Rico, *V. parasitica* from Jamaica, and *V. magna* from North Carolina and the west coast of Florida. Descriptions of 21 new species are in press or in preparation including 5 from Belize (Cohen unpublished), 9 from Panama (Cohen and Morin 1986 [3 species] and unpublished [6 species]), and 6 from Jamaica (Morin and Cohen unpublished). Each species apparently has a restricted habitat distribution and probably has a very limited geographical distribution. These restrictions are perhaps not surprising given their low dispersal, probably due to a life history pattern of near bottom foraging, reproduction by copulation, and the lack of a planktonic phase.

²The genus *Cypridina* was split into several subgenera, including *Vargula*, by Skogsberg in 1920. These were raised to generic status by Poulsen in 1962. Currently there are about 24 described *Vargula* species and 14-20 *Cypridina* species. Luminescence has been found in most *Vargula* species. A few species of *Cypridina* are known to be luminescent but some are not. No other cypridinid genera are known to have luminescent members. Biochemical analysis of ostracode bioluminescence has been done primarily on *Vargula hilgendorfi* from Japan (see Harvey 1952 for details of the early biochemical analyses). Many of these studies have been done since 1962 when *Vargula* became a formal genus. The majority of these studies consistently and incorrectly use the names *Cypridina hilgendorfi* and *Cypridina luciferin*. There has been a very long delay between the systematic renaming of *Vargula hilgendorfi* and a recognition by biochemists of this change; hence one often still sees the usage of *Cypridina* in the literature where it should be *Vargula*.

³Predators I have observed to prey on *Vargula* include: fishes: freckled cardinalfish (*Phaeoptyx conklini*), 3 squirrelfishes (*Holocentrus rufus*, *H. ascensionis*, *Adioryx vexillarius*), and the hardhead silverside (*Atherinomorus stipes*); crustaceans: the shrimps *Stenopus hispidus*, *Rhynchocinetes rigens*, and a small penaeid; the swimming crab *Portunus sebae*; and an unidentified pagurid; cnidarians: the anemone *Aiptasia tagetes* and the cerianthid anemone *Arachnanthus nocturnus*.

⁴Larger, second order predators I have observed attack predators³ on *Vargula* include snappers (Lutjanidae), jacks (Carangidae) and squirrelfishes (Holocentridae). Most, but not all, cases resulted in successful capture.

⁵It is important to distinguish between two types of synchrony: *entrained* and *simultaneous*. Both types of synchrony can potentially occur between individual pulses (or flashes) or between complete or parts of trains (or 'phrases') [i.e. organized clusters of pulses or flashes]. In *entrained synchrony* the stimulus that triggers the luminescent sequence in the receiver is the most recent pulse or train of pulses from its neighbor(s) (i.e. the stimulus is concurrent with the episode in Walker's [1969] terminology). This has also been variously termed leader-follower, paced, wave-like, sweeping, facultative, loose, or homeepisodic synchrony (Walker 1969; Lloyd 1973a, 1973b, 1983; Otte 1980; Case 1984; Cicero 1983—and refs). In *simultaneous synchrony* the stimulus is usually

the preceding emission from the neighbor such that both emit their signals simultaneously (i.e. the stimulus precedes the episode [Walker 1969]). This has also been termed: anticipatory, rhythmic, classic, mass, or proepisodic synchrony (references as above).

Vargula displays appear to show only *entrained synchrony* of both pulses and trains. However, the duration of each pulse and each series of pulses in a train are so long (seconds) relative to the delay between adjacent signalers (milliseconds), that *the majority* of the signal's duration occurs simultaneously between each participating neighbor. Thus, as a consequence of the long duration of each pulse in a train, one can detect not only a wave of entrained synchrony as it sweeps along a reef among hundreds of regularly spaced individuals, but also an *apparent* simultaneous synchrony of the signals during most of the pulse and train (lasting several seconds). True simultaneous synchrony of signals probably does not occur in *Vargula*. Such is not the case in variously synchronizing fireflies. Depending on the species and/or conditions, fireflies may show simultaneous synchrony (e.g. *Pteroptyx malaccae*, *P. tener* [Lloyd 1983, Case 1984 and refs]) or entrained synchrony (e.g. *Photinus knulli*, *P. concisus*, *P. pyralis* [Lloyd 1983, Case 1984, Cicero 1983—and refs]). However, unlike ostracodes, most firefly signals occur as flashes that persist for only a short period of time (few hundred milliseconds). Thus, in those species which show entrained synchrony, there are distinct waves of luminescence because the lead signaler's light is decaying about the time the follower's light is turning on. Some (e.g. *Photinus macdermotti* [Lloyd 1983 and refs]), however, may show flash synchrony without phrase synchrony when a male flashes simultaneously with the second of two flashes in the phrase of its rival.

⁶*Vargula shulmanae* (see Cohen and Morin 1986), known only from the San Blas Islands of the Caribbean coast of Panama, is benthic by day on steep reef escarpments (from depths of 4 to >20m) dominated by diverse corals and gorgonians. They become planktonic, but near the bottom, among the tall gorgonians above these same reefs at night, unless the moon is bright. About 55 minutes after sunset large numbers of males appear in the water column up to about 5m above the reef. They maintain these high numbers for about 1 to 2 hours while they display intensely; thereafter their numbers in the water column drop dramatically. Only occasionally have females been caught in the water column. The male luminescent trains (Fig. 4A) are distinctive and are representative of *shortening train* displays (dominated by widely spaced pulses of long duration that become progressively closer together). Each train, produced from one downward swimming male (moving at about 8cm s⁻¹) surrounded by up to 12 nonsignaling males, contains about 5-8 pulses. Each pulse lasts for over 7s and has a diameter of about 1-2mm. The train is spread out over about a 1.5-2m vertical distance and lasts for about 30-40s. The initial interpulse distance is about 30-50cm. Subsequent pulses are spaced progressively closer until the last two are about 5cm apart. Females are capable of luminescing but do not do so during the luminescent displays. Entrained synchrony occurs between the luminescent trains throughout the reef. The luminescent phases alternate with comparable 30-40s dark phases. Most displays are 75cm or more apart; train densities are fairly low (estimated at about 1m⁻²). This species is not attracted to dead fish or crustaceans; its feeding habits are unknown.

⁷*Vargula contragula* (see Cohen and Morin 1986), also known only from the San Blas Islands of Caribbean Panama, occurs among low profile patch reefs and reef slopes with mixed scleractinian and large gorgonian corals at depths of about 2-10m. Males appear abruptly about 50 min post-sunset if there is no moonlight. They display especially among gorgonian patches and about 1-3m above the bottom. After only about 1 hr the displays terminate abruptly. The luminescent trains (Fig. 4B) are representative of *even train* displays (dominated by many close, but evenly spaced pulses of short duration). Each train is produced obliquely upward at an angle of 30 to 50° by a rapidly swimming (ca. 9cm s⁻¹) male who may be accompanied by up to 6 'silent' males. Pulse duration is relatively short, never more than 4s, and they are rather dim compared to most other species. The first two pulses are separated by about 15cm, but subsequent intervals become rapidly closer so that by about the 5th to the 8th interpulse interval the distance is no more than 1-2cm. Dozens of subsequent pulses retain this close, even

spacing as the ostracode displays over a distance of several meters. However, because the duration of each pulse is short, only about 30cm of each train is visible at any instant in time. The effect is one of a series of luminescent points (about 15 pulses) progressing obliquely up through the water column like a jet contrail. Often the train path is slightly curved laterally and occasionally several individual males will commence signaling together and radiate away from one another as they swim. Reef-wide entrainment of displays occurs, but it is very weak. No females have been caught. The species is presumably benthic in the reef by day; none have been caught in the water column during the day. They are not attracted to carrion, and their feeding habits are unknown.

**Vargula graminicola* (see Cohen and Morin 1986) also is only known from the San Blas region of Caribbean Panama. This unique species is abundant in shallow (3-10m depth) sea grass beds exposed to good water circulation. They are benthic by day and planktonic near the bottom during the night when there is no moonlight. During darkness most of the individuals, including juveniles, females, and males, occur within about 15cm of the bottom, among the sea grasses. However, males in clusters of 2 to 40 regularly rise up to 4m into the water column and produce a spectacular pulsating display (=group pulsing displays: fast group flashes, evenly displayed upward). Each rapidly swimming male (ca. 11cm s⁻¹) produces very bright, short duration (ca. 280ms) pulses in unison with the others in the cluster at regular intervals (ca. 15 to 25cm apart) as they rise vertically or slightly obliquely upward (Fig. 4C). There are usually 8 to 12 group flashes during each pulsating display train. Each train has a total duration of about 18s and a total length of about 1.5 to 2m. Presumably these displays are mating signals made by competing males to the females below. Occasionally females are caught in the water column among the displaying males. They do not participate in the luminescent signaling although they are capable of emitting light (as are all juvenile stages). However, details of mating and copulation are unknown. Brooding females are common at night among the sea grasses. Entrained synchrony between different luminescing clusters occurs over large areas of the sea grass beds (>50m²); with peaks of luminescence at intervals of about 60s. Clusters of displaying males are usually about 15cm to 1m apart so that the density of these rhythmically pulsing displays can be very high (>10m⁻²). The displays commence about an hour post-sunset and continue throughout the night if there is no moonlight until about an hour before dawn; but are most intense during the first two hours. Unlike most other *Vargula* species (except *Vargula hilgen-dorfii*), they are strongly attracted to fish or crustacean carrion. Thus this species can be collected in large numbers with relative ease (ca. 10,000 per hr!).

LITERATURE CITED

- ALEXANDER, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. Pages 35-77 In D. Pimental, Ed. Insects, science and society. Academic Press, New York.
- ANDERSSON, A. 1977. The organ of bellonci in ostracodes: an ultrastructural study of the rod shaped, or frontal organ. Acta Zool. (Stockholm) 58: 197-203.
- BRADBURY, J. W. 1981. The evolution of leks. Pages 138-69 In R. D. Alexander and D. W. Tinkle, Eds. Natural selection and social behavior. Chiron Press, Inc., New York.
- AND R. M. GIBSON. 1983. Leks and mate choice. Pages 109-38 In P. Bateson, Ed. Mate choice. Cambridge Univ. Press, Cambridge.
- BUCK, J. B. AND E. BUCK. 1966. Biology of synchronous flashing fireflies. Nature 211: 562-4.
- . 1978. Toward a functional interpretation of synchronous flashing by fireflies. American Nat. 112: 471-92.
- BURKENROAD, M. D. 1943. A possible function of bioluminescence. J. Mar. Res. 5: 161-4.
- BUSKEY, E. J. AND E. SWIFT. 1985. Behavioral responses of oceanic zooplankton to simulated bioluminescence. Biol. Bull. 168: 263-75.

- CADE, W. 1981. Alternative male strategies: genetic differences in crickets. *Science* 212: 563-4.
- CANNON, H. G. 1931. On the anatomy of a marine ostracod, *Cypridina (Doloria) levis* Skogsberg. *Discovery Rep.* 2: 435-82.
- CASE, J. F. 1980. Courting behavior in a synchronously flashing, aggregative firefly, *Pteroptyx tener*. *Biol. Bull.* 159: 613-25.
- . 1984. Vision in mating behavior of fireflies. Pages 195-222 *In* T. Lewis, Ed. *Insect Communication*. Academic Press, New York.
- CICERO, J. M. 1983. Lek assembly and flash synchrony in the Arizona firefly *Photinus knulli* Green (Coleoptera: Lampyridae). *Coleop. Bull.* 37: 318-42.
- COHEN, A. C. 1983. Rearing and postembryonic development of the myodocopid ostracode *Skogsbergia leneri* from coral reefs of Belize and the Bahamas. *J. Crust. Biol.* 3: 235-56.
- AND J. G. MORIN. 1986. Three new luminescent ostracodes of the genus *Vargula* from the San Blas region of Panama. *Contrib. in Sci., Natural Hist. Mus. of Los Angeles County* (in press).
- CORMIER, M. J. 1978. Comparative biochemistry of animal systems. Pages 75-108 *In* P. J. Herring, Ed. *Bioluminescence in action*. Academic Press, New York.
- DOWNES, J. A. 1969. The swarming and mating flight of Diptera. *Annu. Rev. Ent.* 14: 271-98.
- ELOFSON, O. 1941. Zur Kenntnis der marinen Ostracoden Schwedens mit besonderer Berücksichtigung des Skageraks. *Zoologiska Bidrag. fran Uppsala* 19: 215-534.
- FELDER, D. L. 1982. A report of the ostracode *Vargula harveyi* in the southern Bahamas and its implication in luminescence of a ghost crab, *Ocypode quadrata*. *Crustaceana* 42: 222-4.
- GREENFIELD, M. D. AND K. C. SHAW. 1983. Adaptive significance of chorusing with special reference to the Orthoptera. Pages 1-27 *In* D. T. Gwynne and G. K. Morris, Eds. *Orthopteran mating systems: sexual competition in a diverse group of insects*. Westview Press, Boulder, Colorado.
- HANEDA, Y. 1940. Phenomena of bioluminescence. *Seirigaku Shidoshu* 5: 18-31.
- HARTMANN, G. 1967. Bronns Klassen und Ordnungen des Tierreichs, 5, Abt. 1, Buch 2, Teil 4, Lief. 2: 217-408.
- HARVEY, E. N. 1952. *Bioluminescence*. Academic Press, New York.
- HASTINGS, J. W. 1983. Biological diversity, chemical mechanisms, and the evolutionary origins of bioluminescent systems. *J. Molec. Evol.* 19: 309-21.
- HERRING, P. J. (Ed.) 1978a. *Bioluminescence in action*. Academic Press, New York.
- . 1978b. Bioluminescence in invertebrates other than insects. Pages 199-240 *In* P. J. Herring, Ed. *Bioluminescence in action*. Academic Press, New York.
- . 1985. Bioluminescence in the Crustacea. *J. Crust. Biol.* 5: 557-73.
- AND J. G. MORIN. 1978. Bioluminescence in fishes. Pages 273-329 *In* P. J. Herring, Ed. *Bioluminescence in action*. Academic Press, New York.
- JOHNSON, F. H. AND O. Shimomura. 1978. Introduction of the *Cypridina* system. *In* M. DeLuca, Ed. *Methods in enzymology*. 57: 331-64. Academic Press, New York.
- KORNICKER, L. S. 1969. Relationship between the free and attached margins of the myodocopid ostracod shell. Pages 109-35 *In* J. W. Neale, Ed. *The taxonomy, morphology and ecology of recent Ostracoda*. Oliver and Boyd, Edinburgh.
- . 1975. Antarctic Ostracoda (Myodocopina). *Smithsonian Contrib. Zool.* (163): 1-720.
- . 1984. Cypridinidae of the continental shelves of southwestern North America, the northern Gulf of Mexico, and the West Indies (Ostracoda: Myodocopina). *Smithsonian Contrib. Zool.* (309): 1-29.
- AND J. H. BAKER. 1977. *Vargula tsujii*, a new species of luminescent Ostracoda from Lower and Southern California (Myodocopina: Cypridinidae). *Proc. Biol. Soc. Washington* 90: 218-31.
- AND C. E. KING. 1965. A new species of luminescent Ostracoda from Jamaica, West Indies. *Micropaleontology* 11: 105-10.

- LAPOTA, D. 1983. Bioluminescence in the marine ostracod *Cypridina americana* (Müller, 1890) off Manzanillo, Mexico (Myodocopa: Cypridinidae). Proc. Biol. Soc. Washington 96: 307-8.
- LLOYD, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. Miscel. Pub. Mus. Zool., Univ. Michigan (130): 1-95.
- . 1973a. Model for the mating protocol of synchronously flashing fireflies. Nature 245: 268-270.
- . 1973b. Fireflies of Melanesia: bioluminescence, mating behavior, and synchronous flashing (Coleoptera: Lampyridae). Environ. Ent. 2: 991-1008.
- . 1981. Mimicry in the sexual signals of fireflies. Sci. American 245: 138-45.
- . 1983. Bioluminescence and communication in insects. Annu. Rev. Ent. 28: 131-60.
- MORIN, J. G. 1983. Coastal bioluminescence: patterns and functions. Bull. Mar. Sci. 33: 787-817.
- AND E. L. BERMINGHAM. 1980. Bioluminescent patterns in a tropical ostracod. American Zool. 20: 851 (Abstr.).
- , A. HARRINGTON, K. NEALSON, N. KRIEGER, T. O. BALDWIN AND J. W. HASTINGS. 1975. Light for all reasons: versatility in the behavioral repertoire of the flashlight fish. Science 190: 74-6.
- MÜLLER, G. W. 1893. Ueber Lebensweise und Entwicklungsgeschichte der Ostracoden. Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 23: 355-81.
- NAKAMURA, N. 1954. Study on the ecology of *Cypridina hilgendorfi*. Pages 108-127 In Japanese Soc. of Fisheries, Eds. General view of fisheries. Published by the Japanese Assoc. Adv. Sci., Tokyo.
- OKADA, Y. AND K. KATO. 1949. Studies of luminous animals in Japan. III. Preliminary report on the life history of *Cypridina hilgendorfi*. Bull. Biogeogr. Soc. Japan 14: 22-5.
- OTTE, D. 1980. On theories of flash synchronization in fireflies. American Nat. 116: 587-90.
- POULSEN, E. M. 1962. Ostracoda-Myodocopa. 1: Cypridiniformes-Cypridinidae. Dana Report 57: 1-414.
- SARS, G. O. 1922. Ostracoda. An account of the Crustacea of Norway. 9(1-2): 1-277.
- SHIMOMURA, O. 1982. Mechanism of bioluminescence. Pages 249-76 In Chemical and biological generation of excited states. Academic Press, New York.
- SKOGSBERG, T. 1920. Studies on marine ostracods, 1: Cypridinids, halocyprids and polycopids. Zoologiska Bidrag fran Uppsala, supplement 1: 1-784.
- STEPIEN, C. A. AND R. C. BRUSCA. 1985. Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. Mar. Ecol. Prog. Ser. 25: 91-105.
- SULLIVAN, R. T. 1981. Insect swarming and mating. Florida Ent. 64: 44-65.
- TAKAGI, S. 1936. Ueber Sekretbildung in dem Leuchtorgan von *Cypridina hilgendorfi* Müller, mit besonderer Berücksichtigung der Mitochondrien. Annot. Zool. Japon. 15: 344-9.
- THORNHILL, R. AND J. ALCOCK. 1983. The evolution of insect mating systems. Harvard Univ. Press, Cambridge, MA.
- TSUJI, F. I. 1978. *Cypridina* luciferin and luciferase. In M. DeLuca, Ed. Methods in enzymology. 57: 364-72. Academic Press, New York.
- , R. V. LYNCH AND Y. HANEDA. 1970. Studies on the bioluminescence of the marine ostracod crustacean *Cypridina serrata*. Biol. Bull. 139: 386-401.
- WALKER, T. J. 1969. Acoustic synchrony: two mechanisms in the snowy tree cricket. Science 166: 891-4.
- . 1983. Diel patterns of calling in nocturnal Orthoptera. Pages 45-72 In D. T. Gwynne and G. K. Morris Eds. Orthopteran mating systems: sexual competition in a diverse group of insects. Westview Press, Boulder, Colorado.
- WARNER, J. A. AND J. F. CASE. 1980. The zoogeography and dietary induction of bioluminescence in the midshipman fish, *Porichthys notatus*. Biol. Bull. 159: 231-46.

- , M. I. LATZ AND J. F. CASE. 1979. Cryptic bioluminescence in a midwater shrimp. *Science* 203: 1109-10.
- YATSU, N. 1917. Note on the structure of the maxillary gland of *Cypridina hilgendorfi*. *J. Morph.* 29: 435-40.
- YOUNG, R. E. 1983. Ocean bioluminescence: an overview of general functions. *Bull. Mar. Sci.* 33: 829-45.
- AND C. F. E. ROPER. 1977. Intensity regulation of bioluminescence during countershading in living midwater animals. *Fish. Bull., U. S.* 75: 239-252.

MULTIPLE MATING, SPERM COMPETITION AND THE FERTILITY COMPONENT OF FITNESS IN *DROSOPHILA PSEUDOOBSCURA*

MONTE E. TURNER*

SYNOPSIS

Those aspects of an organism's biology that influence the number of progeny produced make up the fertility component of its fitness. The fertility of both male and female *Drosophila pseudoobscura* is influenced by multiple matings. In the former, rates of multiple matings and the genotypes of females' other mates interact to affect male fitness. Female fecundity and productivity increases with multiple matings, while longevity declines. Mating rates could be the result of these conflicting selection pressures. Density is a non-genetic factor influencing multiple mating. The mechanisms by which multiple matings increase female fertility is not the same in different species of *Drosophila*. In *D. melanogaster*, subsequent matings appear to replenish diminished sperm stores, while in *D. pseudoobscura*, females may absorb sperm for use as a nutrient. These differences emphasize that there need not be single "model systems" even within a genus.

INTRODUCTION

Because many factors over an organism's life contribute to its fitness, this total fitness can be divided into separate components, each of which relates to a specific life stage (Prout 1965, 1969, 1971a, 1971b). This division into smaller fitness components allows for a better understanding of their individual contributions. Two major components are usually recognized, viability and fertility. The viability component of fitness includes parameters such as egg to adult survival and specific age group survival. The aspects of an organisms biology that influence the number of progeny, such as fecundity or male mating success, are included in the fertility component.

While there has been a historical emphasis on the viability component, laboratory experiments with *Drosophila pseudoobscura* have demonstrated that the fertility component can be as large or larger (Anderson and Watanabe 1974). As an illustration imagine two genotypes A_1A_1 and A_2A_2 which have very different fitnesses. If A_1A_1 individuals have more adult offspring than A_2A_2 individuals, it may be that A_1A_1 females

*Monte Turner is an Assistant Professor in the Department of Biology at the University of Akron. His research focuses on the genetic structure of populations. Current address: Department of Biology, University of Akron, Akron, Ohio, 44325.

- , M. I. LATZ AND J. F. CASE. 1979. Cryptic bioluminescence in a midwater shrimp. *Science* 203: 1109-10.
- YATSU, N. 1917. Note on the structure of the maxillary gland of *Cypridina hilgendorffii*. *J. Morph.* 29: 435-40.
- YOUNG, R. E. 1983. Ocean bioluminescence: an overview of general functions. *Bull. Mar. Sci.* 33: 829-45.
- AND C. F. E. ROPER. 1977. Intensity regulation of bioluminescence during countershading in living midwater animals. *Fish. Bull., U. S.* 75: 239-252.

MULTIPLE MATING, SPERM COMPETITION AND THE FERTILITY COMPONENT OF FITNESS IN *DROSOPHILA PSEUDOOBSCURA*

MONTE E. TURNER*

SYNOPSIS

Those aspects of an organism's biology that influence the number of progeny produced make up the fertility component of its fitness. The fertility of both male and female *Drosophila pseudoobscura* is influenced by multiple matings. In the former, rates of multiple matings and the genotypes of females' other mates interact to affect male fitness. Female fecundity and productivity increases with multiple matings, while longevity declines. Mating rates could be the result of these conflicting selection pressures. Density is a non-genetic factor influencing multiple mating. The mechanisms by which multiple matings increase female fertility is not the same in different species of *Drosophila*. In *D. melanogaster*, subsequent matings appear to replenish diminished sperm stores, while in *D. pseudoobscura*, females may absorb sperm for use as a nutrient. These differences emphasize that there need not be single "model systems" even within a genus.

INTRODUCTION

Because many factors over an organism's life contribute to its fitness, this total fitness can be divided into separate components, each of which relates to a specific life stage (Prout 1965, 1969, 1971a, 1971b). This division into smaller fitness components allows for a better understanding of their individual contributions. Two major components are usually recognized, viability and fertility. The viability component of fitness includes parameters such as egg to adult survival and specific age group survival. The aspects of an organisms biology that influence the number of progeny, such as fecundity or male mating success, are included in the fertility component.

While there has been a historical emphasis on the viability component, laboratory experiments with *Drosophila pseudoobscura* have demonstrated that the fertility component can be as large or larger (Anderson and Watanabe 1974). As an illustration imagine two genotypes A_1A_1 and A_2A_2 which have very different fitnesses. If A_1A_1 individuals have more adult offspring than A_2A_2 individuals, it may be that A_1A_1 females

*Monte Turner is an Assistant Professor in the Department of Biology at the University of Akron. His research focuses on the genetic structure of populations. Current address: Department of Biology, University of Akron, Akron, Ohio, 44325.

lay more eggs (fertility) or more A_1A_1 eggs survive to adulthood (viability). In the experiments described here, fitness has been defined in two ways, either as the number of eggs (fecundity) or as the number of adult progeny (productivity) produced by a particular genotype. Productivity includes both fecundity and egg to adult survival, although in a laboratory setting conditions are usually modified such that egg-adult survivals are not significantly different between the tested genotypes. In these cases, results from fecundity and productivity are not qualitatively different. Note that traits such as male mating success are included in the fertility component as a male genotype that mates more often has more offspring and thus a higher fitness. High levels of multiple mating occur in natural populations of *D. pseudoobscura* (Anderson 1974, Cobbs 1977, Levene et al. 1980) as do significant differences in male mating success among certain third chromosome inversion karyotypes (Anderson et al. 1979). Using such differences, the question arises as to how multiple mating and the resulting opportunity for sperm competition affect the fertility component of fitness in *D. pseudoobscura*. Since males and females are affected differently by multiple mating, first results focusing on males will be presented, then results from a female perspective.

MALE FITNESS AND MULTIPLE MATING

Sperm Competition, the competition between sperm from two or more males for the fertilization of a female's eggs, frequently results in the differential utilization of sperm from different ejaculates (Parker 1970). This can have significant effects on male fitness. Sperm precedence refers to the proportion of progeny from a multiply-mated female that are fathered by each male. The preponderance of offspring from the last male has been termed sperm displacement or sperm predominance. The latter term is preferred since it implies no mechanism (Gromko et al. 1984). From a fertility fitness perspective the highest male fitness would be the genotype that maximizes the number of offspring fathered regardless of the order of mating.

If we assume that multiply-mated females have mated with only two males, the total sperm competition fitness component for males is dependent on three parameters; P' , P_1 , and P_2 . P' is the number of offspring fertilized by a male genotype *before* the female remates. P_1 and P_2 are the proportion of offspring fertilized by a male genotype *after* a female remates; P_1 when he was the first male and P_2 when he was the second, (Gromko et al. 1984, Turner and Anderson 1984). From a fitness perspective the important parameter is the total of all three, which give an average number of offspring fertilized by a particular male genotype. As a complication, P_1 and P_2 would have to be weighted by rates of multiple mating and the male mating success for that genotype. These fitnesses could be density dependent, since changing density changes the rate of multiple mating and, therefore, the contribution of P_1 and P_2 to the total. In general, with little remating P' may be the best predictor of a male's reproductive fitness component while in populations with high remating rates, the sum of P_1 and P_2 may be the best predictor. All three parameters (P' , P_1 , P_2) have not been measured for any genotype (in any species) but for some genotypes in *D. pseudoobscura* at least P_1 and P_2 have been measured. Note that from the perspective of any one female $P_1 + P_2$ must equal 1.0 (assuming she has mated twice) but for a particular male $P_1 + P_2$ need not equal 1.0 since the two values are measured in different females.

The determination of P_1 and P_2 requires a means of determining paternity in the offspring of multiply-mated females. In *D. pseudoobscura* two methods of detection have been used, either a recessive morphological marker, orange eyes (Beckenbach 1981; Pruzan-Hotchkiss et al. 1981) or an amylase allozyme marker (Turner and Anderson 1984). A problem with the orange eye marker is it has significantly lower P_1 and

P_2 values (Beckenbach 1981) than wild type (red eye) individuals, while the allozyme marker seems to have no significant effect (Turner and Anderson 1984).

There are no significant differences in P_2 in the naturally occurring genotypes that have been tested. Eight third chromosome gene arrangement karyotypes (Turner and Anderson 1984) and two X-chromosome gene arrangements (Beckenbach 1981) have been used to measure P_2 with the first male genotype constant. In all cases P_2 values ranged from .82 to .90. These results simplify the sperm competition fitness component for *D. pseudoobscura* since for these genotypes the P_2 component can be eliminated, thus any fitness differences must occur through differences in either P' or P_1 .

There are significant differences in P_1 for these *D. pseudoobscura* genotypes. Values of P_1 for eight third chromosome gene arrangement genotypes ranged from .15 to .49 with 6 of 28 pairwise combinations being significant (Turner and Anderson 1984). However, Beckenbach (1981) found no significant P_1 differences between the two X-chromosome gene arrangements. How do these P_1 values relate to observed total fitnesses in laboratory cage populations? The best data are for populations containing the ST (Standard) and CH (Chiricahua) gene arrangements (Dobzhansky and Pavlovsky 1967, Anderson unpubl. data) which have relative fitnesses in the following relationship, ST/CH > ST/ST > CH/CH. The rank order of P_1 values for these genotypes is ST/CH > ST/ST > CH/CH. These parallel results suggest that a portion of the total fitness difference between these *D. pseudoobscura* lines results from differences in the sperm competition abilities of males, and more specifically differences in P_1 .

Male fitness parameters are not constant for any particular genotype, but dependent on the genotype of the other mates of the multiply-inseminated female. For instance, in the measurement of P_1 for third chromosome gene arrangements six crosses had the same genotype second male and P_1 's varied from .12 to .49 (Turner and Anderson 1984). If P_1 had this variation then P_2 for the second male genotype also varied from .88 to .51 depending on the genotype of the first male. Thus, for any genotype the values of P_1 and P_2 are an array of pairwise comparisons with all other genotypes in the population. The possibility that the female genotype influences P_1 and P_2 values has been tested, and there is no statistically significant effect (Turner and Anderson 1984). However, this lack of significance may well be the result of small sample sizes, since there was a great deal of variation observed.

Sperm competition data indicate that a male's fertility component of fitness is a very complex parameter. It is influenced by: rates of multiple mating, male mating success (first and subsequent matings), genotypes of the females other mates, P' , P_1 , P_2 and possibly the female genotype. Many of these parameters are not constants but vary according to other male (and female) genotypes in the population.

MULTIPLE MATING AND FEMALE FITNESS

Although students of sperm competition have focused primarily on males, multiple mating can also influence fitness in females. In *D. melanogaster* both males (Partridge and Farquhar 1981) and females (Kidwell and Malick 1965) show reductions in longevity due to the act of mating. For multiple mating to persist it would seem this decrease in the viability component must be offset by a gain in the reproductive (or some other) component of fitness. Boggs and Gilbert (1979) demonstrated that in three species of butterflies, females absorb part of the male ejaculate and incorporate it into protein. Similarly, *D. mojavensis* females also absorb a portion of the ejaculate, though *D. melanogaster* females do not (Markow and Ankney 1984). Species with this ability may be able to offset the viability disadvantage of multiple mating, since a female with more mates enhances her nutritional state. An increased nutrient uptake allows a female to produce more eggs thus increasing her fitness.

Beckenbach (1981) has shown that *D. pseudoobscura* females will remate within 24 hours after a first mating. In a separate study over 50% of singly-mated females remated when exposed to another male three days after their first mating, (Turner and Anderson 1984). Measurements of fecundity (Beckenbach 1978) or productivity (Turner and Anderson 1983) show that singly-mated females have depleted little of their stored sperm after 1 to 3 days and that remating to replenish stored sperm should not be necessary. How then does multiple mating affect the fertility component of fitness in *D. pseudoobscura* females? Three studies have found that multiply-mated females have a higher fertility component of fitness than females mated once (Beckenbach 1978, Pruzan-Hotchkiss et al. 1981, and Turner and Anderson 1983). The extent of their advantage is dependent on the environment, with a large increase (over 200%) in "poor" environments and a smaller one (about 20%) in "good" environments (Turner and Anderson 1983). These productivity results are consistent with the hypothesis that *D. pseudoobscura* females can and do absorb nutrients from the ejaculate. This is apparent as increased productivity in the poor environment.

Although multiple mating increases the fertility component of fitness, it lowers the viability component in *D. pseudoobscura*. There must be a cost to either the mating itself or the increased egg production because multiply-mated females have significantly lower daily survivals. However, as the fertility advantage outweighs this viability disadvantage, multiply-mated females have a higher overall fitness (Turner and Anderson 1983). Recent results (Hoffman and Harshman 1985) indicate that more than multiple mating may account for this increase. In a study with *D. melanogaster*, females exposed to males after mating but not allowed to remate, had a significant increase (about 35%) in both fecundity and productivity. Their experiments were done under "poor" conditions which was hoped to accentuate any effects. *Drosophila pseudoobscura* was not tested, but it is possible that a portion of the increased fitnesses observed results from a male-produced factor whose effect is to stimulate oviposition in females without mating.

RATES OF MULTIPLE MATING

The first evidence that a *D. pseudoobscura* female in nature would mate with more than one male was a single doubly inseminated female discovered by Koller in 1939. Since then, a number of *D. pseudoobscura* populations have been examined and their frequencies of multiple mating estimated (Dobzhansky et al. 1963, Anderson 1974, Cobbs 1977, Levene et al. 1980). With the exception of an 8% estimate by Dobzhansky et al. (1963), which because of its protocol may have greatly underestimated multiple matings (cf. Levene et al. 1980, for discussion), these estimates range from about 40% (Cobbs 1977) to over 90% (Levene et al. 1980). Although each study used different methods of estimation, the overall conclusion is that natural populations of *D. pseudoobscura* do vary in their frequencies of multiple mating.

With the demonstration that multiply-mated females have significantly more offspring than single-mated females and that the amount of this advantage is dependent on the environment, the potential exists for rates of multiple mating in natural populations to be adaptive, i.e. the result of selection. For example, poor environments might have high rates of multiply-mated females. While in good environments, where a lesser fertility advantage might not offset decreased viability, a lower rate of multiple mating would be expected. A necessary pre-requisite for this is that at some time there was genetic variation influencing whether a female remates. In one laboratory study (Dobzhansky and Pavlovsky 1967) females homozygous for different third chromosome gene arrangements remated at significantly different frequencies. However, this is an isolated result and more investigation is needed.

Selection as a result of fitness differences is not the only factor that could affect rates of multiple-mating. One possible non-genetic influence is density. In *D. pseudoobscura* and *D. persimilis* (a close relative of *D. pseudoobscura*) increasing density increases the frequency of first matings (Spiess and Spiess 1969, Ekstrand and Seiger 1975), and has been hypothesized to have similar effects on multiple matings (Richmond 1976, Levene et al. 1980). However, increasing density decreases the frequency of both first (Jacobs 1960) and second matings in *D. melanogaster* (Gromko and Gerhart 1984). Densities vary widely between different populations and between different seasons in the same population (Dobzhansky and Wright 1947). Most important though, in comparing frequencies of multiple mating with experimental results of productivity, is good and poor environments probably have very different densities (Johnston and Heed 1975). With such differences a knowledge of the effects of density on the frequency of multiple mating is essential to any predictions about rates of multiple mating.

Table 1 shows the effect of different densities on rates of multiple mating in *D. pseudoobscura*. Females that had mated three days previously were confined in vials with *Drosophila media* and another genotype male for 48 hours in several different densities. Their progeny were examined using an electrophoretic assay (see Turner and Anderson 1984) to determine whether they had mated with the second male. Density had a highly significant effect on the frequency of multiple mating ($\chi^2 = 24.91$, 3df, $p < .001$). In general there is an optimal density (20 pairs) and changing from this optimum (either higher or lower) decreases the frequency of multiple matings. The frequencies measured compare closely with rates from natural populations, 40% to 90% for natural populations versus 55% to 91% for the current data (Table 1). How these laboratory densities compare to densities in natural populations is not known. The comparison of rates of multiple mating between temporal samples of the same population would be meaningless without correcting for possible density differences. These results demonstrate the high levels of multiple mating in some natural populations need not be the result of selection to increase multiple matings but could be a byproduct of the density of that particular population.

At lower densities *D. pseudoobscura* and *D. melanogaster* females have opposite responses. It could be argued that in each species their response to density is the result of fitness differences for different density responses. Alternatively, these responses could be a byproduct of another aspect of the reproductive behavior. A number of additional experiments need to be done examining rates of multiple mating before either of these alternatives can be any more than speculation.

TABLE 1. NUMBERS OF MULTIPLY-MATED FEMALES, FREQUENCY OF MULTIPLE MATING AND THE NUMBER OF FEMALES TESTED FOR DIFFERENT DENSITIES OF MALES AND FEMALES.

Density (males:females)	Multiply Mated	Total Tested	Frequency
5:5	11	15	.73
10:10	28	36	.78
20:20	63	69	.91
30:30	43	78	.55
$\chi^2 = 24.91$ $df=3$ $p<.001$			

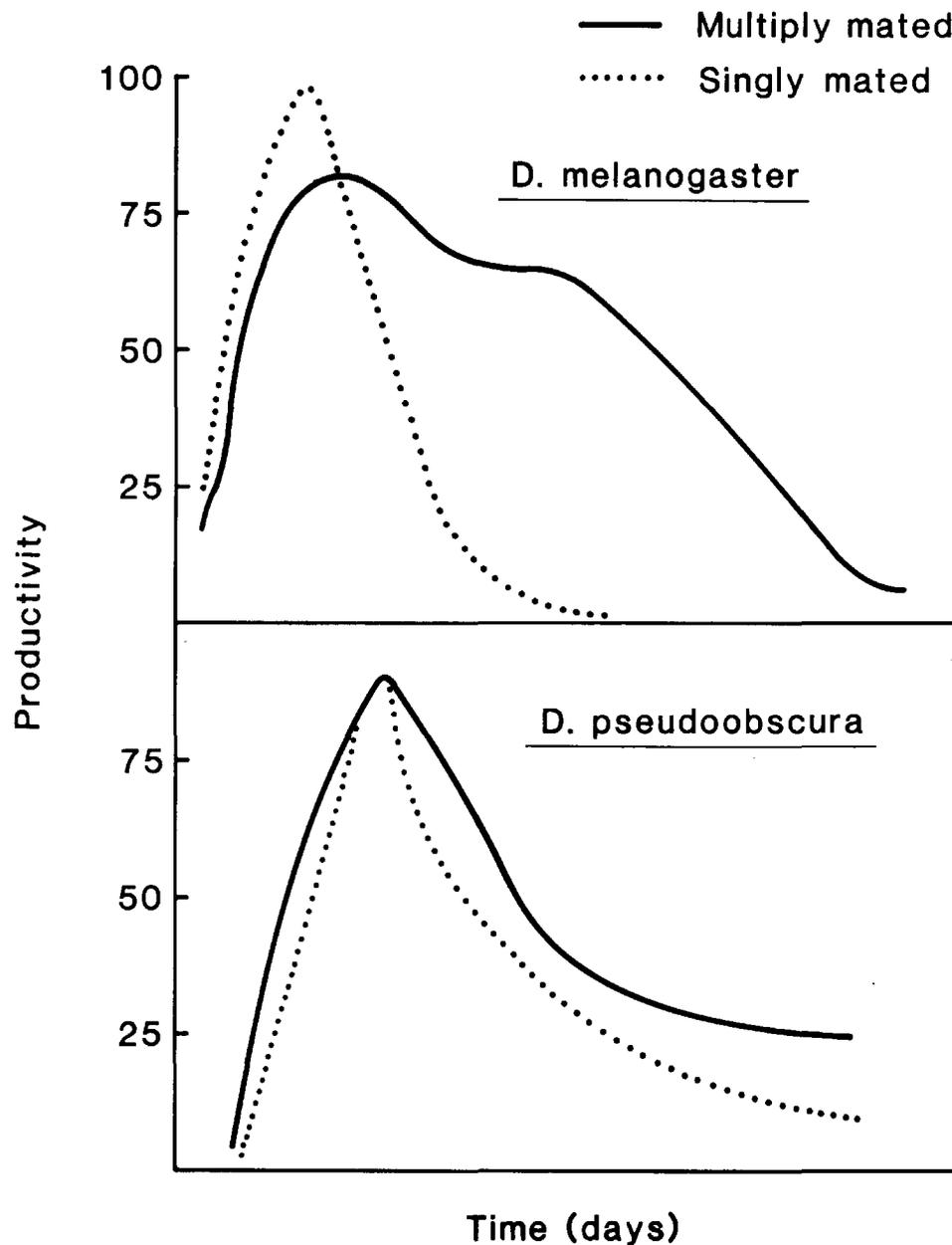


Fig. 1. Generalized daily productivity of *D. melanogaster* (after Pyle and Gromko 1978) and *D. pseudoobscura* (after Turner and Anderson 1983) that have mated singly or multiply.

COMPARISONS TO *D. MELANOGASTER*

Both *D. pseudoobscura* and *D. melanogaster* females experience a fitness advantage with multiple mating, but the nature of their responses are quite different. Figure 1 presents generalized productivity curves for *D. melanogaster* (after Pyle and Gromko 1978) and *D. pseudoobscura* (after Turner and Anderson 1983). The multiply mated *D. melanogaster* female's productivity remains high while the singly mated female's productivity decreases quickly. These curves are of the form expected if multiple mating

were replenishing the sperm load depleted by fertilization. In *D. pseudoobscura* the productivity curves for singly and multiply-mated females have the same shape, but the multiply-mated productivities are consistently higher. This suggests that remating stimulates productivity rather than just replenishing sperm used. Thus the mechanisms through which multiple mated females increase productivity seem different in the two species.

In poor environments, the productivity curves for singly and multiply mated *D. pseudoobscura* females change dramatically (Turner and Anderson 1983). The two curves now have the same shape as the *D. melanogaster* result, but productivities are severely depressed (about 20% of normal). In this poor environment sperm replenishment seems to be occurring. Perhaps replenishment occurs in the poor environment because the females absorbed sperm, while in good environments absorption is reduced. *D. melanogaster* females in poor environments remate at significantly lower rates than females in good environments (Gromko and Gerhart 1984, David et al. 1971). Apparently, sperm replenishment is not needed because the decreased fecundity in poor environments requires fewer sperm for fertilizations. This is observed as a lower rate of multiple mating.

The conclusions from these comparisons are important to general considerations of sperm competition and the fertility component of fitness. The results of sperm competition and multiple mating are species specific, predictions for *D. pseudoobscura* from the *D. melanogaster* data would be wrong and vice versa. In *Drosophila* at least, there is apparently no model system and extensions to other species (both Drosophilids and others) from the results of either *D. melanogaster* or *D. pseudoobscura* should be as testable hypotheses and not as general conclusions. Each species of interest needs to be considered individually in its response to multiple mating and sperm competition.

REFERENCES CITED

- ANDERSON, W. W. 1974. Frequent multiple insemination in a natural population of *Drosophila pseudoobscura*. *Am. Natur.* 108: 709-711.
- ANDERSON, W. W. and T. K. WATANABE. 1974. Selection by fertility in *Drosophila pseudoobscura*. *Genetics* 77: 559-564.
- BECKENBACH, A. T. 1978. The "sex-ratio" trait in *Drosophila pseudoobscura*: fertility relations of males and meiotic drive. *American Natur.* 112: 97-117.
- BECKENBACH, A. T. 1981. Multiple mating and the "sex-ratio" trait in *Drosophila pseudoobscura*. *Evolution* 35: 275-281.
- BOGGS, C. L. AND L. E. GILBERT. 1979. Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. *Science* 206: 83-84.
- COBBS, G. 1977. Multiple inseminations and male sexual selection in natural populations of *Drosophila pseudoobscura*. *American Natur.* 111: 641-656.
- DOBZHANSKY, TH. 1970. *Genetics of the Evolutionary Process*. Columbia Univ. Press, N.Y.
- DOBZHANSKY, TH. AND S. WRIGHT. 1947. *Genetics of Natural populations*. XIV. A response of certain gene arrangements in the third chromosome of *Drosophila pseudoobscura* to natural selection. *Genetics* 32: 142-160.
- DOBZHANSKY, TH., B. SPASSKY, AND T. TIDWELL. 1963. *Genetics of natural populations*. XXXII. Inbreeding and the mutational and balanced genetic loads in natural populations of *Drosophila pseudoobscura*. *Genetics* 48: 361-374.
- DOBZHANSKY, TH. AND O. PAVLOVSKY. 1967. Repeated mating and sperm mixing in *Drosophila pseudoobscura*. *American Natur.* 101: 527-533.
- ECKSTRAND, I. A. AND M. B. SEIGER. 1975. Population density and mating rates in *Drosophila pseudoobscura*. *Evolution* 29: 287-295.
- FOWLER, G. L. 1973. Some aspects of the reproductive biology of *Drosophila*: sperm

- transfer, sperm storage, and sperm utilization. *Adv. Genet.* 17: 293-360.
- GROMKO, M. H. AND P. D. GERHART. 1984. Increased density does not increase remating frequency in laboratory populations of *Drosophila melanogaster*. *Evolution* 38: 451-455.
- GROMKO, M. H., D. G. GILBERT, AND R. C. RICHMOND. 1984. Sperm transfer and use in the repeat mating system of *Drosophila*. In *Sperm Competition and the Evolution of Animal Mating Systems*. R. L. Smith ed., Academic Press, N.Y.
- HOFFMAN, A. A. AND L. G. HARSHMAN. 1985. Male effects on fecundity in *Drosophila melanogaster*. *Evolution* 39: 638-644.
- JACOBS, M. E. 1960. Influence of light on mating of *Drosophila*: the effect of baiting on the behavior and distribution of natural populations. *American Natur.* 109: 207-216.
- KIDWELL, J. F. AND L. E. MALICK. 1965. The effect of genotype, mating status, weight and egg production on longevity in *Drosophila melanogaster*. *J. Hered.* 58: 169-172.
- KOLLER, P. C. 1939. Genetics of natural populations. III. Gene arrangements in populations of *Drosophila pseudoobscura* from contiguous localities. *Genetics* 24: 22-33.
- LEVENE, L., M. ASMUSSEN, O. OLEVERA, J. R. POWELL, M. E. DELAROSA, V. M. SALCEDA, M. I. GASO, J. GUZMAN, AND W. W. ANDERSON. 1980. Population genetics of Mexican *Drosophila*. V. An extremely high rate of multiple insemination in natural population of *Drosophila pseudoobscura*. *American Natur.* 110: 485-486.
- MARKOW, T. A. AND P. F. ANKNEY. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. *Science* 224: 302-303.
- PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525-567.
- PARTRIDGE, L. AND M. FARQUHAR. 1981. Sexual activity reduces lifespan of male fruitflies. *Nature* 294: 580-582.
- PROUT, T. 1965. The estimation of fitness from genotypic frequencies. *Evolution* 19: 546-551.
- PROUT, T. 1969. The estimation of fitnesses from population data. *Genetics* 63: 949-967.
- PROUT, T. 1971a. The relation between fitnesses components and population prediction in *Drosophila* II. Population prediction. *Genetics* 68: 151-167.
- PRUZAN-HOTCHKISS, A., D. DEJIANE AND S. H. FARO. 1981. Sperm utilization in once and twice mated *Drosophila pseudoobscura* females. *American Natur.* 118: 37-45.
- PYLE, D. W. AND M. H. GROMKO. 1978. Repeated mating by female *Drosophila melanogaster*: the adaptive importance. *Experientia* 34: 449-450.
- RICHMOND, R. C. 1976. Frequency of multiple insemination in natural populations of *Drosophila*. *American Natur.* 110: 485-486.
- SPIESS, L. D. AND E. B. SPIESS. 1969. Mating propensity, chromosomal polymorphism and dependent conditions in *Drosophila persimilis*. II. Factors between larvae and adults. *Evolution* 23: 225-236.
- TURNER, M. E. AND W. W. ANDERSON. 1983. Multiple mating and female fitness in *Drosophila pseudoobscura*. *Evolution* 37: 714-723.
- TURNER, M. E. AND W. W. ANDERSON. 1984. Sperm predominance among *Drosophila pseudoobscura* karyotypes. *Evolution* 38: 983-995.

BEHAVIORAL ECOLOGY, MILESTONES

J. E. LLOYD

Dept. of Entomology and Nematology
University of Florida, Gainesville, FL 32611

Behavioral Ecology Symposium-'85 held at Ocho Rios, Jamaica (7 Aug. 1985), was the 7th, and marked a turning point. Papers from the first six Symposia were published in the *Florida Entomologist* in March of each following year, and also in paper-bound separates. (I still have some; ask.) The Ocho Rios Symposium will appear only in the *Florida Entomologist*. The cost of producing separate booklets got to be too much. The papers will appear mostly in March, but some may turn up later in the year.

Also, the editing chores of Symposium-'85 fell upon several volunteers, and I simply read and admired the finished manuscripts, mostly. The editors were, or will be in cases of manuscripts that are still unaccounted for, Ted Burk, Charlie Henry, John Sivinski, Frank Slansky, and Tom Walker. I thank them for doing the heavy work, and making my schedule considerably easier.

Finally, in transition or termination, Symposium-'85 was the last Symposium of the series. I have some firefly stuff to write up and house cleaning to do.

Participants in Symposia past voted unanimously to recognize the valuable contribution that taxonomy in general and certain taxonomists in particular have made to the field of Insect Behavioral Ecology, and present a plaque to the four taxonomists at the Florida State Collection of Arthropods. The plaque was the same sort presented to John



Symposium participants and editors. Front row, l to r: Don Strong, Jeremy McNeil, James Quinn, Monte Turner. Back row: James Morin, George Eickwort, Howard Frank, James Lloyd, Mark Rausher, Tom Walker, John Sivinski. Photographed by Frank Mead, FADCS-DPI. 7 August 1985, Ocho Rios, Jamaica, W.I.



FSCA taxonomists recognized by FES-IBE participants for their contribution to the field of insect behavioral ecology. Left to right: Frank W. Mead, Howard V. Weems, Jr., Harold A. Denmark and Robert E. Woodruff. Frank seems to reveal exasperation with having his photo taken—for years he has been the man *behind* the camera for FES affairs. Photo by Jeffrey W. Lotz, FADCS-DPI.

Alcock last year (See Symposium-'84, page 139). The inscription reads: "To H. A. Denmark, F. W. Mead, H. V. Weems, Jr., and R. E. Woodruff, in grateful recognition of their contributions to the field of Insect Behavioral Ecology through their more than 120 collective years of service to insect taxonomy. From FES-IBE Participants. March 1986." Gents, we want you to know your efforts have been appreciated, and we sing for you.

Participants in Symposia past also voted "to recognize and show appreciation for a valuable published contribution, such as a book or coherent series of publications, to the field of insect behavioral ecology," as they did a year ago with the presentation of a plaque to John Alcock. This year, the recipient is Richard D. Alexander of The University of Michigan. Among the contributions noted in the nomination were his pioneering work on insect communication and the application of behavior to insect systematics. It was noted that "all the leading insect behavioral ecologists have an 'Alexander connection'." Congratulations Dick, and thanks.

I thank the Executive and Program Committees of the Society for their support and cooperation; and also Barbara Hollien for help with technical details, typing mss., mailing ballots, etc. Symposium-'85 was made possible by contributions from IFAS, through the efforts of Dan Shankland, and the Society.





SYMPOSIUM: USE OF PHEROMONES IN TROPICAL CROPS

PREFACE

Insect sex pheromones—They have been hyped and sold by researchers and industry alike as some type of magic elixir to solve the major insect pest control problems of the developed world. The approaches have been imaginative and bold, ranging from spraying the pheromone into the atmosphere to prevent mating, to using traps baited with these potent attractants to decide how to apply pesticide treatments. Many of our colleagues in the less developed areas of the world “have heard the word” and wish to participate in this new pest control phenomenon. Unfortunately, most lack the resources, facilities, and often the skills to develop pheromones for their own use. Frequently, the insects involved are different species, and to develop pheromones to the state-of-the-art uses that now exist for many pest species in North America, Europe, and elsewhere would be an insurmountable task even under the best of circumstances. Therefore, a symposium on the Use of Pheromones in Tropical Crops was held at the 1985 Florida Entomological Society meeting held jointly with our entomological colleagues from the Caribbean Basin and Central and South America, in Ocho Rios, Jamaica, August 5-8. The purpose of the symposium was to demonstrate the usefulness of pheromones in insect pest management projects and to encourage pest managers and entomologists interested in using pheromones in their programs to use the expertise and supplies available to them through research reports and industry, primarily from the United States. Development of such liaisons would allow almost instantaneous transfer of a form of “high technology” to areas which necessarily must still rely on low-level technology to meet the socio-economic needs in their own agrarian lifestyles.

Everett R. Mitchell
Research Leader,
Behavioral Ecology and Reproduction,
Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U. S. Department of Agriculture,
Gainesville, Florida 32604

PHEROMONES: AS THE GLAMOUR AND GLITTER FADE—
THE REAL WORK BEGINS

EVERETT R. MITCHELL

Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U. S. Department of Agriculture,
Gainesville, Florida 32604

ABSTRACT

Sex pheromones have been proclaimed throughout the technologically advanced regions of the world as having great potential for managing insect pests through manipulation of their mating behavior; annihilation by mass trapping; and monitoring and surveys which facilitate control through early detection of pests allowing the timely application of pesticides. Yet, very little of this potential has been realized. How then can pheromones become a part of insect pest control schemes in tropical regions of the world where many countries with meager resources are struggling to introduce modern insect pest management practices? The key lies in education of the scientist-extensionist-farmer connection and a deep commitment to the development to one aspect of sex pheromones: *trapping for monitoring and survey*. The technological tools generally are available; the real work involves developing the relationships between pheromone trap catches with insect populations and plant damage thresholds.

RESUMEN

Las feromonas del sexo se han proclamado a través de las regiones avanzadas tecnológicamente como teniendo gran potencial para administrar plagas de insectos a través de la manipulación del comportamiento de apareamiento; aniquilación por medio de trampas; y el chequeo y muestreo que facilitan el control a través de detección temprana de plagas, así aplicando pesticidas oportunamente. Sin embargo, muy poco potencial se ha realizado. ¿ Como pudieran entonces las feromonas ser parte de un plan para controlar plagas en regiones tropicales del mundo donde muchos países con pocos recursos están luchando para introducir practicas modernas para el manejo de plagas?. La clave se encuentra en la educación del científico—extensionista—farmero, y en un profundo deseo para el desarrollo de un aspecto de las feromonas sexuales: trampas para chequeos y encuestas. Los medios tecnologicos están generalmente disponibles; el verdadero trabajo implica el desarrollo de relaciones entre lo que se atrapa en las trampas de feromonas con las poblaciones de insectos y el umbral de daño de las plantas.

Pheromones constitute one category of the group of chemicals known as "semiochemicals," i.e., messenger chemicals, and they are used throughout the Animal Kingdom for communication and regulation of behavior. Pheromones provide information about potential danger, territory, food, trails, aggregation, sex attraction, mating, and egg laying.

Insect sex pheromones are the most widely and intensely studied of all animal communication systems. During the past 20 years, sex pheromones and attractants have been identified for over 600 different species (Inscoc 1982), and new identifications appear in our scientific literature with almost unbelievable regularity. This great leap forward in pheromone research has been propelled by the development of sophisticated analytical equipment and new techniques which now permit identification using minute quantities of material as low as the picogram level. As might be expected, the large number of pheromone identifications have spawned an even greater number of publica-

tions on pheromone biology, behavior, and potential for utilizing pheromones as tools to control or manipulate insect pests. It is the belief that pheromones can become a significant factor in insect pest control that continues to drive the "pheromone research machine."

I propose here that pheromones can, and indeed, are being used in selected cropping situations to improve insect pest management practices. The key here is "selectivity." Can pheromones be used as a component of insect pest control strategies in tropical environments? Indeed, they can, but as is true in the more temperate regions of the world, ingenuity, creativity, and simplicity are critical to the integration of these powerful tools into any insect pest control system.

USES FOR PHEROMONES IN INSECT PEST MANAGEMENT

Numerous proposals have been put forth on how pheromones may be used to control insects (Mitchell 1981 and papers therein). However, considering the thousands of papers that have been written on insect pheromones, the number of papers detailing actual utilization of pheromones for any purpose is disappointingly low. The reasons for this are many and varied, not the least of which is that most people who have been and continue in pheromone research are involved in identifying pheromones and studying the basics of sex pheromone communication, rather than developing the "how" to put pheromones into practical usage. This does not necessarily indicate a disinterest in developing such information, but more realistically, reflects the work situation in which many researchers find themselves. They often are located in research facilities with little or no direct contact with actual cropping situations, and many also have no practical knowledge of the intricacies of insect pest control.

There are, essentially, three approaches to the use of pheromones in insect pest management: annihilation through mass trapping; disruption of sex pheromone communication; and monitoring with traps. I will not attempt to give an encyclopedic account of all the research which has been reported on each of these approaches. Rather, I will define briefly each approach, and give my opinion as to its potential for adoption as a viable pest control strategy in the tropics and elsewhere.

Mass Trapping—This involves the concentration of many traps in an area with the goal of capturing enough adults to significantly reduce the population. Trapping for annihilation is most effective against species with low birth rates and survivorship, which exist at low equilibrium densities and have density-dependent regulation and low dispersal rate (Barclay 1984). Unfortunately, many pests occur in outbreaks, and as such, their regulation is density-independent most of the time (Barclay & Van Den Driessche 1984). Consequently, suppression of insect pest populations using pheromone-baited traps probably is not a viable alternative to conventional control methods except, perhaps, in isolated situations, such as on an island or in an area newly infested by an introduced insect pest.

Recently, researchers have begun to explore the possibility of eliminating the trap by combining pheromone-pesticide formulations that can be broadcast *en masse*. The success of this annihilation technique likely will depend upon the use of a combination of attractants (pheromone, food) to ensure killing a large proportion of both males and females.

Disruption of Mating Communication—The air permeation technique for disrupting mating communication has been explored around the world by both public agencies and private enterprise for control of a wide variety of insect pests on numerous crops (Mitchell 1981 and papers therein). The premise of this approach is to distribute enough artificial point sources throughout an area such that an insect that relies on the use of a pheromone to locate a mate will be unsuccessful because the atmosphere is permeated

with pheromone. It has yet to be determined whether the insect's inability to find a mate is due simply to confusion or because communication is disrupted as a result of habituation by the perceiving insect. Although much has been written on this approach, the full potential of the mating disruption technique for control of any insect pest has yet to be realized. The mating disruption approach to insect pest control shares the same inherent limitations which characterize the mass trapping approach. In addition, a successful mating-disruption control program is dependent upon a delivery technology that remains in a state of flux and which has not yet achieved an industry standardization critical to grower acceptance. However, the air permeation technique may yet become a useful component in some insect pest control strategies, but the success of this technique will depend upon a careful choice of the target pest. Mating disruption, resulting in subsequent reductions in population numbers and crop damage levels, is achieved only through a complex of events which may affect species differentially, depending upon the insects' behavior and host crop condition. Thus, considerable research is needed before the atmospheric permeation technique will become a significant part of insect pest control strategy.

Monitoring and Surveying—The most immediate and primary use of insect sex pheromones is, and probably will continue to be, as tools to monitor and survey insect populations. Pheromone trap catch data can be used to make judgments on pest control strategy, a few examples of which I cite here.

Sex pheromone traps can provide a realistic estimate of the beginning and ending points of male emergence, flight activity, and migration (Riedl et al. 1976). The distribution and migration of several moth species, including the beet armyworm, *Spodoptera exigua* (Hübner), in California (Trumble & Baker 1984); Egyptian cotton leafworm, *S. littoralis* (Boisduval), in Cyprus (Campion et al. 1977) and Egypt (Nasr et al. 1984); and the black cutworm, *Agrotis ipsilon* (Hufnagel) in the United States corn belt (Levine et al. 1982, Kaster & Showers 1982) have been documented using pheromone traps.

In October 1983, a group of interested scientists, including the author, met in Guadeloupe, F. W. I., to develop a strategy for monitoring the movement of the fall armyworm (FAW), *S. frugiperda* (J. E. Smith), throughout the Caribbean Basin, using sex pheromone traps. Based upon the first year's trapping results, pheromone traps provided a realistic estimate of adult activity peaks in those areas where the FAW resides year-round. Pheromone traps also detected migrant fall armyworm moths as they moved into previously uninfested areas throughout the Eastern United States and Canada.

Data derived from adult surveys can be used to model the development of migrant insect pests once they arrive in uninfested areas. For example, catches of male black cutworm (BCW) moths in pheromone traps give a more reliable indication of the onset of egg laying among migrant females than do catches of BCW moths in light traps. Establishing the start of egg laying is important because it allows the initiation of a temperature-based developmental model using degree days which can predict the presence of BCW larvae. In Iowa, BCW reach the damaging stage 300 Fahrenheit degree-days after the first significant pheromone trap catch. This period usually is about 5 weeks long, but it could be as short as 2 weeks. Because BCW eggs are difficult to find, the model provides far greater efficiency in the pest scouting program (Anonymous 1985).

Pheromone traps also can be used to estimate larval populations and damage levels in crops. Tingle & Mitchell (1981) obtained significant correlations between pheromone-baited trap catches of male tobacco budworm moths (TBW), *Heliothis virescens* (F.), and larval infestations and damage levels in tobacco in Florida. Similarly, Johnson (1983) found a direct relationship between the number of male TBW caught in pheromone traps and egg counts in cotton fields in South Carolina. Silvain & Ti-a-hing

(1985) reported significant correlations between fall armyworm (FAW) larval counts in pasture grasses and adult males caught in pheromone traps in French Guiana and a warning system that enables timely and effective control has been developed (Silvain 1986). Chowdhury et al. (1985) found that pheromone trap catches of FAW males were significantly related to egg mass and larval densities in late-planted sweet corn. These reports provide excellent examples of how catches of male moths can be used effectively to monitor pest development in different cropping situations. This information can be used with other scouting techniques to enhance pest control practices through timing of pesticide applications.

Pheromone trap catch data can be used to discourage automatic spray programs and encourage growers to apply pesticides only when threatened with economically damaging infestations. A recognized method of controlling the boll weevil (BW), *Anthonomus grandis grandis* Boheman, in the lower Gulf Coast of Texas, is to apply early-season insecticide treatments to reduce the number of overwintered adults before they can establish the nucleus of an F_1 generation. Such treatments usually are based upon the intensity of previous years' infestations. Benedict et al. (1985) developed a practical and inexpensive pheromone trapping index system (TI) that can be used to reduce unneeded automatic early-season insecticide sprays. Their method uses cumulative weekly BW trap captures prior to the occurrence of squares (flower buds) sufficiently large for oviposition (one-third grown stage). The square damage used in their indexing system is the accumulative oviposition damage by overwintered BW during the first 2 weeks following appearance of one-third grown squares. Treatments are indicated when the $TI \geq 2.5$. TI of ≤ 1 indicates no insecticide treatment is needed. A TI reading of 1.1 to 2.4 indicates that the treatment decision must be based on the presence of damaged squares or adult BW in the field and on field history. Rummel et al. (1980) previously showed that the trap index method was superior to field inspections for determining the need to treat overwintering BW in West Texas.

Moreno et al. (1985) and Moreno & Kennett (1985) have developed a model for predicting infestations of California red scale (CRS), *Aonidiella aurantii* (Maskell), in California citrus orchards using catches on pheromone-baited sticky traps. The CRS is best controlled with a single application of a scabicide applied after blooming and before the settling of crawlers on the new crop of fruit. The model assumes that some degree of fruit infestation must be accepted. However, their research has shown that navel orange trees in good physiological condition easily can withstand up to 40% fruit infestation (1 or more scale) without apparent damage to the trees at the end of the season. Through proper use of the pheromone trap and proper interpretation of male catches, an assessment of fruit infestation can be made before it occurs. Using this method, some growers have been able to spread the interval for scabicide applications for CRS control up to 36 months.

Gargiullo et al. (1985) developed a model using pheromone-trap data and degree-day summations to predict optional timing for chemical control of the Nantucket pine tip moth (PTM), *Rhyacionia frustrana* (Comstock), on Christmas trees (*Pinus virginiana* Mill.). For each generation, the degree-days are summed commencing on the day of first catch in traps, and continues until a predetermined sum is attained. The day following this attainment is designated as the best date to spray. The choice of insecticide can influence the timing application. For example, optimum dates for spraying a contact insecticide like fenvalerate occurs 1 to 2.5 weeks earlier than for dimethoate, a systemic insecticide. The reason for this difference in timing is that the fenvalerate kills newly hatched PTM larvae, whereas dimethoate is generally most effective against the early larval instars feeding inside of needle mines, fascicle sheaths, and buds.

Management of Pesticide Resistance—One of the newest and most novel uses of pheromones is in the management of pesticide resistance. Suckling et al. (1985) used a

cluster of several pheromone caps strategically placed among suitable host plants to attract males of the lightbrown apple moth (LBAM), *Epiphyas postvittana* (Walker), which then were collected during flights at dusk with sweep nets. The LBAM is a major tortricid pest of apple in New Zealand and Australia. Live traps were not used because the captured moths were in poor condition. Netted moths were treated topically with insecticides to determine the level of pesticide resistance, if any. Using this method, they were able to detect rapidly (within 48 h) the geographic distribution of resistant, susceptible, and possible mixed populations. Using pheromones as a method of collecting samples for insecticide testing to determine the distribution of resistant individuals in an area permitted rapid management decisions on what, when, and where a chemical should be applied. This monitoring method is now an integral aspect of the resistance management of the LBAM in New Zealand.

These are all excellent examples on how pheromones can and are used to manage insect pests. Nevertheless, each insect pest presents a unique set of circumstances which require careful study before pheromones can be put into practical use. How, then, does a person go about developing pheromones as a factor in their pest management scheme?

YOU MUST HAVE DATA

It is elementary, of course, to say that one must have data on which to base one's proposed use of pheromones in insect pest management. But, is it really? Here, I use DATA as an acronym: *Development of Appropriate Technology for Agriculture*. For those who have not done so, I recommend that you read and digest the article "Challenges to International Pest Management Research and Extension in the Third World: Do We Really Want IPM To Work?" by Grace Goodell (1984). Ms. Goodell points out the difficulties of transferring technology in Third World countries from scientists to extensionists and farmers. When such shifts are unsuccessful, and they are more often than we like to admit, such failures often are blamed on "socioeconomic" obstacles which the entomologist perceives as quite simple to resolve in comparison to his or her own challenges. While socioeconomic problems definitely do contribute to failures in technology transfer, *all too often scientists unwittingly design their system for failure because they develop inappropriate technology*. This often is as true for technology transfer in developed as in undeveloped countries. Whether we like to admit it or not, pheromone usage for insect pest control is "high technology." The proper use of pheromones for maximum impact in control situations requires a relatively high level of technical knowledge and skill to collect the data and interpret the results so that decisions and recommendations can be made in insect control situations.

USE THE KISS TECHNIQUE

According to Goodell (1984): "Third World IPM programs often arrive at the farm level as shimmering misfits using sustained rat baiting, *quantitative monitoring of trap catches* [author's emphasis], multicolored handbooks for pest identification, and *lessons on graphing field populations* [author's emphasis]. As such, recommendations from scientists frequently run counter to the farmer's best interests." Insofar as the utilization of sex pheromones for insect pest control is concerned, Goodell's observations are as appropriate to the developed as to the undeveloped world. For some unknown reason, *many scientists seem to equate complexity with usefulness*. On the contrary, the KISS technique—KEEP IT SHORT AND SIMPLE—would appear to be the most prudent approach in developing pheromones for use in insect control. For example, pheromone trap catch degree-day developmental models for the black cutworm and Nantucket pine

tip moth cited here are excellent examples of simple systems which can be used with a minimum of technical training. More complex models requiring extensive data collection and computer-assisted analyses surely will be relegated to the archives of scientific literature, but they will find little or no use in the field. It also is significant that the more successful of the pheromone model systems developed to date have used temperature, i.e., degree days, as the driving force.

ELIMINATE THE FUD FACTOR

New insect management tools always are greeted with a healthy dose of skepticism. Pheromones are no exception. Farmers throughout the world have experience on their side when it comes to pest control practices. They, naturally, are *fearful* of changes, especially with gadgets and terminology which they may have never seen or of which they have never heard. They are *uncertain* if they should become a willing participant in an experiment with their livelihood; after all, they stand to lose the most if things do not go as advertised. This uncertainty often translates to *doubt* that the new approach—for example, the use of pheromone traps to schedule insecticide sprays—is worth the risk of shifting from an automatic spray schedule to one of wait-and-see. Elimination of the FUD factor—FEAR, UNCERTAINTY, DOUBT—is difficult to overcome under the best of circumstances; the less sophisticated the farmer clientele, the more difficult it will be. Education is the key here. Scientists must work hand-in-hand with extensionists and FARMERS if the value of pheromones as a pest management tool is to be realized. Goodell (1984) summarized the plight of the small farmer in the Third World thusly:

Of all the various components of modern agriculture . . . , IPM is the most demanding. To the small farmer IPM remains the cutting edge of scientific farming. But as the traditional farmers strain to catch up with the challenging improvements available to them, they often find themselves in a no-man's-land between technological change for which scientists assume responsibility, and those aspects of change which depend on the limited resources of Third World extension programs.

Much of the same can be said for the developed world, especially where the use of pheromones is concerned.

THE HARD WORK BEGINS

Entomologists have numerous opportunities to develop unique ways of introducing pheromones into the management of insect pests. In some cases, pheromone traps can be used to survey insect pests over large areas to alert farmers to possible infestations from migrant and local pests. In other cases, pheromones can be used locally on a field-by-field basis to schedule spray treatments or even to release parasitoids for maximum effectiveness. In both instances, much data must be gathered on the biology of the pest and its relation to its natural enemies, and to wild and cultivated hosts. In many cases, plant infestations and crop damage data already are being gathered in the course of present insect pest management programs. *The introduction of pheromone traps would be a natural extension of these programs.* Simplified models developed from these data then could be used to improve pest management practices through more judicious use of pesticides and conservation of natural enemies.

Most pheromones identified to date have been for species native to the temperate and subtropical regions of the world. However, sex pheromones or attractants have been identified for more than 50 species which are of major importance to agriculture in the Caribbean Basin and Central and South America. These pheromones often can be purchased already formulated and ready for use in traps. Moreover, effective traps

have been designed and are available for most of these species. Persons seriously considering developing pheromones for use in context of their own insect control programs are encouraged to take advantage of the vast amount of research already done on pheromone formulation and trap design, and to use their talent, experience, and energy to commence gathering the necessary data to forge the link between pheromone trap catches and insect pest populations. This truly is a unique opportunity for the economic entomologists of the Caribbean and Central and South American regions (and indeed in North America also) to adapt a form of high technology to their areas at nominal costs; the major costs of identification, formulation, and trap design having already been borne to a large extent by their North American friends and neighbors.

END NOTE

Mention of a commercial or proprietary product does not constitute an endorsement by the USDA.

REFERENCES CITED

- ANONYMOUS. 1985. Ag Consultant and Fieldman, March 1985. pp 20-21. Article quoting W. E. Showers. Research Entomologist, Corn Insects Research Laboratory, USDA, Ankeny, Iowa and S. E. Taylor, Climatologist, Iowa State University, Ames.
- BARCLAY, HUGH J. 1984. Pheromone trapping models for pest control: Effects of mating patterns and immigration. *Res. Popul. Ecol.* 26: 303-311.
- BARCLAY, HUGH J., AND PAULINE VAN DEN DRIESSCHE. 1984. Pheromone trapping for male annihilation: A density dependent model. *Prot. Ecol.* 7: 281-289.
- BENEDICT, J. H., T. C. URBAN, D. M. GEORGE, J. C. SEGERS, D. J. ANDERSON, G. M. MCWHORTER, AND G. R. ZUMMO. 1985. Pheromone trap thresholds for management of overwintered boll weevils (Coleoptera: Curculionidae). *J. Econ. Ent.* 78: 169-171.
- CAMPION, D. G., B. W. BETTANY, J. B. MCGINNINGLE, AND L. R. TAYLOR. 1977. The distribution and migration of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in relation to meteorology on Cyprus, interpreted from maps of pheromone trap samples. *Bull. Ent. Res.* 67: 501-522.
- CHOWDHURY, M. A., R. B. CHALFANT, AND J. R. YOUNG. 1985. Relationship of pheromone trap catches of fall armyworm (Lepidoptera: Noctuidae) with egg and larval density in late planted sweet corn. *Environ. Ent.* (in press).
- GARGIULLO, P. M., C. W. BERISFORD, AND J. F. GODBEE, JR. 1985. Prediction of optimal timing for chemical control of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), in the Southeastern Coastal Plain. *J. Econ. Ent.* 78: 148-154.
- GOODELL, GRACE. 1984. Challenges to international pest management research and extension in the Third World: Do we really want IPM to work? *Bull. Ent. Soc. America* 30: 18-26.
- INSCOE, M. N. 1982. Insect attractants, attractant pheromones, and related compounds. *In: Insect Suppression with Controlled Release Pheromone Systems*, Vol. II, pp. 201-295. (Eds. A. F. Kydonieus and Morton Beroza). CRC Press, Boca Raton, Florida.
- JOHNSON, DONALD R. 1983. Relationship between tobacco budworm (Lepidoptera: Noctuidae) catches when using pheromone traps and egg counts in cotton. *J. Econ. Ent.* 76: 182-183.
- KASTER, L., AND WILLIAM B. SHOWERS. 1982. Evidence of spring immigration and autumn reproductive diapause of the adult black cutworm in Iowa. *Environ. Ent.* 11: 306-312.
- LEVINE, E., S. L. CLEMENT, L. V. KASTER, A. J. KEASTER, W. G. RUESINK, W.

- B. SHOWERS, AND F. T. TURPIN. 1982. Black cutworm, *Agrotis ipsilon* (Lepidoptera: Noctuidae), pheromone trapping: A regional research effort. Bull. Ent. Soc. America 28: 139-142.
- MITCHELL, EVERETT R. (EDITOR). 1981. Management of Insect Pests with Semiochemicals: Concepts and Practice. Plenum Press, New York. 514 pp.
- MORENO, D. S., C. E. KENNETT, H. S. FORSTER, R. W. HOFFMANN, AND D. L. FLAHERTY. 1985. Predicting CRS infestations by trapping males. California Agric. (May-June) 39: 10-12.
- MORENO, D. S., AND C. E. KENNETT. 1985. Predictive year-end California red scale (Homoptera: Diaspididae) orange fruit infestations based on catches of males in the San Joaquin Valley. J. Econ. Ent. 78: 1-9.
- NASR, EL-SAYED, M. R. TUCKER, AND D. G. CAMPION. 1984. Distribution of moths of the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in the Nile Delta interpreted from catches in a pheromone trap network in relation to meteorological factors. Bull. Ent. Res. 74: 487-494.
- RIEDL, H., R. A. CROFT, AND A. J. HOWITT. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological time models. Canadian Ent. 108: 449-460.
- RUMMEL, D. R., J. R. WHITE, S. C. CARROLL, AND C. R. PRUITT. 1980. Pheromone trap index system for predicting need for overwintered boll weevil control. J. Econ. Ent. 73: 806-810.
- SILVAIN, J. F., AND J. TI-A-HING. 1985. Prediction of larval infestation in pasture grasses by *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from estimates of adult abundance. Florida Ent. 68: 686-691.
- SILVAIN, J. F. 1986. Use of pheromone traps as a warning system against attacks of *Spodoptera frugiperda* larvae in French Guiana. Florida Ent. 69: 000-000.
- SUCKLING, D. M., D. R. PENMAN, R. B. CHAPMAN, AND C. H. WEARING. 1985. Pheromone use in insecticide resistance surveys of lightbrown apple moths (Lepidoptera: Tortricidae). J. Econ. Ent. 78: 204-207.
- TINGLE, F. C., AND E. R. MITCHELL. 1981. Relationships between pheromone trap catches of male tobacco budworm, larval infestations, and damage levels in tobacco. J. Econ. Ent. 74: 437-440.
- TRUMBLE, J. T., AND T. C. BAKER. 1984. Flight phenology and pheromone trapping of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in southern coastal California. Environ. Ent. 13: 1278-1282.

USE OF PHEROMONE TRAPS AS A WARNING SYSTEM AGAINST ATTACKS OF SPODOPTERA FRUGIPERDA LARVAE IN FRENCH GUIANA

J. F. SILVAIN
Laboratoire d'Entomologia appliquée
Institut Français de Recherche Scientifique pour le
Développement en Coopération
Centre ORSTOM de Cayenne
B.P. 165, 97323 Cayenne Cedex, French Guiana

ABSTRACT

Experiments in French Guiana since 1979 have shown that it is possible to use pheromone traps in improved pastures, to enable not only a follow-up of the seasonal

- B. SHOWERS, AND F. T. TURPIN. 1982. Black cutworm, *Agrotis ipsilon* (Lepidoptera: Noctuidae), pheromone trapping: A regional research effort. Bull. Ent. Soc. America 28: 139-142.
- MITCHELL, EVERETT R. (EDITOR). 1981. Management of Insect Pests with Semiochemicals: Concepts and Practice. Plenum Press, New York. 514 pp.
- MORENO, D. S., C. E. KENNETT, H. S. FORSTER, R. W. HOFFMANN, AND D. L. FLAHERTY. 1985. Predicting CRS infestations by trapping males. California Agric. (May-June) 39: 10-12.
- MORENO, D. S., AND C. E. KENNETT. 1985. Predictive year-end California red scale (Homoptera: Diaspididae) orange fruit infestations based on catches of males in the San Joaquin Valley. J. Econ. Ent. 78: 1-9.
- NASR, EL-SAYED, M. R. TUCKER, AND D. G. CAMPION. 1984. Distribution of moths of the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in the Nile Delta interpreted from catches in a pheromone trap network in relation to meteorological factors. Bull. Ent. Res. 74: 487-494.
- RIEDL, H., R. A. CROFT, AND A. J. HOWITT. 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological time models. Canadian Ent. 108: 449-460.
- RUMMEL, D. R., J. R. WHITE, S. C. CARROLL, AND C. R. PRUITT. 1980. Pheromone trap index system for predicting need for overwintered boll weevil control. J. Econ. Ent. 73: 806-810.
- SILVAIN, J. F., AND J. TI-A-HING. 1985. Prediction of larval infestation in pasture grasses by *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from estimates of adult abundance. Florida Ent. 68: 686-691.
- SILVAIN, J. F. 1986. Use of pheromone traps as a warning system against attacks of *Spodoptera frugiperda* larvae in French Guiana. Florida Ent. 69: 000-000.
- SUCKLING, D. M., D. R. PENMAN, R. B. CHAPMAN, AND C. H. WEARING. 1985. Pheromone use in insecticide resistance surveys of lightbrown apple moths (Lepidoptera: Tortricidae). J. Econ. Ent. 78: 204-207.
- TINGLE, F. C., AND E. R. MITCHELL. 1981. Relationships between pheromone trap catches of male tobacco budworm, larval infestations, and damage levels in tobacco. J. Econ. Ent. 74: 437-440.
- TRUMBLE, J. T., AND T. C. BAKER. 1984. Flight phenology and pheromone trapping of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) in southern coastal California. Environ. Ent. 13: 1278-1282.

USE OF PHEROMONE TRAPS AS A WARNING SYSTEM AGAINST ATTACKS OF SPODOPTERA FRUGIPERDA LARVAE IN FRENCH GUIANA

J. F. SILVAIN
Laboratoire d'Entomologia appliquée
Institut Français de Recherche Scientifique pour le
Développement en Coopération
Centre ORSTOM de Cayenne
B.P. 165, 97323 Cayenne Cedex, French Guiana

ABSTRACT

Experiments in French Guiana since 1979 have shown that it is possible to use pheromone traps in improved pastures, to enable not only a follow-up of the seasonal

evolution of adult *Spodoptera frugiperda* populations, but also to estimate, a week in advance, the subsequent abundance of larvae in these pastures. Based on these results, an experimental warning network for attacks of *S. frugiperda* larvae in pastures and on pluvial rice was installed in July 1983. The results confirmed earlier observations and showed that the *S. frugiperda* populations evolved in the same fashion all along the coastal strip of French Guiana. Today, a warning network of nine stations helps broadcast regular warning messages to cattle breeders, thus enabling them to monitor their pastures at the right times and to carry out insecticide treatments as necessary.

RESUMEN

Experimentos en la Guayana Francesa desde 1979, han demostrado que es posible usar trampas de feromonas en pastizales mejorados, no solo para permitir una subsecuente evolución temporal de las poblaciones del adulto de *Spodoptera frugiperda*, pero también para estimar con una semana de anticipo, la subsecuente abundancia de larvas en estos pastos. Basado en estos resultados, una red experimental de aviso de ataques por larvas de *S. frugiperda* en pastos y en arroz pluvial, fue instalada en Julio de 1983. Los resultados confirman observaciones previas y demostraron que poblaciones de *S. frugiperda* evolucionaron en la misma forma a lo largo de la costa de la Guayana Francesa. Hoy, una red de aviso de 9 estaciones, ayuda a transmitir mensajes regulares de advertencia a los ganaderos, pudiendo ellos chequear sus pastos en los momentos oportunos y aplicar insecticidas cuando es necesario.

Since 1976, imported pasture grasses have been planted over large surfaces of improved pasture-land in French Guiana. Simultaneously, population outbreaks of *Mocis latipes* (Guenée) and *Spodoptera frugiperda* (J. E. Smith) larvae have been observed. During the rainy season, these larvae damage old and new pastures; and in the latter case, the introduction of pasture grasses could become endangered. These insects appeared as veritable limiting factors in the development of cattle breeding in French Guiana.

For lack of a regular monitoring program, these larval outbreaks were usually discovered too late, and despite insecticide treatments, the loss of large quantities of vegetation could not be avoided, nor could the advent, a few weeks thereafter, of new larval outbreaks on the same pastures. To rectify this situation, it was necessary to develop a system aimed at forewarning cattle-breeders about imminent larval outbreak risks. But, for very practical reasons, such a system based on monitoring of larval populations would never do; consequently, we tried to see if it was possible to use pheromone traps as a method of predicting the development of *S. frugiperda* larval populations and, subsequently, as a method of warning. This step became a challenge, considering the divergent opinions of various scientists on the subject of using pheromone traps as an effective monitoring method for *S. frugiperda* populations (Mitchell 1979, All 1980, Barfield et al. 1980, Sparks 1980, Starratt & McLeod 1982). However, their selective character, the ease and simplicity with which they can be used, as well as the reasonable cost of pheromone traps strongly urged us to make the attempt.

This paper reports experiments carried out between 1979 and 1985 which led to the installation in French Guiana of a network of warning stations equipped with pheromone traps to alert about possible *S. frugiperda* larvae attacks.

DEMONSTRATING THE EFFICIENCY OF PHEROMONE TRAPS AS A METHOD OF PREDICTING THE EVOLUTION OF *S. FRUGIPERDA* LARVAL POPULATIONS.

Starting in 1979, we began testing the efficiency of these traps in a cattle-farm in

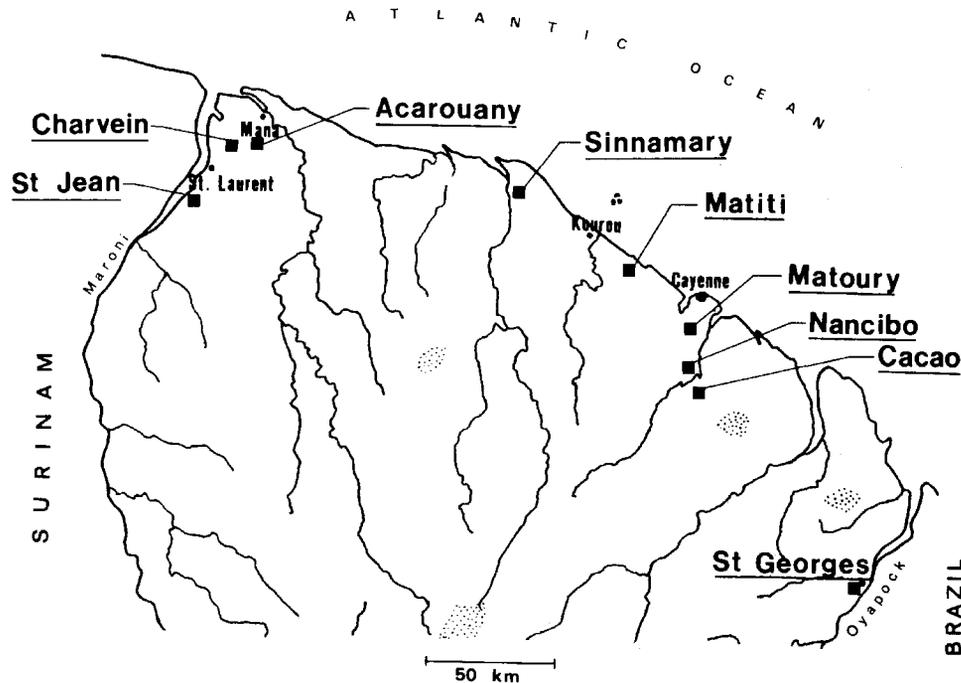
Matoury, not far from Cayenne (cf. Map 1). Three Zoecon Pherocon 1 C sticky traps, baited with 25mg of (Z)-9-dodecen-1-ol acetate in Conrel hollow fiber dispensers were operated every weekend. A blacklight trap was operated on Mondays and Thursdays and, with the help of a sweep net, larval populations were sampled on Tuesdays and Fridays (Silvain & Ti A Hing 1985). Several lessons were gleaned from this experiment:

—A strong, positive and very significant correlation (Spearman's Rank Correlation coefficient higher than 0.65 between November 1979 and April 1983) exists between the results obtained through the pheromone and blacklight trap systems (Silvain 1984, Silvain & Ti A Hing 1985). Considering the fact that blacklight traps attract mostly females (80%) (Silvain & Ti A Hing 1985), this result leads to the conclusion that, in the case of improved pastures in French Guiana, the development of male and female populations occurs in a similar fashion in the course of time, yet another advantage of pheromone traps.

—There is a strong positive and very significant (higher than 0.70) correlation between the results obtained through pheromone traps and those of larval densities in the pastures a week later. A slightly lower correlation is found between the results of moth captures and those of larval catches during the same week (Silvain & Ti A Hing 1985). Those results show that pheromone traps can be used not only to follow the seasonal development of *S. frugiperda* larval populations, but also to predict the future development of these populations on the study site.

—Adult and larval *S. frugiperda* populations are generated monthly during most of the year, and normally these generations are well separated. These findings are of great importance in the setting-up of a warning system, because they show that predictions about the periods when new generations will appear can be made well in advance.

—There are positive, low or moderate, but still significant correlations between the development of adult and larval populations and the pluviometry 3, 4 and 5 weeks earlier.



Map 1: Location of the warning stations

In 1982, a second monitoring station for noctuid populations was installed in Sinnamary, and this helped confirm the results obtained in Matoury. For both moth and larval catches, the results obtained in Sinnamary between 1982 and 1984 were positively correlated to those in Matoury, 100 km to the south-east (Silvain 1983, Silvain 1984). This observation led to the belief that the seasonal development of *S. frugiperda* populations in pastures along the costal strip followed the same general pattern.

It is possible that the highly positive character of results obtained in French Guiana may be due to the nature of the crop observed (low perennial pasture grasses) and to the adoption of a method of use of pheromone traps which tended to minimize the principal defect of the type of trap chosen, i.e. its rapid saturation (Tingle & Mitchell 1975). Also, it may be noted that we haven't tried to directly compare the number of moths and larvae caught, since this would give coefficients with a relative low correlation; but rather to compare the development within a given period of these two variables with the help of a Spearman rank correlation test. The main idea was to first show that a peak in moth catches in pheromone traps was followed by a peak in larvae captured in the pastures.

What remained was to expand these types of experiments to other sites along French Guiana's coast, to verify whether results obtained from Matoury and Sinnamary could be applied to the whole of the coastal strip, and to install an operational warning system in collaboration with the Plant Protection Service.

INSTALLATION OF AN EXPERIMENTAL WARNING NETWORK

EQUIPMENTS AND METHODS USED

Beginning in July 1983, 7 new monitoring stations of noctuid populations gradually were set up in pastures and on pluvial rice (cf. Map 1). Table 1 shows the nature of experiments conducted at each station. Two types of pheromone traps and dispensers were used: sticky Albany Sentry Wing traps baited with a commercial pheromone in Albany hollow fiber dispensers, and International Pheromone Moth Traps baited with a mixture originating from Dr. Mitchell's Laboratory in rubber septum dispensers. The two pheromones contained a mixture of the 4 compounds recommended by Mitchell, i.e. the Z7DDA, Z9DDA, Z9TDA and Z11HDA. The Albany traps were operated as described above, whereas the IPM traps were permanently positioned and their contents emptied every Tuesday and Friday and the pheromone changed every two weeks. Sampling of larval populations continued as before.

RESULTS OBTAINED

Comparison of the moth captures recorded in the different sites—There were 3 periods of abundant *S. frugiperda* moths between July 1983 and March 1985 at practically all the stations (cf. Fig. 1a).

—The July to August period in 1983.

—The November-December 1983 to April 1984 period, during which the largest populations occurred in January and especially in February 1984.

—The May-September period in 1984, during which the most abundant populations were observed in July-August.

This relatively simultaneous appearance of moths at the different sites explains the homogeneity in the correlation coefficients obtained at the different stations. Positive and significant correlations existed in all the cases, except for results obtained from Charvein. This confirms the hypothesis that the evolution of *S. frugiperda* populations follows the same general pattern all along French Guiana's coastal strip, thus supporting

TABLE 1. EXPERIMENTATIONS CARRIED OUT IN EACH STATION OF THE EXPERIMENTAL WARNING SYSTEM

Locality	Type of Crops	Experimentations Carried Out
St. Georges de l'Oyapock	Pasturegrasses	P.T. 1* (2)**
Cacao	Pluvial rice	P.T. 1 (3) L.T. ***
Nancibo	Pasturegrasses	P.T. 2 (3)
Matoury	Pasturegrasses	P.T. 1 (4) et P.T. 2 (1) L.T. Larval sampling with sweep net
Matiti-Macouria	Pasturegrasses	P.T. 2 (3)
Sinnamary	Pasturegrasses	P.T. 1 (4) Larval sampling with sweep net
Acarouany	Pasturegrasses	P.T. 1 (3) L.T. Larval sampling with sweep net
Charvein	Pluvial rice or sorghum	P.T. 1 (2) Larval sampling
St. Jean	Pasturegrasses	P.T. 1 (3)

*P.T. 1: Monitoring of male *Spodoptera frugiperda* populations with Albany Scentry™ Wing Trap, baited with commercial pheromone.

P.T. 2: Monitoring of male *Spodoptera frugiperda* populations with International Pheromone Moth Traps baited with pheromone furnished by the Insect Attractants Lab. (U.S.D.A. Gainesville).

**No. of traps used.

***L.T.: Monitoring of adult *Spodoptera frugiperda* populations with blacklight trap.

the validity of warnings based on these results. At Charvein, in a sorghum crop, *S. frugiperda* populations were able to persist at an abundant level during the dry period, which was not the case in habitats having only pasture grasses. Pluvial rice crops grown in the same site and at Cacao did not influence the development of adult *S. frugiperda* populations.

During the October 1984-March 1985 period, adult populations persisted at a relatively low level at the various stations with the exception of Matiti; and *S. frugiperda* were only caught sporadically at Cacao and Nancibo. This situation seems to be linked to the absence of a dry season in October-November 1984, and again to the absence of a marked rainy season from December 1984 to February 1985. In Matiti, where the populations increased dramatically from January to March 1985, the wet/dry season and dry/wet season transitions were slightly more pronounced than at the other stations.

During practically the entire period of study, and at all the different sites, a succession of well separated moth generations occurred ca. every 4 or 5 weeks.

Influence of the type of trap used—The results obtained from the two types of traps were very similar with significant ($p > 0.01$) rank correlation coefficients among the results from Matiti (IPM traps) and those from Matoury (0.51) and Sinnamary (0.57)

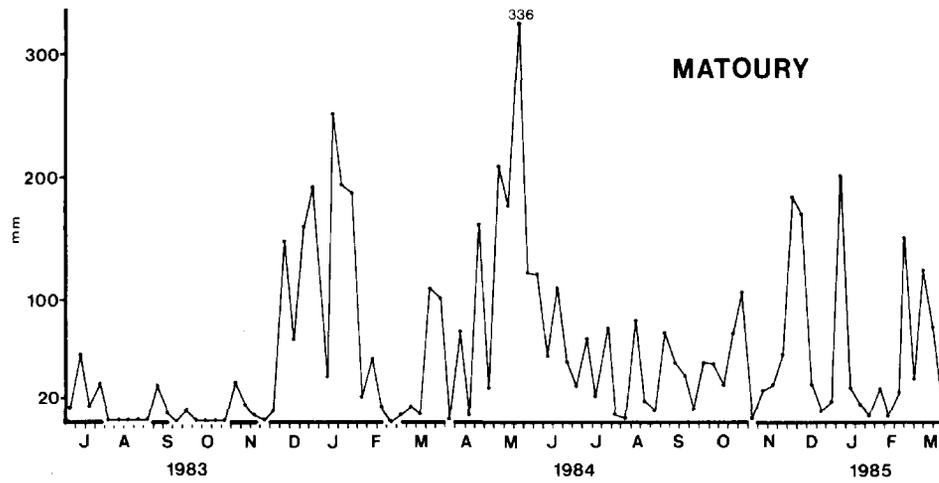


Fig. 1c. Rainfall in Matoury, F. G.

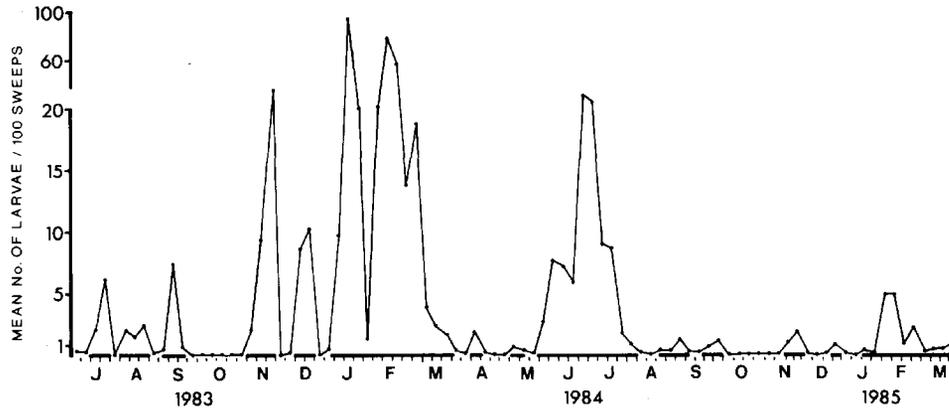


Fig. 1b. *Spodoptera frugiperda* arvae per 100 sweeps on improved pastures.

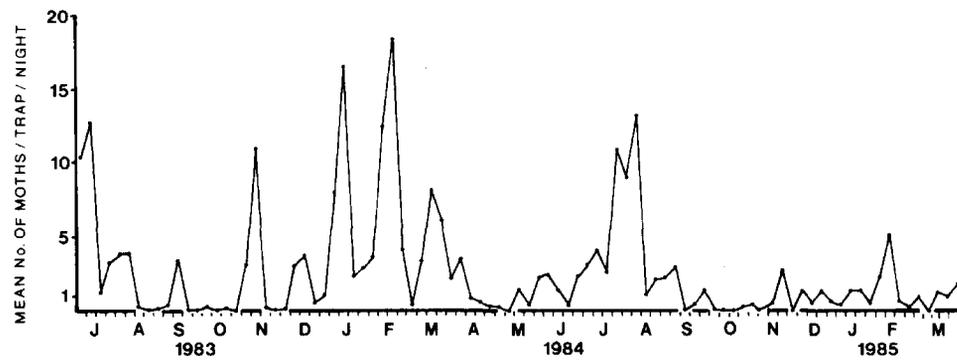


Fig. 1a. *Spodoptera frugiperda* moths captured per night in pheromone traps. Matoury, F. G. 1983-1985.

where Albany traps were used. (It is interesting to note that if the month of March 85 is excluded from these comparisons, we arrive at coefficients of 0.68 and 0.60 with Sinnamary and Matoury, respectively). The same was true of the results obtained from Nancibo (IPM traps) and Cacao (Albany traps) ($r_s=0.69$, $p>0.01$)

Correlations between pheromone trap moth captures and larvae caught—At the three stations located in pastures where a seasonal development of larval populations had been tracked, we again found positive and very significant correlations between moth catches in a given week and larval densities during the same week and particularly with larval densities in the following week (correlation with larvae caught during the following week: Acarouany: $r_s=0.44$, $t=4.54$, $p>0.01$; Sinnamary: $r_s=0.48$, $t=5.13$, $p>0.01$; Matoury: $r_s=0.55$, $t=6.28$, $p>0.01$). In the Matoury and Sinnamary sites, rank correlation coefficients obtained are lower than those observed earlier; however, we consider this decrease to be linked with the low level of *S. frugiperda* larval populations during a major portion of the study period. We compared highly fluctuating moth captures in Acarouany and Sinnamary with populations of larvae which were close to zero level during half of the experimentation time. An analysis of results obtained between September 83 and March 84 in Matoury confirms this hypothesis. During this period of dense adult and larval populations (cf. Fig. 1a & 1b), the rank correlation coefficient existing between moth and larvae catches, made a week later, reached 0.81 ($t=7.02$, $p>0.01$). Similarly, a calculation of existing rank correlation coefficients, during period of dense populations, between pheromone trap results and larval abundance the following week in Sinnamary and Acarouany, revealed far higher correlations between the two population estimates than those observed during the entire study period (Sinnamary: November 83-May 84: $r_s=0.69$, $t=5.01$, $p>0.01$; Acarouany: July-November 1983: $r_s=0.67$, $t=3.82$, $p>0.01$). These results support the soundness of choosing of pheromone traps as a method of forewarning the development of *S. frugiperda* larval populations in pastures. This method appears as the most efficient one at times when adult and larval populations are most abundant, which also corresponds exactly with the periods when a warning is most urgently needed.

The results obtained from sorghum crops and pluvial rice to date are not sufficient to permit any definite conclusions.

Correlations between moth trapping, larval abundance and rainfall—In Matoury, between July 83 and March 85, positive, weak, but still significant correlations ($p=0.01$) were again observed between pheromone trap catches during a given week and the rainfall of 3 ($r_s=0.26$) or 4 ($r_s=0.22$) weeks before (cf. Fig. 1a & 1c). The same was true for larval abundance and rainfall in the preceding 4 ($r_s=0.26$, $p=0.01$) and 5 ($r_s=0.25$, $p=0.01$) weeks (cf. Fig. 1b & 1c). These results confirm the belief that rainfall has a definite place among the factors contributing to the seasonal evolution of *S. frugiperda* populations.

WARNING ABOUT *S. FRUGIPERDA* LARVAE ATTACKS

BASIS OF THE WARNING

Results obtained between July 83 and March 84 emphasize the 3 essential points upon which the warning procedure depends:

—A new generation of moths and then larvae appears every 4 to 5 weeks at each of the stations. Hence, it is possible to predict, a month in advance, the approximate date when the next generations will appear for any given station.

—Pheromone traps help to predict one week in advance how the larval populations present in a given week will develop. This respite is enough to warn farmers who then will be able to carry out insecticide treatments before its too late, if densities necessitate action.

—The adult *S. frugiperda* populations develop over time in a similar manner all along the French Guiana coastal strip; so all the sites in this zone covered by the warning network will be protected.

Therefore, a 2-fold prediction of larval outbreaks in pastures will be undertaken. The first predicts the period when monthly generations of moths and larvae appear, using moth captures. The second predicts the weekly magnitude of these larval populations, from the most recent results. Rainfall during the preceding weeks also are taken into consideration.

COMPOSITION AND BROADCASTING OF WARNING MESSAGES

Every Monday, we analyze and synthesize results coming from the different stations. Every 15 days, this synthesis appears in a press-release published on Fridays in the agricultural supplement of the major local newspaper. Should there be a risk of larval outbreak, the farmers are forewarned by means of this printed message as well as radio broadcasts. A direct warning by telephone to one or many cattle breeders may occur.

FUTURE PROSPECTS

The warning network consists of nine stations. We are replacing sticky traps at all the stations, with International Pheromone Moth Traps because of their high level of efficiency (Mitchell, personal comm., as well as our own observations) and the greater facility with which they can be used. Pheromones from INRA's Chemical Mediator Laboratory (France) have replaced pheromones from Albany. We are progressively entrusting the Plant Protection Service with the management of the warning network. Nevertheless, we shall continue testing new pheromones and traps for efficiency, and these could be proposed eventually to improve the validity of warnings issued. In the future, we hope to include in the system for monitoring *S. frugiperda* populations, another pheromone trap system for *Mocis latipes* populations to provide warning about the risks of subsequent larval outbreaks of this species.

CONCLUSION

The results of 5 years of work in French Guiana confirm that pheromone traps for the *Spodoptera frugiperda* males can be effectively used as a warning method about damages caused by larvae of this pest in improved pastures. The installation of a warning network permits farmers to protect their pastures precisely when necessary and to take adequate measures at the right moment for *S. frugiperda* larval outbreaks. During the months to come, a modernization of equipment and methods in use should contribute further in ameliorating the performance of pheromone traps and consequently, in improving the validity of warnings issued.

ACKNOWLEDGEMENTS

I thank Dr. E. R. Mitchell for inviting me to participate in this symposium and for supplying pheromones, D. Dauthuille for his assistance and suggestions, S. Boucher, J. Ti-A-Hing (ORSTOM) for technical assistance, and technicians from Plant Protection Service (SPV) and others for their field assistance. I want to thank Dr. J. McNeil (Université Laval, Québec, Canada) for reviewing this manuscript.

REFERENCES CITED

- ALL, J. N. 1980. Reducing the lag between research synthesis and practical implementation of pest management strategies for the fall armyworm: introduction to the fall armyworm conference 1980. *Florida Ent.* 63: 357-61.
- BARFIELD, C. S., J. L. STIMAC AND M. A. KELLER. 1980. State of the art for predicting damaging infestations of fall armyworm. *Florida Ent.* 63: 364-405.
- MITCHELL, E. R. 1979. Monitoring adult populations of the fall armyworm. *Florida Ent.* 62: 91-98.
- SILVAIN, J. F. 1983. Etude de faisabilité d'un réseau d'avertissement des attaques de noctuelles. March 82-April 83 report to the "Préfecture de la Guyane". 20p.
- SILVAIN, J. F. 1984. Etude de faisabilité d'un réseau d'avertissement des attaques de noctuelles. April 83-April 84 report to the "Conseil Général de la Guyane". 11p.
- SILVAIN, J. F., M. REMILLET, AND G. TAVAKILIAN. 1984. Le programme d'étude des noctuelles nuisibles aux graminées fourragères en Guyane française. Proceedings of the C.F.C.S. seventeenth Annual Meeting. Venezuela: 116-130.
- SILVAIN, J. F. 1984. Premières observations sur l'écologie de *Spodoptera frugiperda* (J. E. Smith) et *Mocis latipes* (Guenée), noctuelles déprédatrices des graminées fourragères en Guyane française. In "Les Colloques de l'INRA", n°24: Prairies guyanaises et élevage bovin: 243-272.
- SILVAIN, J. F. AND J. TI A HING. 1985. Prediction of larval infestation in pasture grasses by *Spodoptera frugiperda* (Lepidoptera:Noctuidae) from estimates of adult abundance. *Florida Ent.* 68: 686-91.
- SPARKS, A. N. 1980. Pheromones: potential for use in monitoring and managing populations of the fall armyworm. *Florida Ent.* 63: 406-10.
- STARRAT, A. N. AND D. G. R. MCLEOD. 1982. Monitoring fall armyworm, *Spodoptera frugiperda* (Lepidoptera:Noctuidae), moth population in southwestern Ontario with sex pheromone traps. *Canadian Ent.* 114: 545-9.
- TINGLE, F. C. AND E. R. MITCHELL. 1975. Capture of *Spodoptera frugiperda* and *S. exigua* in pheromone traps. *J. of Econ. Ent.* 68: 613-615.

GRANDLURE: USE IN BOLL WEEVIL CONTROL AND ERADICATION PROGRAMS IN THE UNITED STATES

W. A. DICKERSON
Boll Weevil Eradication Research Unit
Agricultural Research Service
U. S. Department of Agriculture
4116 Reedy Creek Road
Raleigh, North Carolina 27607

ABSTRACT

The grandlure-baited boll weevil trap is an essential component of most, if not all, boll weevil control programs. While there are other minor uses of grandlure, the major use is as an attractant for the boll weevil trap. The Southeastern Boll Weevil Eradication Program uses the grandlure-baited boll weevil trap to determine areawide distribution of boll weevils, field-by-field presence of boll weevils, where and when to apply insecticide treatments and suppress very low populations of boll weevils.

REFERENCES CITED

- ALL, J. N. 1980. Reducing the lag between research synthesis and practical implementation of pest management strategies for the fall armyworm: introduction to the fall armyworm conference 1980. *Florida Ent.* 63: 357-61.
- BARFIELD, C. S., J. L. STIMAC AND M. A. KELLER. 1980. State of the art for predicting damaging infestations of fall armyworm. *Florida Ent.* 63: 364-405.
- MITCHELL, E. R. 1979. Monitoring adult populations of the fall armyworm. *Florida Ent.* 62: 91-98.
- SILVAIN, J. F. 1983. Etude de faisabilité d'un réseau d'avertissement des attaques de noctuelles. March 82-April 83 report to the "Préfecture de la Guyane". 20p.
- SILVAIN, J. F. 1984. Etude de faisabilité d'un réseau d'avertissement des attaques de noctuelles. April 83-April 84 report to the "Conseil Général de la Guyane". 11p.
- SILVAIN, J. F., M. REMILLET, AND G. TAVAKILIAN. 1984. Le programme d'étude des noctuelles nuisibles aux graminées fourragères en Guyane française. Proceedings of the C.F.C.S. seventeenth Annual Meeting. Venezuela: 116-130.
- SILVAIN, J. F. 1984. Premières observations sur l'écologie de *Spodoptera frugiperda* (J. E. Smith) et *Mocis latipes* (Guenée), noctuelles déprédatrices des graminées fourragères en Guyane française. In "Les Colloques de l'INRA", n°24: Prairies guyanaises et élevage bovin: 243-272.
- SILVAIN, J. F. AND J. TI A HING. 1985. Prediction of larval infestation in pasture grasses by *Spodoptera frugiperda* (Lepidoptera:Noctuidae) from estimates of adult abundance. *Florida Ent.* 68: 686-91.
- SPARKS, A. N. 1980. Pheromones: potential for use in monitoring and managing populations of the fall armyworm. *Florida Ent.* 63: 406-10.
- STARRAT, A. N. AND D. G. R. MCLEOD. 1982. Monitoring fall armyworm, *Spodoptera frugiperda* (Lepidoptera:Noctuidae), moth population in southwestern Ontario with sex pheromone traps. *Canadian Ent.* 114: 545-9.
- TINGLE, F. C. AND E. R. MITCHELL. 1975. Capture of *Spodoptera frugiperda* and *S. exigua* in pheromone traps. *J. of Econ. Ent.* 68: 613-615.

GRANDLURE: USE IN BOLL WEEVIL CONTROL AND ERADICATION PROGRAMS IN THE UNITED STATES

W. A. DICKERSON
Boll Weevil Eradication Research Unit
Agricultural Research Service
U. S. Department of Agriculture
4116 Reedy Creek Road
Raleigh, North Carolina 27607

ABSTRACT

The grandlure-baited boll weevil trap is an essential component of most, if not all, boll weevil control programs. While there are other minor uses of grandlure, the major use is as an attractant for the boll weevil trap. The Southeastern Boll Weevil Eradication Program uses the grandlure-baited boll weevil trap to determine areawide distribution of boll weevils, field-by-field presence of boll weevils, where and when to apply insecticide treatments and suppress very low populations of boll weevils.

RESUMEN

Las trampas cebadas con "grandlure" del gorgojo del algodón, es un compuesto esencial de la mayoría, si no de todos los programas de control del gorgojo del algodón. Mientras que hay otros usos menores de "grandlure", el mayor uso es como un atrayente para atrapar al gorgojo del algodón. El Programa de Erradicación del Sudeste del Gorgojo del Algodón, usa trampas cebadas con "grandlure" para determinar el área de distribución de los gorgojos del algodón, la presencia de campo-por-campo del gorgojo del algodón, y dónde y cuándo hacer los tratamientos de insecticidas.

Female boll weevils, *Anthonomus grandis* Boheman, were observed by Cross & Mitchell (1966) in a series of field tests conducted in 1963 to be attracted to male boll weevils at distances greater than 30 feet. Subsequent to these observations, Keller et al. (1964) reported that the male boll weevil emitted a substance which attracted the female boll weevil. Hardee et al. (1969) determined this male produced pheromone attracted both male and female weevils in the spring and fall. Tumlinson et al. (1969) isolated, identified and synthesized the pheromone into four active components, two terpenoid alcohols and two aldehydes. These four synthesized components are referred to collectively as grandlure.

An effective grandlure-baited trap and dispensing system for grandlure have been under constant development for almost twenty years.

One of the keys to utilizing grandlure as a tool for boll weevil control is a dispensing system that provides controlled release of the pheromone over a protracted period. Early methods of dispensing grandlure employed by Tumlinson et al. (1969) included firebrick. This technique while providing an effective means for bioassay allowed the grandlure to be released within a few hours. Subsequent dispenser improvements by McKibben et al. (1971, 1980), Hardee et al. (1972, 1974, 1975), McKibben (1976) and Bull (1976) have led to the development of several efficient systems for releasing grandlure over a 1-4 week period.

Equally important to an efficient dispenser is an effective trap. Numerous early trap designs were evaluated by Cross et al. (1969). These field tests indicated a wing trap coated with a sticky material was the most effective design. However, traps developed later by Leggett & Cross (1971) and Mitchell & Hardee (1974) represented important steps in providing practical grandlure-baited boll weevil traps suitable for routine use. Essentially, the trap described by Mitchell & Hardee (1974) with modifications by Dickerson et al. (1981) and Dickerson (1985) has become the trap design in most common use.

The synthesis of grandlure and the development of an inexpensive and efficient trap and grandlure dispenser has led to the widespread use of grandlure-baited boll weevil traps. The use of grandlure as an attractant for traps is a vital part of essentially all boll weevil control programs in the U. S. today.

I will focus primarily on the use of grandlure in conjunction with boll weevil eradication in the southeastern U. S. However, before I discuss this aspect, I would like to briefly review two other uses of grandlure for boll weevil control.

1. *Pinhead square treatment:*

Cotton squares must be larger than pinhead stage in order to support boll weevil reproduction. Insecticides applied just prior to this critical stage of cotton growth will often eliminate most of the emerged overwintered weevils from the cotton field before reproduction can be initiated. Rummel et al. (1980) developed an index for assessing the need for chemical control during this time based on the number of weevils captured in grandlure-baited boll weevil traps during the 6-week period immediately prior to the pinhead square stage of cotton. Similar indexing systems are currently in use by most

boll weevil infested cotton producing areas of the U. S. Essentially, this principal of early season boll weevil control was proposed by Ewing & Parencia (1949) long before grandlure was discovered. However, the incorporation of the grandlure-baited boll weevil trap into their early season approach has greatly increased its impact on boll weevil control.

2. Modified trap crop:

The concentration of insects onto small plantings of preferred hosts has long been suggested as an efficient means to control insect pests. L. O. Howard (1896) suggested this trap crop approach for boll weevil shortly after this cotton pest was detected in Texas. Except for Isely (1924), relatively little additional research on trap crops was reported until Bradley (1967) found that periodic applications of insecticides to early planted border strips of cotton delayed subsequent infestations of boll weevil on nearby younger cotton. Research conducted by Lloyd et al. (1972) and Boyd (1973) indicated that the newly synthesized boll weevil pheromone, grandlure, could attract and concentrate weevils into small areas of a cotton field where limited amounts of chemicals could then be applied for their control. In this approach, grandlure is applied to a few rows of cotton adjacent to boll weevil hibernation sites. As weevils accumulate, insecticide treatments are applied to this limited area, thus preventing or reducing the need for subsequent field-wide treatment. This procedure essentially works in the same way as a conventional trap crop. Gilliland et al. (1976) reported that plantings of early fruiting cotton containing grandlure-bait stations were effective for suppressing emerging boll weevil populations.

Despite these encouraging reports, trap crops have received limited use and are not widely recommended as a means of early season weevil control. However refinements in this approach, including the use of grandlure, may result in renewed interest. Some current drawbacks to the use of grandlure in this system include the expense of the grandlure, critical timing of application, and the availability of a suitable grandlure formulation and dispenser system for this special use. Until these limiting factors are resolved, this potentially highly effective approach to boll weevil control will not be widely used.

3. Boll weevil eradication:

Boll weevil eradication was the expressed goal for the Boll Weevil Research Laboratory at the dedication of that facility in March of 1962. Eradication techniques developed there and in other Federal and State laboratories are currently being utilized by the Southeastern Boll Weevil Eradication Program. All cotton (over 200,000 acres) grown in Virginia, North Carolina, and South Carolina is included in this program. Grandlure-baited boll weevil traps are a key tool used to evaluate areawide and field-by-field populations of boll weevils over this 3-State area. This information allows the application of the most appropriate suppression measures to eradicate the boll weevil. The central role of the grandlure-baited boll weevil trap in the Southeastern Boll Weevil Eradication Program is well illustrated by listing yearly program activities for this 30-month program.

1983

- Map 1983 cotton fields.
- Place grandlure-baited boll weevil traps around cotton fields at 1 trap per 10 acres (July).
- Applications of insecticide for diapause control.

1984

- Place grandlure-baited boll weevil traps around the sites of 1983 cotton fields at 1 trap per acre (April).
- Map 1984 cotton fields.

- Place grandlure-baited boll weevil traps around 1984 cotton fields at 1 trap per acre (May).
- Application of insecticide at pinhead square stage of cotton.
- Application of insecticide for reproduction control.
- Application of insecticide for diapause control.

1985

- Place grandlure-baited boll weevil traps around the sites of 1984 cotton fields at 1 trap per acre (April).
- Map 1985 cotton fields.
- Place grandlure-baited boll weevil traps around 1985 cotton fields at 1 trap per acre (May).
- Application of insecticide at pinhead square stage of cotton.
- Application of insecticide for reproduction control.
- Application of insecticide for diapause control.

The integration of the biology of the boll weevil, phenology of the cotton plant, and program activities are illustrated in Figure 1. The eradication program was initiated in July of 1983 with areawide trapping followed by intensive applications of insecticide to prevent boll weevils from entering diapause. Limited trapping was continued throughout the winter to detect boll weevil movement during periods of warm weather. The intensive trapping of the previous years' cotton field sites and current cotton plantings during the spring evaluate the need for insecticide applications at the pinhead square stage of cotton to prevent boll weevil reproduction. After cotton begins fruiting in late June and early July, grandlure-baited traps placed inside field margins and/or around field borders detect additional weevils entering the cotton fields from overwintering sites. Lloyd et al. (1983) reported that under conditions of low weevil populations, this intensive spring and early summer trapping is often sufficient to prevent weevil reproduction, thus eliminating the need for additional insecticide application. In late August and September as cotton stops fruiting, pheromone production by the boll weevil declines and the attractiveness of the grandlure-baited trap increases. During this period, the number of weevils captured in traps is a very sensitive indicator used to direct field-by-field insecticide treatments for diapause control. As boll weevil populations continue to decline during the course of the boll weevil eradication program, traps become increasingly efficient as the competing sources of pheromone become fewer and fewer.

The grandlure-baited boll weevil trap serves as the eyes and ears for managing the Southeastern Boll Weevil Eradication Program. The trap is the tool used to determine: (1) areawide distribution of boll weevils; (2) field-by-field presence of weevils; and (3) when and where to apply chemical treatment. Under conditions of very low weevil population, the trap may also provide significant suppression of emerging overwintered boll weevils. Eradicating the boll weevil from the southeastern U. S. would be very difficult, if not impossible, and certainly more costly, without grandlure and the boll weevil trap.

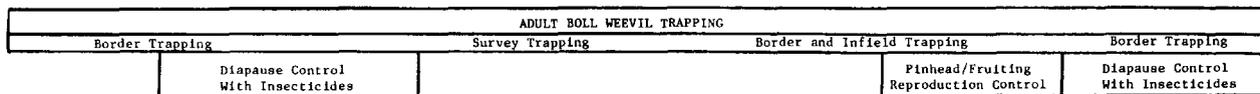
In 1985, the Southeastern Boll Weevil Eradication Program used over 400,000 boll weevil traps and approximately 2,750,000 dispensers containing 10 mg. of grandlure each. While the grandlure-baited boll weevil trap is not the only use for grandlure in boll weevil control programs, current and near future uses will likely center around trapping programs. I estimate that at least 99% of the grandlure produced in the U. S. is used as attractant in boll weevil traps.

REFERENCES CITED

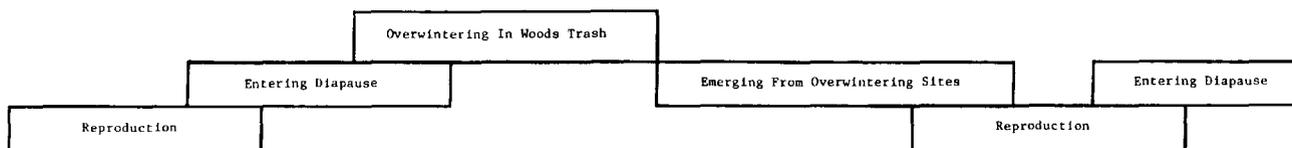
BRADLEY, J. R., JR. 1967. Oriented movement of the boll weevil in response to trap

Boll Weevil Eradication Program

Eradication Technology



Seasonal History of Boll Weevil



Plant Growth

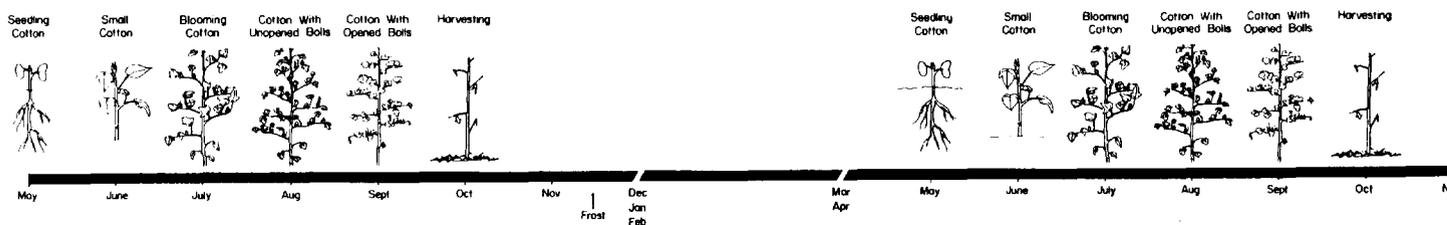


Fig. 1. The application of boll weevil eradication technology in relation to plant growth and the seasonal activity of the boll weevil.

- crop plantings, foliage color, and sex pheromone. 73 pp. Ph.D Dissertation, Louisiana State University, Baton Rouge, LA.
- BOYD, F. J. 1973. Progress report on the Pilot Boll Weevil Eradication Experiment. Proc. 1973 Beltwide Cotton Prod.-Mech. Conf. pp. 20-22.
- BULL, D. L. 1976. Formulation of grandlure. In Detection and Management of the Boll Weevil with Pheromone. Texas. Agri. Exp. Sta., Research Monograph No. 8, pp. 5-8.
- CROSS, W. H., AND H. C. MITCHELL. 1966. Mating behavior of the female boll weevil. J. Econ. Entomol. 59: 1503-1507.
- DICKERSON, W. A. 1985. Boll Weevil Trap. U.S. Patent application No. 734,647.
- DICKERSON, W. A., G. H. MCKIBBEN, E. P. LLOYD, J. F. KEARNEY, J. J. LAM, JR., AND W. H. CROSS. 1981. Field evaluation of a modified infield boll weevil trap. J. Econ. Entomol. 74: 280-282.
- EWING, K. P., AND C. R. PARENIA, JR. 1949. Early-season applications of insecticides for cotton insect control. U.S. Dept. of Agri., Bureau of Entomology and Plant Quarantine E-792, 9 pp.
- GILLILAND, F. R., JR., W. R. LAMBERT, J. R. WEEKS, AND R. L. DAVIS. 1976. Trap crop for boll weevil control in boll weevil suppression, management, and elimination technology. ARS-S-71, U.S. Dept. of Agri.
- HARDEE, D. D., W. H. CROSS, AND E. B. MITCHELL. 1969. Male boll weevils are more attractive than cotton plants to boll weevils. J. Econ. Entomol. 62: 165-169.
- HARDEE, D. D., T. M. GRAVES, G. H. MCKIBBEN, W. L. JOHNSON, R. C. GUELDNER, AND C. M. OLSEN. 1974. A slow-release formulation of grandlure, the synthetic pheromone of the boll weevil. J. Econ. Entomol. 67: 44-46.
- HARDEE, D. D., G. H. MCKIBBEN, R. C. GUELDNER, E. B. MITCHELL, J. H. TUMLINSON, AND W. H. CROSS. 1972. Boll weevils in nature respond to grandlure, a synthetic pheromone. J. Econ. Entomol. 65: 97-100.
- HARDEE, D. D., G. H. MCKIBBEN, AND P. M. HUDDLESTON. 1975. Grandlure for boll weevils: controlled release with a laminated plastic dispenser. J. Econ. Entomol. 68: 477-479.
- HOWARD, L. O. 1896. The maximum cotton boll weevil. U.S. Dept. of Agri. Bureau of Entomol. Circ. 14 (2nd ser.). 8 pp.
- KELLER, J. C., E. B. MITCHELL, G. MCKIBBEN, AND T. B. DAVICH. 1964. A sex attractant for female boll weevils from males. J. Econ. Entomol. 57: 609-610.
- LEGGETT, J. E., AND W. H. CROSS. 1971. A new trap for capturing boll weevils. U.S. Dept. of Agri., Coop. Econ. Insect Report 21: 773-774.
- LLOYD, E. P., J. E. LEGGETT, AND A. W. HARTSTACK. 1983. Pheromones for survey, detection, and control in cotton insect management with special reference to the boll weevil. R. L. Ridgway, E. P. Lloyd, and W. H. Cross, eds. Agri. Handbook No. 589, ARS, USDA, Washington, D.C. pp. 179-205.
- LLOYD, E. P., W. P. SCOTT, K. K. SHAUNAK, F. C. TINGLE, AND T. B. DAVICH. 1972. A modified trapping system for suppressing low-density populations of overwintered boll weevils. J. Econ. Entomol. 65: 1144-1147.
- MCKIBBEN, G. H. 1976. Composition for attracting the cotton boll weevil. U.S. Patent 3,803,303.
- MCKIBBEN, G. H., D. D. HARDEE, T. B. DAVICH, R. C. GUELDNER AND P. A. HEDIN. 1971. Slow-release formulations of grandlure, the synthetic pheromone of the boll weevil. J. Econ. Entomol. 64: 317-319.
- MCKIBBEN, G. H., W. L. JOHNSON, R. EDWARDS, E. KOTTER, J. F. KEARNEY, T. B. DAVICH, E. P. LLOYD, AND M. C. GANYARD. 1980. A polyester-wrapped cigarette filter for dispensing grandlure. J. Econ. Entomol. 73: 250-251.
- MITCHELL, E. B., AND D. D. HARDEE. 1974. Infield traps: a new concept in survey and suppression of low populations of boll weevils. J. Econ. Entomol. 67: 506-508.

- RUMMEL, D. R., J. R. WHITE, S. C. CARROLL, AND G. R. PRUITT. 1980. Pheromone trap index system for predicting need for overwintered boll weevil control. *J. Econ. Entomol.* 73: 806-810.
- TUMLINSON, J. H., D. D. HARDEE, R. C. GUELDNER, A. C. THOMPSON, P. A. HEDIN AND J. P. MINYARD. 1969. Sex pheromones produced by male boll weevil: isolation, identification, and synthesis. *Science (Washington)* 166: 11010-1012.

USE OF PHEROMONES IN THE BOLL WEEVIL DETECTION AND CONTROL PROGRAM IN PARAGUAY

W. H. WHITCOMB

Professor Emeritus, University of Florida
Research Coordinator, Fito Technica Florida, Inc.
P.O. Bx 2458, Gainesville, FL 32601

AND

R. M. MARENGO
Ministry of Agriculture
Asuncion, Paraguay

ABSTRACT

Although the boll weevil, *Anthonomus grandis* Boem., arrived in South America before 1949, it was not discovered in Brazil until 1983. Now, however, the boll weevil is expected, momentarily, in neighboring Paraguay. A network of pheromone traps to intercept the boll weevil has been set up both on the Paraguay/Brazil border and in important cotton producing areas of Paraguay.

RESUMEN

Aunque el picudo Mexicano, *Anthonomus grandis* Boem., llegó a Sudamérica antes de 1949, no fué descubierto en Brasil sino hasta 1983. Ahora, no obstante, se espera que el picudo Mexicano llegue al Paraguay muy pronto. Una serie de trampas de feromona para interceptar al picudo se han colocado en la frontera de Paraguay/Brasil y en las zonas importantes de producción de algodón en Paraguay.

The cotton boll weevil, *Anthonomus grandis* Boheman, a pest of North American cotton for over 50 years, was discovered in South America on 20 Nov. 1949. Specimens taken at Tocoron, 20 km south of Maracay, Venezuela, were found to be *A. grandis* (Ron-Pedrique 1950, Whitcomb 1952, Whitcomb & Britton 1953). The identification was confirmed on 30 Nov. 1949 by C. F. W. Muesebeck from specimens forwarded to Washington, D.C., U.S.A. Final determination was made by L. L. Buchanan from dissections of the genitalia.

Serious yield losses were reported by cotton growers all over Venezuela. The economic impact was severe. By 1950, the Atlantic coast of Colombia was heavily infested.

For over 30 years, no other South American countries reported new boll weevil infestations. However, in Feb. 1983 the boll weevil was discovered near Sao Paulo,

- RUMMEL, D. R., J. R. WHITE, S. C. CARROLL, AND G. R. PRUITT. 1980. Pheromone trap index system for predicting need for overwintered boll weevil control. *J. Econ. Entomol.* 73: 806-810.
- TUMLINSON, J. H., D. D. HARDEE, R. C. GUELDNER, A. C. THOMPSON, P. A. HEDIN AND J. P. MINYARD. 1969. Sex pheromones produced by male boll weevil: isolation, identification, and synthesis. *Science (Washington)* 166: 11010-1012.

USE OF PHEROMONES IN THE BOLL WEEVIL DETECTION AND CONTROL PROGRAM IN PARAGUAY

W. H. WHITCOMB

Professor Emeritus, University of Florida
Research Coordinator, Fito Technica Florida, Inc.
P.O. Bx 2458, Gainesville, FL 32601

AND

R. M. MARENGO
Ministry of Agriculture
Asuncion, Paraguay

ABSTRACT

Although the boll weevil, *Anthonomus grandis* Boem., arrived in South America before 1949, it was not discovered in Brazil until 1983. Now, however, the boll weevil is expected, momentarily, in neighboring Paraguay. A network of pheromone traps to intercept the boll weevil has been set up both on the Paraguay/Brazil border and in important cotton producing areas of Paraguay.

RESUMEN

Aunque el picudo Mexicano, *Anthonomus grandis* Boem., llegó a Sudamérica antes de 1949, no fué descubierto en Brasil sino hasta 1983. Ahora, no obstante, se espera que el picudo Mexicano llegue al Paraguay muy pronto. Una serie de trampas de feromona para interceptar al picudo se han colocado en la frontera de Paraguay/Brasil y en las zonas importantes de producción de algodón en Paraguay.

The cotton boll weevil, *Anthonomus grandis* Boheman, a pest of North American cotton for over 50 years, was discovered in South America on 20 Nov. 1949. Specimens taken at Tocoron, 20 km south of Maracay, Venezuela, were found to be *A. grandis* (Ron-Pedrique 1950, Whitcomb 1952, Whitcomb & Britton 1953). The identification was confirmed on 30 Nov. 1949 by C. F. W. Muesebeck from specimens forwarded to Washington, D.C., U.S.A. Final determination was made by L. L. Buchanan from dissections of the genitalia.

Serious yield losses were reported by cotton growers all over Venezuela. The economic impact was severe. By 1950, the Atlantic coast of Colombia was heavily infested.

For over 30 years, no other South American countries reported new boll weevil infestations. However, in Feb. 1983 the boll weevil was discovered near Sao Paulo,

Brazil (Barbosa et al. 1983, Sobrinho & Lukefahr 1983). In November, the boll weevil was found in Northeastern Brazil. It became obvious that neither Paraguay nor Argentina could escape infestation by the boll weevil much longer.

In March 1984, the senior author was contracted by the Food and Agricultural Organization of the United Nations to determine whether or not the boll weevil had already invaded Paraguay. He contacted Willard Dickerson, a United States Department of Agriculture authority on boll weevil detection in Raleigh, North Carolina. Plans were made for a network of pheromone traps for weevil detection along the Paraguay/Brazil border and throughout the cotton-producing areas of Paraguay.

Cotton production in Paraguay is very different from cotton cultivation in other Latin American countries. There are over 135,000 small farms. Few of the plantings are over 2 ha; there are almost no large haciendas. Slash and burn farming, where the jungle is cut down and abandoned three years later, is common in much of South America but is rare in Paraguay. The farms are mostly owner-operated, non-mechanized operations that depend on oxen, horses, or mules for energy. Farmers have little capital, use almost no fertilizer, and spend less than US\$50 per year on pesticides. Because of fertile soil east of the Paraguay River, the effort of the farmers and an unusually well-adapted variety of cotton, Paraguayan cotton farmers compete well on the world market. Production of 1,200 kg of cotton/ha is not unusual. The variety of cotton grown at present in Paraguay, Reba P279, is a precocious type of short-staple cotton developed by geneticists of the French Cotton and Tropical Fiber Institute (I.R.C.T.). The origin of this variety is Allen A50T crossed with Stoneville B1439 in the Central Africa Republic. Allen is a variety from Chad in Africa and this variety traces much of its ancestry to pre-boll weevil, long season upland American cotton. Much of the cotton is marketed in France.

The network of pheromone traps was first established during March-April 1984. The purpose of the network was twofold. The 1st objective was to determine if the boll weevil was already present in Paraguay. The 2nd objective was to determine when and where the boll weevil would appear. The arrival of the boll weevil in Paraguay was deemed almost inevitable due to its rapid spread in Brazil. The boll weevil project was under the auspices of F.A.O. and the Ministry of Agriculture of Paraguay. Ing. Alberto Alvarez, Director of Agricultural Research was the ministerial representative in charge. The senior author traveled to Paraguay twice. His first assignment was from March-May 1984; the second was from March-July 1985. Ing. Caesar Caballero directed the field research during 1984; Ing. Rosa Maria Marengo directed field research in 1985. The pheromone traps have been in continuous operation since April 1984 and will be serviced continuously until the weevil is taken.

The traps used were Hercon Boll Weevil Scout™ Trap (Hercon Div. Health-Chem Corp., 1107 Broadway, NY, NY 10010), originally recommended by Willard Dickerson of APHIS (U.S.D.A.) (Fig. 1). Traps are placed on 1.5-m-high bamboo stakes which are split at the tip. The pheromone is placed in the plastic perforated cage. There was difficulty with lids being blown off in the wind. This problem was solved with narrow elastic tape stretched from holes on one side, over the top to holes on the other side and knotted at each end. Additional difficulties arose from vandalism and theft. This problem was resolved partially by positioning traps as inconspicuously as possible, and by initiating a publicity campaign to educate people in the importance of the traps.

Traps were placed in or on the edges of cotton fields in 15 separate areas varying in size, with 50 or more to an area. The 15 areas are as follows: Caaguzú, Hernandarias, La Paloma, Saltos del Guaira, Corpus Christi, Ipé Jhu, Capitán Bado, Cruce Liberación, Concepción, Mayor Martínez, Coronel Bogado, Ybycui, Loma Plata, Yby Yaú, and Caacupé.

The areas between Hernandarias and Capitan Bado received special attention; this

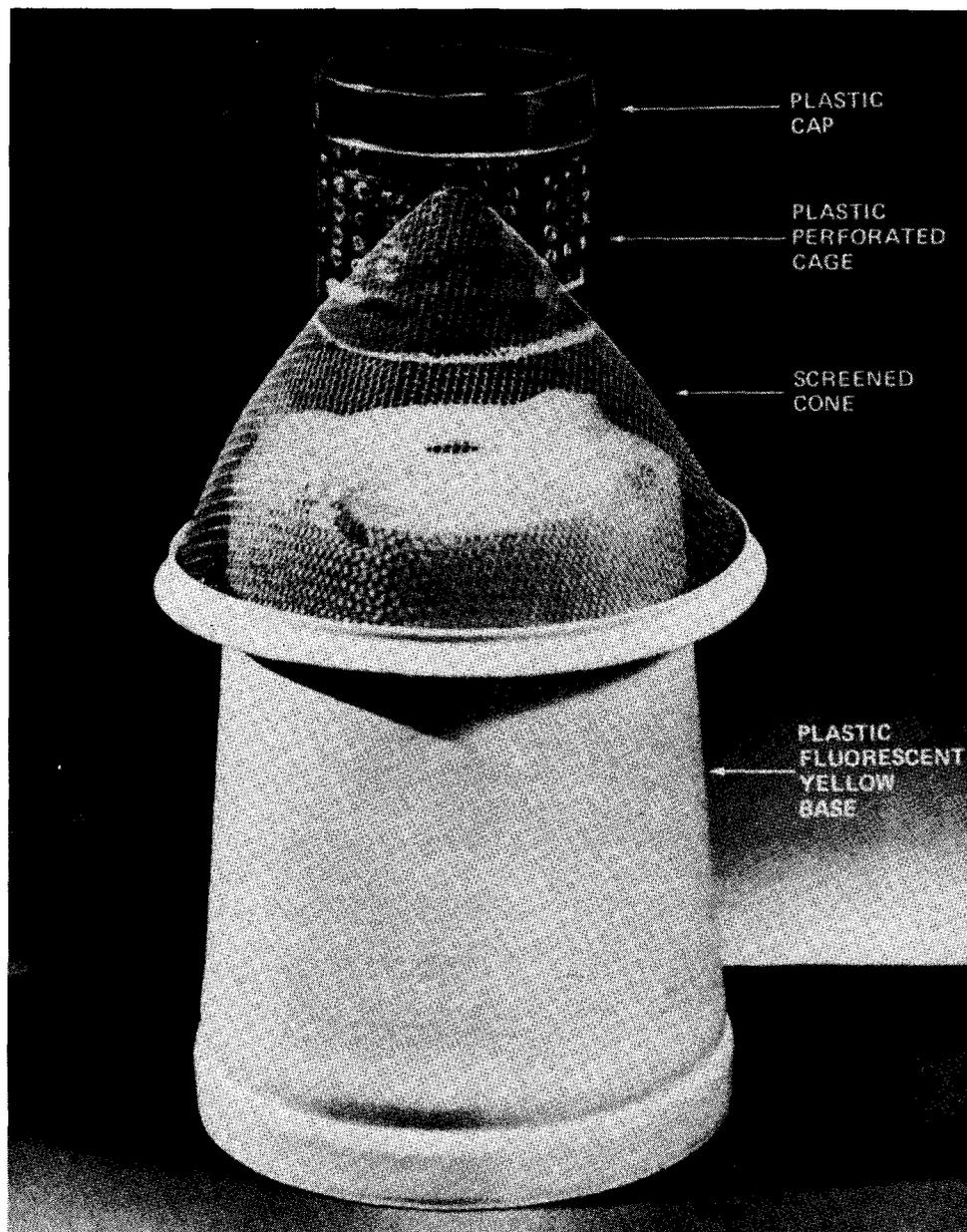


Fig. 1. Hercon Boll Weevil Scout™ Trap.

zone is situated directly in the apparent path of the spreading weevil infestation. Near Saltos del Guaira, La Paloma, Corpus Christi, and Ipé Jhu, Brazilian and Paraguayan cotton fields are only a few meters apart. They are so close that care had to be taken not to place traps in Brazil. Coronel Bogado, Mayor Martínez, and Ybycui were far from the border but received special attention as key cotton growing areas. Ten traps were placed at the cotton research station at Caacupé. Isolated pheromone traps were located at gins and crucial transportation points. Emphasis was placed on examining traps once a week. At times, this was difficult because of lack of transportation. As an added precaution, all traps were examined by a supervisor once a month. All specimens collected in the traps were brought to the cotton research laboratory at Caacupé. They

were then sorted and the weevils were separated and examined for possible *Anthonomus* species which were forwarded to specialists for identification.

To date, no boll weevils have been taken in any of the traps in Paraguay. Apparently, the boll weevil is not yet present in Paraguay. Boll weevils are now present near the Brazilian state of Parana. *Anthonomus grandis* can be expected in Paraguay at any time. It is entirely possible that following the late dispersal in May and June 1986, boll weevils will be taken in the pheromone traps in Paraguay.

Once the weevils are present in Paraguay, pheromone traplines will be expanded in as many areas as possible to indicate the first seasonal appearance. Early season treatment of boll weevil hot spots is a crucial part of present day boll weevil pest management. In Paraguay, insecticide will not be used until the weevils are actually present in the field. Four distinct methods will be used to locate boll weevils before the appearance of cotton squares. Pheromone traps have proven themselves valuable in this regard in several countries (Gilliland and Rummell 1978). In Paraguay, they will be used in conjunction with a 2nd method, the planting of trap crops. Trap crops are sown weeks before the actual crop and begin squaring early, attracting most of the weevils in the vicinity. The 3rd approach is still experimental and utilizes mixtures of pheromones and other attractants applied to cotton planted at the normal time. Theoretically, this approach could be useful, but is still unproven. Examination of terminals in non-squaring cotton was used effectively by Dwight Isely over 60 years ago (Isely 1926). This method is time consuming, but could be quite effective, especially in conjunction with the pheromone traps, in the small Paraguayan cotton field. Timing for mid- and late-season insecticide applications in Paraguay will depend upon sequential sampling of punctured squares.

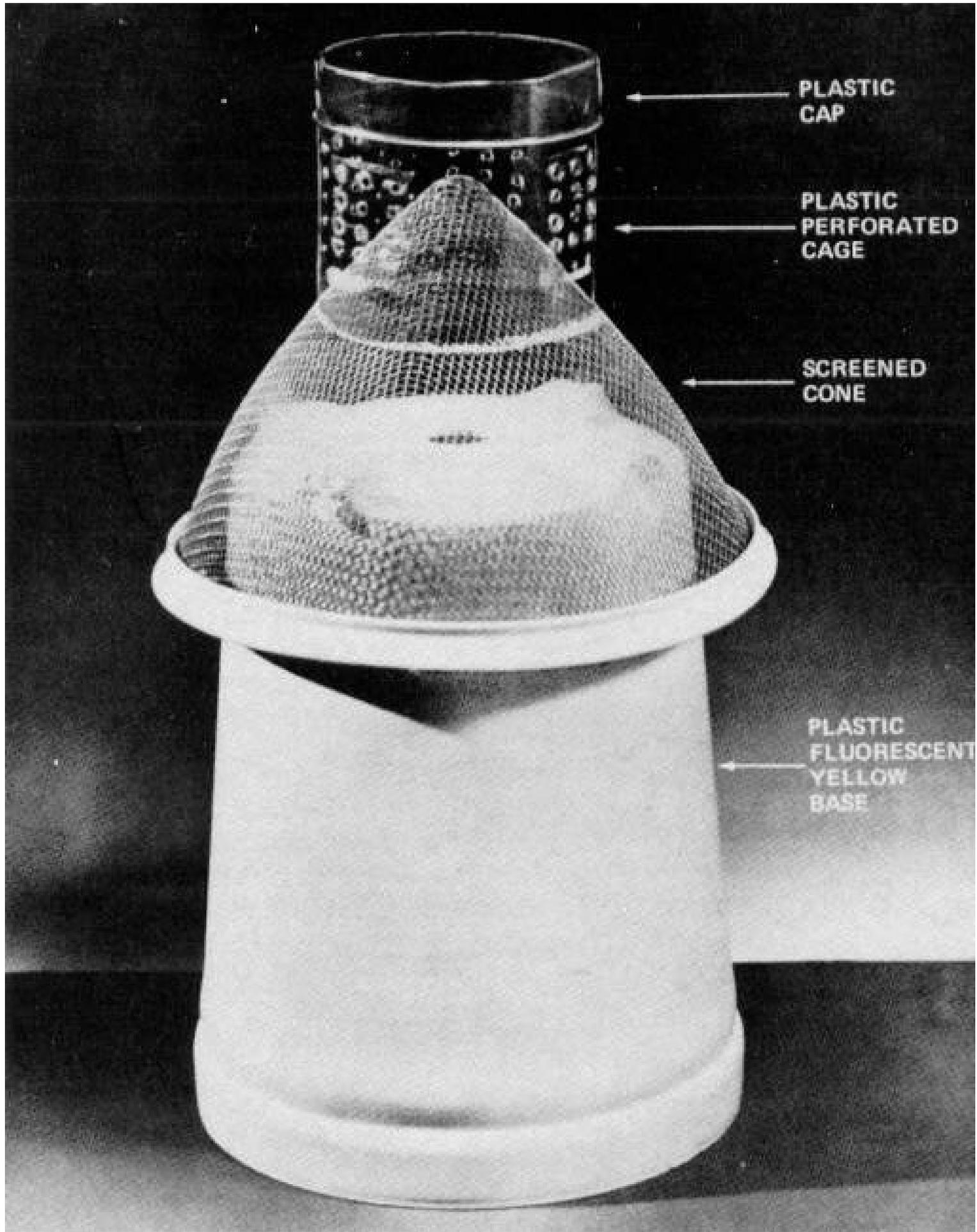
Pheromones, as a survey tool, have revolutionized much of tropical pest management. If one needs to know when the mature sex forms of a given insect pest are present, there is no better method. Counts from traps baited with grandlure can demonstrate the presence of both male and female boll weevils. Paraguay is depending on this survey tool for the very survival of its cotton industry.

END NOTE

This investigation was instigated and funded by the Food and Agricultural Organization of the United Nations. Florida Agricultural Experiment Stations Journal Series No. 6989.

LITERATURE CITED

- BARBOSA, S., R. BRAGA SOBRINHO, M. J. LUKEFAHR. 1983. Relatório sobre o ocorrência do bicudo do algodoeiro *Anthonomus grandis* Boheman no Brasil, e recomendações para su erradicação. Campina Grande Embrapa C.NPA: 1-12.
- GILLILAND, F. R. JR. AND D. R. RUMMELL. 1978. The role of pheromone for boll weevil detection and suppression. pg. 84-95 in L. O. Warren. 1978. The Boll Weevil Management Strategies, Southern Cooperative Series 228: 1-124.
- ISELY, DWIGHT. 1926. Early summer dispersion of boll weevil with special reference to dusting. University of Arkansas Bull. 204: 3-17.
- RON-PEDRIQUE, A. 1950. El picudo del algodón en Venezuela. El Agricultor Venezolano 14(141): 24-28.
- SOBRINHO, R. BRAGO, M. J. LUKEFAHR. 1983. Bicudo (*Anthonomus grandis* Boheman) Nova Ameaca A Cotonicultura Brasileira. Embrapa Documentos 22: 3-32.
- WHITCOMB, W. H. 1952. La lucha contra el picudo del algodón. Sus peculiaridades en el tropico. Revista Shell 1: 52-58.
- WHITCOMB, W. H. AND L. A. BRITTON. 1953. The control of cotton boll weevil *Anthonomus grandis* Boheman in Venezuela. The Empire Cotton Growing Review 30(3):178-181.



PLASTIC
CAP

PLASTIC
PERFORATED
CAGE

SCREENED
CONE

PLASTIC
FLUORESCENT
YELLOW
BASE

PHEROMONES AND PARAPHEROMONES IN THE CONTROL OF TEPHRITIDS

JOHN M. SIVINSKI AND CARROL CALKINS

Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U. S. Department of Agriculture,
Gainesville, Florida 32604

ABSTRACT

The complex lives of tephritids are mediated by a variety of chemical cues. Those involved with feeding, host location, mating, and oviposition have been used in control. *Feeding*—recent work suggests that tropical adult fruit flies feed for the most part on leaf surface bacteria. New attractants based on bacteria and their by-products may soon be available. *Host location*—host odors, colors and shapes can attract flies and are presently used in integrated pest management. These stimuli are frequently added to traps baited with sexual pheromone and parapheromones. *Mating*—males, particularly in lekking species, release pheromones that attract both males and virgin females. These compounds are produced in a morphologically broad range of glands. Parapheromones are compounds, often originally derived from plants, that attract sexually mature males and more rarely, females. Their role in fruit fly bionomics is unknown, though they may coincidentally resemble pheromones or be pheromone precursors. The principal uses of sex attractants have been in male eradication and monitoring; however, in the future they may also be useful in quality control. *Oviposition*—females in a number of pestiferous species mark oviposition sites with a pheromone that discourages egg laying by subsequent females. Chemical identification of these substances has proved difficult, but field trials suggest that they may be used to protect fruit crops.

RESUMEN

La vida compleja de tephritidos es regulada por una variedad de apuntes químicos. Aquellos envueltos con la alimentación, localizar hospederos, apareamiento, y oviposición se han usado para su control. *Alimentación*—reciente trabajo sugiere que moscas adultas tropicales se alimentan en su mayor parte de bacterias en la superficie de la hoja. Nuevos atrayentes basados en bacterias y sus productos secundarios, pudieran estar disponibles muy pronto. *Localizar hospedero*—olor del hospedero, colores y formas pueden atraer moscas y son actualmente usadas en la administración integral de plagas. Estos estímulos son frecuentemente añadidos a trampas cebadas con feromonas sexuales y con paraferomonas. *Apareamiento*—machos, particularmente en las especies "lekking" echan feromonas que atraen a machos y hembras vírgenes. Estos compuestos son producidos por un número de glandulas morfológicamente diversas. Las paraferomonas son compuestos que a menudo originalmente se derivaron de plantas, y que atraen a machos sexualmente maduros y más raramente a las hembras. Su función en la bionomía de las moscas de frutas es desconocida, aunque ellas pueden coincidentalmente parecerse a las feromonas o ser precursoras de feromonas. El uso principal de los atrayentes sexuales ha sido en la erradicación y chequeo de los machos, sin embargo, en el futuro ellos también pudieran ser útiles en el control de calidad. *Puesta de huevos*—las hembras, en un número de especies de plagas, marcan el lugar donde ponen los huevos que desalenta a otras hembras de poner huevos. La identificación química de estas substancias ha probado ser difícil pero pruebas en el campo sugieren que ellas pudieran ser usadas para proteger los cultivos de frutas.

On an arthropodean scale, the lives of fruit flies can be extraordinarily eventful. Some superlatives include: learning of host plants and pheromones (Prokopy et al.

1982a, Roitberg and Prokopy 1981), regular dispersions to feeding areas up to 100 km away (Drew et al. 1984), intricate dual-strategy male mating systems with elaborate lek centered courtships and highly discriminating females (Burk 1981, Sivinski and Burk 1986) and the exploitation of chemically and morphologically complex bodies (fruit) for larval development.

Much of this behavioral exuberance is mediated through chemical cues and this in turn offers a number of opportunities for control through chemical manipulation. Entomologists concerned with the attraction/repulsion of tephritids have concentrated their efforts on fruit fly feeding, host location, mating and oviposition. Only the latter two involve pheromones (*sensu strictu*). However, much of tephritid control has been and remains to be done with feeding/host cues. Since these kairomones are often applied in parallel to and conjunction with pheromones and parapheromones, they deserve some brief discussion here as well.

ADULT FEEDING

Tephritids feed on extrafloral nectaries, sap flows, bird dung and occasionally flowers (i.e., *Dacus curcurbitae* Coq.; Bateman 1972). However, most were thought to subsist on homopteran honeydew (e.g., Hagen 1958). Australian work on *Dacus* spp. has challenged this assumption and reemphasized the role of leaf surface bacteria in diet, particularly the diet of species in the humid tropics where conditions do not allow the accumulation of insect excretions (Drew et al. 1983; Courtice and Drew 1984; see also work on *Anastrepha fraterculus* (Wied.) by Malavasi et al. 1983). The large numbers of bacteria in tephritid crops have been noted for many years, but were thought to be largely symbionts (Petri 1910). Now these microbial masses are being reinterpreted as the result of consumption and a new generation of bacterial based attractants may be in the wings, although some controversy exists regarding the present work.

In the meantime, bacteria are being exploited in food traps. Commonly used protein hydrolysate baits apparently owe much of their attractiveness to the bacteria they nurture. Gow (1954) noted that the addition of antibiotics lowers the effectiveness of protein lures and Morton and Bateman (1981) found ammonium, probably the result of bacterial degradation, to function as the principal attractant in such solutions (see also, Courtice and Drew 1984). Amino acids act as feeding stimulants once contact is made (for similar effect in *Anastrepha*, see Sharp and Chambers 1983).

Food baits are used in both population monitoring and control. The standard liquid filled trap is the McPhail trap, an invaginated glass bottle based on an ancient Chinese design for the capture of blow flies. These have been particularly useful for detection of *Anastrepha* spp., for which no other practical attractant exists. Sprayed mixtures of protein bait and insecticide (typically malathion, which is relatively nontoxic to mammals, or naled) are classic means of tropical tephritid control (see Drew et al. 1978). In temperate regions, poisoned protein hydrolysates have not always proven more effective than insecticides alone in controlling *Rhagoletis* spp. (Reissig 1977).

HOST LOCATION

Plants and their fruits can be conspicuous by their shape, color, and odor. Location of hosts by their specific shape seems rare, although *Platyparea poecoloptera* (Schrank) are attracted to asparagus-like and *Urophora affinis* Fraunfeld to composit-like forms (Eckstein 1931, Zwolfer 1970). The apple maggot, *Rhagoletis pomonella* Walsh, is drawn to fruit-like spheres and circles (see Prokopy and Roitberg 1984 for recent discussion). *R. pomonella* is attracted to apple volatiles (Prokopy et al. 1973, Fein et al. 1982), and synthetic apple volatiles increase the performance of traps (Reissig et al. 1982,

Swift 1982). Host odors also lure the olive fly, *D. oleae* (Gmelin) (Fiestas Ros de Ursinos et al. 1972). Contact arrestants and repellents of *Rhagoletis* spp. occur in host and nonhost tissue, respectively (Bush et al., cited in Prokopy 1977). A number of plants produce chemicals attractive to tephritids, but often their role, if any, in fruit fly bionomics is obscure (Keiser et al. 1975; see discussion of parapheromones below).

This is an appropriate point to mention the role of color in control. Wavelengths reflected from foliage and fruit can be highly attractive. *Rhagoletis* spp. are drawn to fluorescent yellows, and sticky yellow boards alone suppress populations in cherry and blueberry (Prokopy 1976, Boller and Remund 1981). Sticky red spheres are also useful against apple maggot and have been used in integrated pest management procedures (Prokopy 1975, 1985). *Ceratitidis capitata* (Wied.) and *Dacus* spp. (with the exception of *D. cucurbitae*) are lured to yellow, while *Anastrepha suspensa* (Loew) is most attracted by orange, (Bateman 1976, Greany et al. 1977, de Souza et al. 1984). Striping in the case of *A. suspensa* and checkering in *D. tryoni* (Froggatt) increased the effectiveness of colored decoys (Davis et al. 1984, Hill and Hooper 1984).

Traps containing food, host, or sexual lures are often colored as well, although in the case of the olive fly, *D. oleae*, yellow did not boost the value of MacPhail traps until a sticky compound was placed on the outside (Bateman 1976, Prokopy and Economopoulos 1975). This emphasizes the importance, when designing traps, of understanding the behavior of flies as they approach and land upon a surface. Davis et al. (1984) found that Caribbean fruit flies generally landed on the underside of foliage and thus modified the Jackson trap (a folded cardboard tent with an inserted floor) so that there was a ceiling adhesive. Mediterranean fruit flies tend to land on upper surfaces and walk to lower surfaces. This suggests that an upper surface adhesive placed on floor inserts of a Jackson trap is the most efficient means of trapping this species (Hendrichs and Aluja, personal communication).

MATING—PHEROMONES AND PARAPHEROMONES

The meeting of the sexes is not a simple procedure in the Tephritidae, particularly among polyphagous tropical and subtropical species. Host unpredictability has placed a selective emphasis on males' advertising their qualities to passing females rather than searching fruit for available mates (Burk 1981, Prokopy 1980, Sivinski and Burk 1986). Males of these tropical species frequently aggregate in leks where intense competition has further elaborated their distance signals and courtship displays. In *Anastrepha*, *Ceratitidis* and *Dacus* there are acoustic, visual, and pheromonal signals directed at mate-searching females (e.g. Sivinski et al. 1984). This barrage of male-produced stimuli complicates the study and manipulation of any one signaling system.

Another complication in the application of pheromones for control arises from the lek mating system. Males who join mating aggregations are believed to have a greater probability of inseminating a female. They are therefore attracted to the signals of other males. A rule-proving exception is the nonlekking *Rhagoletis cerasi* L. where male pheromone is not attractive to other males; (see Katsoyannos 1982). On the other hand, while temperate females mate every week or less, tropical females tend to copulate much less frequently, perhaps only once in a lifetime (Bateman 1976, Prokopy and Roitberg 1984). Thus the proportion of the female population responding to sexual signals at any one time can be quite small (Burk and Calkins 1983), especially in comparison to food baited traps which tend to attract more females (1.4 to 1.8X in Caribbean fruit fly, Perdomo et al. 1976). Often, pheromones and parapheromones are referred to as "male lures". This is an overstatement. When equal numbers of males and *receptive* females are exposed to male baited traps they are captured in roughly equal numbers (Perdomo et al. 1976). This propensity for sexual attractants in the field to capture males

but not females influences control strategies, as we shall see later.

As implied earlier, attractant pheromones in tropical frugivorous tephritids are emitted by males; with the exception of *D. oleae*, where both sexes produce similar pheromones (Baker et al. 1980, Mazomenos and Pomonis 1982). Those that have been identified, at least in part, tend to be multicomponent blends (Baker et al. 1982, Gariboldi et al. 1983, Nation 1983, Battiste et al. 1983), and may include substances active at either close or long ranges (Bellas and Fletcher 1979). The bizarre papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, appears to be exceptional in possibly having only a single component pheromone (Landolt et al. 1985). Many *Dacus* spp. puff out "smoke"; red or orange inorganic phosphate crystals coated with long chain hydrocarbons (C25-29) that resemble cuticular waxes (Ohinata et al. 1982). It is possible these evolved as a means of projecting nonvolatile cuticular contact pheromones and so expanded the flies' broadcast range. One might wonder if the color of smoke has a communicative function as well.

Different genera have evolved a variety of pheromone glands; in *Dacus*, male and female glands are located in the rectum. In *Anastrepha*, large glandular cells are present in the pleural region of the abdomen. There also are sexually dimorphic salivary glands. In *Rioxa pornia* (Walker), there are similar pleural and salivary glands from which in the latter case. A foam (with pheromone ?) is produced that females consume during copulation. In medfly, pleural glands and dimorphic salivary glands are combined with ductless glands in the last abdominal segment. Finally, in *Rhagoletis* there are no specialized glands but pheromones may arise in the gut (Nation 1981).

Pheromones are perceived in *D. tryoni*, the Queensland fruit fly, by sensors on the antennae, maxillary palps, and last segment of the ovipositor (Giannakakis and Fletcher 1981, Metcalf et al. 1983). If such a receptor topography is general it might account for a peculiar behavior noted in Caribbean and Mediterranean fruit flies. Females often sit on the undersides of leaves with their ovipositors stuck upward perpendicular to their bodies. The action seems purposeful but puzzling. Can sensillae on the ovipositor pick up airborne chemicals and could it be erected to act as a sort of third antenna?

The range of fruit fly pheromones show considerable variance. Those of *D. tryoni* and *D. neohumeralis* attract males from several meters away (Bellas and Fletcher 1979). The pheromone of *D. oleae* works well at 80 m (Delerio et al. 1982), while the medfly synthetic attractant, trimedlure, is effective to at least 20 m (Delrio and Zumreoglu 1982). The champion is another parapheromone, methyl eugenol, which attracts Oriental fruit flies, *D. dorsalis*, from distances of up to 1 km (Steiner 1969).

Parapheromones, such as the above mentioned methyl eugenol and trimedlure, are something of a mysterious blessing (Table 1). Often as not, they have been discovered by accident and are frequently, but not always, derived from plants (kerosene was a

TABLE 1. THE MAJOR PARAPHEROMONES USED IN FRUIT FLY CONTROL—FROM CHAMBERS (1979).

Compound	Pest species for which used
Methyl eugenol	Oriental fruit fly, <i>Dacus dorsalis</i> ; Mango fruit fly, <i>D. zonatus</i>
Cuelure 4-(p-hydroxyphenyl)- 2-butanone acetate	Melon fly, <i>D. curcubitae</i> ; Queensland fruit fly, <i>D. tryoni</i>
Trimedlure <i>tert</i> -butyl 4 (or 5)-chloro-2-methyl- cyclohexanecarboxylate	Mediterranean fruit fly, <i>Ceratitidis capitata</i> Natal fruit fly, <i>C. rosa</i>

favorite at the turn of the century, Severin and Severin 1915). Methyl eugenol was found to be the active ingredient in the classic attractant, citronella oil, while the essential oils of the seeds of *Angelica archangelica* L. were popular medfly attractants before the discovery of trimedlure (see citations in Guiotto et al. 1980). Ether extracts of any number of plants can attract flies (61 of 232 in Keiser et al. 1975). In the case of the Australian plant *Zieria smithii*, whose crushed leaves attract *D. cacuminatus* (Hering), its essential oils are ca. 85% 0-methyl eugenol (Fletcher et al. 1975). It is believed that the majority of such plants do not serve as food, shelter, or mating sites but since the natural histories of most tephritids are poorly known, it is probably premature to make such a generalization.

Parapheromones undoubtedly fill some sexual role. Females of some *Dacus* spp. respond to them at the same time and in much the same manner as they would to pheromone (Fitt 1981a). Mediterranean and Oriental fruit fly females will even be attracted to parapheromones in the field when their males are trapped out (Steiner et al. 1965, Nakagawa et al. 1970). To females they are apparently something like a pheromone, but do not compete well with the real thing. There is certainly little species specificity in parapheromones. Seventy-nine species of *Dacus* in the South Pacific are attracted by either cue lure or methyl eugenol (Drew 1974, Drew and Hooper 1981; only the jackfruit fruit fly *D. umbrosus* F. responds to both, Umeya and Hirao 1975).

The reaction of males to parapheromones both substantiates and obscures their status as pheromonal surrogates. Males are more attracted to parapheromones as they mature sexually but in at least some *Dacus* spp. they are most responsive at the time of day opposite their peak period of sexual activity (Brieze-Stegeman et al. 1978, Fitt 1981b). Once males arrive at a methyl eugenol site they "pulse" their mouthparts and lick the lure. Fitt (1981b) has found metabolites of methyl eugenol in the pheromone of *D. tryoni* 24 h after ingestion, which suggests it may be a pheromone precursor that is sought by males when available but which is not strictly necessary for pheromone production. A somewhat similar case may occur in neotropical euglossine bees, many of which are specialized pollinators of orchids. Males visit flowers solely to gather floral scents from which to construct pheromones and some are highly attracted to eugenol (Williams and Whitten 1983). Unfortunately the generality of the argument is shaken by the relative unpalatability of trimedlure. It is preferable to use fumigant insecticides in conjunction with trimedlure since the insects are not likely to eat it (Drew et al. 1978).

Whatever the role of parapheromones in tephritid biology it is believed that there is room for improvement in fruit fly attractants. Methyl eugenol is more effective at trapping the Oriental fruit fly than trimedlure is in capturing Mediterranean fruit fly. This suggests to Fletcher (1977) an untapped responsiveness in the medfly. Early work with *C. capitata* sex pheromone shows it to be at least as effective as trimedlure, and bears the promise of further improvement (Zümreoglin 1983). Fletcher (1977) also notes that the pheromone of *D. tryoni* is more successful than the classic parapheromone attractant, cue lure. All of this presages the arrival of more effective baits with further research. There is a particular sense of urgency concerning lures for Oriental fruit fly since methyl eugenol has recently been found to cause liver cancer in rats (Mitchell et al. 1985).

What can be done with available lures? As noted, tropical fruit fly attractants catch mostly males. Even so, male annihilation through lure/toxicant mixtures have eradicated Oriental fruit fly from a number of islands (Koyama et al. 1984; note these authors found that male numbers must be suppressed to 1% of their former level before there is a detectable fall in fruit infestation). Suppressions of wild males is, of course, useful before a sterile release. There is extensive literature on how, when and where to apply lure/toxicant mixtures. The interested reader should consider the following and their bibliographies: Nakamori and Soemori (1981), Chambers (1977, 1979), Drew et al.

(1978), Boving et al. (1980), Hart et al. (1966), Barclay and van den Driessche (1984), Cunningham et al. (1975). Also, note subsequent citations under discussion of monitoring since there is considerable overlap in techniques. Pheromones and parapheromones have proved to be particularly useful in monitoring populations and warning of introductions. For instance, methyl eugenol has discovered and aided in the eradication of at least 11 forays of Oriental fruit fly into Los Angeles County, California (Anonymous 1984). An introduction to the literature is as follows: trap design and presentation of the lure (Drew et al. 1978, Hooper and Drew 1978, Ibrakin et al. 1979, Jones et al. 1983, King and Landolt 1984, Nakagawa et al. 1979, 1981, Rice et al. 1984, Leonhardt et al. 1984, refer to earlier discussion of host cues for further trap literature) lure mixture (Hooper 1978), and height placement of traps (Holbrook and Fujimoto 1969, Hooper and Drew 1979). Pheromones may have an expanding role in quality control, i.e. making sure that domesticated sterile flies can respond to sexual signals in a competitive manner (Boller et al. 1981).

OVIPOSITION

A female fruit fly puts its eggs into a closed environment. Beneath the fruit surface can lurk hidden con- and heterospecific competitors (note that *D. dorsalis* larvae can suppress the development of *Ceratitidis capitata*; Keiser et al. 1974). Numerous larvae in a single small fruit would destroy the fruit before maturity; thus, multiparasitism would be detrimental. It behooves the first female to oviposit in a fruit to advertise the fact and subsequent females to heed the warning. This has led to the evolution of oviposition deterring pheromones in all of the major pestiferous fruit fly genera (Prokopy 1981).

As might be expected, the greater the potential for competition the more developed such marking systems become. For instance, in the western cherry fruit fly, *Rhagoletis indifferens* Curran, the natural host can support a single larva and the marker is quite effective in discouraging further egg laying (Mumtaz and Alinizee 1983). At the other extreme the melon hosts of *D. curcubitae* can support hundreds, even thousands, of larvae, and females do not use oviposition deterring pheromones (Prokopy and Koyama 1982). In *A. fructeculus* females put more marker on smaller fruit, thereby investing more material to avoid more acute competition (Prokopy et al. 1982b).

These pheromones have, for the most part, resisted chemical analysis, though in *D. oleae* the marker is simply olive juice from the oviposition puncture smeared over the fruit by the fly (Cirio 1971, Prokopy and Roitberg 1984). In this case, the actual repellent chemical resides in the oil fraction (Girolami et al. 1981). In *R. pomonella*, at least one major component is produced in the posterior of the midgut (Prokopy et al. 1982c). There can be cross specific recognition of oviposition deterring pheromones (Averill and Prokopy 1982).

Under laboratory conditions the pheromones of some species can persist for up to 12 days, but their effective duration in the field is much less (Katsoyannos 1975). However, older larvae are not "invisible" to foraging females. *D. tryoni* can recognize occupied fruit pulp by its chemical composition, even after larvae are removed (Fitt 1984). *A. suspensa* senses larval feeding sounds and prefers to lay eggs on silent sites (Sivinski, unpublished data).

Once identified and synthesized, oviposition repellents could be an attractive means of control (Prokopy 1972). To date, individual cherry trees have been effectively protected from *R. cerasi* by deterring pheromones (Katsoyannos and Boller 1980). However, a potential drawback is that these "warnings" tend to lose force as hosts become scarce and females are deprived of opportunity to oviposit (Mumtaz and Aliniazee 1983, Roitberg and Prokopy 1983). In *R. pomonella*, females encountering marked fruit are

more likely to disperse relatively long distances (Roitberg et al. 1984). One can imagine circumstances in which increased dispersion from a localized infestation would be counterproductive to control. Note that deterring pheromones serve as a kairomone of the *Rhagoletis* egg parasite *Opius lectus* Gahan, and so might serve to concentrate natural enemies (Prokopy and Webster 1978).

We hope this brief review has introduced the reader to some of the problems and solutions in controlling fruit flies through pheromones and parapheromones.

END NOTE

We thank R. Heath, P. Landolt, and J. Nation for numerous improvements in the manuscript.

REFERENCES CITED

- ANONYMOUS. 1984. No rest for the weary: the Oriental is back in LA. *Citrograph* 69: 243-244.
- AVERILL, A., AND R. J. PROKOPY. 1982. Oviposition-detering fruit marking pheromone in *Rhagoletis zephyria*. *J. Georgia Ent. Soc.* 17: 315-319.
- BATEMAN, M. A. 1972. The ecology of fruit flies. *Ann. Rev. Entomol.* 17: 493-518.
- . 1976. Fruit flies. Pages 11-49 in V. L. Delucchi, ed. *Studies in Biological Control*. Cambridge University Press, Cambridge.
- BATTISTE, M. A., L. STREKOWSKI, D. P. VANDERBILT, M. VISNICK, AND R. KING. 1983. Anastrephin and epianastrephin novel lactone components isolated from the sex pheromone blend of male Caribbean and Mexican fruit flies. *Tetrahedron Lett.* 24: 2611-2614.
- BOHN, R., R. H. HERBERT, AND R. A. LOMER. 1982. Chemical components of the rectal gland secretions of male *Dacus cucurbitae*, the melon fly. *Experientia* 38: 232-233.
- BAKER, R., R. H. HERBERT, AND R. A. LOMER. 1982. Chemical components of the rectal gland secretions of male *Dacus cucurbitae*, the melon fly. *Experientia* 38: 232-233.
- BARCLAY, J. H., AND P. VAN DEN DRIESSCHE. 1984. Pheromone trapping for male annihilation: a density dependent model. *Prot. Ecol.* 7: 281-289.
- BELLAS, T. E., AND B. S. FLETCHER. 1979. Identification of the major components in the secretion from the rectal pheromone glands of the Queensland fruit flies *Dacus tryoni* and *Dacus neohumensis* (Diptera: Tephritidae). *J. Chem. Ecol.* 5: 795-803.
- BOLLER, E. F., B. I. KATSOYANNOS, U. REMUND, AND D. L. CHAMBERS. 1981. Measuring, monitoring and improving the quality of mass-reared Mediterranean fruit flies, *Ceratitidis capitata* Wied. *Zeit. Ange. Entomol.* 92: 67-83.
- , AND U. REMUND. 1981. Zum Stand alternativer Bekämpfungsverfahren gegen die Kirschenfliege, *Rhagoletis cerasi* L.: Abschluss der Forschungsperiode 1962-1979 in der Schweiz. *Mitt. drsch. Ges. angew. Ent.* 2: 223-227.
- BOVING, P. A., R. T. CUNNINGHAM, AND R. G. WINTERFIELD. 1980. Tropical fruit fly control. *Adv. Agric. Tech. Western Series No. 14*, USDA Oakland.
- BRIEZE-STEGEMAN, R., M. A. RICE, AND G. H. S. HOOPER. 1978. Daily periodicity in attraction of male tephritid fruit flies to synthetic chemical lures. *J. Australian Entomol. Soc.* 17: 341-346.
- BURK, T. 1981. Signaling and sex in acalypterate flies. *Florida Ent.* 64: 30-43.
- , AND C. CALKINS. 1983. Medfly mating behavior and control strategies. *Florida Ent.* 66: 3-18.
- CHAMBERS, D. L. 1977. Attractants for fruit fly survey and control. Pages 327-244 in H. H. Shorey and J. J. McKelvey, Jr., eds. *Chemical control of insect behavior*. John Wiley & Sons, New York.

- . 1979. Diptera (fruit and vegetable crops, veterinary and medical pests. Pages 38-46 in W. L. Roelofs, ed. Establishing Efficacy of Sex Attractants and Disruptants for Insect Control. Entomol. Soc. America 97 pp.
- CIRIO, U. 1971. Reperti sul meccanismo stimola-resposta nell' ovideposizione del *Dacus oleae* Gmelin (Diptera, Trypetidae). Redia 52: 577-600.
- COURTICE, A. C., AND R. A. I. DREW. 1984. Bacterial regulation of abundance in tropical fruit flies (Diptera: Tephritidae). Australian Zool. 21: 251-267.
- CUNNINGHAM, R. T., D. L. CHAMBERS, AND A. G. FORBES. 1975. Oriental fruit fly: thickened formulations of methyl eugenol in spot applications for male annihilation. J. Econ. Ent. 68: 861-863.
- DAVIS, J. C., H. R. AGEE, AND D. L. CHAMBERS. 1984. Trap features that promote capture of the Caribbean fruit fly. J. Agric. Ent. 1: 236-248.
- DELRIO, G., A. P. ECONOMOPOULOS, P. V. ECONOMOPOULOS, G. H. HANIATAKIS, AND P. PROTA. 1982. Comparative field studies on food, sex, and visual attractants for the olive fruit fly. Page 92 in International Symposium on Fruit Flies of Economic Importance. CEC/IOBC, Athens, Greece.
- DELRIO, G., AND A. ZUMREOGLU. 1982. Attractability range and capture efficiency of medfly traps. Page 89 in International Symposium on Fruit Flies of Economic Importance. CEC/IOBC, Athens, Greece.
- DESOUYA, H., O. DEOLWEIRA PAVAN, AND I. SILVA. 1984. Oviposition and alignment behavior of *Ceratitis capitata* (Diptera: Tephritidae) on colored spheres. Revta. Brasileira. Ent. 28: 11-14.
- DREW, R. A. I. 1974. The responses of fruit fly species (Diptera: Tephritidae) in the South Pacific area to male attractants. J. Australian Ent. Soc. 13: 267-270.
- , A. C. COURTICE, AND D. S. TEAKLE. 1983. Bacteria as a natural source of food for adult fruit flies (Diptera: Tephritidae). Oecologia 60: 279-284.
- , AND G. H. S. HOOPER. 1981. The responses of fruit fly species (Diptera: Tephritidae) in Australia to various attractants. J. Australian Ent. Soc. 20: 201-205.
- , G. H. S. HOOPER, AND M. A. BATEMAN. 1978. Economic fruit flies of the South Pacific region. Watson Ferguson and Co., Brisbane, Australia.
- , M. P. ZALUCKI, AND G. H. S. HOOPER. 1984. Ecological studies of Eastern Australian fruit flies (Diptera: Tephritidae) in their endemic habitat. Oecologia 64: 267-272.
- ECKSTEIN, F. 1931. Über die Verwendung ion Kodermitteln zur Schdlingsbekämpfung. Ziet. Ang. Ent. 18: 726-743.
- ECONOMOPOULOS, A. P., AND A. PAPADOPOULOS. 1983. Wild olive fruit flies caught on sticky traps with odor, color and combinations of the two attractants. Redia 66: 409-416.
- FEIN, B. L., W. H. REISSIG, AND W. L. ROELOFS. 1982. Identification of apple volatiles attractive to the apple maggot, *Rhagoletis pomonella*. J. Chem. Ecol. 8: 1473-1487.
- FIESTAS ROSE DE USMOS, J. A., E. CONSTANTE, R. OURAN, AND A. RONCERO. 1972. Etude d'un attractif naturel pour *Dacus oleae*. Ann. Ent. Soc. France 41: 1-129.
- FITT, G. 1981a. Responses by female Dacinae to "male" lures and their relationship to patterns of mating behavior and pheromone response. Ent. Exp. & Appl. 29: 87-97.
- . 1981b. The influence of age, nutrition and time of day on the responsiveness of male *Dacus opiliae* to the synthetic lure methyl eugenol. Ent. Exp. & Appl. 30: 83-90.
- . 1984. Oviposition behavior of two tephritid fruit flies, *Dacus tryoni* and *Dacus jorvisi*, as influenced by the presence of larvae in the host fruit. Oecologia 62: 37-46.
- FLETCHER, B. S. 1977. Behavioral responses of Diptera to pheromones, allomones, and kairomones. Pages 129-148 in H. H. Shorey and J. J. McKelvey, Jr. eds. Chemical Control of Insect Behavior. John Wiley & Sons, New York.

- , M. A. BATEMAN, N. K. HART, AND J. A. LAMBERTON. 1975. Identification of a fruit fly attractive in an Australian plant *Zieria smithii* as o-methyl eugenol. *J. Econ. Ent.* 68: 815-816.
- GARIBOLDI, P., L. VEROTTA, AND R. F. ANELLI. 1983. Studies on the sex pheromone of *Dacus oleae* analysis of substances contained in the rectal glands. *Experientia* 39: 502-505.
- GIANNAKAKIS, A., AND B. S. FLETCHER. 1981. Ablation studies related to the location of the sex pheromone receptors of the Queensland fruit fly, *Dacus tryoni* (Froggatt) (Diptera: Tephritidae). *J. Australian Ent. Soc.* 20: 9-12.
- GIROLAMI, V., A. VIANELLO, A. STAPAZZON, E., RAGAZZI, AND G. VERONESE. 1981. Ovipositional deterrents in *Dacus oleae*. *Ent. Exp. & Appl.* 29: 177-188.
- GOW, P. L. 1954. Proteinaceous bait for the Oriental fruit fly. *J. Econ. Ent.* 47: 153-160.
- GREANY, P. D., H. R. AGEE, A. K. BURDITT, AND D. L. CHAMBERS. 1977. Field studies on color preferences of the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). *Ent. Exp. & Appl.* 21: 63-70.
- GUIOTTO, A., P. MANZINI, G. PASTORINI, AND P. RODIGHIERO. 1980. Synthesis and attractiveness for *Ceratitis capitata* Wied. males of Δ_3 -cyclohexenylalkylcarbinol acetates. *Il Farmaco Ed. Sc.* 35(6): 440-446.
- HAGEN, K. S. 1958. Honeydew as an adult fruit fly diet affecting reproduction. *Proc. Int. Congr. Ent.* X, 1956, Montreal 25-30.
- HANIOTAKIS, G. E., AND G. SKYRIANOS. 1981. Attraction of the olive fruit fly to pheromone, McPhail, and color traps. *J. Econ. Ent.* 74: 58-60.
- HART, W. G., L. F. STIENER, R. T. CUNNINGHAM, S. NAKAGAWA, G. FASCAS. 1966. Glyceride of lard as an extender for cue lure med lure and methyl eugenol in formulations for programs of male annihilation. *J. Econ. Ent.* 59: 1395-1400.
- HILL, A. R., AND G. H. S. HOOPER. 1984. Attractiveness of various colours to Australian tephritid fruit flies in the field. *Ent. Exp. & Appl.* 35: 119-128.
- HOLBROOK, F. R., AND M. S. FUJIMOTO. 1969. Mediterranean fruit flies and melon flies trapped at various heights with synthetic lures. *J. Econ. Ent.* 62: 962-963.
- HOOPER, G. H. S. 1978. Effect of combining methyl eugenol and cue lure on the capture of male tephritid fruit flies. *J. Australian Ent. Soc.* 17: 189-190.
- , AND R. A. I. DREW. 1978. Comparison of the efficiency of two traps for male tephritid fruit flies. *J. Australian Ent. Soc.* 17: 95-97.
- , AND R. A. I. DREW. 1979. Effect of height of trap on capture of tephritid fruit flies with cue lure and methyl eugenol in different environments. *Environ. Ent.* 8: 786-788.
- IBRAHIM, A. G., G. SINGH, AND H. S. KING. 1979. Trapping of the fruit flies, *Dacus* spp. (Diptera: Tephritidae) with methyl eugenol in orchards. *Pestanika* 2: 58-61.
- JONES, O. T., J. C. LISK, C. LONGHURST, AND P. E. HOWSE. 1983. Development of a monitoring trap for the olive fruit fly, *Dacus oleae* (Gmelin) (Diptera: Tephritidae), using a component of its sex pheromone as lure. *Bull. Ent. Res.* 73: 97-106.
- KATSOYANNOS, B. I. 1975. Oviposition-detering, male-arresting, fruit-marking pheromone in *Rhagoletis cerasi*. *Environ. Ent.* 4: 801-807.
- . 1982a. Male sex pheromone of *Rhagoletis cerasi* L. (Diptera, Tephritidae): factors affecting release and response and its role and the mating behavior. *Zeit. Ang. Ent.* 94: 187-198.
- . 1982b. Captures of *Ceratitis capitata* and *Dacus oleae* flies (Diptera: Tephritidae) by McPhail and rebel color traps suspended on host and nonhost trees in Cheos, Greece. Page 90 in *International Symposium on Fruit Flies of Economic Importance*. CEC/IOBC, Athens, Greece.
- , AND E. F. BOLLER. 1980. Second field application of oviposition deterring pheromone of the European cherry fruit fly, *Rhagoletis cerasi* L. (Diptera: Tephritidae). *Zelt. Ang. Ent.* 89: 278-281.
- KEISER, I., E. J. HARRIS, D. H. MEYASHITA, M. JACOBSON, AND R. E. PERDUE, JR. 1975. Attraction of ethyl ether extracts of 232 botanicals to Oriental fruit flies, melon flies, and Mediterranean fruit flies. *Lloydia* 38: 141-152.

- , R. M. KOBAYASHI, D. H. MEYASHITA, E. J. HARRIS, E. L. SCHNEIDER, AND D. L. CHAMBERS. 1974. Suppression of Mediterranean fruit flies by Oriental fruit flies in mixed infestations of guava. *J. Econ. Ent.* 67: 355-360.
- KING, J. R., AND P. J. LANDOLT. 1984. Rate of loss of trimedlure from cotton wicks under South Florida field conditions. *J. Econ. Ent.* 77: 221-224.
- KOYAMA, J., T. TERUYA, AND K. TANAKA. 1984. Eradication of the Oriental fruit fly (Diptera: Tephritidae) from the Okiwawa islands by a male annihilation method. *J. Econ. Ent.* 77: 468-672.
- LANDOLT, P. J., R. R. HEATH, AND J. R. KING. 1985. Behavioral responses of female papaya fruit flies, *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae) to male produced sex pheromone. *Ann. Ent. Soc. America* (in press).
- LEONHARDT, B. A., R. E. RICE, E. M. HARTE, AND R. T. CUNNINGHAM. 1984. Evaluation of dispensers containing trimedlure, the attractant for the Mediterranean fruit fly (Diptera: Tephritidae). *J. Econ. Ent.* 77: 744-749.
- MALAWASI, A., J. S. MORGANTE, AND R. J. PROKOPY. 1983. Distribution and activities of *Anastrepha fraterculus* (Diptera: Tephritidae) flies on host and nonhost trees. *Ann. Ent. Soc. America* 76: 286-292.
- MAZAMENOS, B. E., AND J. E. POMONIS. 1982. Male olive fruit fly pheromone: isolation, identification and lab bioassays. Pages 96-103 in *International Symposium on Fruit Flies of Economic Importance*. CEC/IOBC, Athens, Greece.
- METCALF, R. L., W. C. MITCHELL, AND E. R. METCALF. 1983. Olfactory receptors in the melon fly *Dacus cucurbitae* and the Oriental fruit fly, *Dacus dorsalis*. *Proc. Nat. Acad. Sci. USA* 80: 3143-3147.
- MITCHELL, W. C., R. L. METCALF, E. R. METCALF, AND S. METCALF. 1985. Candidate substitutes for methyl eugenol as attractants for the area-wide monitoring and control of the Oriental fruit fly *Dacus dorsalis* Hendel (Diptera: Tephritidae). *Environ. Ent.* 14: 176-181.
- MORTON, T. C., AND M. D. BATEMAN. 1981. Chemical studies on proteinaceous attractants for fruit flies, including the identification of volatile constituents. *Australian J. Agric. Res.* 32: 905-916.
- MUMTAZ, M. M., AND M. T. ALINIAZEE. 1983. The oviposition-detering pheromone in the eastern cherry fruit fly, *Rhagoletis indifferens* Curran (Dipt., Tephritidae). *Ziet. Ang. Ent.* 96: 83-93.
- NAKAGAWA, S., G. J. FARIAS, AND L. F. STEINER. 1970. Response of female Mediterranean fruit flies to male lures in the relative absence of males. *J. Econ. Ent.* 63: 227-229.
- , E. J. HARRIS, AND I. KEISER. 1981. Performance of capture in capturing Mediterranean fruit flies in Steiner plastic or cardboard sticky traps. *J. Econ. Ent.* 74: 244-245.
- , H. J. HARRIS AND T. ORAGO. 1979. Control release of trimedlure from a three-layer laminated plastic dispenser. *J. Econ. Ent.* 72: 625-627.
- NAKAMORI, H., AND H. SOEMORI. 1981. Attractiveness of methyl eugenol to the Oriental fruit fly, *Dacus dorsalis* Hendel, applied with various absorbents. *Bull. Okinawa Prof. Agric. Exp. Stn.* 6: 47-61.
- NATION, J. L. 1981. Sex-specific glands in tephritid fruit flies of the genera *Anastrepha*, *Ceratitidis*, *Dacus* and *Rhagoletis* (Diptera: Tephritidae). *Int. J. Insect Morph. & Embryol.* 10: 121-129.
- . 1983. Sex pheromone of the Caribbean fruit fly: chemistry and field ecology. Pages 109-110 in *IUPAC Pesticide Chemistry: Human Welfare and the Environment*, Vol. 2. J. Miyamoto and P. C. Kearney (eds). Pergamon Press, New York.
- OHINATA, K., M. JACOBSON, R. M. KOBAYASHI, D. L. CHAMBERS, M. S. FUJIMOTO, AND H. H. HEGA. 1982. Oriental fruit fly and melon fly: biological and chemical studies of smoke produced by males. *J. Environ. Sci. & Health A17*: 197-216.
- PERDOMO, A., J. NATION, AND R. M. BARANOWSKI. 1976. Attraction of female and male Caribbean fruit flies to food-baited and male-baited traps under field conditions. *Environ. Entomol.* 5: 1208-1210.

- PETRI, L. 1910. Untersuchung über die Darmbakterien der Olivenfliege. Zentr. Bakt. Parasitenk. Infekt. 26: 357-367.
- PROKOPY, R. J. 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. Environ. Ent. 1: 326-332.
- . 1975. Apple maggot control by sticky red spheres. J. Econ. Ent. 68: 197-198.
- . 1977. Stimuli influencing trophic relations in Tephritidae. Colloq. Int. CNRS 265: 305-336.
- . 1980. Mating behavior of frugivorous Tephritidae in nature. Pages 37-46 in Proceedings of a Symposium on Fruit Fly Problems, Kyoto and Naha, August 9-12, 1980.
- . 1981. Epideictic pheromones that influence spacing patterns of phytophagous insects. Pages 181-213 in D. A. Nordlund, R. L. Jones, and W. J. Lewis, eds. Semiochemicals: Their Role in Pest Control. John Wiley & Sons, New York.
- . 1985. A low-spray apple-pest-management program for small orchards. Canadian Ent. 117: 581-585.
- , A. L. AVERILL, S. S. COOLEY, AND C. A. ROITBERG. 1982a. Associative learning in egg laying site selection by apple maggot flies. Science 218: 76-77.
- , A. MALAVASI, AND J. S. MORGANTE. 1982b. Oviposition deterring pheromone in *Anastrepha fraterculus* flies. J. Chem. Ecol. 8: 763-771.
- , A. L. AVERILL, C. M. BARDINELLI, E. S. BOWDAN, S. S. COOLEY, R. M. CRNJAR, E. A. DUNDULIS, C. A. ROITBERG, P. J. SPATCER, J. H. TUMLINSON, AND B. L. WEEKS. 1982c. Site of production of an oviposition-deterring pheromone component in *Rhagoletis pomonella* flies. J. Insect Physiol. 28: 1-10.
- , AND A. P. ECONOMOPOULOS. 1975. Attraction of laboratory cultured and wild *Dacus oleae* flies to sticky coated McPhail traps of different colors and odors. Environ. Ent. 4: 187-192.
- , V. MOERICKE, AND G. L. BUSH. 1973. Attraction of apple maggot flies to odor of apples. Environ. Ent. 2: 743-749.
- , AND J. KOYAMA. 1982. Oviposition site partitioning in *Dacus cucurbitae*. Ent. Exp. & Appl. 31: 428-432.
- , AND B. D. ROITBERG. 1984. Foraging behavior of true fruit flies. American Sci. 72: 41-49.
- , AND R. P. WEBSTER. 1978. Oviposition-deterring pheromone of *Rhagoletis pomonella* as a kairomone for its egg parasitoid *Opius lectus*. J. Chem. Ecol. 4: 481-494.
- REISSIG, W. H. 1977. Response of the apple maggot, *Rhagoletis pomonella* and the cherry fruit fly *R. fausta* (Diptera: Tephritidae), to protein hydrolysate bait sprays. Canadian Ent. 109: 161-164.
- , B. L. FEIN, AND W. L. ROELOFS. 1982. Field tests of synthetic apple volatiles as apple maggot (Diptera: Tephritidae) attractants. Environ. Ent. 11: 1294-1298.
- REITH. 1980. Identification and synthesis of the major sex pheromone of the olive fly *Dacus oleae*. J. Chem. Soc. Chem. Commun. 1: 52-54.
- RICE, R. E., R. T. CUNNINGHAM, AND B. A. LEONHARDT. 1984. Weathering and efficacy of trimedlure dispensers for attraction of Mediterranean fruit flies (Diptera: Tephritidae). J. Econ. Ent. 77: 750-756.
- ROITBERG, B. D., R. S. CAIRL, AND R. J. PROKOPY. 1984. Oviposition deterring pheromone influences dispersal distance in tephritid fruit flies. Ent. Exp. & Appl. 35: 217-220.
- , AND R. J. PROKOPY. 1981. Experience required for pheromone recognition by the apple maggot fly. Nature 292: 540-541.
- . 1983. Host deprivation influence on response of *Rhagoletis pomonella* to its

- oviposition deterring pheromone. *Physiol. Ent.* 8: 69-72.
- SEVERIN, H. H. P., AND H. C. SEVERIN. 1915. Kerosene traps as a means of checking up the effectiveness of a poisoned bait spray to control the Mediterranean fruit fly (*Ceratitis capitata* Weid.) with a record of beneficial insects captured in the kerosene. *J. Econ. Ent.* 8: 329-338.
- SHARP, J. L., AND D. L. CHAMBERS. 1983. Aggregation response of *Anastrepha suspensa* (Diptera: Tephritidae) to proteins and amino acids. *Environ. Ent.* 12: 923-928.
- SIVINSKI, J., AND T. BURK. 1986. Reproductive and mating behavior. In A. S. Robinson and G. Hooper, eds. *Fruit Flies – Biology, Natural Enemies, and Control*. Elsevier, Amsterdam. (In press)
- , ———, AND J. C. WEBB. 1984. Acoustic courtship signals in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *Anim. Behav.* 32: 1011-1016.
- STEINER, L. F. 1969. Control and eradication of fruit flies on citrus. *Proc. First Int. Citrus Symp.* 28: 881-887.
- , W. C. MITCHELL, E. J. HARRIS, T. T. KOZUMA, AND M. S. FUJIMOTO. 1965. Oriental fruit fly eradication by male annihilation. *J. Econ. Ent.* 48: 961-964.
- SWIFT, F. C. 1982. Field tests of visual and chemical lures for apple maggot flies. *J. Econ. Ent.* 75: 201-206.
- UMEYA, K., AND J. HIRAO. 1975. Attraction of the jackfruit fly, *Dacus umbrosus* F. (Diptera: Tephritidae) and lace wing *Chrysopa* spp. (Neuroptera: Chrysopidae) by lure traps baited with methyl eugenol and cue-lure in the Philippines. *Appl. Ent. Zool.* 10: 60-62.
- WILLIAMS, N. H., AND W. M. WHITTEN. 1983. Orchard floral fragrances and male euglossine bees: methods and advances in the last sesquidecade. *Biol. Bull.* 164: 355-395.
- ZÜMREOGLU, A. 1983. Field cage evaluations of the male sex pheromone (methyl (*E*)-6-nonenoate) of the Mediterranean fruit fly (*Ceratitis capitata* Wied.). Pages 495-499 in R. Cavallora, ed. *Fruit Flies of Economic Importance*. Proc. CEC/IOBC Int. Symp. Athens. A. A. Bakema, Rotterdam.
- ZWOLFER, H. 1970. Investigations on the host-specificity of *Urophora affinis* Fraunfeld (Diptera: Trypetidae). *Comm. Int. Biol. Cont. Prog. Dept.* 26 (Weed Projects for Canada).

SEX PHEROMONE GLAND OF THE NAVEL ORANGEWORM,
AMYELOIS TRANSITELLA (LEPIDOPTERA: PYRALIDAE)
LOCATION, BIOASSAY AND *IN VITRO* MAINTENANCE

ASOKA SRINIVASAN¹, J. A. COFFELT², PHILLIPA NORMAN¹,
AND BEVERLY WILLIAMS¹

ABSTRACT

Anatomical studies of the sex pheromone gland of the female navel orangeworm, *Amyelois transitella* (Walker), revealed the gland to be a broad, chevron-shaped structure located on the ventrolateral surface of the intersegmental membrane between abdominal segments VIII and IX. Support for this finding was obtained by bioassay and gas chromatographic analyses of extracts that were prepared from various portions of the terminal abdominal segments of female moths. Histological examination showed that the gland consists of a single layer of specialized columnar epidermal cells.

Sex pheromone glands were obtained from surface-sterilized abdominal segments of 2 to 3-day-old virgin females and subsequently cultured for up to 7 days in either chemically defined or modified Grace's medium. Bioassays of extracted medium in which sex pheromone glands had been maintained indicated that more pheromone was recovered from modified Grace's medium than from the chemically defined growth substrate.

RESUMEN

Estudios anatómicos de la glándula de feromona sexual de la *Amyelois transitella* (Walker), reveló que la glándula era una estructura ancha en forma de cheurón localizada en la superficie ventro-lateral de la membrana intersegmental entre los segmentos abdominales VIII y IX. Este descubrimiento es apoyado por bio-ensayo y análisis de gas cromatográfico de extractos que fueron preparados de varias porciones de los segmentos terminales del abdomen de polillas hembras. Exámenes histológicos demostraron que la glándula consiste de una sola capa de células especializadas de epidermis columnar.

Glándulas de feromonas sexuales fueron obtenidas de la superficie esterilizada de segmentos abdominales de hembras vírgenes de 2 a 3 días de edad, y subsecuentemente cultivadas hasta 7 días en un medio químicamente definido o en el medio Grace modificado. Bio-ensayos del medio extraído en el cual las glándulas de feromonas sexuales han sido mantenidas, indicaron que más feromonas fueron recuperadas del medio Grace modificado, que de sustratos de medios químicamente definidos.

Although recent studies have revealed much about the biosynthesis of lepidopteran sex pheromones, more detailed and comparative studies of biosynthetic pathways would be facilitated greatly if the pheromone-producing tissue could be maintained in tissue culture (Roelofs & Bjostad 1984). Also, in spite of extensive studies on the chemistry of lepidopteran sex pheromones only limited information is available on the control mechanisms involved in the development and activity (production and/or release of pheromone) of sex pheromone glands, and most of these studies have been conducted *in vivo* (Cardé & Webster 1981, Sasaki et al. 1983, Raina & Klun 1984, Webster & Cardé 1984). Again, the understanding of the control mechanisms would be enhanced

¹Biology Department, Tougaloo College, Tougaloo, MS 39174.

²Insect Attractants, Behavior, and Basic Biology Research Laboratory, Agric. Res. Serv., USDA, Gainesville, FL 32604.

greatly if the sex pheromone gland could be maintained under defined conditions in tissue culture. Ultimately, successful tissue culture of pheromone glands could result in the establishment of *in vitro* pheromone production systems that would facilitate isolation and identification of the biologically active compounds.

Two studies of the *in vitro* culture of sex pheromone glands of pyralid moths have been reported. White et al. (1972) found that 50 or 100 $\mu\text{g/ml}$ of juvenile hormone (JH) were essential for maintaining the integrity of the gland of female sugarcane borers, *Diatraea saccharalis* (F.), in tissue culture. In contrast, Srinivasan et al. (1979) reported that the gland of the female Indian meal moth, *Plodia interpunctella* (Hübner), was successfully maintained *in vitro* without the addition of exogenous JH. This apparent contradiction regarding the JH requirement prompted the present investigation of the *in vitro* maintenance of the gland of another pyralid, the navel orangeworm, *Amyelois transitella* (Walker). *A. transitella*, a major pest of almonds in California, was selected because some aspects of the biology and chemistry of its sex pheromone are known (Srinivasan 1969, Coffelt et al. 1979a,b). Also, Oberlander (1976) had reported the successful *in vitro* maintenance of imaginal discs and fat bodies of *A. transitella*.

This paper reports the requirements for *in vitro* maintenance of the sex pheromone gland of this species and also presents behavioral data that suggests that sex pheromone can be extracted from cultured glands.

MATERIALS AND METHODS

Moths used in this study were reared as described by Coffelt et al. (1979a) at $27 \pm 1^\circ\text{C}$ and ca. 60% RH under a 14:10 (L:D) photoperiod. Photophase and scotophase light intensities were >250 and ca. 0.3 lux, respectively. The larval diet was wheat bran, honey, glycerol (u.s.p.) and tap water (24:2:2:1, vol:vol) that had been autoclaved 15 min at 120°C . Brewer's yeast powder (5% by wt.) was added after autoclaving.

Bioassays and chemical analyses were conducted using the procedures of Coffelt et al. (1979a,b) to confirm the location of the glands. Extracts for these studies were prepared in the following manner: the terminal segments of the abdomen of 2 to 3-day-old sexually mature females were extruded by gently squeezing the base of the abdomen, and then cut into 3 sections over a small piece of dry ice under a dissecting microscope at 10X magnification. The 1st section was the tip of the 9th segment (fraction A), the 2nd section consisted mainly of the intersegmental region between segments VIII and IX (fraction B), and the 3rd section consisted of the remaining portions of the 8th and 7th segments (fraction C). Hexane extracts were prepared from each of the 3 sections (fractions A, B and C), and the volume of the solvent was adjusted to yield 1×10^{-2} female equivalents (FE) per 10 μl . The solutions were bioassayed using activation as a response criterion (Coffelt et al. 1979a). Applicators treated only with hexane served as controls. Gas chromatographic analyses were conducted on a 1.8-m x 2-mm (ID) glass column packed with 3% OV-1- on 100/200 mesh Gas Chrom-Q; and temperature programmed from 100°C at injection to 220°C at 6°C per min.

The procedure for tissue culture of *A. transitella* glands was similar to that of Srinivasan et al. (1979) for *P. interpunctella*. Material for tissue culture was obtained from surface-sterilized (15-20 min immersion of whole insect in 0.1% HgCl_2 solution containing 0.1% Triton-X-100) 2 to 3-day-old unmated females. The abdominal tips that contained the glands were rinsed several times in culture medium before being placed in culture. Groups of 10 glands were cultured in sterile glass Petri dishes each containing 1 ml of the culture medium. Cultures were maintained in an incubator at 25°C and 65% RH. Growth substrates investigated were chemically defined Grace's medium, a modified Grace's medium containing whole egg ultrafiltrate, fetal calf serum and bovine

serum albumin fraction V (Yunker et al. 1967), and Ringer's solution (Carolina Biological Co.).

At periodic intervals (1, 3 and 6 days), 2 to 4 glands were removed from these cultures or from virgin females of similar age, fixed in alcoholic Bouin's solution, washed several times with deionized water, and stored in 70% ethanol for histological studies. These studies were conducted using the standard techniques for paraffin-embedded tissue. The abdomens of 2 to 3-day-old virgin females were fixed in alcoholic Bouin's solution for 12 h. The tissue was first embedded in 3% agar before being embedded in paraffin. Sections were cut at 6 μ and stained with hematoxylin and counterstained with eosin.

The glands and medium in which they were cultured were separately extracted after 144 h (6 days) of incubation. Unused medium was also extracted to serve as a control. All extracts were bioassayed in serial dilution to establish the relative quantities of pheromone present in each preparation.

RESULTS AND DISCUSSION

The sex pheromone gland of female *A. transitella* is a broad, chevron-shaped structure that is located on the ventrolateral surface of the intersegmental membrane between abdominal scleromata VIII and IX. Figure 1A shows a longitudinal section of the gland of a 2 to 3-day-old female. It consists of a single layer of specialized columnar epidermal cells; its location and morphology are strikingly similar to that reported by Smithwick & Brady (1977) for the confamilial *P. interpunctella*. Bioassays of the extracts of various abdominal parts (Table 1), revealed that >90% of the pheromone (based on additional bioassays of serial dilutions) (see Coffelt et al. 1979a) was contained in fraction B prepared from the intersegmental region between abdominal segments VIII and IX. The low level of male response observed in fractions A and C was probably due to contamination of the surface of the segment during the process of extrusion of the abdominal tip. Gas chromatographic analysis of the biologically active fraction showed the presence of a single peak with a retention time (11.4 min) coincident with synthetic (*Z,Z*)-11,13-hexadecadienal, a previously identified pheromone component of *A. transitella* (Coffelt et al. 1979b). No pheromone was found in analyses of fractions A and C.

Earlier studies by both Dickens (1936) and Srinivasan (1969) reported the gland in

TABLE 1. COMPARISON OF THE RESPONSE OF *A. TRANSITELLA* MALES TO THE FEMALE SEX PHEROMONE EXTRACTS PREPARED FROM THE 3 DIFFERENT SECTIONS OF 25 ABDOMINAL TIPS.^a

Treatment	% Male response ^d	\pm S.E.
Control ^b	3.8 a	2.6
Fraction A ^b	16.3 b	3.7
Fraction B ^c	80.8 c	3.3
Fraction C ^b	16.3 b	4.2

^aFraction A—Section of the tip of segment IX; fraction B—intersegmental region between segments VIII and IX; and fraction C—remaining portion of segments VII and VIII.

^bBased on 12 replications of 10 males/replication.

^cBased on 18 replications of 10 males/replication.

^dValues followed by the same lower case letter are not significantly different at the 5% level by Duncan's New Multiple Rang Test.

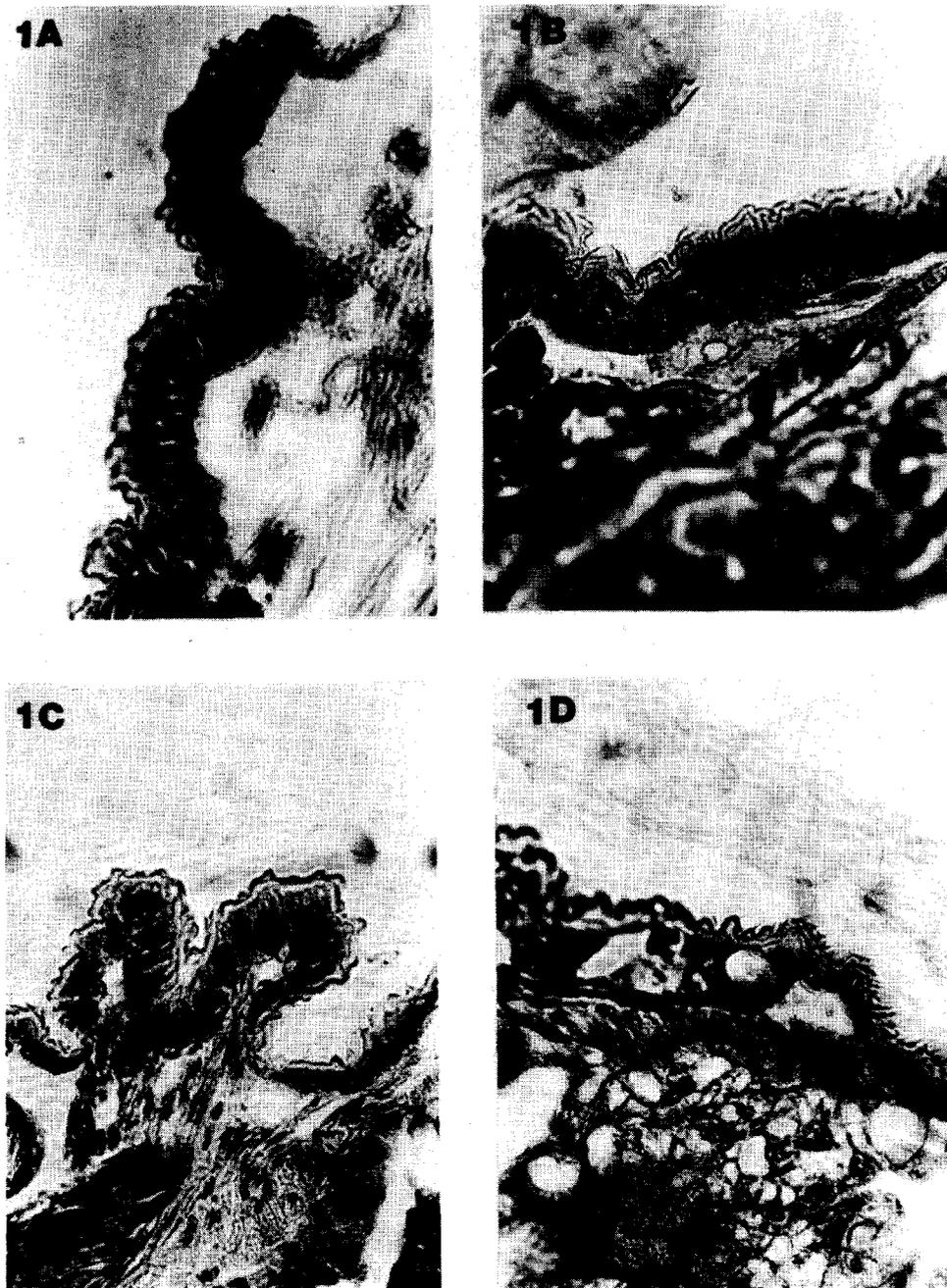


Fig. 1. Sections of 2 to 3-day-old virgin female *A. transitella* glands. (A) Before being placed in culture; (B) after 7 days in chemically defined Grace's medium; (C) after 7 days in modified Grace's medium; and (D) after 7 days in Ringer's solution.

A. transitella females to be a ring of glandular epithelium. However, careful examinations during this study revealed it to be ventrolateral and chevron-shaped. Serial sections of the dorsal region did not show the presence of glandular epithelial cells. Even though *A. transitella* is 2-3X larger than *P. interpunctella*, the gland cells are similar in size to the *P. interpunctella* cells (Smithwick & Brady 1977). We did not determine

TABLE 2. DETECTION OF THE FEMALE SEX PHEROMONE OF *A. TRANSITELLA* BY BIOASSAY FROM TEN GLANDS MAINTAINED IN TISSUE CULTURE FOR 144 H.¹

Source	% Male response ²	
	Defined medium	Modified medium
Gland extract	10.0 a	23.3 b
Medium extract	6.7 a	50.0 c

¹Based on 3 replications of 10 males/replication.

²Values followed by the same lower case letter are not significantly different at the 5% level by Duncan's New Multiple Range Test.

the actual surface area occupied by the gland but it appeared slightly larger than that of *P. interpunctella* although not as large as the relative size of the moth would suggest.

Figure 1A shows the gland of a 2-3-day-old virgin female *A. transitella* before it was placed in culture. There was no detectable difference in the histological appearance of the cells of isolated glands maintained in either chemically defined Grace's medium (Fig. 1B), or modified Grace's medium (Fig. 1C). However, the cells in the glands maintained in Ringer's solution had disintegrated (Fig. 1D). Bioassays revealed the presence of sex pheromone only in the extracts prepared from the modified Grace's medium in which the glands had been incubated for 144 h (Table 2). Further analysis of these extracts by as chromatography indicated that quantities of sex pheromone recovered were below the detection limits (<0.1 ng/FE).

Like *P. interpunctella* (Srinivasan et al. 1979), the *A. transitella* glands did not require exogenous JH in the medium as reported by White et al. (1972) for the sugarcane borer and also could be maintained structurally in chemically defined Grace's medium. The materials present in the modified Grace's medium, thus were not essential for gland survival, but were necessary if pheromone was to be recovered from the culture medium.

END NOTES

This research was supported in part by NIH Grants I-F34G1706251 and 5-506RR8110. Mention of a commercial or proprietary product does not constitute an endorsement by the USDA.

REFERENCES CITED

- CARDÉ, R. T., AND R. P. WEBSTER. 1981. Endogenous and exogenous factors controlling insect sex pheromone production and response, particularly in the Lepidoptera, pp. 977-990. *In: Regulation of Insect Development and Behavior International Conference*, M. Kloza [ed.]. Wyroclaw Tech. University Press.
- COFFELT, J. A., K. W. VICK, L. L. SOWER, AND W. T. MCCLELLAN. 1979a. Sex pheromone mediated behavior of the navel orangeworm, *Amyelois transitella*. *Environ. Ent.* 8: 587-90.
- , ———, P. E. SONNET, AND R. E. DOOLITTLE. 1979b. Isolation, identification, and synthesis of a female sex pheromone of the navel orangeworm, *Amyelois transitella* (Lepidoptera: Pyralidae). *J. Chem. Ecol.* 5: 955-66.
- DICKENS, G. R. 1936. The scent glands of certain Phycitidae (Lepidoptera). *Trans. Royal Ent. Soc. (Lond.)* 85: 331-62.
- OBERLANDER, H. 1976. Hormonal control of growth and differentiation of insect tissues cultured *in vitro*. *In Vitro* 12: 225-35.

- RAINA, A. K., AND J. A. KLUN. 1984. Brain factor control of sex pheromone production in the female corn earworm moth. *Science* 225: 531-533.
- ROELOFS, W. L., AND L. B. BJOSTAD. 1984. Biosynthesis of lepidopteran pheromones. *Bio-organic Chem.* 12: 279-298.
- SASAKI, M., L. M. RIDDLEFORD, J. W. TRUMAN, AND J. K. MOORE. 1983. Reevaluation of the role of the corpora cardiaca in calling and oviposition behavior of giant silk moths. *J. Insect Physiol.* 29: 695-705.
- SMITHWICK, E. G., AND U. E. BRADY. 1977. Histology of the sex pheromone gland in developing female Indian meal moths, *Plodia interpunctella*. *J. Ga. Ent. Soc.* 12: 13-29.
- SRINIVASAN, ASOKA G. S. 1969. Sex pheromone of the navel orangeworm, *Paramyelois transitella* (Walker) (Phycitidae: Lepidoptera): Its biological and ecological significance. Ph.D. Dissertation, Univ. Calif., Berkeley, 119 pp.
- , J. A. COFFELT, AND H. OBERLANDER. 1979. *In vitro* maintenance of the sex pheromone gland of the female Indian meal moth, *Plodia interpunctella* (Hübner). *J. Chem. Ecol.* 6: 653-62.
- WHITE, M. R., R. L. AMBORSKI, JR., AND G. E. AMBORSKI. 1972. Organ culture of the terminal abdominal segment of an adult female lepidopteran. *In Vitro* 8: 30-6.
- YUNKER, L. E., J. L. VAUGHN, AND J. CORY. 1967. Adaptation of an insect cell line (Grace's antherae cells) to medium free of insect hemolymph. *Science* 155: 1565-66.

INFLUENCE OF CABBAGE CULTIVAR AND FREQUENCY OF INSECTICIDE APPLICATION ON DAMAGE BY THE CABBAGE LOOPER (LEPIDOPTERA:NOCTUIDAE)

R. N. STORY AND F.J. SUNDSTROM

Department of Entomology

Department of Horticulture

Louisiana Agricultural Experiment Station

Louisiana State University Agricultural Center

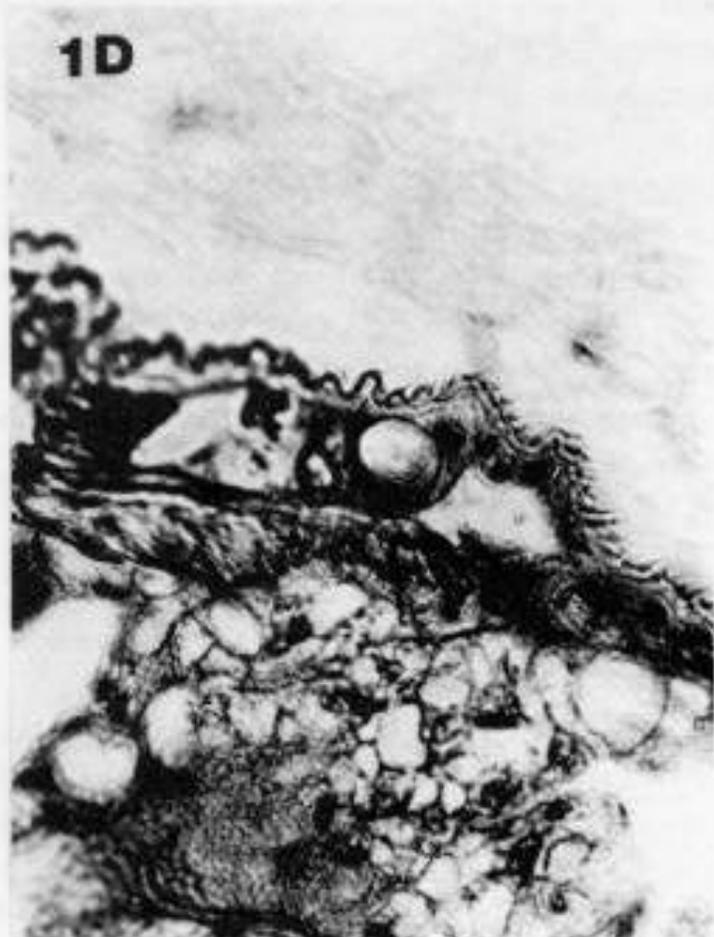
Baton Rouge, Louisiana 70803

ABSTRACT

Field tests were conducted to investigate the effect of cabbage cultivar and frequency of insecticide application on cabbage looper, *Trichoplusia ni* (Hübner), damage in both the spring and fall seasons. The mean number of frame and wrapper leaves varied significantly among the cultivars, and the number of days to harvest also differed. Both insecticide frequency and cultivar had significant effects on the amount of cabbage looper damage to the leaves (percent leaf damage and leaf rating) and heads (percent damage) of ten cultivars. In considering both leaf and head damage over both seasons, 'Rio Verde', 'Super Market', 'Superette', and 'Gourmet' sustained the least amount of damage. The interactions between cultivar and insecticide frequency for both seasons were not significant, indicating that the ten cultivars responded to the three levels of insecticide frequency in a similar manner. There was an additive effect of cabbage resistance and insecticide, where the resistant cultivars performed the best regardless of the frequency of pesticide application.

RESUMEN

Se hicieron pruebas de campo para investigar el efecto de la variedad de col y la

1A**1B****1C****1D**

- RAINA, A. K., AND J. A. KLUN. 1984. Brain factor control of sex pheromone production in the female corn earworm moth. *Science* 225: 531-533.
- ROELOFS, W. L., AND L. B. BJOSTAD. 1984. Biosynthesis of lepidopteran pheromones. *Bio-organic Chem.* 12: 279-298.
- SASAKI, M., L. M. RIDDLEFORD, J. W. TRUMAN, AND J. K. MOORE. 1983. Reevaluation of the role of the corpora cardiaca in calling and oviposition behavior of giant silk moths. *J. Insect Physiol.* 29: 695-705.
- SMITHWICK, E. G., AND U. E. BRADY. 1977. Histology of the sex pheromone gland in developing female Indian meal moths, *Plodia interpunctella*. *J. Ga. Ent. Soc.* 12: 13-29.
- SRINIVASAN, ASOKA G. S. 1969. Sex pheromone of the navel orangeworm, *Paramyelois transitella* (Walker) (Phycitidae: Lepidoptera): Its biological and ecological significance. Ph.D. Dissertation, Univ. Calif., Berkeley, 119 pp.
- , J. A. COFFELT, AND H. OBERLANDER. 1979. *In vitro* maintenance of the sex pheromone gland of the female Indian meal moth, *Plodia interpunctella* (Hübner). *J. Chem. Ecol.* 6: 653-62.
- WHITE, M. R., R. L. AMBORSKI, JR., AND G. E. AMBORSKI. 1972. Organ culture of the terminal abdominal segment of an adult female lepidopteran. *In Vitro* 8: 30-6.
- YUNKER, L. E., J. L. VAUGHN, AND J. CORY. 1967. Adaptation of an insect cell line (Grace's antherae cells) to medium free of insect hemolymph. *Science* 155: 1565-66.

INFLUENCE OF CABBAGE CULTIVAR AND FREQUENCY OF INSECTICIDE APPLICATION ON DAMAGE BY THE CABBAGE LOOPER (LEPIDOPTERA:NOCTUIDAE)

R. N. STORY AND F.J. SUNDSTROM

Department of Entomology

Department of Horticulture

Louisiana Agricultural Experiment Station

Louisiana State University Agricultural Center

Baton Rouge, Louisiana 70803

ABSTRACT

Field tests were conducted to investigate the effect of cabbage cultivar and frequency of insecticide application on cabbage looper, *Trichoplusia ni* (Hübner), damage in both the spring and fall seasons. The mean number of frame and wrapper leaves varied significantly among the cultivars, and the number of days to harvest also differed. Both insecticide frequency and cultivar had significant effects on the amount of cabbage looper damage to the leaves (percent leaf damage and leaf rating) and heads (percent damage) of ten cultivars. In considering both leaf and head damage over both seasons, 'Rio Verde', 'Super Market', 'Superette', and 'Gourmet' sustained the least amount of damage. The interactions between cultivar and insecticide frequency for both seasons were not significant, indicating that the ten cultivars responded to the three levels of insecticide frequency in a similar manner. There was an additive effect of cabbage resistance and insecticide, where the resistant cultivars performed the best regardless of the frequency of pesticide application.

RESUMEN

Se hicieron pruebas de campo para investigar el efecto de la variedad de col y la

frecuencia de la aplicación de insecticidas sobre el daño de *Trichoplusia ni* (Hubner) durante la primavera y el otoño. El promedio de hojas de marco y de hojas de envoltura varió significativamente entre las variedades, así como el número de días para la cosecha. La frecuencia de insecticidas, así como la variedad, tuvieron efectos significantes en la cantidad de daño de las hojas (porcentaje de daño y la clasificación de las hojas), y las cabezas (porcentaje de daño) de diez variedades. Cuando se considera el daño de las hojas y de las cabezas durante ambas estaciones, 'Rio Verde', 'Super Market', y 'Superette', sostuvieron los menores daños. La interacción entre las variedades y la frecuencia de insecticidas en ambas estaciones no fue significativa, indicando que las diez variedades respondieron a la frecuencia de los tres niveles de insecticidas en una forma similar. Hubo un efecto aditivo de la resistencia de la col e insecticida, donde las variedades resistentes lo hicieron mejor, no importando la frecuencia de la aplicación de insecticidas.

The cabbage looper, *Trichoplusia ni* (Hübner), is a major pest of cabbage, *Brassica oleracea* L., in the United States. Insecticidal control of this pest is an essential component of cabbage production in the southeastern U.S. Several researchers have evaluated commercial cabbage cultivars for their susceptibility to cabbage looper damage (Brett & Sullivan 1974, Radcliffe & Chapman 1966a,b, Creighton et al. 1981). Some cultivars have a low level of resistance to the cabbage looper, but this resistance is inadequate as a control by itself. Host plant resistance in cabbage must therefore be used in conjunction with insecticides. Chalfant & Brett (1967) found that resistant cabbage cultivars sustained less damage than susceptible cultivars when insecticides were applied on a regular schedule. There appeared to be an additive effect of host plant resistance and insecticide. The objective of the present study was to evaluate commonly grown cabbage cultivars in the southeast for damage by the cabbage looper and to study the effect of insecticide application frequency on the amount of leaf and head damage.

MATERIALS AND METHODS

The study was conducted at the Hill Farm, Louisiana State University, Baton Rouge, LA during the fall (1981) and spring (1982) seasons. Ten cabbage cultivars were seeded into peat pots (Jiffy 7's®) in the greenhouse and transplanted in the field at 30 days. Seedlings were spaced 30 cm apart on rows 1.2m wide. A split-plot experimental design with 4 replications was used with cultivar as the whole plot and frequency of insecticide application as the subplot. The cabbage was planted in 8 rows 30 m in length, with individual plots 6.7 m in length. No buffer areas were used. The following cultivars were utilized: 'Market Prize', 'Green Boy', 'Sun-Up', 'Hybrid 15', 'Earliana', 'Gladiator', 'Gourmet', 'Superette', 'Super Market', and 'Rio Verde'. There were 3 levels of insecticide application: no insecticide, one mid-season application, and 3 middle to late season applications of permethrin. Insecticides were applied with a hand-held CO₂ pressurized sprayer delivering 741 l/h at 2.77 kg per cm² through a single spray nozzle containing a D-3 disc, No. 25 core, and 16 mesh strainer. In the spring season, permethrin was applied on April 7, 14, and 23 on treatments receiving 3 applications, and on April 14 on treatments receiving one application. In the fall season, permethrin was applied on October 28 and November 12 and 20 on treatments receiving 3 applications, and on November 12 on treatments receiving one application. Cabbage was evaluated for damage at maturity by taking both leaf damage and head damage counts. Leaf damage counts were made by counting the number of damaged and undamaged frame and wrapper leaves on each plant. Damaged leaves were defined as those with 1 or more holes $\geq 2\text{cm}^2$ in area. Leaf ratings were calculated by determining the mean number of leaves per plant with holes present. Percent leaf damage was also determined. The

number of damaged and undamaged heads were counted at harvest; percent head damage was calculated from these data. The number of days from transplanting to harvest for each cultivar was recorded. Data were analysed with Analysis of Variance and Duncan's Multiple Range Test was used for mean separation. The least significant difference test was used to compare interactions.

RESULTS AND DISCUSSION

The frequency of pesticide application had a significant effect on the amount of leaf and head damage during both seasons (Table 1). Cabbage looper leaf damage was similar in the spring and fall.

The mean number of frame and wrapper leaves varied significantly among the cultivars, ranging from 12.6 in Earliana to 18.3 in Gourmet (Table 2). There were also differences in the number of days to harvest (Table 2). The early maturing cultivars

TABLE 1. EFFECT OF THE FREQUENCY OF PERMETHRIN APPLICATION ON CABBAGE DURING THE FALL (1981) AND SPRING (1982) SEASONS. BATON ROUGE, LA.

No. Applications	Leaf Rating ^{a,b}		Percent Leaf Damage ^{a,c}		Percent Head Damage ^a	
	Spring	Fall	Spring	Fall	Spring	Fall
0	5.6a	6.5a	35.1a	39.2a	25.9a	45.6a
1	3.8b	3.8b	23.8b	22.7b	10.1b	23.4b
3	2.5c	0.6c	13.7c	3.6c	1.9c	17.3c

^aNumbers followed by the same letter are not significantly different ($P>0.05$) by Duncan's MRT.

^bMean number of frame and wrapper leaves per plant with 1 or more feeding holes $\geq 2\text{cm}^2$ in area.

^cPercentage of frame and wrapper leaves per plant with 1 or more feeding holes $\geq 2\text{cm}^2$ in area.

TABLE 2. MEAN NUMBER OF FRAME AND WRAPPER LEAVES AT MATURITY AND DAYS TO HARVEST FOR TEN CABBAGE CULTIVARS, AVERAGED OVER THE FALL (1981) AND SPRING (1982) SEASON.

Cultivar	No. Frame and Wrapper Leaves ^a		Days to Harvest ^b
	Mean	SD	Mean
Gourmet	18.3a	0.41	92
Superette	18.1a	0.89	90
Green Boy	17.9a	0.87	96
Market Prize	17.7a	0.45	88
Rio Verde	17.6a	0.61	102
Super Market	17.3a	0.77	88
Gladiator	17.1a	0.84	92
Hybrid 15	14.9b	0.70	86
Sun-Up	14.6b	0.40	80
Earliana	12.6c	1.09	74

^aMeans followed by the same letter are not significantly different, Duncan's multiple range test.

^bMean number of leaves of cultivar 'Earliana' for fall season only.

'Earliana' and 'Sun-Up' (74 and 80 days to harvest, respectively) had fewer leaves than the full season cultivars. Two indices of leaf damage, leaf rating and percent leaf damage, were calculated to quantify leaf feeding. Leaf ratings do not adjust for differences in the total leaf number, and at high damage levels there would be a bias because cultivars with fewer leaves would have lower ratings. Percent leaf damage adjusts for leaf number differences, but low damage levels may show a bias because cultivars with fewer leaves would have higher ratings. Therefore, both indices have limitations, but because leaf damage in this study was low to moderate (0.6-6.5 mean leaves damaged per plant), leaf ratings were selected as a better measure of leaf damage.

Both head and leaf damage varied significantly among the cultivars (Table 3). There was a significant correlation between leaf rating and percent leaf damage for all cultivars. 'Rio Verde', 'Super Market', and 'Superette' sustained the least amount of leaf damage while 'Hybrid 15' and 'Green Boy' had relatively high levels of leaf damage. Analysis of variance indicated a significant difference between seasons for both leaf ratings and percent leaf damage. This seasonal difference in leaf damage was primarily attributable to the performance of the two early maturity cultivars 'Earliana' and 'Sun-Up'. An analysis of variance without these two cultivars revealed a nonsignificant seasonal effect. Both cultivars sustained relatively heavy leaf damage in the spring but not in the fall. These differences may have been attributable to their early maturation and harvest. It is plausible that during the fall season these cultivars escaped some injury because they were harvested 1 to 3 weeks before the full season cultivars. In the spring most damage may have been sustained earlier in the season and, if so, an early harvest would not have enabled them to escape injury. This hypothesis is supported by the fact that head damage was much higher in the fall than the spring. In considering both leaf and head damage collectively over both seasons, 'Rio Verde', 'Super Market', 'Superette' and 'Gourmet' sustained the least amount of damage.

Significant differences in percent head damage were present in the spring season but not the fall. The cultivars 'Green Boy', 'Super Market', 'Gourmet', and 'Superette' sustained the least amount of head damage of those cultivars evaluated for head damage in both seasons, while 'Earliana', 'Market Place', and 'Sun-Up' had relatively high levels of damage. 'Rio Verde', not evaluated in the spring, had less head damage than all other cultivars except 'Green Boy' in the fall. 'Rio Verde' and 'Gladiator' in the spring and 'Hybrid 15' in the fall were not evaluated for head damage because the heads were inadvertently harvested before being evaluated.

The relationship between leaf and head damage was inconsistent between seasons. Correlations between leaf and head damage were significant in the spring season for cultivars in the control and single spray treatment, but not significant for the cultivars receiving 3 permethrin applications. This trend is expected, because permethrin will eliminate loopers which have caused leaf damage, thereby preventing head damage from occurring. In the fall season correlations between head and leaf damage were nonsignificant for all 3 levels of permethrin application frequency. Significant differences in head damage among the cultivars were not present in the fall.

In evaluating the level of resistance of cabbage cultivars to cabbage looper damage, leaf damage is a better index than head damage because it represents feeding which accumulated over a period of 2 to 3 months. Head damage occurs during a much shorter period of time, since the outer leaves of the head are the last exposed leaves of the plant to develop.

The interactions between cultivar and permethrin frequency on cabbage cultivar leaf damage during both seasons were not significant, indicating that the ten cultivars responded to the three levels of permethrin frequency in a similar manner (Table 4). In general, within each season cultivars which sustained less damage in the controls also sustained less damage with both 1 or 3 permethrin applications. This indicates that

TABLE 3. INFLUENCE OF CULTIVAR ON CABBAGE LOOPER DAMAGE DURING THE FALL (1981) AND SPRING (1982) SEASONS. BATON ROUGE, LA.

	Leaf Ratings ^{a,b}			Percent Leaf Damage ^{a,c}			Percent Head Damage ^a	
	Mean	Spring	Fall	Mean	Spring	Fall	Spring	Fall
Rio Verde	2.9	2.8a	3.0abc	17.1	16.5a	17.8ab	—	21.9a
Super Market	3.3	2.7a	3.9abcd	19.1	15.7a	22.4abcd	10.6abc	22.2a
Superette	3.3	2.9a	3.7abcd	18.2	16.3a	20.2abc	1.4a	30.6a
Gourmet	3.5	3.1a	3.9abcd	19.1	17.0	21.2abcd	4.6ab	26.6a
Sun-Up	3.8	4.8 bc	2.7ab	25.8	32.9 bc	18.7ab	17.8 bcd	31.3a
Earliana	3.9	5.7 c	2.1a	30.1	45.2 d	16.4a	26.1 d	46.5a
Market Prize	3.9	3.2nbc	4.6 de	21.9	18.1a	25.8 bcd	16.0 bcd	37.6a
Gladiator	3.9	4.3abc	3.4 bcd	22.8	25.6ab	20.1abc	—	30.1a
Green Boy	4.1	3.4ab	4.8 e	22.9	19.0a	26.9 cd	4.2ab	21.4a
Hybrid 15	4.8	5.4 c	4.3 cde	32.2	35.8 c	28.6 d	20.2 cd	—

^aNumbers followed by the same letter are not significantly different ($P>0.05$) by Duncan's MRT.

^bMean number of frame and wrapper leaves per plant with 1 or more feeding holes $\cong 2\text{cm}^2$ in area.

^cPercentage of frame and wrapper leaves per plant with 1 or more feeding holes $\cong 2\text{cm}^2$ in area.

TABLE 4. INFLUENCE OF PERMETHRIN SPRAY FREQUENCY ON CABBAGE LOOPER LEAF DAMAGE (LEAF RATING) FOR TEN CABBAGE CULTIVARS, SPRING AND FALL SEASONS.

Cultivar	Insecticide Spray Frequency ^a					
	Spring			Fall		
	0	1	3	0	1	3
Rio Verde	4.7ab	2.7a	1.0a	5.5abc	3.3abc	0.2a
Super Market	4.8ab	2.6a	0.7a	6.5 bcde	4.5 bc	0.6a
Superette	3.5a	2.9ab	2.4ab	5.3abc	4.5 bc	1.1a
Gourmet	5.5ab	2.0a	1.8ab	8.2 ef	2.8ab	0.6a
Sun-up	7.0 b	4.2ab	3.2ab	4.6ab	3.3 bc	0.3a
Earliana	7.2 b	7.1 bc	2.8ab	4.3a	1.4a	0.5a
Market Prize	4.2a	2.9ab	2.5ab	7.8 ef	5.1 c	0.8a
Gladiator	7.1 b	3.7ab	2.2ab	6.7 cdef	2.9ab	0.7a
Green Boy	5.1ab	3.7ab	1.4ab	8.5 f	5.3 c	0.6a
Hybrid	7.1 b	5.4 bc	3.6 b	7.5 def	4.8 bc	0.6a

^aNumbers followed by same letter are not significantly different(P>0.05), LSD test.

there is an additive effect of host plant resistance in cabbage and insecticide. Chalfant & Brett (1967) obtained similar results with the cabbage looper on cabbage. The two early maturing cultivars 'Earliana' and 'Sun-Up' were inconsistent in their performance between seasons, but within each season they responded to insecticide frequency in a manner similar to the other cultivars. These data indicate that the use of resistant cabbage cultivars alone could reduce the number of insecticide treatments needed to control the cabbage looper.

REFERENCES CITED

CHALFANT, R. B. AND C. H. BRETT. 1967. Interrelationship of cabbage variety, season, and insecticide control of the cabbage looper and imported cabbageworm. J. Econ. Entomol. 60: 687-690.

CREIGHTON, C. S., T. L. MCFADDEN, AND M. L. ROBBINS. 1981. Comparative control of caterpillars on cabbage cultivars treated with *Bacillus thuringiensis*. J. Georgia Entomol. Soc. 16: 361-367.

BRETT, C. H. AND M. J. SULLIVAN. 1974. The use of resistant varieties and other cultural practices for control of insects on crucifers in North Carolina. N.C. State Univ. Agr. Exp. Sta. Bull. 449, 31 pp.

RADCLIFF, E. B. AND R. K. CHAPMAN. 1966a. Plant resistance to insect attack in commercial cabbage varieties. J. Econ. Entomol. 59: 116-120.

RADCLIFFE, E. B. AND R. K. CHAPMAN. 1966b. Varietal resistance to insect attack in various cruciferous crops. J. Econ. Entomol. 59: 120-125.

LEAFHOPPERS (HOMOPTERA: CICADELLIDAE) AND
PLANTHOPPERS (HOMOPTERA: DELPHACIDAE) IN
SOUTHERN FLORIDA RICE FIELDS

R. H. CHERRY AND D. B. JONES
University of Florida, IFAS
Everglades Research and Education Center
P. O. Drawer A
Belle Glade, Florida 33430

AND

F. W. MEAD
Florida Dept. Agric. and Consumer Services
Division of Plant Industry
P. O. Box 1269
Gainesville, Florida 32602

ABSTRACT

Leafhoppers (Homoptera: Cicadellidae) and planthoppers (Homoptera: Delphacidae) were collected with sweep nets in southern Florida rice fields during 1983 and 1984. The most abundant leafhopper was *Graminella nigrifrons* (Forbes) and the most abundant planthopper was *Delphacodes propinqua* (Fieber). Total numbers of leafhoppers in rice fields rose quickly after spring plantings and remained relatively constant from May to October. In contrast, individual leafhopper species were more variable in seasonal population trends. *Sogatodes oryzicola* (Muir), a vector of hoja blanca was also detected.

RESUMEN

Salta hojas (Homoptera: Cicadellidae) y salta plantas (Homoptera: Delphacidae) se recogieron con Jabecas en campos arroceros del sur de la Florida durante 1983 y 1984. Se discuten las distintas especies de importancia económica que se encontraron. El salta hojas más abundante fue el *Graminella nigrifrons* (Forbes) y el salta plantas más abundante fue el *Delphacodes propinqua* (Fieber). El número total de salta hojas en los campos arroceros aumentó rápidamente después de las siembras de primavera, manteniéndose relativamente constante de Mayo a Octubre. Sin embargo, las poblaciones de algunas especies de salta hojas mostraron cambios estacionales dramáticos. También se detectó a *Sogatodes orizicola* (Muir), un vector de la hoja blanca.

Rice was grown for grain in the Everglades agricultural area of southern Florida during the 1950's. Commercial production was stopped in 1957 by the United States Federal Government after the hoja blanca (white leaf) disease was found in the area. The lifting of controls on production by the Federal Government in 1974 made it possible again to harvest Florida rice for grain (Alvarez 1978). Since 1977 rice production in the area has grown to nearly 4,000 ha and drying and milling facilities have been established (Rohrman & Alvarez 1984). Currently, ca. 85% of Florida rice is grown in the Everglades agricultural area.

Several species of leafhoppers and planthoppers are serious pests of rice in different areas of the world and frequently occur in numbers large enough to cause complete drying of the crops. In addition to the damage resulting from direct feeding, leafhoppers and planthoppers are vectors of most presently known rice virus diseases (Pathak 1968). Other than a brief description of leafhoppers and planthoppers in Everglades rice fields

by Genung et al. (1979), little is known of the species composition or seasonal population dynamics of leafhoppers and planthoppers occurring in Florida rice. In this study, we describe the relative abundance of leafhoppers (Cicadellidae) and planthoppers (Delphacidae) occurring in southern Florida rice fields.

MATERIALS AND METHODS

Eight commercial rice fields in the Everglades agricultural area of southern Florida were sampled with 38.1-cm-diameter sweep nets each year during the 1983 and 1984 growing seasons. During much of the growing season, these rice fields were kept flooded and were underlain with soft muck. Sweep nets were thus used because they are light and portable. Southwood (1978) discusses advantages and limitations of sweep net sampling for insects. Each field was ca. 16 ha and fields were located throughout the Everglades agricultural area to obtain a representative sample of insect populations. All fields were subject to normal rice production practices including planting dates that ranged from March 1 through May 12. Each field was sampled weekly by making 100 consecutive sweeps (180°) taken about 50 meters into the field to avoid possible edge effects. Sweeping began 6 weeks after planting and continued through harvest. Eight fields were removed from production after one harvest during August to September and eight fields were removed from production after one ratoon crop during October to November. After collection, insects were frozen for later counting. Only adults of the leafhoppers and planthoppers were counted because of the large number of insects collected and to facilitate taxonomic identification. An overall survey of the relative abundance of the leafhopper and planthopper species was determined from 42 random samples containing 6060 leafhoppers and planthoppers identified by F. W. Mead. Thereafter, the seasonal abundance of the total number of leafhoppers and 3 most abundant leafhopper species was determined. These latter 3 species were ca. 97% of all leafhoppers collected. Delphacid seasonal abundance was not determined because of the low numbers of these insects collected.

RESULTS AND DISCUSSION

The relative abundance of leafhoppers and planthoppers in sweep net samples in Florida rice fields is shown in Table 1. Leafhoppers outnumbered planthoppers ca. 41 to 1. Genung et al. (1979) also reported that leafhoppers were more abundant on Everglades rice than planthoppers. Generally, leafhoppers feed on the leaves and upper parts of rice plants, whereas planthoppers confine themselves to the basal parts (Pathek 1968). Thus, our sweep net samples probably overestimated leafhoppers relative to planthoppers present in the rice. The most abundant leafhopper was the blackfaced leafhopper, *Graminella nigrifrons* (Forbes). This species has a wide distribution on grasses in the eastern United States and breeds on rice (Stoner & Gustin 1967). This species is also a vector of several corn stunting pathogens (Nault & Bradfute 1979). The second most abundant leafhopper was *Draeculacephala portola* Ball which is the most common *Draeculacephala* in eastern and central United States and has been reported in Cuban rice fields (Young & Davidson 1959). Since this insect is common on sugarcane in the southern United States (Pemberton & Charpentier 1969) and is a recognized sugarcane pest in Florida (Strayer 1975), some *D. portola* probably immigrated into the rice fields from the numerous sugarcane fields in the Everglades area. Abbott & Ingram (1942) reported the transmission of chlorotic streak of sugarcane by *D. portola* but, Pemberton & Charpentier (1969) thought that the insect transmission of chlorotic streak had not been adequately demonstrated in light of more recent studies. The most abundant planthopper was *Delphacodes propinqua* (Fieber) which is also a vector of maize

TABLE 1. RELATIVE ABUNDANCE¹ OF LEAFHOPPERS AND PLANTHOPPERS IN FLORIDA RICE FIELDS.

Cicadellidae	Number	% of Total
<i>Graminella nigrifrons</i> (Forbes)	3891	65.8
<i>Draeculacephala portola</i> Ball	988	16.7
<i>Balclutha incisa</i> (Matsumara)	884	14.9
<i>Draeculacephala producta</i> (Walker)	51	0.9
<i>Balclutha hebe</i> Kirkaldy	40	0.7
Other species ²	61	1.0
	5915	100.0
Delphacidae	Number	% of Total
<i>Delphacodes propinqua</i> (Fieber)	79	54.5
<i>Perkinsiella saccharicida</i> Kirkaldy	20	13.8
<i>Saccharosydne saccharivora</i> (Westwood)	12	8.3
<i>Sogatella kolophon</i> (Bmr.)	12	8.3
<i>Sogatodes molinus</i> Fennah	12	8.3
Other species ³	10	6.9
	145	100.1

¹Based on random samples identified by F. W. Mead (see text).

²*B. guajanae* (DeLong), *Exitianus exitiosus* (Uhler), *Hortensia similis* (Walker), *Macrosteles fascifrons* (Stal), *Planicephalus flavicosta* (Stal).

³*Delphacodes puella* (Van Duzee), *Pissonotus piceus* Van Duzee, *Sogatodes oryzicola* (Muir).

rough dwarf virus (Breck 1979). The second most abundant planthopper was the sugarcane delphacid, *Perkinsiella saccharicida* Kirkaldy. This species is a serious sugarcane pest of Australian origin. Besides direct damage to sugarcane by feeding and ovipositional activities, the insect is also a vector of the virus that causes Fiji disease in sugarcane. The first North American record of *P. saccharicida* was reported in 1982 in Palm Beach County, Florida. Subsequent surveys revealed the delphacid throughout southern Florida (Sosa 1983). Another delphacid detected in this study is *Sogatodes oryzicola* (Muir). This insect is a vector of hoja blanca which is one of the most destructive rice diseases in the Western Hemisphere (Harris 1979). Fortunately, hoja blanca currently is not known to exist in the United States. Detection of *S. oryzicola* in this study is the first report of the insect in the United States in more than a decade.

The seasonal population trends of leafhoppers in the sweep net samples are shown in Fig. 1. Total numbers of leafhoppers rose quickly in April and remained relatively constant (Range = 44 to 78 adults/100 sweeps) from May until October, decreasing to 26 adults/100 sweeps in November. In contrast to the total leafhopper numbers, the 3 most abundant leafhopper species showed more variable seasonal trends. The early increase of leafhoppers in rice fields during April and May was almost wholly (> 97%) due to *G. nigrifrons*. During June to August, *G. nigrifrons* remained > 75% of all leafhoppers, and then declined to lower levels during September to November. Genung & Mead (1969) also found a decline in *G. nigrifrons* populations after August in pasture grasses in southern Florida. *D. portola* populations increased slowly during April to June and remained somewhat constant (Range = 8 to 23 adults/100 sweeps) thereafter. In contrast to *G. nigrifrons* or *D. portola*, *Balclutha incisa* (Matsumara) increased rapidly during the late summer to fall period and during October was the most abundant leafhopper species. Reasons for this October increase in *B. incisa* are not known, but

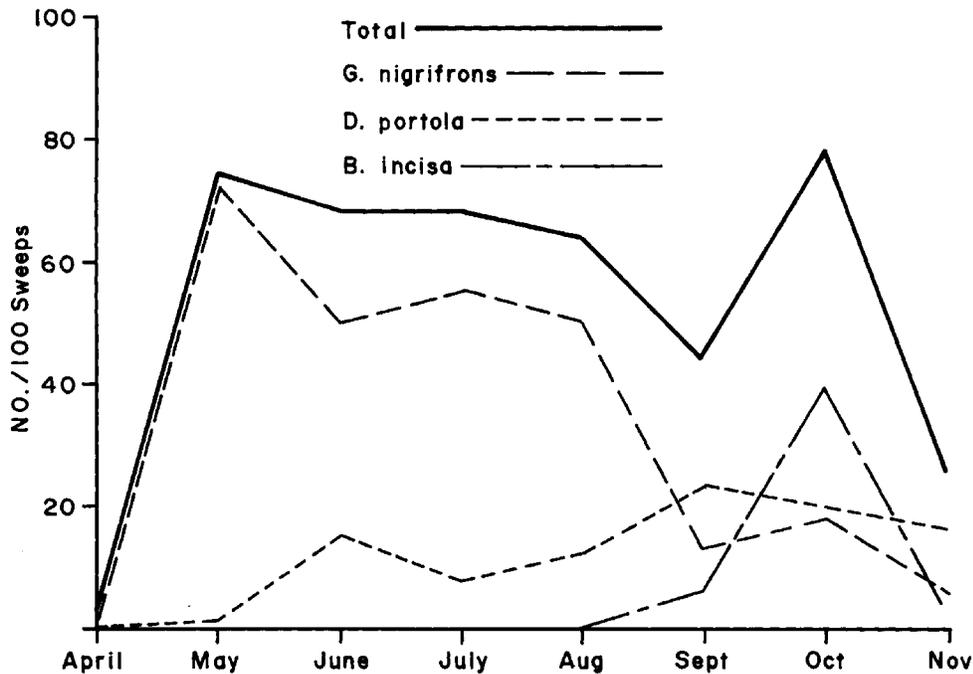


Fig. 1. Mean adult leafhoppers per 100 sweeps in eight Florida rice fields sampled each year during 1983 and 1984. Each field was sampled weekly with 100 continuous 180° sweeps with a 38.1 cm diameter sweep net. Fields were located throughout the Everglades agricultural area of southern Florida.

may be related to the weedy condition of a few of the ratooned rice fields.

In conclusion, Genung et al. (1979) have noted that leafhoppers are often very abundant on southern Florida rice and may contribute to the unthrifty appearance and discoloration often observed in the rice. Currently, southern Florida rice growers have expressed no concern for leafhopper or planthopper populations in their rice fields and *S. orizicola* was the only rice disease vector detected in our survey. However, several economically important leafhopper and planthopper species including potential disease vectors are present in the fields and may increase rapidly in numbers. Presently, we have little understanding of the impact of leafhoppers and planthoppers on southern Florida rice production or how these insects are interacting with other local crops such as corn and sugarcane. These above subjects warrant future research, especially if rice acreage continues to increase in southern Florida.

ACKNOWLEDGMENTS

We express our gratitude to the numerous rice growers who allowed us use of their fields and Dr. J. P. Kramer for help in identifying some specimens and Dr. J. Alvarez for the Spanish translation. This is Agricultural Experiment Station Journal Series No. 6376 and FDACS, DPI, Bur. Entomology Contribution No. 610.

REFERENCES CITED

ABBOTT, E. V., AND J. W. INGRAM. 1942. Transmission of chlorotic streak of sugar

- cane by the leaf hopper *Draeculacephala portola*. Phytopathology 32: 99-100.
- ALVAREZ, J. 1978. Potential for commercial rice production in the Everglades. Economic Information Report 98. Food and Resource Economics Dept., Univ. of Florida.
- BRCAK, J. 1979. Leafhopper and planthopper vectors of plant disease agents in central and southern Europe, pp. 97-155. In Maramorosch, K., and K. Harris (eds.), Leafhopper vectors and plant disease agents. Academic Press, New York.
- GENUNG, W. G., AND F. W. MEAD. 1969. Leafhopper populations (Homoptera: Cicadellidae) on five pasture grasses in the Florida Everglades. Florida Ent. 52: 165-170.
- GENUNG, W. G., G. H. SNYDER, AND V. E. GREEN, JR. 1979. Rice-field insects in the Everglades. Belle Glade AREC Research Rept. EV-1979-7.
- HARRIS, K. F. 1979. Leafhoppers and aphids as biological vectors: vector-virus relationships, pp. 217-309. In Maramorosch, K., and K. Harris (eds.), Leafhopper vectors and plant disease agents. Academic Press, New York.
- NAULT, L. R., AND O. E. BRADFUTE. 1979. Corn stunt: involvement of a complex of leafhopper-borne pathogens, pp. 561-587. Ibid.
- PATHAK, M. D. 1968. Ecology of common insect pests of rice. Ann. Rev. Ent. 13: 257-294.
- PEMERTON, C. E., AND L. E. CHARPENTIER. 1969. Insect vectors of sugar cane virus diseases, pp. 411-427. In J. R. Williams, J. R. Metcalfe, R. W. Mungomery, and R. Mathes (eds.), Pests of sugar cane. Elsevier, New York.
- ROHRMANN, F., AND J. ALVAREZ. 1984. Costs and returns for rice production on muck soils in Florida, 1984. Economic Information Report 202. Food and Resource Economics Dept., Univ. of Florida.
- SOSA, O., JR. 1983. Sugarcane delphacid discovered in Florida. Sugar J. 45: 16.
- SOUTHWOOD, T. R. 1978. Ecological methods with particular reference to the study of insect populations. Second Edition. Chapman and Hall, New York.
- STONER, W. N., AND R. D. GUSTIN. 1967. Biology of *Graminella nigrifrons* (Homoptera: Cicadellidae), a vector of corn (maize) stunt virus. Ann. Entomol. Soc. America 60: 496-505.
- STRAYER, J. 1975. Sugarcane insect control. Florida Coop. Ext. Serv. Entomol. Rept. 40.
- YOUNG, D. A., JR., AND R. H. DAVIDSON. 1959. A review of leafhoppers of the genus *Draeculacephala*. USDA Tech. Bull. 1198.

ARTHROPODS ON BRAZILIAN PEPPERTREE,
SCHINUS TEREBINTHIFOLIUS
(ANACARDIACEAE), IN SOUTH FLORIDA

J. R. CASSANI
Lee County Hyacinth Control District
Post Office Box 06005
Fort Myers, Florida 33906

ABSTRACT

Arthropods on *Schinus terebinthifolius* Raddi were collected by hand and with a sweep net every other week between 8 May 1979 and 29 July 1980 at three sites in Lee County, Florida. Of the 115 arthropod species identified, 46 (40.0%) were phytophagous, 59 (51.3%) predatory, and 10 (8.7%) miscellaneous. The six most frequently occurring species belonged to either the Formicidae or Araneae. The most frequently (65.5%) occurring phytophagous sp. was a bush cricket (*Cyrtoxipha* sp.). The phytophagous

- cane by the leaf hopper *Draeculacephala portola*. Phytopathology 32: 99-100.
- ALVAREZ, J. 1978. Potential for commercial rice production in the Everglades. Economic Information Report 98. Food and Resource Economics Dept., Univ. of Florida.
- BRCAK, J. 1979. Leafhopper and planthopper vectors of plant disease agents in central and southern Europe, pp. 97-155. In Maramorosch, K., and K. Harris (eds.), Leafhopper vectors and plant disease agents. Academic Press, New York.
- GENUNG, W. G., AND F. W. MEAD. 1969. Leafhopper populations (Homoptera: Cicadellidae) on five pasture grasses in the Florida Everglades. Florida Ent. 52: 165-170.
- GENUNG, W. G., G. H. SNYDER, AND V. E. GREEN, JR. 1979. Rice-field insects in the Everglades. Belle Glade AREC Research Rept. EV-1979-7.
- HARRIS, K. F. 1979. Leafhoppers and aphids as biological vectors: vector-virus relationships, pp. 217-309. In Maramorosch, K., and K. Harris (eds.), Leafhopper vectors and plant disease agents. Academic Press, New York.
- NAULT, L. R., AND O. E. BRADFUTE. 1979. Corn stunt: involvement of a complex of leafhopper-borne pathogens, pp. 561-587. Ibid.
- PATHAK, M. D. 1968. Ecology of common insect pests of rice. Ann. Rev. Ent. 13: 257-294.
- PEMERTON, C. E., AND L. E. CHARPENTIER. 1969. Insect vectors of sugar cane virus diseases, pp. 411-427. In J. R. Williams, J. R. Metcalfe, R. W. Mungomery, and R. Mathes (eds.), Pests of sugar cane. Elsevier, New York.
- ROHRMANN, F., AND J. ALVAREZ. 1984. Costs and returns for rice production on muck soils in Florida, 1984. Economic Information Report 202. Food and Resource Economics Dept., Univ. of Florida.
- SOSA, O., JR. 1983. Sugarcane delphacid discovered in Florida. Sugar J. 45: 16.
- SOUTHWOOD, T. R. 1978. Ecological methods with particular reference to the study of insect populations. Second Edition. Chapman and Hall, New York.
- STONER, W. N., AND R. D. GUSTIN. 1967. Biology of *Graminella nigrifrons* (Homoptera: Cicadellidae), a vector of corn (maize) stunt virus. Ann. Entomol. Soc. America 60: 496-505.
- STRAYER, J. 1975. Sugarcane insect control. Florida Coop. Ext. Serv. Entomol. Rept. 40.
- YOUNG, D. A., JR., AND R. H. DAVIDSON. 1959. A review of leafhoppers of the genus *Draeculacephala*. USDA Tech. Bull. 1198.

ARTHROPODS ON BRAZILIAN PEPPERTREE,
SCHINUS TEREBINTHIFOLIUS
(ANACARDIACEAE), IN SOUTH FLORIDA

J. R. CASSANI
Lee County Hyacinth Control District
Post Office Box 06005
Fort Myers, Florida 33906

ABSTRACT

Arthropods on *Schinus terebinthifolius* Raddi were collected by hand and with a sweep net every other week between 8 May 1979 and 29 July 1980 at three sites in Lee County, Florida. Of the 115 arthropod species identified, 46 (40.0%) were phytophagous, 59 (51.3%) predatory, and 10 (8.7%) miscellaneous. The six most frequently occurring species belonged to either the Formicidae or Araneae. The most frequently (65.5%) occurring phytophagous sp. was a bush cricket (*Cyrtoxipha* sp.). The phytophagous

hemipterans *Hyalymenus potens* (Alydidae) and *Leptoglossus phyllopus* (Coreidae) also occurred frequently especially when *Schinus* fruit was abundant. No significant herbivory was observed on *S. terebinthifolius* at any time during the survey. A list of insect species recorded from *S. terebinthifolius* in Florida by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry between 1934 and 1981 is incorporated and discussed.

RESUME

Se coleccionaron artrópodos en *Schinus terebinthifolius* Raddi a mano y con redes de ciega cada otra semana entre Mayo 8, 1979 y Julio 29, 1980, en 3 sitios en el Condado de Lee en la Florida. De las 115 especies de artrópodos identificadas, 46 (40%) eran fitófagas, 59 (51.3%) eran depredadores, y 10 (8.7%) eran misceláneas. Las seis especies que ocurrieron más frecuentemente pertenecían a la Formicidae o a la Araneae. La especie de fitófago que ocurrió con más frecuencia fue el grillo *Cyrtoxipha*. Los fitófagos hemípteros *Hyalymenus potens* (Alydidae) y *Leptoglossus phyllopus* (Coreidae) también ocurrieron frecuentemente, especialmente cuando la fruta *Schinus* era abundante. No se observó ningún herbívoro significativo en *S. terebinthifolius* en ningún momento durante la encuesta. Se incorpora y se discute una lista de las especies obtenidas de *S. terebinthifolius* de la Florida por el Departamento de Agricultura y Servicios al Consumidor de la Florida, División de la Industria de Plantas, entre 1934 y 1981.

The woody shrub *Schinus terebinthifolius* Raddi (Anacardiaceae), is an aggressive colonizer throughout south Florida. A native of Argentina, Paraguay and Brazil, it is thought to have been introduced into Florida as an ornamental during the 1840's (Ewel et al. 1982). *S. terebinthifolius* is also found in southern Arizona and southern California and is naturalized in over 20 countries (Ewel et al. 1982). The plant is called Florida Holly, Christmas Berry, Brazilian pepper and Brazilian peppertree (BP), which is the approved common name (WSSA 1984). BP is reported as a "sparse species" in its native range, but reaches heights of 13m and often grows as an impenetrable thicket invading and disrupting a variety of habitats including hammocks and mangrove forests in Florida (Ewel et al. 1982). Areas disturbed by human activities or hurricanes are often the most aggressively invaded (Alexander & Crook 1973). The influx of urban development associated with a disruption of natural hydrological cycles by the construction of canals and other water control structures in south Florida during recent years, has essentially "opened the door" for *Schinus* invasion. A variety of control strategies including herbicides, burning and bulldozing have been undertaken in localized areas as Everglades National Park and Sanibel Island with limited success (Koepp 1979, Pierce 1979).

The introduction of three exotic insect species, *Crasimorpha infuscata* Hodges (Lep.:Gelechiidae), *Episimus utilis* Zimmerman (Lep.: Tortricidae) and *Bruchus atronotatus* Pic (Col.:Bruchidae), for biological control of BP in Hawaii between 1954 and 1961 resulted in the bruchid and tortricid becoming established but with little effect on the plant's dispersal (Julien 1982, C. J. Davis pers. com.). However, those species or other insect or pathogen control agents present in the native range of *Schinus* spp. may be more suitable in south Florida. For example, there are several species of shrubby *Schinus* in the northwest region of Argentina where fruits are severely attacked by undescribed bruchid species in the genus *Lithraeus* (A. L. Teran pers. com.).

The objective of this survey was to provide a better understanding of the arthropod fauna on BP in south Florida in order to identify arthropods that may have potential for manipulation as control agents and to provide a basis for further work on arthropod control agents of BP.

MATERIALS AND METHODS

Three sites in Lee County, Florida, dominated by BP growth, were surveyed every other week between 8 May 1979 and 29 July 1980. Site 1 was located on Sanibel Island on Tarpon Bay Road between Gulf Drive and Periwinkle Way (T46S, R22E, S26). This site is characterized as a narrow roadside strip of BP growing on a roadside ditch spoil bank. Site 2 was located in Fort Myers west of Marsh Avenue between Ballard Road and Madison Avenue (T44S, R25E, S17). This site consisted of intermittent stands of BP growing in a field of mixed grass spp. and a variety of herbs. Site 3 was located near Tice Road approximately 200m east of Interstate 75 (T44S, R25E, S10), and was of a similar habitat and surrounding plant community as Site 2.

Arthropod collection methods included sweeping and hand collecting. Forty standard sweeps were made on BP at each site with a 30-cm-diam. sweep net. The area of vegetation swept ranged from approximately 0.6m to 2.4m above ground level and included leaf, flower and fruiting portions of the plants. Arthropods were also collected by hand for a 5-min. period at each site and notes were made concerning their location on the plant and related behavior. The contents of the sweep net samples were returned to the laboratory in plastic bags and kept frozen until they could be sorted. Hand collected samples were transported in killing jars and stored as above.

The compilation of insects collected from BP by DPI (Florida Department of Agriculture and Consumer Services, Division of Plant Industry) workers was made from identification slips on record at DPI headquarters in Gainesville. The DPI file included 221 individual collections made on BP in south Florida during the following years: 1934, 1935, 1939, 1948, 1950, 1954, 1956, 1958-74, 1977-81. Due to the lengthy list of insect species and the subjective and non-comprehensive nature of the DPI survey, only those insect spp. collected on more than one date were included in this compilation.

RESULTS AND DISCUSSION

In the Lee County (LCHCD) survey, 115 arthropod species were collected of which 46 (40.0%) were phytophagous and 59 (51.3%) predatory (Tables 1 and 2). Those species categorized as miscellaneous are also included in Table 2. A total of 44 species are listed from the DPI survey of which 37 (84.1%) are phytophagous, 5 (11.4%) predatory and 2 (4.5%) miscellaneous. DPI field agents are trained to scout for pests of agriculture as evidenced by the high percentage of phytophagous species from this survey. The six most common species from the LCHCD survey were either ants (Formicidae) or spiders (Araneae). Dead BP branches resulting from periodic freezing temperatures provide a suitable nesting habitat for the arboreal formicids, *Pseudomyrmex mexicanus*, *P. brunneus*, *Crematogaster clara* and *Camponotus floridanus* which are important predators of small arthropods and of eggs and young of larger ones (Trager pers. com.). A small inconspicuous bush cricket (*Cyrtolipha* sp.) was the most common phytophagous species from the LCHCD survey. Blatchley (1920) reports *C. gundlachi* Saussure and *C. gundlachi columbiana* Caudell as occurring in Florida on shrubs and small trees usually near water.

During October through March when BP fruit is plentiful, the most conspicuously abundant and commonly occurring species are *Hyalymenus potens* (Alydidae), the *Leptoglossus* group, primarily *L. phyllopus*, and the scutellerids *Symphylus caribeus* and *Sphyrocoris obliquus*, all of which imbibe juice from ripening fruit. The effect of feeding by true bugs on the normal development of BP fruit and eventual effect on the seed is unknown, however, there was no evidence of a decline in seedling density and distribution in areas that were surveyed. Aggregations of immature *H. potens* and *Leptoglossus* spp. were often observed on clusters of BP fruit indicating that oviposition

probably also occurs on BP. Hussey (1952) also observed *L. phyllopus* and *L. gonagra* on BP fruit.

Many of the most frequently occurring insects from the DPI survey (Table 1) are major or minor pests of agriculture. *Diaprepes abbreviatus* (sugarcane root borer) is a pest of sugarcane, citrus and other crops (Hill 1975). *Pulvinaria psidii* (green shield scale) is a minor pest of guava and mango (Hill 1975). Major pests of citrus including *Aleurocanthus woglumi* (citrus blackfly) and *Coccus viridus* (soft green scale) were collected from BP but infrequently during the DPI survey.

The only commonly occurring species from the LCHCD survey that is a significant agricultural pest is *Leptoglossus phyllopus*, a major pest of citrus. During serious infestations it causes premature color break and fruit drop (Mead 1971). *L. phyllopus* also heavily infests at times a variety of other crops including tomato, bean, bell pepper and curcubits which are important winter vegetable crops in south Florida (Mead 1971). Other species of *Leptoglossus* are also pests. BP growing in proximity to agricultural areas probably supports large populations of vegetable damaging coreids, pentatomids and scutellerids especially during October through December when BP fruiting is at its peak and winter vegetable crops are nearing harvest. Scale insects were never very numerous during the LCHCD survey. On several occasions the coccinellids *Azya luteipes* and *Cycloneda* sp. were observed preying on scales. None of the phytophagous arthropods collected from BP as a part of the LCHCD survey were observed causing significant damage to the plant nor was extensive herbivory of any type observed.

Ewel et al. (1982) reported 29 species of insects visiting male and female BP flowers in Everglades National Park. Only three of these 29 species were also collected in the LCHCD survey indicating that the arthropod fauna on BP is probably influenced to a large extent by the composition and diversity of the surrounding plant communities. None of the phytophagous insects reported here are thought to utilize BP exclusively. This is not surprising since BP has been present in Florida for a relatively short period. Only 9 (12%) of the 74 phytophagous species in Table 1 were common to both the DPI and LCHCD surveys. This suggests that sampling sites over a greater geographical range and or other habitat types may have been more appropriate for the LCHCD survey.

The compatibility of an introduced biological control agent with the existing arthropod fauna of BP will depend in part on its susceptibility to predation by ants and spiders which are the most common groups on this plant. Soft bodied larvae with limited defense mechanisms that occur on exposed portions of the plant would seem to be the most susceptible to foraging ants and spiders.

Due to its prolific dispersal and aggressive colonization of rapidly increasing disturbed areas, BP remains a significant component of the flora in south Florida. Introduction of an exotic phytophagous arthropod may be economically feasible, if suitable agents can be found, considering the high cost of present control activities in some areas. Despite the problems associated with BP, the plant is still being used as an ornamental, mostly at older residences where scattered plants were already growing prior to construction and were allowed to remain as a part of the landscape. Introduction of a leaf feeding insect for control of *Schinus* would result in a conflict of interest since the plant is still used for landscape purposes. Control by a leaf feeding insect, even if possible, is probably impractical. An agent that damages or consumes a large percentage of flowers or seeds may be a long-term solution to the problem of seed dispersal and the continued invasion of *Schinus* to uninfested areas.

ACKNOWLEDGMENTS

Arthropod identifications were made by: G. B. Edwards (Araneae), J. E. Eger (Scutelleridae), R. E. Froeschner (Alydidae), A. B. Hamon (Coccidae), F. C. Harmston

TABLE 1. PHYTOPHAGOUS ARTHROPODS COLLECTED FROM *SCHINUS TERREBINTGHIFOLIUS*.

Taxon	Stages Collected ¹	Assoc. ²	Months Collected ³	% Frequency of Occurrence LCHCD Survey (Site) ⁴	% Frequency of Occurrence DPI Survey ⁵
COLEOPTERA					
Cantharidae					
<i>Chauliognathus marginatus</i> (Fabr.)	A	B,L,F	III,V,X	17.2(2)	—
Chrysomelidae					
<i>Blepharida rhois</i> (Forst.)	A	L	V-VII	—	3.6
Curculionidae					
<i>Diaprepes abbreviatus</i> (L.)	all	L,B,R	III-IX	—	4.1
Elateridae					
<i>Conoderus</i> sp.	A	L	VIII	3.4(3)	—
<i>Glyphonyx</i> sp.	A	—	V-VII	10.3(2)	—
<i>Melonotus</i> sp.	A	L	VII	3.4(2)	—
Scarabaeidae					
<i>Euphoria sepulcharis</i> (F.)	A	B	III,V,IX	6.9(2)	1.0
<i>Pachystethus marginatus</i> (Fab.)	A	—	VI,X	—	1.0
<i>Trigonopeltastes delta</i> (Forst.)	A	L,B,S	IX,XI	—	1.0
DIPTERA					
Tephritidae					
<i>Tephritis subpura</i> (Johnson)	A	L	VIII	—	1.4
HEMIPTERA-HOMOPTERA					
Acanaloniidae					
<i>Acanalonia latifrons</i> (Walker)	A	—	VII	3.4(1)	—
Aleyrodidae					
<i>Aleurocanthus woglumi</i> Ashby	I	—	VII,IX	—	2.3
Alydidae					
<i>Hyalymenus</i> sp.	I,A	L,S	I,XII	—	1.4
<i>Hyalymenus potens</i> Torre-Bueno	I,A	F	I-V,X-XII	41.4(2,3)	—
Aphididae					
<i>Aphis gossypii</i> Glover	I,A	—	IV,X	—	1.0

Cercopidae						
<i>Clastoptera undulata</i> Uhler	A	—	VII, XI	34.5(1-3)	—	—
<i>Clastoptera xanthocephala</i> Germa	A	—	III, VI, IX	10.3(2)	—	—
Cicadellidae						
<i>Chlorotettix minimus</i> Baker	A	—	V	3.4(2)	—	—
<i>Draeculacephala portola</i> Ball	A	—	II	3.4(2)	—	—
<i>Graphocephala coccinia</i> (Forster)	A	—	I-III, V-VIII, IX, XII	51.7(1-3)	—	—
<i>Graphocephala versuta</i> (Say)	A	—	VII	3.4(2)	—	—
<i>Homalodisca coagulata</i> (Say)	A	—	V, VII, XI	10.3(2)	—	—
<i>Oncometopia nigricans</i> (Walker)	A	—	III, IV, VI, VII, IX	27.6(2,3)	—	—
<i>Stragania robusta</i> (Uhler)	A	—	II, VI	6.9(1,3)	—	—
Coccidae						
<i>Ceroplastes</i> sp.	A, I	S, L	III, VIII-X	—	—	1.8
<i>Ceroplastes ceriferus</i> (And.)	A, I	—	X, XII	—	—	1.0
<i>Ceroplastes cirripediformis</i> Comstock	A, I	L, S	II, III, V, VII, XII	—	—	4.5
<i>Ceroplastes floridensis</i> Comstock	A, I	L, S	I-III, V, VIII-X	—	—	5.0
<i>Coccus accuminatus</i> (Sign.)	A, I	L, S	I-VII, IX	—	—	6.3
<i>Coccus hesperidum</i> L.	A, I	L, S	III, IV, VI, X	3.4(2)	—	1.4
<i>Coccus viridis</i> (Green)	A	L	I, X	—	—	1.8
<i>Kilifia accuminata</i> (Sign.)	A, I	L, S	I-III, VI, VIII	20.7(2,3)	—	2.3
<i>Parasaissetia nigra</i> (Nietner)	A, I	L, S	V, X	—	—	1.0
<i>Protopulvinaria pyriformis</i> Comst.	A, I	S	V, VII	—	—	1.0
<i>Pulvinaria psidii</i> Maskel	A, I	L	I-X	31.0(1-3)	—	13.1
<i>Saissetia coffeae</i> (Walker)	A, I	L, S	I-III, V-VIII	3.4(1)	—	2.3
Coreidae						
<i>Acanthocephala femorata</i> (F.)	A	F	V	3.4(2)	—	—
<i>Leptoglossus concolor</i> (Walker)	A	F, L	I, III, VIII, X-XII	17.2(2,3)	—	1.0
<i>Leptoglossus gonagra</i> (F.)	A, I	F, L	I-IV, VIII, XI	20.7(2,3)	—	1.0
<i>Leptoglossus oppositus</i> (Say)	A, I	F, L	I	3.4(2)	—	—
<i>Leptoglossus phyllopus</i> (L.)	A, I	—	I, V, VIII, X-XII	37.9(2,3)	—	—
<i>Spartocera</i> sp.	I	L	VI	—	—	1.0

TABLE 1. (Continued)

Taxon	Stages Collected ¹	Assoc. ²	Months Collected ³	% Frequency of Occurrence LCHCD Survey (Site) ⁴	% Frequency of Occurrence DPI Survey ⁵
Diaspididae					
<i>Howardia biclavis</i> (Comstock)	A,I	S	IV,VI,X	—	1.4
<i>Pinaspis strachani</i> (Cooley)	A,I	—	V,VI,X	—	1.0
<i>Pseudaonidia duplex</i> (Cockerel)	A,I	S	IV	—	1.0
<i>Pseudaonidia trilobitiformis</i> (Green)	A,I	L	I,X	—	1.4
Largidae					
<i>Largus davisii</i> Barber	A	—	VII	3.4(3)	—
Lygaeidae					
<i>Oncopeltus fasciatus</i> (Dallas)	A,I	L,S	IV,VI,XI	3.4(2)	1.0
Membracidae					
<i>Spissistilus festinus</i> (Say)	A	—	X-XII	6.9(3)	—
<i>Umbonia crassicornis</i> (Amyot & Serville)	A,I	—	VII	—	1.0
Ortheziidae					
<i>Orthezia insignis</i> Browne	A,I	S,L	VI	—	1.0
Pentatomidae					
<i>Acrosternum marginatum</i> (P. De B.)	I	L	VII	—	1.0
<i>Euschistus servus</i> (Say)	A,I	—	V-VIII,XII	17.2(2,3)	—
<i>Loxa flavicollis</i> (Drury)	A	—	I,IV,VII	10.3(1-3)	—
<i>Nezara viridula</i> (L.)	A,I	L	I,II,IV,XII	17.2(2,3)	1.0
<i>Piezodorus guildinii</i> (Westwood)	A	—	I,II	6.9(2)	—
<i>Thyanta perditor</i> (F.)	A	—	I,II	6.9(3)	—
Pseudococcidae					
<i>Geococcus coffeae</i> Green	A,I	L,R	I,X,XII	—	1.4
<i>Phenacoccus solani</i> Ferris	A,I	R	X	—	1.0

Scutelleridae						
<i>Chelysoma guttatutum</i> (Her.-Sch.)	A	F	XI	3.4(2)	—	
<i>Dioleus chrysorrhoeus</i> (Fabr.)	A	—	VIII	3.4(2)	—	
<i>Sphyrocoris obliquus</i> (Germar)	A,I	—	I,X-XII	20.7(2,3)	—	
<i>Symphylus</i> sp.	A	—	I-III	13.8(2,3)	—	
<i>Symphylus caribbeanus</i> Kirkaldy	A	—	I-III,V	17.2(2,3)	—	
Tropiduchidae						
<i>Pelitropis rotulata</i> Van Duzee	A	—	VI,VII	10.3(1,2)	—	
LEPIDOPTERA						
Arctiidae						
<i>Hyphantria cunea</i> Drury	L	L	VII,IX	—	1.0	
Lycaenidae						
Sp. A	A	L	V,VIII,XI	10.3(3)	—	
ORTHOPTERA						
Acrididae						
<i>Melanoplus</i> sp.	A,I	L	VI,VIII,IX	10.3(3)	—	
<i>Paroxya</i> sp.	A	L	VI	3.4(3)	—	
<i>Schistocera</i> sp.	A	L	VI	3.4(3)	—	
Gryllidae						
<i>Cyrtoxipha</i> sp.	A,I	L	I-VIII,XI,XII	65.5(1-3)	—	
Tettigoniidae						
<i>Pterophyla</i> sp.	A,I	L	VII,XI,XII	10.3(2,3)	—	
<i>Neoconocephalus</i> sp.	A,I	L	VII,IX,XII	13.8(2)	—	
THYSANOPTERA						
Thripidae						
<i>Selenothrips rubrocinctus</i> (Giard)	A,I	L,B	III,VI,VII,IX,XI	—	4.1	

¹A = adult, I = immature

²L = leaves, B = bloom, S = stem, F = fruit, R = root

³includes both surveys

⁴Lee County Hyacinth Control District

⁵Division of Plant Industry, Florida Department of Agriculture and Consumer Services

TABLE 2. PREDACEOUS AND MISCELLANEOUS ARTHROPODS COLLECTED FROM *SCHINUS TERREBINTHIFOLIUS*.

Taxon	Stages Collected ¹	Assoc. ²	Months Collected ³	% Frequency of Occurrence LCHCD Survey (Site) ⁴	% Frequency of Occurrence DPI Survey ⁵
ACARI					
Phytoseiidae					
<i>Amblyseius hibisci</i> (Chant)	A	—	III, V	—	1.0
<i>Typhlodromalus peregrinus</i> (Muma)	A, I	—	XII	—	1.0
Tydeidae					
<i>Lorryia formosa</i> Cooreman	—	L	VII, IX	—	1.0
<i>Tydeus</i> sp.	A, I	L, S	VI, XII	—	1.0
ARANEAE					
Anyphaenidae					
<i>Aysha</i> sp.	—	—	I-VIII, X-XII	89.7(1-3)	—
<i>Aysha velox</i>	—	—	I, II, VII, XI, XII	24.1(2,3)	—
<i>Teudis mordax</i> (O. P. Cambridge)	—	—	II	3.4(2)	—
Araneidae					
<i>Acanthepeira</i> sp.	—	—	VI	3.4(3)	—
<i>Avaneus pagnia</i> (Walckenaer)	—	—	IV	3.4(2)	—
<i>Eriophora ravilla</i> (Kock)	—	—	II, VII, IX-XI	17.2(2,3)	—
<i>Gasteracantha cancriformis</i> (L.)	—	—	III, VIII	10.3(1)	—
<i>Neoscona arabesca</i> (Walckenaer)	—	—	I	3.4(2)	—
<i>Tetragnatha</i> sp.	—	—	II-IV, IX-XI	20.7(1-3)	—
<i>Tetragnatha guatemalensis</i> O. P. Cambridge	—	—	I	3.4(3)	—
Clubionidae					
<i>Chiracanthium inclusum</i> (Hentz)	—	—	V, VIII	10.3(3)	—
<i>Clubiona</i> sp.	—	—	VI	10.3(3)	—
<i>Trechelas</i> sp.	—	—	V	3.4(2)	—

Dictynidae						
<i>Dictyna altamira</i> (Gertsch & Davis)	—	—	X	3.4(2)	—	
Linyphiidae						
<i>Eperigone cf. serrata</i> Ivie & Barrows	—	—	XII	3.4(3)	—	
Lycosidae						
<i>Pardosa longispinata</i> Tullgren	—	—	VII	3.4(1)	—	
<i>Mysmena</i> sp.	—	—	V	3.4(1)	—	
Oxyopidae						
<i>Peucetia viridans</i> (Hentz)	—	—	I-V, VII, IX-XII	44.8(2,3)	—	
Pisauridae						
<i>Dolomedes</i> sp.	—	—	VI	6.9(3)	—	
<i>Pisaurina undulata</i> (Keyserling)	—	—	VII, VIII	10.3(3)	—	
Salticidae						
<i>Hentzia palmarum</i> (Hentz)	—	—	I-VIII, X-XII	75.9(1-3)	—	
<i>Lyssomanes viridis</i> (Walckenaer)	—	—	I, III-V, VI, X	27.6(2-3)	—	
<i>Metaphidipus galathea</i> (Walckenaer)	—	—	II, XII	6.9(2)	—	
<i>Phidipus regiosus</i> C. L. Koch	—	—	VI, X, XII	10.3(2)	—	
<i>Thiodina</i> sp.	—	—	I, III	10.3(2)	—	
<i>Thiodina sylvana</i> (Hentz)	—	—	III, X	6.9(2,3)	—	
<i>Zygoballus</i> sp.	—	—	VII	6.9(3)	—	
Thomisidae						
<i>Misumenopus</i> sp.	—	—	VII	3.4(2)	—	
<i>Misumenopus oblongus</i> (Keyserling)	—	—	XI	3.4(2)	—	
COLEOPTERA						
Coccinellidae						
<i>Azya luteipes</i> Muls.	A	—	VII	6.9(2)	—	
<i>Cycloneda</i> sp.	A	—	I, V, VI, VIII, XI	17.2(1-3)	—	
DIPTERA						
Bibionidae						
<i>Plecia nearctica</i> Hardy	A	L	IV, V, IX	13.8(2,3)	—	

TABLE 2. (Continued)

Taxon	Stages Collected ¹	Assoc. ²	Months Collected ³	% Frequency of Occurrence LCHCD Survey (Site) ⁴	% Frequency of Occurrence DPI Survey ⁵
Dolichopodidae					
<i>Chrysotus</i> sp.	A	L	V-VII, XI	13.8(1-3)	—
<i>Condylostylus</i> sp.	A	L	V-VIII, XI, XII	34.5(1-3)	—
<i>Condylostylus chrysoprasinus</i> (Wik.)	A	L	VI, VII	6.9(3)	—
<i>Condylostylus crinitus</i> (Aldr.)	A	L	VI	6.9(2,3)	—
<i>Condylostylus mundus</i> (Wied.)	A	L	VII, VIII	6.9(3)	—
Otitidae					
<i>Euxestus abdominalis</i> (Loew)	A	—	II, VII	—	1.0
Sarcophagidae					
<i>Blaesoxipha opifera</i> (Coq.)	A	—	X	3.4(2)	—
<i>Erythrandra picipes</i> B & B	A	L	IV	3.4(3)	—
<i>Oxysarcodexia ventricosa</i> (Wulp)	A	L	VI	3.4(3)	—
<i>Ravinia derelicta</i> (Walk.)	A	L	VI	3.4(3)	—
<i>Sarcodexia alata</i> (Ald.)	A	L	II	3.4(2)	—
Stratiomyidae					
<i>Hermetia illucens</i> (L.)	A	L	VII	3.4(2)	—
Syrphidae					
Sp. A	A	—	I	3.4(1)	—
Sp. B	A	—	II-IV	10.3(2)	—
HEMIPTERA-HOMOPTERA					
Pentatomidae					
<i>Euthyrhynchus floridanus</i> (L.)	A	LS	IV, V, VII	3.4(2)	1.8
Phymatidae					
<i>Phymata fasciata</i> (Gray)	A	—	V	3.4(3)	—
HYMENOPTERA					
Apidae					
<i>Apis mellifera</i> L.	A	B	VI, IX, X	17.2(1-3)	—

Formicidae					
<i>Brachymyrmex</i> sp.	—	—	V	3.4(3)	—
<i>Camponotus floridanus</i> (Buckley)	—	—	III, VI-X	44.8(1,3)	—
<i>Camponotus pavidus</i> Wheeler	—	—	V, VII	6.9(2)	—
<i>Camponotus rasilis</i> Wheeler	—	—	VI, VII	10.3(3)	—
<i>Camponotus tortuganus</i> Emery	—	—	VI, VIII	13.8(1,3)	—
<i>Cardiocondyla</i> sp.	—	—	VII	6.9(2,3)	—
<i>Colobopsis impressa</i> Roger	—	—	I, III-IX, XII	75.9(2,3)	—
<i>Conomyrma flavopecta</i> (Smith)	—	—	VII-IX	10.3(3)	—
<i>Crematogaster ashmeadi</i> Mayr	—	—	VI	3.4(1)	—
<i>Crematogaster clara</i> Mayr	—	—	I, III, V-X, XII	72.4(2,3)	—
<i>Paratrechina bourbonica</i> (Forel)	—	—	VI, VII	6.9(3)	—
<i>Pheidole dentata</i> Mayr	—	—	VII	3.4(1)	—
<i>Pseudomyrmex ejectus</i> Smith	—	—	I, III-X	65.5(1-3)	—
<i>Pseudomyrmex elongatus</i> (Mayr)	—	—	I, III, VII	10.3(2,3)	—
<i>Pseudomyrmex mexicanus</i> (Roger)	—	—	II, XII	89.7(1-3)	—
<i>Pseudomyrmex pallidus</i> (Smith)	—	—	I, VI	6.9(3)	—
<i>Solenopsis geminata</i> (Fabr.)	—	—	VI, IX	6.9(4)	—
<i>Tapinoma litorale</i> Wheeler	—	—	I	3.4(2)	—
Halictidae					
Sp. A.	—	B	X, XI	6.9(2)	—
NEUROPTERA					
Chrysopidae					
<i>Chrysopa</i> sp.	A	L	I, XI	10.3(2)	—
Mantispidae					
<i>Mantispa</i> sp.	A	L	VI, VII, X, XI	13.8(2,3)	—
PSOCOPTERA					
Psocidae					
<i>Cerastipsocus venosus</i> (Burmeister)	A, I	—	VI	—	1.0

¹A = adult, I = immature

²L = leaves, S = stem

*includes both surveys

⁴Lee County Hyacinth Control District

⁵Division of Plant Industry, Florida Department of Agriculture and Consumer Services

(Dolichopodidae), F. W. Mead (Hemiptera, Homoptera), R. I. Sailer (Hemiptera), J. C. Trager (Formicidae), R. E. Woodruff (Coleoptera, Orthoptera). I thank G. Buckingham, R. M. Baranowski, W. E. Caton, R. T. Cunningham, C. J. Davis, J. Ewel, G. Y. Funasaki, D. H. Habeck, J. M. Kingsolver, F. W. Mead, A. T. Teran and H. V. Weems for providing valuable suggestions and or assistance in compiling information on *Schinus*.

REFERENCES CITED

- ALEXANDER, T. R. AND A. G. CROOK. 1973. Recent and long-term vegetation changes and patterns in South Florida: Part I: Preliminary report. South Florida Environmental Project. University of Miami, Coral Gables, Fl. 224 pp.
- BLATCHLEY, W. S. 1920. Orthoptera of Northeastern America With Especial Reference To The Faunas of Indiana and Florida. Nature Pub. Co., Indianapolis, Indiana. 784 pp.
- EWEL, J. J., D. S. OJIMA, D. A. KARL, AND W. F. DEBUSK. 1982. *Schinus* in successional ecosystems of Everglades National Park. South Florida Research Center Report T-676. 141 pp.
- HILL, D. S. 1975. Agricultural Insect Pests of the Tropics and Their Control. Cambridge Univ. Press, Cambridge, London. 516 pp.
- HUSSEY, R. F. 1952. Food plants and new records for some Hemiptera in Florida. Fla. Ent. 35: 117.
- JULIEN, M. H., ed. 1982. Biological control of weeds: A world catalogue of agents and their targets. Commonwealth Agri. Bur., Farnham Royal Slough, England. 108 pp.
- KOEPF, W. P. 1979. The status of *Schinus* manipulation in Everglades National Park. Pages 45-47 in *Schinus*. Technical proc. of techniques for control of *Schinus* in South Florida: a workshop for area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fl.
- MEAD, F. W. 1971. Leaf-footed bug, *Leptoglossus phyllopus* (Linnaeus) (Hemiptera:Coreidae). Entomology Circular No. 107, Fl. Dept. Agri. and Consumer Serv., Division of Plant Industry, Gainesville, Fl.
- PIERCE, D. A. 1979. Brazilian pepper (*Schinus* sp.) control on the J. N. "Ding" Darling National Wildlife Refuge. Page 53 in *Schinus*. Technical proc. of techniques for control of *Schinus* in South Florida: a workshop for natural area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fl.
- WEED SCIENCE SOCIETY OF AMERICA (WSSA). 1984. Composite list of weeds. Weed Sci. 32 (Suppl. 2): 137 pp.

TERRESTRIAL ARTHROPODS OF NORTHWEST FLORIDA
SALT MARSHES: DIPTERA (INSECTA)

JORGE R. REY

University of Florida - IFAS
Florida Medical Entomology Laboratory
200 9th Street S.E.
Vero Beach, Florida 32962
U.S.A.

AND

EARL D. MCCOY

Department of Biology
University of South Florida
Tampa, Florida 32620
U.S.A.

ABSTRACT

A report on the species of Diptera captured in nearly 16,000 sweeps of various types of salt marsh vegetation in northwest Florida is presented. A total of 87 species belonging to 58 genera and 25 families was collected in the 15-month study. These numbers are similar to those found in other North American marshes, when the same types of vegetation and sampling methods are compared. Approximately 75% of the species and 78% of the genera captured in Florida had been reported previously from other marshes in North America. The more common families in Florida, in terms of numbers of species captured, were the Ephydriidae, Muscidae, Ceratopogonidae, Chloropidae, and Culicidae.

RESUMEN

Se presentan datos sobre las especies de moscas capturadas en casi 16,000 pases con jabecas en las marismas del noroeste de la Florida. Un total de 87 especies pertenecientes a 58 géneros y 25 familias fueron capturados durante el programa de muestreo de 15 meses de duración. Estos números son similares a los que se encuentran en otras marismas de América del Norte si se comparan los mismos tipos de vegetación y métodos de muestreo. Aproximadamente 75% de las especies y 78% de los géneros capturados en la Florida han sido reportados previamente de otras marismas en América del Norte. Las familias más comunes en la Florida fueron la Ephydriidae, Muscidae, Ceratopogonidae, Chloropidae y Culicidae.

Below, we present a report on the dipteran fauna of *Juncus - Spartina* salt marshes located in northwest Florida, U.S.A. We include a list of the species collected, and data on their relative abundances and patterns of habitat utilization. This information was obtained during a 15-month study of the terrestrial arthropod fauna of marshes within the St. Marks National Wildlife Refuge, in Wakulla County, Florida (30.09° N, 29.12° W). Results for other arthropod groups have been reported previously (McCoy & Rey 1981a,b, Rey & McCoy 1982, 1983), or will be forthcoming. An analysis of diversity and abundance patterns of the complete arthropod fauna of these marshes is in preparation.

METHODS

All specimens were collected by removal sweeping during the period June 1975 to August 1976. A total of 132 samples was taken at 20 sites located within the 4 major

vegetation zones occurring in these marshes (see below). Samples were taken monthly or quarterly between 1100 and 1500 h, on bright, windless days. Each sample consisted of 120 sweeps using standard methods for vegetation sweeping (Southwood 1966). After sweeping, the nets were emptied into plastic bags which were returned to the laboratory for processing. The contents of the bags were hand-sorted under a dissecting microscope and all specimens recovered were assigned to morphospecies. Reference collections were then sent to appropriate specialists for final identifications.

Four marsh zones were sampled: (1) *Spartina* fringe; a narrow band of *Spartina alterniflora* Loisel; (smooth cordgrass) found along shorelines, tidal creeks, and marsh channels. (2) *Juncus roemerianus* Scheele (black rush) marsh; extensive, monospecific stands of black rush, that occur at slightly higher elevations than the *Spartina* fringe, and dominate the St. Marks marshes. (3) *Distichlis spicata* meadows; a mixed community in which *Distichlis spicata* (L.) Greene (seashore saltgrass) predominates over other species such as *Spartina patens* (Ait.) Muhl. (slender cordgrass), *Borrchia frutescens* (L.) DC. (sea oxeye), and *Limonium carolinianum* (Walt.) Britt. (sea lavender). This habitat occurs as isolated patches above the *Juncus*, and is inundated only by seasonal high tides. (4) Halophytic shrub zone; a narrow zone occurring between the *Spartina* and the *Juncus* zones, on sand levies deposited by storm winds and tides. The vegetation consists primarily of groundsel (*Baccharis halimifolia* L.), marsh elder (*Iva frutescens* L.), Christmas berry (*Lycium carolinianum* Walt.), and wax myrtle (*Myrica cerifera* L.). This zone is flooded only by storm tides.

More complete descriptions of the sampling methods used during the study are given in McCoy & Rey (1981a, b), and site descriptions in Rey (1981) and McCoy & Rey (1981a).

RESULTS

The seasonal occurrence and the relative abundance of the species captured in each habitat are presented in Table 1. A total of 87 species belonging to 58 genera, and representing 25 families of Diptera, was identified from our collections. Excluded from the total are 9 morphospecies whose reference specimens were damaged while in route to specialists. They represented single collections and therefore could not be replaced.

The numbers of species captured in the different marsh zones are: *Spartina* fringe - 65 species, *Juncus* marsh - 54 species, *Distichlis* meadows - 53 species, halophytic shrubs - 46 species. Of these, 10 species were collected exclusively in *Spartina*, 6 in *Juncus*, 5 in *Distichlis*, and 2 in the shrubs. Approximately 75% of the flies that were identified to species have also been collected in other North American marshes (Bickley & Seek 1975, Blanton & Wirth 1979, Davis 1978, Davis & Gray 1966, Kale 1964, Lane 1969, Marples 1964, Wall 1973). In total, 78.1% of the genera found at St. Marks, have been reported from other North American tidal marshes.

DISCUSSION

In a compilation of available data on insects of the 'maritime zones' of Georgia, North Carolina, and South Carolina, Davis (1978) reported a total of 136 species of Diptera, distributed among 83 genera and 30 families. These totals however, are not directly comparable to our data (87 species, 58 genera, and 25 families); Davis' list includes species which were captured in a variety of habitats which either do not occur at St. Marks or were not sampled during our study (Rey & McCoy 1982). In addition, his list includes a large number of species reported only from soil collections or from sticky traps at ground level, or represented only by aquatic larval forms collected by dipping. Many of these species obviously were not collected by sweeping. For example, of ten

species of tabanids in Davis' list, only one is reported as occurring in sweep-net collections; the others are represented by larval forms collected from salt marsh soil or adults collected in canopy traps. Because adult tabanids are strong fliers and can easily escape an approaching net, they usually are missed by sweep sampling. If tabulation is restricted to genera and species captured by sweeping similar habitats, Davis' list reduces to approximately 80 species and 50 genera, numbers similar to those reported here. The composition of the dipteran fauna of St. Marks appears to resemble that of other North American marshes more closely than the composition of other orders that we have examined previously. Figure 1 shows the percentage of the total number of genera and species of various orders held in common by St. Marks and other North American marshes. Although the proportions of hemipteran, homopteran, and dipteran genera held in common are comparable (83%, 72%, and 78%, respectively), the proportion of common species is much higher for the Diptera than for any other order examined thus far.

The composition at the family level also appears to be similar to that reported by Davis (1978). The five most common families in Georgia, North Carolina and South Carolina (excluding the Tabanidae) are: Dolichopodidae (17.7% of the total number of species), Chloropidae (15.4%), Ephydriidae (14.0%), Ceratopogonidae (7.3%), and Culicidae (6.0%). At St. Marks, the five most common families are: Ephydriidae (19.6%), Muscidae (15.0%), Ceratopogonidae (12.8%), Chloropidae (10.3%), and Culicidae (5.7%). Thus, 4 of the 5 families with the most species are the same at both locations, and their relative dominances are similar. The exceptions are the Dolichopodidae on the Atlantic Coast and the Muscidae at St. Marks.

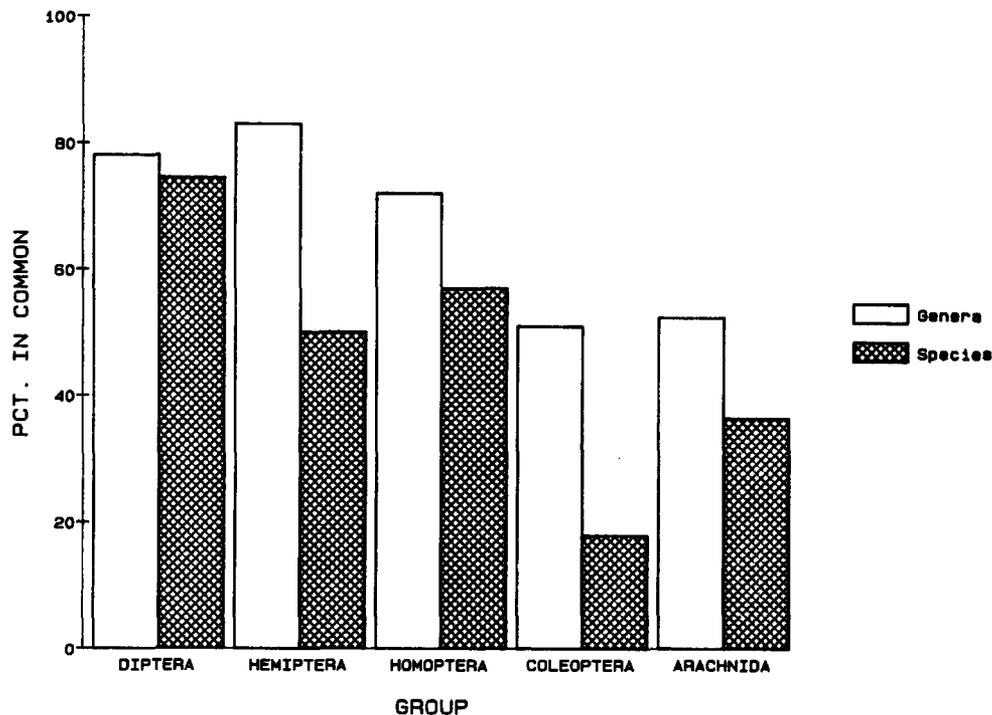


Fig 1. Proportions of the number of species and genera held in common by St. Marks and other North American marshes.

TABLE 1. SPECIES OF DIPTERA IDENTIFIED FROM ST. MARKS MARSHES. LETTERS REFER TO THE 4 HABITAT TYPES: S = *Spartina alterniflora* FRINGE, J = *Juncus roemerianus* MARSH D = *Distichlis spicata* MEADOWS, B = HALOPHYTIC SHRUB ZONE. ONE ASTERISK FOLLOWING THESE LETTERS DESIGNATE THE SPECIES AS "COMMON" (3-10 INDIVIDUALS IN A SINGLE COLLECTION), 2 ASTERISKS AS "VERY COMMON" (10+ INDIVIDUALS), AND NO ASTERISK AS "UNCOMMON" (FEWER THAN 3 INDIVIDUALS).

TAXON	MONTH											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
TIPULIDAE												
<i>Limonia floridana</i> (Osten Sacken)							J	J			D	
Gen. sp. indet.	S										B	
CULICIDAE												
<i>Aedes sollicitans</i> (Walker)			S* J	S J D	S	S B	D*		S* D	S* D B	J* D	
<i>Aedes taeniorhynchus</i> (Wiedemann)					J D			B				
<i>Anopheles atropos</i> Dyar & Knab										S**		
<i>Anopheles bradleyi</i> King				S* J								
<i>Culex salinarius</i> Coquillett										S*		
CERATOPOGONIDAE												
<i>Culicoides furens</i> (Poey)		D			D B				D**	D* J	S J	
<i>Culicoides melleus</i> (Coquillett)		S* J	S* J**	J* B	J* S**		D* J	J* B*	J*	S** J D* B*	S J D B	S* D B
<i>Culicoides mississippiensis</i> Hoffman	D	D J	D J	S J D S*	J					D	J D*	J D*
<i>Dasyhelea grisea</i> (Coquillett)	J								S J			
<i>Dasyhelea</i> sp. 2									D			
<i>Dasyhelea</i> sp. 3	S	J	D		B			S B	D	S J** D* B*	S	
<i>Dasyhelea</i> sp. 4								B		D		D
<i>Forcipomyia</i> sp.			B							D S		
<i>Atrichopogon</i> sp.		D	S		B					S** J** D**	J	B
<i>Bezzia</i> sp.			S* J** D**B	J*							S	
<i>Stilobezzia beckae</i> Wirth					D							

CHIRONOMIDAE

Orthocladus sp. B D J* D J J* D S* D B

Microtendipes anticus (Walker)

J
J*D

Gen. sp. indet.

SCIARIDAE

Bradysia sp. B

SCATOPSIDAE

Gen. sp. indet. J

STRATIOMYIDAE

Brachycara slossonae (Johnson) J*

S* B

Sargus sp. S

TABANIDAE

Tabanus nigrovittatus (Macquart) D D S* J* J B

Chrysops fuliginosus Wiedemann J

Chrysops atlanticus Pechuman S

ASILIDAE

Laphystia litoralis Curran S

S

Laphystia sp. 2 S** B S S*

S* J

EMPIDIDAE

Gen. sp. indet. B

DOLICHOPODIDAE

Pelastoneurus lamellatus Loew B S* J S* D* D*

B
S D

S* D*
B
S** D**

Paracleius alternans (Loew) J S S J S S

PIPUNCULIDAE

Tomosaryella sp. J J S D S* J J B

D* B

OTITIDAE

Chaetopsis apicalis Johnson S J* J* D** S** J** S** J** S** J* S* J S** J* J D* S* J** S J* S* J*

D**B

D** B*

D** B

D* B*

D** B

D* B*

D

D** B

D

D** B

D

D* J

D** J*

Chaetopsis fulvifrons (Macquart) D J S** J* S* J S* J S J S* D* D

D** B

D**

D*

D**

S

B

J

S

J

Chaetopsis aenea (Wiedemann) D S J S* J

S*

S B

D** S*

Gen. sp. indet.

Rey & McCoy: Salt Marsh Diptera

TABLE 1. (CONTINUED)

TAXON	MONTH											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
TEPHRITIDAE												
<i>Tephritis stigmatica</i> (Coquillett)	D	B*	J		B	S J				S D	J	
LAUXANIDAE												
Gen. sp. indet.											D	
LONCHAEIDAE												
<i>Lonchaea</i> sp.			D B									
CANACIDAE												
<i>Canace snodgrassii</i> Coquillett	B										S J	
Gen. sp. indet.	B		S							S** D**	D	B
EPHYDRIDAE												
<i>Dimecoenia fuscifemur</i> Steyskal	J		J D	S* J*	J B				D*	S J	J	D
<i>Dimecoenia spinosa</i> (Loew)					J		S		S* J			
<i>Dimecoenia austrina</i> (Coquillett)		D S	S* J*	S** J	J** D**	S* B*	B J	S B	S* J	D** S**	D S*	J*
<i>Cressonomyia hinei</i> (Cresson)			D	D				J		J** B	J*	
								S** B*		S** D*		
<i>Polytrichophora agens</i> Cresson			S	S	D		J	J		J* B		
<i>Polytrichophora</i> sp. 2				J				J		S**	J S	
<i>Notiphila bispinosa</i> Cresson	S J** B**	S* B	D* J**	S J*	S D B	S	S*	J B	S** J D*	S* J D*	D	S J* B
<i>Clanoneurum americanum</i> Cresson			J	D				S J B*		S*	D*	J
<i>Hydrellia valida</i> Loew			S D J	D	D B	S B		J B		S* J	D B	
<i>Psilopa flavida</i> Coquillett					D							
<i>Psilopa</i> sp. 2											D*	
<i>Leptopsilopa</i> sp. 1		B*		D						D		
<i>Leptopsilopa</i> sp. 2										D		
<i>Ceropsilopa costalis</i> Wirth	D B	S									S* B	S*
<i>Ceropsilopa</i> sp.			D									

TABLE 1. (CONTINUED)

TAXON	MONTH											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
<i>Lispe</i> sp.	B									S*		S
<i>Phaonia</i> sp. 1	B	B		S						S		
<i>Phaonia</i> sp. 2			S J	D	B					S	D	
<i>Phaoniinae</i> gen. sp. indet.					B					D	J	
<i>Musca domestica</i> L.										S		
Gen. sp. indet.		S*									J	
Gen. sp. indet.											J	
SARCOPHAGIDAE												
<i>Sarcophaga johnsoni</i> Aldrich			S	S	D		S B	S		D		
<i>Tricharaea simplex</i> (Aldrich)								S				

ACKNOWLEDGMENTS

The authors wish to thank Red Gidden and Joe White of the St. Marks National Wildlife Refuge for their cooperation during the course of this study. We also wish to thank the following for providing determinations for some of our specimens: L. P. Lounibos and J. R. Linley (Florida Medical Entomology Laboratory); G. W. Byers (University of Kansas); B. A. Harrison (Walter Reed Biosystematic Unit); W. N. Mathis (Smithsonian Institution); and R. J. Gagné, B. V. Peterson, C. W. Sabrosky, F. C. Thompson, W. W. Wirth, and N. E. Woodley, (Systematic Entomology Laboratory, United States Department of Agriculture). Phil Lounibos and John Linley provided many helpful comments on an earlier draft of this manuscript. University of Florida, Institute of Food and Agricultural Sciences Journal Series No. 6418

REFERENCES CITED

- BICKLEY, W. E. AND T. R. SEEK. 1975. Insects in four Maryland marshes. Univ. Maryland Agric. Exper. Sta. Misc. Publ. 870.
- BLANTON, F. S. AND W. W. WIRTH. 1979. The Sand Flies (*Culicoides*) of Florida (Diptera Ceratopogonidae). Arthropods of Florida and Neighboring Land Areas vol. 10. Florida Dept. of Agriculture and Consumer Services, Gainesville.
- DAVIS, L. V. 1978. Class Insecta. Pages 186-220 *In*: An Annotated Checklist of the Biota of the Coastal Zone of North Carolina (R. G. Zingmark, Ed.). Univ. South Carolina Press, Columbia.
- , AND H. E. GRAY. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. *Ecol. Monogr.* 36: 275-95.
- KALE, H. W. 1964. Food of the long-billed marsh wren, *Tematodytes palustris griseus*, in the salt marshes of Sapelo Island, Georgia. *Oriole* 29: 47-61.
- LANE, R. S. 1969. The insect fauna of a coastal salt marsh. M. A. Thesis, San Francisco State College.
- MARPLES, T. G. 1964. A radionuclide tracer study of arthropod food chains in a *Spartina* marsh ecosystem. Ph.D. Dissertation, Univ. of Georgia.
- MCCOY, E. D., AND J. R. REY. 1981a. Terrestrial arthropods of Northwest Florida salt marshes: Coleoptera. *Florida Ent.* 64: 405-11.
- , AND ———. 1981b. Patterns of abundance, distribution, and alary polymorphism among the salt marsh Delphacidae Homoptera: Fulgoroidea) of Northwest Florida. *Environ. Ent.* 6: 285-91.
- REY, J. R. 1981. Ecological biogeography of arthropods on *Spartina* islands in Northwest Florida. *Ecol. Monogr.* 51: 237-65.
- , AND E. D. MCCOY. 1982. Terrestrial arthropods of Northwest Florida salt marshes: Hemiptera and Homoptera. *Florida Ent.* 65: 241-8.
- , AND ———. 1983. Terrestrial arthropods of Northwest Florida salt marshes: Araneae and pseudoscorpiones (Arachnida). *Florida Ent.* 66: 497-503.
- SOUTHWOOD, T. R. E. 1966. *Ecological Methods with Particular Reference to the Study of Insect Populations.* Methuen and Co., London.
- WALL, W. J., JR. 1973. The intertidal sand and salt marsh invertebrate fauna associated with the bloodsucking Diptera of Cape Cod, Massachusetts. *Environ. Ent.* 2: 681-4.

ANTS OF THE ARCHBOLD BIOLOGICAL STATION,
HIGHLANDS COUNTY, FLORIDA
(HYMENOPTERA: FORMICIDAE)

MARK DEYRUP

Archbold Biological Station

P. O. Box 2057

Lake Placid, Florida 33852

and

JAMES TRAGER

Archer Road Entomology Lab

University of Florida

Gainesville, Florida 32611

ABSTRACT

The 102 species of ants known to occur on the Archbold Biological Station in Highlands Co., Florida are listed with annotations on their habitat and microhabitat preferences and timing of nuptial flights. The diversity of the fauna results from the confluence of several biogeographic groups of ants. Several species are endemic to the xeric scrub of central Florida, which was an insular refugium during Pleistocene or Pliocene flooding. About 20 species are exotic, of which 6 have invaded scrub habitats. The invasibility of south Florida to exotic ants and the biogeographic affinities of native ants are discussed.

RESUMEN

Se registran las 102 especies de hormigas ya conocidas de la Estación Biológica Archbold en el condado Highlands en la Florida. Se presentan informaciones sobre el habitat y el microhabitat preferidos y sobre la sazón del vuelo nupcial. La diversidad de esa fauna resulta de la confluencia de varios grupos biogeográficos de hormigas. Algunas especies son endémicas del matorral xérico de la Florida central, que era un refugio insular durante inundaciones de la Pleistoceno o Plioceno. Aproximadamente 20 especies de esta fauna son exóticas, de las cuales 6 han colonizado el matorral xérico. Se trata de la invasibilidad de la Florida meridional por hormigas exóticas y de las afinidades de las biogeográficas de las hormigas nativas.

INTRODUCTION

The Archbold Biological Station (ABS) is a permanent ecological reserve located at the south end of the Lake Wales Ridge in Highlands County, Florida. The main property consists of about 4,377 acres, including an 80-acre lake; there is also a 8-acre tract (Price Memorial Tract) on the north side of Lake Placid.

The ant fauna of the ABS is of special interest for several reasons, one of which is the biogeography of the region. The Lake Wales Ridge is a series of former islands isolated during the Pleistocene or Pliocene flooding of peninsular Florida (Laessle 1968). The ridge is presently characterized by excessively drained sandy soil. Both the history and soil conditions of the area contribute to a relatively high proportion of endemism among species and subspecies of certain groups of plants and animals (Hubbell 1961). The presence or absence of endemic forms of ants is therefore of interest with respect to the biogeography of the region and the biogeography of ants. A second reason for the study is the apparent ecological importance of ants at the ABS. Preliminary obser-

vations suggested that ants are both diverse and abundant in most habitats. An understanding of the ant fauna is a useful step toward the long-term goal of a better understanding of the invertebrate ecology of the ABS. Finally, we regard the ants of the ABS as an important research resource. Our list informs the scientific community about the ants available for study at the ABS.

There have been no intensive surveys of ants in any part of southern Florida; this study provides baseline information that will be useful in documenting the invasion of exotic species and shifts in the ranges of native species.

Several workers have previously studied ants at the ABS or specimens from the ABS. These projects dealt with species of *Formica* (Schneirla 1944), *Conomyrma* (Smith 1944), *Pheidole* (Naves 1985), *Solenopsis (Diplorhoptrum)* (Thompson 1980), *Camponotus* (Walker 1983), and *Paratrechina* (Trager 1984). Current projects include studies of the genera *Pseudomyrmex* (R. Klein) and *Conomyrma* (Trager, in preparation). There have been no previous attempts to compile a complete list of ants of the ABS.

MATERIALS AND METHODS

The ant survey began in December 1980, and continued through the summer of 1984. Four kinds of traps were used. The first was a series of small vials with perforated tops that permit entry to small ants. These vials were baited with commercial canned tuna fish, buried, and left overnight. The second type of trap consisted of small plastic cups baited with canned pet food, set out, and retrieved as soon as they were invaded by ants. Two small malaise traps in a sand pine scrub area were used continuously from June 1983 through 1984 to trap alates. An ultraviolet light was used to trap alates at night. Tullgren extraction was used to obtain ants and associated arthropods from about 300 samples of litter of various types. Ants were also found by searching for entrances in soil and by breaking open logs and twigs. Rocks do not naturally occur at the Archbold Biological Station, and the small number of imported rocks present were not important collection sites.

The vegetation types of the ABS have been classified and mapped by Abrahamson, et al. (1984). The following classification is taken from a vegetation map prepared in 1983 by these authors. The categories SP, NS and MOrr are original.

RS: Southern Ridge Sandhill. Open woodland of south Florida slash pine (*Pinus elliotii* var *densa* Little and Dorman), xerophytic oaks (*Quercus laevis* Walter, *Q. myrtifolia* Willdenow, *Q. chapmanii* Sargent, *Q. geminata* Small), and scrub hickory (*Carya floridana* Sargent). Understory composed of wire grass (*Aristida stricta* Michaux), scrub palmetto (*Sabal etonia* Swingle), and herbs. On well-drained upland soil.

RSt: Southern Ridge Sandhill with turkey oak (*Quercus laevis*).

RSh: Southern Ridge Sandhill with scrub hickory (*Carya floridana*).

SS: Sand Pine Scrub. Dense to widely-scattered stands of sand pine (*Pinus clausa* Chapman) with understory dominated by xerophytic oak and other shrub species or rosemary (*Ceratiola ericoides* Michaux). On well-drained deep sandy soil.

SSr: Sand Pine Scrub with rosemary (*Ceratiola ericoides*).

SSo: Sand Pine Scrub with oak (*Quercus* spp.)

SF: Scrubby Flatwoods. Low shrubby growth of xerophytic oaks (*Quercus inopina* Ashe, *Q. chapmanii*, *Q. geminata*) and palmettos (*Serenoa repens* Bartram and *Sabal etonia*) typically with widely-scattered south Florida slash pines and often sand pines. On well-drained sandy soil.

SFi: Scrubby Flatwoods with inopina oak (*Quercus inopina*).

SFl: Scrubby Flatwoods with sand live oak (*Quercus geminata*).

FL: Flatwoods. Open stands of south Florida slash pine of extremely low to moderate densities. Understory and ground cover of varying combination of grasses, herbs, saw palmetto (*Serenoa repens*), and shrubs (*Lyonia* spp., *Vaccinium* spp., *Befaria racemosa* Ventnat, *Ilex glabra* Linnaeus). On soils with organic hardpan restricting drainage.

FLw: Flatwoods with wiregrass (*Aristida stricta*).

FLc: Flatwoods with cutthroat grass (*Panicum abscissum* Swallen).

FLg: Flatwoods with gallberry (*Ilex glabra*) and fetterbush (*Lyonia lucida* Lamarck).

FLp: Flatwoods with saw palmetto (*Serenoa repens*).

BH: Bayhead. Dense forests of broadleaved evergreen trees (*Gordonia lasianthus* Linnaeus, *Persea borbonia* Linnaeus, *Magnolia virginiana* Linnaeus) on muck soil subject to periodic flooding. Undergrowth of shrubs, including wax myrtle (*Myrica cerifera* Linnaeus), dahoon holly (*Ilex cassine* Linnaeus), highbush blueberry (*Vaccinium corymbosum* Linnaeus), and abundant ferns (*Osmunda* spp.).

SP: Seasonal Pond. Open seasonally flooded depressions, usually with distinctly zoned vegetation dominated by grasses or shrubby *Hypericum edisonianum* Small and often bordered by a dense band of saw palmettos. Soils ranging from sandy to highly organic.

SPb: Seasonal Pond with broomsedge (*Andropogon brachystachys*).

SPc: Seasonal Pond with cutthroat grass (*Panicum abscissum*).

SPh: Seasonal Pond with *Hypericum edisonianum*.

MO: Man-modified.

MOl: Man-modified, landscaped, park-like.

MOr: Man-modified, roadside.

MOrr: Man-modified, railroad.

NS: *Nyssa biflora* Walter swamp.

All records listed below have associated pinned and labelled voucher specimens. These specimens have been divided between the reference collection of the Archbold Biological Station and the Florida State Collection of Arthropods, Gainesville.

ANNOTATED LIST OF SPECIES

The species listed below are arranged according to their order in the Formicidae part of Catalog of Hymenoptera in America North of Mexico (Smith 1979). We have refrained as much as possible from innovations in nomenclatural usage. A number of species have manuscript names that have not been published; in some cases the names were presented in theses that may not be published in the near future. In such cases we do not list the unpublished name, but give the appropriate unpublished name in the annotations. Subspecific names are used primarily when there is reason to believe that the subspecies will eventually be given specific rank. Abbreviations of vegetation type are explained above. Unless otherwise indicated, malaise trap records are from the SSo habitat. Habitat information is presented in Table 1.

Neivamyrmex Borgmeier

Of the three species of *Neivamyrmex* found in Florida only *N. opacithorax* is known from southern Florida (Watkins 1976). Army ants escaped notice at the Archbold Biological Station until 1983, and workers have never been seen in the open. Possibly, the desert-like conditions of upland areas of southern Florida forces army ants to become nocturnal or exclusively subterranean; Creighton (1950) speculates that arid conditions explain the cryptic nature of army ants in the southwestern United States. Flightless

TABLE 1. COLLECTION DATA BY HABITAT. NUMBERS REFER TO NUMBER OF OCCASIONS A SPECIES WAS TAKEN IN A HABITAT. SEE METHODS FOR HABITAT CATEGORIES.

	RSt	RSh	SSr	SSo	SFl	SFi	FL	FLw	FLc	FLg	FLp	BH	SPb	SPc	SPh	Mo	MOl	MOr	MOrr	NS
<i>Amblyopone pallipes</i>	3	12		3						1		1	1							
<i>Aphaenogaster ashmeadi</i>	2										1	1								
<i>Aphaenogaster flemingi</i>				1										3		2				
<i>Aphaenogaster floridana</i>							1			1	1									
<i>Aphaenogaster texana</i>	2											9								
<i>Aphaenogaster treatae</i>					2															
<i>Brachymyrmex depilis</i>	1	4	2	10	3	3				2	1	1	4		2		1			
<i>Brachymyrmex obscurior</i>																		3		
<i>Camponotus abdominalis floridanus</i>				1		2					1	3			4		1		1	
<i>Camponotus castaneus</i>	3	1		1		1						2					1			
<i>Camponotus impressus</i>		1		3								1				1	4			1
<i>Camponotus rasilis</i>																				
<i>Camponotus socius</i>																				
<i>Camponotus tortuganus</i>	1		1	1						1	1									
<i>Camponotus nearcticus</i>	2			1		1	1													
<i>Camponotus pavidus</i>												1					1			2
<i>Cardiocondyla emeryi</i>				1			1						1	1	1		8			
<i>Cardiocondyla nuda</i>																	8			
<i>Cardiocondyla venustula</i>																	2			
<i>Cardiocondyla wroughtonii</i>																1				
<i>Conomyrma flavopecta</i>			1	1	1															
<i>Conomyrma smithi</i>	1												2							
<i>Conomyrma</i> sp. 1	2	2	1	2	7										1					
<i>Conomyrma</i> sp. 2	1			2	1					1	2		2	4	6	2	8		1	
<i>Conomyrma</i> sp. 3	4	1		2				2		2			1	1						
<i>Crematogaster ashmeadi</i>	2				5	1						1					6		1	1
<i>Crematogaster clara</i>	2			5						1			1	1				1	1	
<i>Crematogaster minutissima</i>																				1

TABLE 1. (CONTINUED)

	RSt	RSh	SSr	SSo	SFl	SFi	FL	FLw	FLc	FLg	FLp	BH	SPb	SPc	SPh	Mo	MOI	MOr	MOr	NS
<i>Crematogaster</i> sp.				2				1					1	1				1		
<i>Cyphomyrmex fuscus</i>	1				1							1					2		1	
<i>Cyphomyrmex minutus</i>	2											2					3			1
<i>Discothyrea testacea</i>		1				1					1		1		1					1
<i>Eurhopalothrix floridana</i>																1				
<i>Formica archboldi</i>												1		9		1				
<i>Formica pallidefulva</i>	1	1			2															
<i>Hypoponera inexorata</i>	1	4		2	2					1	1									
<i>Hypoponera opaciceps</i>	1																4		2	
<i>Hypoponera opacior</i>	6	8	3	5	3	1	2		1	1	2	9	1	3	2		2		1	
<i>Hypoponera punctatissima</i>		1				2						2	1	1			3		1	1
<i>Iridomyrmex pruinosus</i>		2	6		10									4			1	1	1	
<i>Leptothorax elongata manni</i>																				
<i>Leptothorax pergandei floridanus</i>	3	3			2									2						
<i>Leptothorax texanus</i>	2		1		1															
<i>Leptothorax wheeleri</i>	1																			
<i>Monomorium floricola</i>																	3			
<i>Monomorium pharaonis</i>																				
<i>Monomorium viridum</i>	2	4	1	2	10				1	2			7	1	1		1		2	
<i>Myrmecina americana</i>												1								
<i>Neivamyrmex opacithorax</i>	1																			
<i>Ochetomyrmex auropunctatus</i>	1															2	2			
<i>Odontomachus brunneus</i>								1		3	2	6	1	4	2		1		2	1
<i>Odontomachus clarus</i>	3	1		6	3	1					1		1		4					
<i>Pachycondyla stigma</i>	1		1	3					1	1	3	2	1							1
<i>Paratrechina arenivaga</i>	1	1		1	2	1					1			2						
<i>Paratrechina bourbonica</i>																2	1			1
<i>Paratrechina concinna</i>														1	2					
<i>Paratrechina faisonensis</i>					1							12								

Florida Entomologist 69(1)

March, 1986

TABLE 1. (CONTINUED)

	RSt	RSh	SSr	SSo	SFl	SFi	FL	FLw	FLc	FLg	FLp	BH	SPb	SPc	SPh	Mo	MOl	MOr	MOrr	NS
<i>Solenopsis</i> sp.	12	2	2	12	5	3				4	4	10		8	3		1		1	
<i>Strumigenys eggersi</i>	4	14		9	2	2					3						5			1
<i>Strumigenys louisianae</i>		1	1																	
<i>Strumigenys rogeri</i>		2			1	1				1	1	8	1							
<i>Tapinoma litorale</i>				1							2									
<i>Tapinoma melanocephalum</i>		1									1					2	2		1	
<i>Tetramorium bicarinatum</i>											2									
<i>Tetramorium simillimum</i>						1										1	13			
<i>Trachymyrmex septentrionalis</i>	2	4	2	3	1							1								1
<i>Trichoscapa membranifera</i>																1				1
<i>Xenomyrmex floridanus</i>	1		5									1								1

queens restrict the dispersal of army ants; water barriers may have prevented the other two species of army ants from reaching southern Florida. We collected *N. texanus* Watkins on the Lake Wales Ridge in Avon Park, about 54 miles north of the Archbold Biological Station.

opacithorax (Emery). Workers in nest of *Paratrechina phantasma* in firelane. Males were collected in malaise traps; the flight period was concentrated in September and October both years. Total individuals in 1983-4 were grouped as follows: Aug.:3; Sept.:25; Oct.:24; Nov.:3.

Amblyopone Erichson

Smith (1979) does not include Florida in the range of either of the two eastern species of *Amblyopone*, but *A. pallipes* has been reported from Welaka (Van Pelt 1958) and Dunedin (M. R. Smith 1930).

pallipes (Haldeman). At base of dead and live pines; *Quercus myrtifolia* litter; *Q. geminata* litter; *Q. laevis* stump; hickory litter. Males were collected in malaise traps. In 1983, out of 39 males, 22 were captured in Aug. and Sept., but there was no late summer increase in captures in 1984.

Platythyrea Roger

punctata (Smith). At the base of live magnolia; under bark of suspended dead branch; on rotten stump. Males in malaise traps in Sept.-Nov.

Proceratium Roger

croceum (Roger). In rotten pine log. Males in malaise traps in June-Aug. Not previously reported south of Putnam Co. (Van Pelt, 1958).

Discothyrea Roger

testacea (Roger). In deep pine litter; at base of live pine; in dead palmetto trunk; in *Andropogon* tussock.

Pachycondyla Smith

stigma (Fabricius). In rotten pine wood; under bark of dead pine; under bark of dead *Gordonia*, in rotten *Gordonia*, in litter at base of *Lyonia ferruginea*. Alates from nests in Sept., Dec. Males in malaise traps in SFi in June.

Hypoponera Santschi

inexorata (Wheeler). In pine litter, hickory litter, *Quercus chapmanii* litter, turkey oak litter; rosemary litter; litter of *Befaria racemosa* leaves.

opaciceps (Mayr). Under railroad ties; in lawn thatch; pine litter, in *Melaleuca* log; in *Quercus laevis* litter. Alates in flight in June, Sept.-Feb. From the continuously monitored malaise traps 20 specimens (out of a total of 24) are from the months Oct.-Dec., suggesting a late fall flight season.

opacior (Forel). In pine litter; rotten pine; *Quercus geminata* litter; rotten oak; oak litter; hickory litter; cutthroat tussock; under dead *Serenoa repens*; *Quercus chapmanii* litter; pine-sweetbay litter; magnolia litter; wire grass litter; broomsedge tussock; *Quercus myrtifolia* litter; flying squirrel nest box; grape-oak litter. Alates in flight June-July, Oct.-Dec. Not previously reported south of Putnam Co. (Van Pelt 1958); we have collected specimens from several sites south of the Archbold Biological Station, including Key Largo.

punctatissima (Roger). In cutthroat tussock, broomsedge tussock, base of dead pine; base of live pine; base of *Nyssa biflora*; under dead branch on ground; tree hole in *Quercus laurifolia*; in rotten pine; in rotten *Melaleuca*; under fallen post.

Leptogenys Roger

elongata manni Wheeler. No workers seen from ABS. Males in malaise trap July-Dec. In both 1983 and 1984 the majority of specimens (29 out of 45) were collected in Oct. Taxonomic note: Trager (in preparation) will show that the Florida *Leptogenys*, long considered a subspecies of the Texas species, *L. elongata*, is in fact a distinct species.

Odontomachus Latreille

There are apparently three species of *Odontomachus* in Florida. The taxonomy of these species will be discussed in a separate paper. We use the name *O. brunneus* somewhat differently than Brown in his 1976 revision of the genus, in that we consider *O. ruginodis* (found in Dade and Monroe counties to the south of ABS) a distinct species.

brunneus (Patton). At base of live pine, in cutthroat tussock, under dead pine; nest in rotten pine log, base of *Nyssa biflora*, in broomsedge tussock, under dead palmetto. Alates in nest in Sept.; alates at light May, June, Dec.

clarus Roger. In broomsedge tussock; at base of oak; in *Befaria racemosa* litter; under log; in stomach of armadillo. Males in malaise traps: this species was the most abundant ant in malaise trap samples. More than 2,000 specimens were collected during the summer and fall of 1983. The general flight pattern is several large flights from late July through November.

ruginodis Wheeler. We have not seen *ruginodis* at ABS, but a male captured in September 1979 is deposited in the Florida State Collection of Arthropods in Gainesville.

Pseudomyrmex Lund

There are six species of this genus living on the Archbold Biological Station, according to Ward's 1985 revision of the genus. Three are similar-appearing yellow species whose coexistence in Florida was not recognized by Creighton (1950) or Smith (1979).

cubaensis Forel. In twig of *Callicarpa americana* MOI; on picnic table MOI; alates Nov., Dec., and Jan. Ward (1985) has shown that this species is distinct from *elongatus* and is more widely distributed in Florida.

ejectus (F. Smith). On *Quercus laurifolia*; on *Myrica cerifera*; nest in dead grape vine; nest in dead weed stalk; nest in twig of *Callicarpa americana* in flying squirrel nest box. Alates in nest in Mar., at ultraviolet light in Oct., Mar., June.

elongatus (Mayr). On *Myrica cerifera*; nest in dead grape vine.

mexicanus (Roger). On trunk of pine; on flower of *Ilex cassine*; making hole and robbing nectar from flower of *Vaccinium corymbosum*; at tuna bait on pine; nest in *Sambucus* twig; nest in stem of *Callicarpa americana*; nest in pine twig; nest in dead grape vine. Alates in nest Oct., alates in flight in May-July, Oct.

pallidus (Smith). Several nests in broomsedge culms; in stem of *Lacnanthes caroliniana*; in stem of *Smilax*. Alates in flight Oct.-Dec.

seminole Ward. Nests in broomsedge culms; on flower of *Ilex cassine*; in stem of *Lacnanthes caroliniana* (Lamarck). Alates in nest in Jan., Feb., Nov. This species may be distinguished from *P. delicatulus* and *P. pallidus* by the following characters: head of worker in profile with distance between eye and upper edge of head about equal to the malar space; worker with a pair of faint black spots on the first gastral tergite; queen more than 6 mm in length; male genitalia not triangular in profile.

simplex (F. Smith). On twig of pine; on trunk of dying pine; on twig of *Persea humulis*; on *Myrica cerifera*; nest in culm of broomsedge. Alate in flight in Oct.

Pogonomyrmex Mayr

badius (Latreille). On bare sand in open areas. Alates in flight in June-July. At the Archbold Biological Station males of this species are entirely reddish brown, not bicolored (blackish brown with light brown gaster) as they are elsewhere. Mating between

sibs at the nest entrance may be the rule in this population.

Aphaenogaster Mayr

ashmeadi (Emery). In deep pine litter; at pet food bait; at base of pine stump. Not previously collected south of Pasco Co. (Carroll 1975).

flemingi (Smith). In dry cutthroat seasonal pond; nest in opening, under grass clump, near Lake Placid; in stomach of armadillo. Vegetation types: SPc (3), MO (2), SSo (1). Not previously collected south of Alachua Co. and Putnam Co. (Carroll 1975).

floridana (Smith). Nests at edge of sand road. Not previously reported south of Alachua Co. (Carroll 1975).

texana (Emery). At base of pine; at base of *Gordonia lasianthus*; at pet food baits; nest in rotten pine log; nest in rotten *Melaleuca* log. Carroll (1975) recognizes this species as *A. carolinensis* Wheeler, elevating Wheeler's varietal name to species rank. We use the name *texana* because Carroll's work has not yet been published.

treatae (Forel). Under *Quercus inopina*; nest under *Q. inopina*. Not previously reported south of Polk Co. (Carroll 1975).

Pheidole Westwood

Pheidole adrianoi Naves. At tuna bait; at pet food bait; at cookie crumbs; in open sand; under *Quercus inopina*; under *Ximenia americana* Linnaeus; under *Licania michauxii* Prance; at edge of drive; prey of *Brachynemurus* sp. Alates at ultraviolet light in June.

dentata (Mayr). At pet food baits; base of pine; on palmetto leaf; on cement walk; under *Quercus chapmanii*, in pine litter; base of *Gordonia lasianthus*; under bovine dung; *Quercus myrtifolia* litter, *Carya floridana* litter; at base of *Nyssa biflora*; in stomach of armadillo. Alates at light in June.

dentigula Smith. At base of live pine; in dead pine; *Lyonia* litter; oak-pine litter; hickory litter; *Quercus myrtifolia* litter; *Q. chapmanii* litter; *Q. laevis* litter; palmetto-pine litter; pine litter, *Ligustrum* litter; hollow in live pine; base of *Gordonia lasianthus*. Alates at light in June.

floridana Emery. In hickory litter; *Quercus geminata* litter; *Q. myrtifolia* litter; at tuna bait; at pet food bait; under bark of dead pine; at base of live pine; cutthroat tussock; broomsedge tussock; in lawn; in rotten log; palmetto-pine litter; pine litter; *Ceratiola* litter; *Gordonia* litter; Magnolia litter; *Nyssa biflora* litter; in dead palmetto trunk. Alates at ultraviolet light in June.

metallescens Emery. In hickory litter; *Quercus chapmanii* litter, *Lyonia* litter; wire grass litter; at tuna bait; at pet food bait; at rolled oats bait. Alates in malaise trap in July.

moerens Wheeler. On pavement by ABS building; in *Andropogon* tussock by Lake Placid.

morrissi Forel. At tuna bait; at pet food bait; at base of live *Pinus elliottii*; in *Andropogon brachystachys* tussock; nest in open gravel along railroad; in sandy firelanes; taking nectar from *Euthamia minor* (Michaux).

littoralis Cole. Nests (12 seen) in open sand of fire lanes; only one nest seen in vegetation (SSr). Taxonomic note: Naves (1985) in his monograph on Florida *Pheidole* gives this form specific rank.

Cardiocondyla Emery

emeryi Forel. At pet food bait; on live pine; in lawn litter; dead specimen on back of chrysopterid larva; at edge of lake; in bay twig; in pine twig.

nuda (Mayr). At pet food bait; in lawn. Alates in flight in July, Oct., Dec.

venustula Wheeler. Lake edge; edge of lawn.

wroughtonii (Forel). Lake edge.

Crematogaster Lund

ashmeadi Mayr. In dead twig of *Rhus copallina*; in dead branch of *Pinus clausa*; in dead twig of hickory; in *Eupatorium* stem; in dead *Quercus laevis*; in dead *Lyonia ferruginea*; in dead leaves of large *Tillandsia*. Alates in flight in Apr., June-Aug., Oct., Dec.; alates in nest in Oct.

clara Mayr. In dead *Hypericum edisonianum*; in rotten log; on flower of *Opuntia compressa*; on grasses; in grass stem; in dead twig of *Pinus elliottii*.

minutissima Mayr. In rotten *Melaleuca* log; litter at base of *Nyssa biflora*. Alates at ultraviolet light in June.

Crematogaster sp. An undescribed species resembling *C. ashmeadi* in the following characters: small size; short, thick propodeal spines; a single erect hair on each thoracic humerus; short appressed pubescence on the head. Unlike *C. ashmeadi*, this species has clear reddish-yellow head and thorax, contrasting sharply with the blackish gaster. All colonies found to date were in pine trees, in contrast with *C. ashmeadi*, which nests in a variety of situations.

Monomorium Mayr

floricola (Jerdon). On *Morus rubra*; on *Clerodendrum*; in twig of *Callicarpa americana*.

pharaonis (Linnaeus). Abundant in Archbold Biological Station buildings.

viridum Brown. At pet food bait; in open sand of fire lane; in gravel along railroad; tending aphids on *Palafoxia*; on *Opuntia compressa*; on *Clerodendrum* flowers. Alates at ultraviolet light in June.

Xenomyrmex Forel

floridanus Emery. In *Sambucus* twig; in hickory twig; in *Pinus clausa* twig; in malaise traps; on table under *Quercus laurifolia*. Alates in malaise trap in Oct. and Dec.

Solenopsis Westwood

carolinensis Forel. Under log by railroad; in nest of *Monomorium viridum* by roadside.

geminata (Fabricius). In wet sand near seasonal pond; in gravel along railroad; along edge of lake. Alates at ultraviolet light in Apr., May, Oct.; alates in nest in July. This species occurs in red and black color phases. Only the red form was found on the main Archbold Biological Station property, but the black form occurs in moist situations near the edge of the *Nyssa* swamp on the Lake Placid property.

globularia (Smith). At pet food bait; in rotten pine log; in dead palmetto stump in fire lane.

invicta Buren. At pet food bait; along roadside; in stomach contents of armadillo. Alates in malaise traps in Jan., Feb., May-Sept., Dec.; alate in stomach of armadillo in Jan.

nickersoni Thompson. In rotten pine log; at base of large slash pine; *Andropogon* tussock; sand pine litter; cutthroat tussock; *Quercus laevis* litter; hickory litter; pine and palmetto litter; *Ceratiola* litter. This is a recently described species (Thompson 1982) not included in the Hymenoptera catalog.

pergandei Forel. Under fence post; under rock; in nest of *Monomorium viridum*; in nest of *Aphaenogaster floridana*; in gravel along railroad. Alates in nest in Sept.

picta Emery. In dead branch of *Pinus elliottii*; in dead branch in crown of *Pinus clausa*; in nest box of flying squirrel; in "trash pile" on back of chrysopid larva.

tennesseensis Smith. In pine litter; in palmetto and pine litter; in hickory and pine

litter; at base of dead pine; in *Quercus geminata* litter; in *Q. virginiana* litter; in *Q. myrtifolia* litter; in *Q. laevis* litter; in rotten pine log; in hickory litter; in dead palmetto stem; *Lyonia ferruginea* litter; cutthroat tussock; *Vaccinium* sp. litter; *Schinus* litter; magnolia litter; wire grass litter; *Ceratiola* litter.

Solenopsis sp. In cutthroat tussock; in palmetto litter; *Lyonia ferruginea* litter; wire grass litter; pine litter; *Ceratiola* litter; palmetto and pine litter; in rotten pine log; in pine stump; magnolia litter; loose bark at base of pine; *Quercus laevis* litter; *Q. myrtifolia* litter; *Q. geminata* litter; *Befaria racemosa* litter; under log near railroad; hickory litter. This small yellow *Diplorhoptum* resembles *S. carolinensis*, but has short sparse hair on the vertex and a conspicuous glabrous midline on the front of the head. This species may prove to be a southern variant of *S. texana* Emery.

Leptothorax Mayr

pergandei floridanus Emery. At pet food bait; in hickory litter; in oak litter; in pine litter; nest in buried dead *Lyonia* stem; nest in buried hickory nut. Alates at ultraviolet light in May.

texanus Wheeler. At tuna bait; at pet food bait.

wheeleri Smith. On dead *Pinus elliottii*.

Myrmecina Curtis

americana Emery. In rotten pine log.

Tetramorium Mayr

bicarinatum (Fabricius). On flowers of *Erechtites*; nest in stump of bay tree. Taxonomic note: This species was long known as *T. guineense*. Bolton (1977) has shown that the type of *guineense* is in fact a *Pheidole* and that *bicarinatum* is the next available name.

simillimum (Smith). At pet food bait; on fallen orange; at base of *Pinus clausa*; at base of *Pinus elliottii*; on *Morus rubra*; in lawn; at base of *Quercus laurifolia*, under fence post; in "trash pile" on back of chrysopid larva; at edge of lake.

Ochetomyrmex Mayr

europunctatus (Roger). Under raccoon feces; under fence post; at lake edge. Alates in flight in June-Aug., Oct.-Dec.

Strumigenys Smith

The distribution of species of *Strumigenys* in Florida is discussed by Deyrup and Trager (1984).

eggersi Emery. *Pinus elliottii* litter; *P. clausa* litter, base of standing dead pine; pine and hickory litter; hickory litter; *Ligustrum* litter; *Schinus* litter; *Quercus laevis* litter; *Q. laevis* stump; *Q. geminata* litter; *Q. laurifolia* litter; *Q. myrtifolia* litter; *Q. virginiana* litter; *Nyssa biflora* litter; *Ceratiola ericoides* litter; dead palmetto stem; base of live palmetto.

louisianae Roger. In *Quercus geminata* litter; in *Pinus clausa* litter.

rogeri Emery. In litter at base of *Pinus elliottii*; under rotten pine; pine and hickory litter; *Quercus chapmanii* litter; magnolia and *Gordonia* litter; at base of dead magnolia.

Smithistruma Brown

All species of *Smithistruma* are scarce at the Archbold Biological Station, and apparently confined to the more mature areas of a hickory ridge. Mature sand pine scrub areas, which are more mesic than the hickory ridge and have more pockets of deep litter, did not provide any specimens of *Smithistruma*.

clypeata (Roger). Oak-hickory litter. This not previously reported south of Putnam Co. (Van Pelt 1958).

creightoni (Smith). In *Quercus geminata* litter; in *Pinus clausa* litter. Not previously reported south of Putnam Co. (Van Pelt 1985).

dietrichi (Smith). In hickory litter. Not previously reported south of Putnam Co. (Van Pelt 1958); we have collected specimens in Dade Co.

talpa (Weber). In *Quercus geminata* litter; in hickory litter; in *Vaccinium myrsinites* litter; in oak and hickory litter. Not previously reported south of Putnam Co. (Van Pelt 1958).

Trichoscapa Emery

membranifera (Emery). In moist disturbed area; in *Nyssa sylvatica* litter.

Quadristruma Brown

emmae (Emery). In *Pinus elliottii* litter; in *P. clausa* litter; under dead *P. elliottii*, in *Quercus geminata* litter; in *Q. chapmanii* litter; in *Q. laevis* stump; in *Q. myrtifolia* litter; in *Q. laevis* litter; in cutthroat tussock; in *Andropogon* tussock; in dead palmetto stem; in *Ligustrum* litter; in hickory litter; in wire grass litter; in *Gordonia* litter; under *Melaleuca* log; in *Nyssa sylvatica* litter. The single published U. S. record of this species is from Homestead (Smith 1979). *Q. emmae* is well established in several sites we have visited in Dade Co. and Monroe Co.; we have not collected it north of the Archbold Biological Station.

Eurhopalothrix Brown and Kempf

floridana Brown and Kempf. In dead palmetto stem. Previously known only from Highlands Hammock State Park (Brown & Kempf 1960). In addition to a collection from the Archbold Biological Station, we have collected this species in Dade Co. (Matheson Hammock), Monroe Co. (Key Largo), Marion Co. (Ocala National Forest), and Alachua Co. (Gainesville). This species is possibly a tropical exotic (Brown & Kempf 1960). Specimens have also been collected in Tamaulipas, Mexico (W. L. Brown, personal communication).

Cyphomyrmex Mayr

The *rimosus* group of this genus is currently undergoing revision by Snelling, who provided the names used here.

fuscus Emery. In rotten log; along lake shore, on mud; in abandoned fire ant mound; under board. Alates in flight in May, June, Oct.-Dec. This species has long been confused with *C. minutus*, but is clearly distinguished by larger size, darker color, sharp and prominent thoracic protuberances. This species is known from southern South America, and has not previously been reported from the United States, though we have found it to be common throughout Florida.

minutus Mayr. In hickory litter; at base of dying *Pinus clausa*; in *Nyssa biflora* litter; in grass tussock on lake shore; in fern litter; under fence post; in *Ligustrum* litter; under palmetto stump. Alates in flight in June, Oct.; alates in nest under fallen fence post in Jan. This species is not found in northern Florida.

Trachymyrmex Forel

septentrionalis (McCook). In hickory leaf litter; nest in open fire lane; at base of dying *Pinus clausa*; under *Lyonia ferruginea*; at pet food bait; in lawn. Alate in malaise trap in June, Nov.; aggregation of males (on scrub oak) being eaten by scrub jays in July.

Iridomyrmex Mayr

There is widespread verbal agreement that the species below (*I. pruinosus*) should be transferred to *Forelius*.

pruinosus (Roger). At pet food bait; nests in open sand. Alates at ultraviolet light in June.

Conomyrma Forel

The genus *Conomyrma* presents special taxonomic problems for our study: of the five species at the Archbold Biological Station three are undescribed and the names of the other two have not been applied consistently. There are descriptions of the undescribed species in an unfinished manuscript by Trager. We will not refer to the manuscript names here because of the possibility of creating further taxonomic tangles should other names be chosen for these species.

flavopecta (Smith). Nests in open sand. Alates in nest: 11-VII-84. This species may be recognized by its striking coloration: the head and gaster are black, the thorax bright orange. The name *flavopecta* has been applied incorrectly to the more widely distributed *Conomyrma* sp. 2.

smithi Cole. Sharing nest with *Conomyrma* sp. 2. Vegetation types: SPb (2), RSt (1). *C. smithi* is a varietal name (Cole 1936), appearing in the 1979 catalog as a synonym of *C. insana* (Buckley): *Dorymyrmex pyramicus* var. *smithi*. We cannot follow our conservative policy and refer to this species as a form of either *insana* or *pyramicus*, because neither name refers correctly to any species found in our area. *C. smithi* is recognized by its solid dark-brown color. The antennal scapes are relatively short and the head relatively broad compared with other *Conomyrma* species in south Florida. This species is a temporary nest parasite of *Conomyrma* sp. 2.

Conomyrma sp. 1. Nests in open sand; at pet food bait. This yellow species is unusually elongate and slender. No published names have been applied to this species, which is known only from the Archbold Biological Station.

Conomyrma sp. 2. Nests in sand around grasses, especially in man-modified habitats; at pet food bait; on *Euthamia minor*, in lawn; on flower of *Ilex cassine*. Alates at ultraviolet light in Sept.-Nov., May. Alates in nest in July. There is some variation in color and in queen size, and we may be dealing with more than one species. Specimens in collections are usually labelled *C. pyramicus* or *C. flavopecta*.

Conomyrma sp. 3. Nests in paths in scrub; at pet food bait. Alates in malaise trap in June and July. This small species is easily identified by the pronounced dorsal angle of the mesonotum and the shining, hairless gaster. In the field this species bears a remarkable resemblance to *Pheidole morrisi* and light forms of *P. dentata*. No published names have been applied to this species.

Tapinoma Foerster

litorale Wheeler. In dead grape vine; in dead *Smilax* vine; in dead hickory twig.

melanocephalum (Fabricius). In base of palmetto; on *Clerodendrum* flowers; on *Baccharis*; on flower of *Ilex cassine*; in rotten log.

Brachymyrmex Mayr

depilis Emery. In rotten log; in *Pinus clausa* litter; in *P. elliotti* litter; in palmetto and pine litter; in *Quercus geminata* litter; in cutthroat tussock; in *Andropogon* tussock; in dead oak branch on ground; in *Lyonia ferruginea* litter; in *Befaria racemosa* litter; in pine stump; in dead palmetto stem; in hickory litter; under bear feces; in *Vaccinium* litter. Alates in flight in June-Aug., Dec.

obscurior Forel. On *Baccharis*; in grass along roadside.

Camponotus Mayr

abdominalis floridanus (Buckley). In hollow stick; under log; in dead palmetto trunk; under pieces of bark below standing dead pine; tending membracids on palmetto flower stalk; tending aphids on *Palafoxia*; on flowers of *Ilex cassine*; on extrafloral nectaries of *Crotolaria mucronata*; on *Erechtites* flower. Although this is the commonest *Camponotus* on the Archbold Biological Station, no flights of alates have been

observed. In other parts of Florida, the flights occur shortly after sunset during the summer rainy season.

castaneus (Latreille). In hickory litter; in *Pinus elliottii*; feeding on fallen tangerine; tending aphids on *Palafoxia*; on flower of *Erechtites*. Alates at ultraviolet light in Jan.-May, Dec. This species has nocturnal mating flights in late winter and early spring.

impressus (Roger). On flower of *Ilex cassine*; on large laurel oak; in hickory twig; in grape vine; in malaise trap. Alates at ultraviolet light in Apr.-June.

nearcticus Emery. On large *Pinus elliottii*; under bark of *P. elliottii*; in squirrel nest box on pine; on large *P. clausa*. Nests at the Archbold Biological Station and elsewhere in Florida are always in large pine trees.

pavidus Wheeler. This species is apparently the form described by Wheeler as *C. fallax rasilis* var. *pavidus*. The form is considered a distinct species (*C. pavidus*) by Blum (1981). This form differs in morphology and nest site from the sympatric *Camponotus* sp. 1 and *C. sayi* (= *C. rasilis* Wheeler). In stump of *Quercus laevis*; on flower of *Erechtites*; in dead bay twig; in small branch of *Q. laurifolia*. Alate at ultraviolet light in Apr.

rasilis Emery. Alates at light in Jan. and Mar. This has been considered a form of *C. sayi* but is here considered a separate species. A recent study of mandibular gland compounds supports the separation of this form (Blum 1981), but the taxonomy of the complex has not been formally reviewed.

socius Roger. Specimens were collected in 1965 on the Archbold Biological Station, but this large, conspicuous, day-foraging ant was not seen during the present study. We conclude that this species is rare or extinct on the Archbold Biological Station. The reduction of open ground in the sandhill habitats of the Archbold Biological Station, due to the exclusion of fire, might have contributed to the disappearance of this species.

tortuganus Emery. In dead pine; under log; in dead saw palmetto; under bark of standing dead pine. Alates at ultraviolet light in Sept.-Nov.

Paratrechina Motschulsky

Trager (1984) recently described 5 new species from the United States, of which 3 occur at the Archbold Biological Station.

arenivaga (Wheeler). At pet food baits; nests in open fire lane in small clearings, and near seasonal ponds. Alates in nest in Oct., Dec., Jan.

bourbonica (Forel). On *Sida cordifolia*; in tree hole in *Quercus laurifolia*; under bark of dead bay tree. Alates in nest in Dec.; alates in flight Oct.-Dec.

concinna Trager. In rotten log in pond; under pine bark on ground. Alates in nest in Dec.

faisonensis (Forel). In *Pinus elliottii* litter; in magnolia litter; in magnolia-Gordonia litter; at pet food bait. This species, synonymized under *arenivaga* by Creighton (1950), was recently shown (Trager 1984) to differ from *arenivaga* in ecology, color, and male genital characters.

longicornis (Latreille). On pavement by buildings; under laurel oak.

phantasma Trager. Nests in open sand. Alates in nest Oct. and Dec. This species is most abundant in Highlands County, with only a few scattered populations to the north.

vividula (Nylander). Under *Melaleuca* log. Vegetation type: MO (1).

wojciki Trager. In *Andropogon* tussock; in cutthroat tussock; *Pinus elliottii* litter; in rotten log; in large fallen bromeliad; under *Cladonia* mat; in *Vaccinium* litter; in hickory litter; in *Quercus myrtifolia* litter; at pet food bait. Alates in nest Jan.-Mar., Sept.-Nov.

Formica Linnaeus

archboldi Smith. In cutthroat tussock; in *Andropogon* tussock. Alate in flight in May.
pallidefulva Latreille. At pet foot bait. Alates at light in June.

SUMMARY AND DISCUSSION

BIOGEOGRAPHY OF ARCHBOLD BIOLOGICAL STATION ANTS

With 102 species of ants, the Archbold Biological Station has, by a considerable margin, the most diverse known ant fauna from any single locality in the United States. One reason for the richness of the ant fauna is the great diversity of habitats occurring on the Archbold Biological Station. Another reason is a confluence of faunistic elements at the south end of the Lake Wales Ridge. A third reason is the susceptibility of the area to colonization by exotics. The biogeographic groups of ants that mingle at the Archbold Biological Station are described briefly below. Our analysis is relatively unsophisticated because there are no state-wide surveys of Florida ants and because there have been few studies of phylogenetic relationships between Florida species and those in other areas, such as the West Indies or Texas. The species we have assigned to the various groups are listed in Table 2. We have assigned species to faunal groupings on the basis of distribution data in the Catalog of Hymenoptera (Smith 1979), and our own observations.

The widespread eastern ant fauna, which includes some transcontinental and even circumpolar species groups, is chiefly composed of forest-dwelling species. Typical species ranges extend north to Canada and west to Illinois. In the Florida panhandle, where there is a southward extension of the southern mixed hardwood forest (Greller 1980), several northern ants occur, which are apparently absent from the rest of Florida. Examples of these ants are *Camponotus americanus* Mayr, *C. subbarbatus* Emery, *Leptothorax curvispinosus* Mayr, *L. schaumii* Roger (Bhatkar and Whitcomb, unpublished collection data), and *Formica subsericea* Say (Wilson & Francoeur 1974). A more dilute representation of the eastern ant fauna is found in north-central Florida, where there is a very broad transition zone between southern mixed hardwood forest and temperate broadleaved evergreen forest (Greller 1980). A finger of the transition zone extends down the Lake Wales Ridge to the northern border of Highlands County (Greller 1980). Somewhere between Alachua County and the south end of the Lake Wales Ridge the eastern ant fauna becomes even sparser: 13 widespread eastern species found in Alachua County and Putnam County (Van Pelt 1958) do not occur on the Archbold Biological Station. These species are *Aphaenogaster fulva* Roger, *A. lamellidens* Mayr, *Pheidole pilifera* (Roger), *Crematogaster lineolata* (Say), *Ponera pennsylvanica* Buckley, *Smithistruma ornata* (Mayr), *S. pulchella* (Emery), *Lasius alienus* (Foerster), *Lasius neoniger* Emery, *Prenolepis imparis* (Say), *Camponotus pennsylvanicus* (DeGeer), *Tapinoma sessile* (Say), and *Dolichoderus pustulatus* Mayr. An additional species in this group is *Polyergus lucidus* Mayr (Trager & Johnson 1984). About 10 widespread eastern ants occur at the Archbold Biological Station (Table 2). A number of these (*Amblyopone pallipes*, *Smithistruma clypeata*, *Formica pallidefulva*) are usually associated on the Archbold Biological Station with xeric hammock habitats, such as mature SSo and mature RSh. Since such habitats are rare south of the Lake Wales Ridge, this may be the southernmost limit of several ants.

The southeastern ant fauna is a varied group, including arenicolous species that occur as far north as New Jersey and Illinois, as well as pine woods inhabitants that are found inland as far north as Tennessee. Many of these ants appear to be of southwestern origin, as disjunct populations or closely related species often occur in Texas or even further west. Some of these species are restricted to scrub and sandhill habitats; such

TABLE 2. GEOGRAPHIC RANGES OF ANTS FOUND ON THE ARCHBOLD BIOLOGICAL STATION.

Eastern or Nearctic Species		
<i>Amblyopone pallipes</i>	<i>Formica pallidefulva</i>	<i>Pheidole morrisi</i>
<i>Aphaenogaster treatae</i>	<i>Iridomyrmex pruinosus</i>	<i>Solenopsis carolinensis</i>
<i>Brachymyrmex depilis</i>	<i>Myrmecina americana</i>	<i>Smithistruma clypeata</i>
<i>Camponotus castaneus</i>		
Southeastern Species		
<i>Aphaenogaster ashmeadi</i>	<i>Crematogaster</i> sp.	<i>P. dentigula</i>
<i>A. flemingi</i>	<i>Discothyrea testacea</i>	<i>P. floridana</i>
<i>A. floridana</i>	<i>Formica archboldi</i>	<i>P. metallescens</i>
<i>A. texana</i>	<i>Hypoconera inexorata</i>	<i>Pheidole adrianoi</i>
<i>Camponotus abdominalis</i>	<i>H. opaciceps</i>	<i>Pogonomyrmex badius</i>
<i>C. impressus</i>	<i>H. opacior</i>	<i>Proceratium croceum</i>
<i>C. rasilis</i>	<i>Leptogenys elongata manni</i>	<i>Pseudomyrmex brunneus</i>
<i>C. socius</i>	<i>Leptothorax pergandei</i>	<i>P. pallidus</i>
<i>C. tortuganus</i>	<i>L. texana</i>	<i>Solenopsis geminata</i>
<i>C. nearcticus</i>	<i>L. wheeleri</i>	<i>S. globularia</i>
<i>C. pavidus</i>	<i>Monomorium viridum</i>	<i>S. nickersoni</i>
<i>Conomyrma flavopecta</i>	<i>Neivamyrmex opacithorax</i>	<i>S. pergandei</i>
<i>C. smithi</i>	<i>Odontomachus brunneus</i>	<i>S. picta</i>
<i>Conomyrma</i> sp. 1	<i>Odontomachus clarus</i>	<i>S. tennesseensis</i>
<i>Conomyrma</i> sp. 2	<i>Paratrechina arenivaga</i>	<i>Solenopsis</i> sp.
<i>Conomyrma</i> sp. 3	<i>P. concinna</i>	<i>Smithistruma creightoni</i>
<i>Crematogaster ashmeadi</i>	<i>P. faisonensis</i>	<i>S. dietrichi</i>
<i>C. clara</i>	<i>P. phantasma</i>	<i>S. talpa</i>
<i>C. minutissima</i>	<i>P. wojciki</i>	<i>Strumigenys louisianae</i>
	<i>Pheidole dentata</i>	<i>Trachymyrmex septentrionalis</i>
West Indies and South Florida Species		
<i>Brachymyrmex obscurior</i>	<i>Pheidole litoralis</i>	<i>P. seminole</i>
<i>Cyphomyrmex minutus</i>	<i>Platythyrea punctata</i>	<i>Tapinoma litorale</i>
<i>Eurhopalothrix floridana</i>	<i>Pseudomyrmex elongatus</i>	<i>Xenomyrmex floridanus</i>
<i>Pachycondyla stigma</i>	<i>P. simplex</i>	
Exotic Species		
<i>Cardiocondyla emeryi</i>	<i>M. pharaonis</i>	<i>Quadristruma emmae</i>
<i>C. nuda</i>	<i>Ochetomyrmex</i>	<i>Solenopsis invicta</i>
<i>C. venustula</i>	<i>auropunctatus</i>	<i>Strumigenys eggersi</i>
<i>C. wroughtonii</i>	<i>Paratrechina bourbonica</i>	<i>S. rogeri</i>
<i>Cyphomyrmex fuscus</i>	<i>P. longicornis</i>	<i>Tapinoma melanocephalum</i>
<i>Hypoconera</i>	<i>P. vividula</i>	<i>Tetramorium bicarinatum</i>
<i>punctatissima</i>	<i>Pheidole moerens</i>	<i>T. simillimum</i>
<i>Monomorium floricola</i>	<i>Pseudomyrmex mexicanus</i>	<i>Trichoscapa membranifera</i>

species are discussed in more detail below. The southeastern ant fauna includes about 61 species found on the Archbold Biological Station. There is little decrease in numbers of species between north-central Florida and the Archbold Biological Station; the only species to drop out are *Neivamyrmex texanus* Watkins, *N. carolinensis* (Emery), *Cryptopone gilva* (Roger), *Leptothorax bradleyi* Wheeler, and *Crematogaster vermiculata*

Emery. The last species is restricted to bald cypress (Buren 1968), which does not occur on the Archbold Biological Station.

A distinctive fauna of apparently native ants is shared by southern Florida and the West Indies. Some species extend into northern areas of Florida. Of 9 species in this group at the Archbold Biological Station, 4 do not reach north-central Florida. Three species found in the Florida Keys, *Camponotus planatus* Roger, *Leptothorax allardycei* (Mann), and *Zacryptocerus varians* (Smith), do not occur at the Archbold Biological Station.

A group of about 22 exotic tropical ants includes representatives of all major tropical areas. Most species in this group are intolerant of severe cold, and are therefore confined in the United States to Florida, with the exception of the species that live indoors. These exotics are discussed in more detail below.

COMPARISON OF FAUNAL SURVEYS OF FLORIDA ANTS

A comprehensive comparison of the ant fauna of the Archbold Biological Station and that of other sites in Florida is hampered by a lack of comparable surveys. Van Pelt's survey (1958) of the ants of the Welaka Reserve (Putnam Co.) is the only other study of the ants of a single locality. There are two regional surveys, one a study of the ants of the Florida Keys (Wilson 1964), the other an unpublished survey by A. P. Bhatkar and W. H. Whitcomb of the ants of the Red Hills region in northern Leon County. Although all these surveys seem to have been intensive, there is reason to suspect that Berlese funnel sampling in the Archbold Biological Station and Welaka surveys was much more extensive than in the other two surveys. Taxonomic problems beset all the surveys: several important Florida genera, including *Conomyrma*, *Pheidole*, *Paratrechina*, *Camponotus*, and *Solenopsis*, were in need of revision at the time of the surveys. In recent years these taxonomic problems have been partially resolved. Another problem is invasions of certain exotics since the time of the earlier studies.

In spite of all these discrepancies among the Florida surveys, they seem similar enough to allow a simple analysis that is not very sensitive to the addition or subtraction of a few species in a particular fauna. Such a test is provided by Sorensen's coefficient of similarity (Southwood 1978): $C_s = 2j/(a+b)$, where "j" is the species common to both sites, "a" the total species at one site, "b" the total species at the other. The results are arranged in decreasing order of similarity.

$$\text{Welaka-Red Hills: } C_s = 2(55)/(76+84) = .69$$

$$\text{Welaka-ABS: } C_s = 2(59)/(76+102) = .66$$

$$\text{ABS-Red Hills: } C_s = 2(56)/(84+102) = .60$$

$$\text{ABS-Florida Keys: } C_s = 2(52)/(30+102) = .39$$

$$\text{Welaka-Florida Keys: } C_s = 2(18)/(76+30) = .34$$

$$\text{Red Hills-Florida Keys: } C_s = 2(17)/(84+30) = .30$$

These results are just as one might predict from the geographic locations of the four sites. Each fauna is most like that of its nearest neighbor along a north-south transect. The mainland sites are much more similar to each other than to the Florida Keys. The Keys differ from the mainland in the depauperate nature of their fauna. Wilson (1964) attributes this low diversity to large-scale perturbations, particularly hurricanes, which may eradicate most terrestrial ants.

The diversity of ant fauna at the Archbold Biological Station relative to that of Florida as a whole appears surprisingly high. We have compiled from various sources a checklist of Florida ants, including known undescribed species. This list includes 166 spp., so that the Archbold Biological Station includes 61% of the ants known from Florida. This contrasts with the situation in the herpetofauna: the Archbold Biological Station has 61 species of herps (J. N. Layne 1978, unpublished list) out of the Florida

fauna of 150 species (Ashton and Ashton 1974), or 41% of the fauna. This might be interpreted as an indication that herps tend to have more locally restricted species than ants, but it is more likely an indication that the ant fauna of the Archbold Biological Station is much better known than that of Florida in general. Several parts of the state that might be expected to have locally restricted populations, such as the Miami, Pensacola, Everglades, and Appalachian areas, have not been surveyed.

ANTS OF SCRUB AND SANDHILL HABITATS

The species of scrub and sandhill environments are of special interest to us, as a principal mission of the Archbold Biological Station is the study of organisms found in these habitats. Several species of ants are apparently restricted to scrub and sandhill environments, and represent the only localized concentration of endemic ants in eastern North America. The following list summarizes our information on scrub and sandhill ants.

Species occurring in scrub and sandhill: 59

Species generally restricted to scrub and sandhill at ABS: 10

Exotic species in scrub and sandhill: 6

Exotic species restricted to scrub and sandhill: 0

Scrub and sandhill endemics: 4

The most striking feature of these numbers is the very large number of species that live in scrub and sandhill habitats compared to the number of species restricted to these habitats. We had expected that the harsh environment of scrub and sandhill, with heat, exposure, periodic droughts and fires, would have resulted in a small, tightly structured community of ants showing specific adaptations for a rigorous environment. We ascribe the large number of facultative scrub inhabitants to two factors. One factor is the importance of microhabitat. Even in open, recently burned scrub a dead log or a small accumulation of litter provides cooler and moister refugia for colonies of certain ants, some of which, such as *Camponotus abdominalis floridanus* and *C. tortuganus*, may be abundant and conspicuous scrub inhabitants. The other factor is successional change: after an area has escaped burning for a decade or more it becomes increasingly mesic and suitable for many ants not found in the early stages of the same plant community. A recently burned area, especially the "rosemary bald" (SSr), is dominated by scrub and sandhill obligates.

The species restricted to scrub and sandhill habitats vary in their geographic ranges. Three species, *Pogonomyrmex badius*, *Solenopsis globularia littoralis*, and *Leptothorax texanus davisii*, are widely distributed in sandy habitats through the eastern United States. One species, *Pheidole littoralis* is widespread in well-drained sandy areas in southern Florida, but absent from the rest of the United States. There are 5 species that are apparently endemic to Florida scrub and sandhill: *Conomyrma flavopecta*, *Conomyrma* spp. 1 and 3, *Odontomachus* sp., *Pheidole adrianoi*, *Paratrechina phantasma*. *Paratrechina wojciki* is endemic to central Florida, but found in a variety of habitats. These species might be analogous to some endemic reptiles, such as *Sceloporus woodi*, *Tantilla relicta*, *Stilosoma extenuatum*, *Rhineura floridana*, and *Neoseps reynoldsi*, whose ancestors probably came from western North America, or from Central America via western North America, before the Pleistocene an became isolated in the xeric uplands of central Florida (Auffenberg 1982). A number of additional species were probably once confined to these xeric upland refugia and spread to other parts of Florida and the southeastern United States in post-glacial times. Probable examples are *Pogonomyrmex badius*, *Solenopsis globularia littoralis*, *Leptothorax texanus davisii*, *Pheidole floridana*, *P. sitarches littoralis*, *Camponotus abdominalis floridanus*, *C. tortuganus*, *Aphaenogaster floridanus*, and *A. flemingi*. These species

may be historically analogous to the herps *Gopherus polyphemus*, *Ophisaurus compressus*, *Rana grylio*, and *Rhadinaea flavilata* (Boyles 1966).

There are no endemic genera of Florida ants. The closest approach to an endemic genus is *Pogonomyrmex badius*, included above in the list of species probably originating in central Florida uplands. *P. badius* belongs to a distinctive species group that differs from all southwestern *Pogonomyrmex* species in having polymorphic workers (Cole 1968). In contrast, there are 3 endemic Florida genera of herps, all restricted to xeric uplands (Auffenberg 1982). A glance at the representatives of these genera dispels any idea that this taxonomic contrast originates in a tendency of herpetologists to define genera more narrowly than do myrmecologists. The dispersal and colonization ability of ants, generally far superior to that of herps, are factors that would decrease the probability of the very protracted isolation required to protect an ancient relict or to permit radical morphological adjustment to better exploit an emergent ecological niche.

EXOTIC ANTS

Between 20 and 24 species of ants on the Archbold Biological Station are not native to Florida. The 4 species whose status is questionable are Neotropical species that may have been introduced before any surveys of Florida ants. The reasons for suspecting these 4 (out of 12 species with West-Indian-Neotropical distribution) are as follows. *Pachycondyla stigma* is a pantropical species (Smith 1979). In 1932 this species, which is very common today, was known only from Lake Worth in Palm Beach County (Wheeler 1932). *P. stigma* was reported from the Archbold Biological Station in 1943 (Schneirla 1944). *Brachymyrmex obscurior* is "possibly introduced" (Smith 1979); at the Archbold Biological Station it inhabits disturbed sites. *Pseudomyrmex simplex* has not been reported from Florida until 1985 (though it might have been confused with *P. pallidus*) and like *P. mexicanus*, may have been recently introduced. The speed with which *P. mexicanus* became completely naturalized throughout Florida at least as far north as Gainesville (Whitcomb et al. 1972), casts vague doubts on the native status of other Florida *Pseudomyrmex* species, especially *P. cubaensis* and *P. elongatus*. There is no good way to establish whether any Florida-Neotropical species are native. Suggestive evidence for exotic origin would be: documentation of rapid range expansion; infraspecific character states linking Florida populations with distant Neotropical populations; restriction to disturbed habitats; flightless queens. It is tempting, in view of the scarcity of West Indian elements in the native herpetofauna (Auffenberg 1982) and scarab fauna (Woodruff 1973), to assume that most Florida-West Indian ants are exotic, but the relatively good colonizing capacity of ants makes independent establishment plausible in most cases.

The 22 verified exotic ants on the Archbold Biological Station vary widely in the extent to which they are restricted to man-modified environments. There are 2 species, *Monomorium pharaonis* and *Paratrechina longicornis*, that are restricted to buildings and adjacent gardens. Species confined to man-modified environments are *Pheidole moerens*, *Cardiocondyla nuda*, *C. venustula*, *C. wroughtonii*, *Monomorium floricola*, *Tetramorium bicarinatum*, *Wasmannia auropunctata*, *Tapinoma melanocephalum*, *Trichoscapa membranifera*, *Paratrechina bourbonica*, *P. vividula*, and the suspected exotic *Brachymyrmex obscurior*. Species that regularly colonize natural habitats are *Pseudomyrmex mexicanus*, *Hypoponera punctatissima*, *Cardiocondyla emeryi*, *Solenopsis invicta*, *Tetramorium simillimum*, *Strumigenys eggersi*, *S. rogeri*, *Quadris-truma emmae*, *Cyhomymyrmex fuscus* and the suspected exotics *Pachycondyla stigma* and *Pseudomyrmex simplex*.

The relatively large number of exotics in natural habitats can be attributed to several factors. The warmer parts of Florida, isolated as they are from mainland Neotropica,

are truly insular in nature, and the ant fauna is correspondingly depauperate and subject to invasion by tramps. The numerous sea ports with direct traffic between nearby tropical areas provide access to Florida. Finally, the natural habitats of the Archbold Biological Station and of much of southern Florida are subject to frequent natural disturbances in the form of fires and floods which may make these habitats more easily invaded by ants associated with man-made disturbances.

A series of 6 sites that we assume represents a gradient from insular or disturbed sites to mainland or undisturbed sites show a decreasing percentage of exotic ants.

Florida Keys (Wilson 1964): 30.0% exotics (9 spp.)

Archbold Biological Station: 19.6% exotics (20 spp.)

Welaka Reserve (Van Pelt 1958): 10% exotics (7 spp.)

Red Hills (Bhatkar and Whitcomb, unpublished): 9.5% exotics (8 spp.)

In an even more dramatic contrast to the situation in Florida, in a recent survey of the ants of Utah (Allred 1982) only 1 exotic was found among 169 species of ants. It is true that the Utah survey concentrated on rural areas, but the back roads of Florida are literally lined with the nests of exotic ants.

The number of exotic ant species at the Archbold Biological Station is not only large compared with other sites, but is also large relative to the number of exotics in some other groups of insects. Among the Archbold Biological Station butterflies, for example, there is only 1 exotic out of 65 species, among scarabs there are 6 exotics out of 76 species, among bees there is 1 exotic out of 52 species. One possible explanation is that alate female ants are relatively poor long-range dispersers relative to stronger-flying insects, so that subtropical Florida was not saturated with naturally immigrating ants from the Neotropics long before the arrival of humans. A complementary explanation is that ants, while poor dispersers, are excellent colonizers, hence species may frequently become established from a single introduction. Once a single fertile female establishes herself in a suitable habitat her chance of founding a breeding population is good because of the likelihood of mating among her offspring, of which large numbers are concentrated in one place over a period of at least a year. An analogous situation occurs in the beetles of the family Scolytidae. Almost all recently established Florida species are members of the tribe Xyleborini or in the genus *Hypothenemus*; in both these groups sib matings within the parental gallery are the rule (Wood 1977).

The same factors that permit the establishment of an exotic population normally ensure the eventual abundance of that species, but this may not hold throughout the new range of the species, and may change over time. Several exotics are rare at the Archbold Biological Station; these species are *Cardiocondyla venustula*, *C. wroughtonii*, *Paratrechina vividula*, *Pheidole moerens*, and *Trichoscapa membranifera*. *C. venustula* and *T. membranifera* are the only species we have not found in dense populations elsewhere in Florida.

MISSING ANTS

Several species of ants that might be expected to occur at the Archbold Biological Station have not been found. *Dolichoderus pustulatus* Mayr occurs in low flatwoods at Welaka (Van Pelt 1958) and in the Everglades (Wheeler 1932), but not at the Archbold Biological Station. *Prionopelta antillana* Forel is widespread in South America and in the West Indies; a population reported from Juniper Springs in Ocala State Forest (Smith 1979) was still thriving in 1985. The absence of this species from the Archbold Biological Station provides evidence that the Ocala population may be exotic. *Neivamyrmex texanus* Watkins was found at Lake Wales in 1983; this site is 54 miles north of

the Archbold Biological Station. *Aphaenogaster lamellidens* Mayr is reported from Highlands Co. (Carroll 1975).

ACKNOWLEDGMENTS

The work of James Trager at the Archbold Biological Station was supported in part by a grant from the Archbold Biological Station. We would like to thank William Brown, Jr. (Cornell University), and Roy Snelling (Los Angeles Natural History Museum) for identifying specimens of ants. Nancy Deyrup assisted in the collection and preparation of specimens. The manuscript was typed and the tables prepared by Dorothy Carter. James Layne, Fred Lohrer, and Lawrence Battoe (Archbold Biological Station) all provided helpful suggestions for improving the manuscript.

REFERENCES CITED

- ABRAHAMSON, W. G., A. F. JOHNSON, J. N. LAYNE, AND P. A. PERONI. 1984. Vegetation of the Archbold Biological Station: an example of the southern Lake Wales Ridge. *Florida Sci.* 47: 209-250.
- ALLRED, D. M. 1982. Ants of Utah. *Gt. Basin Natur.* 42: 415-511.
- ASHTON, R. E., JR. AND P. S. ASHTON. 1981. Handbook of reptiles and amphibians of Florida. Part One. The Snakes. Windward Publ. Inc., Miami. 176 pp.
- AUFFENBERG, W. 1982. Florida environments and their herpetofaunas. Part III. Herpetogeography. *Florida Herpetol.* 4: 1-36.
- BOLTON, B. 1977. The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Oriental and Indo-Australian regions, and in Australia. *Bull. British Mus. Nat. Hist. (Entomol.)* 36: 67-151.
- BLUM, M. S. 1981. Sex pheromones in social insects: Chemotaxonomic potential. Pp. 163-174 in P. E. Howse and J. L. Clement (Eds.) *Biosystematics of social insects*. Academic Press, London and New York. 436 pp.
- BOYLES, J. M. 1966. Zoogeography of the herpetofauna of central Florida. Unpublished Ph.D. dissertation, Univ. Alabama. 164 pp.
- BROWN, W. L. 1953. Revisionary studies in the ant tribe Dacetini. *American Midl. Natur.* 50: 1-137.
- BROWN, W. L. 1976. Contribution toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomol.* 19: 67-171.
- BROWN, W. L., AND W. W. KEMPF. 1960. A world revision of the ant tribe Basicerotini (Hym. Formicidae). *Studia Entomol.* 3: 161-249.
- BUREN, W. F. 1968. A review of the species of *Crematogaster sensu strictu*, in North America (Hymenoptera, Formicidae). Part II. Descriptions of new species. *J. Georgia Entomol. Soc.* 3: 91-121.
- CARROLL, J. F. 1975. Biology and ecology of ants of the genus *Aphaenogaster* in Florida. Unpublished Ph.D. Dissertation, Univ. Florida, Gainesville.
- COLE, A. C., JR. 1968. *Pogonomyrmex* harvester ants. Knoxville, Univ. Tennessee Press. 222 pp.
- CREIGHTON, W. S. 1950. The ants of North America. *Bull. Mus. Comp. Zool.* 104: 1-583.
- DEYRUP, M., AND J. TRAGER. 1984. *Strumigenys rogeri*, an African Dacetine ant new to the U. S. *Florida Entomol.* 67: 512-516.
- GRELLER, A. M. 1980. Correlation of some climate statistics with distribution of broadleaved forest zones in Florida, U.S.A. *Bull. Torrey Bot. Club* 107: 189-219.
- HUBBELL, T. H. 1961. Endemism and speciation in relation to Pleistocene changes in Florida and the southeastern coastal plain. *Eleventh Int. Congr. Entomol., Wien 1960*, 1: 466-469.
- LAESSLE, A. M. 1968. Relationship of sand pine scrub to former shore lines. *Q. J. Florida Acad. Sci.* 30: 269-286.

- NAVES, M. A. 1985. A monograph of the genus *Pheidole* in Florida (Hymenoptera: Formicidae). *Insecta Mundi* 1: 53-90.
- SCHNEIRLA, T. C. 1944. Results of the Archbold Expeditions. No. 51. Behavior and ecological notes on some ants from south-central Florida. *American Mus. Novit.* 1261: 1-5.
- SMITH, D. R. 1979. Superfamily Formicoidea. Pp. 1312-1467 in K. V. Krombein, P. D. Hurd, Jr., D. R. Smith, B. D. Burks (eds.) *Catalog of Hymenoptera in America north of Mexico*. Smithsonian Institution Press, Washington, D. C.
- SMITH, M. R. 1930. A list of Florida ants. *Florida Entomol.* 14: 1-6.
- SMITH, M. R. 1944. Additional ants recorded from Florida, with descriptions of two new subspecies. *Florida Entomol.* 27: 14-17.
- SOUTHWOOD, T. R. E. 1978. *Ecological methods*. New York, John Wiley and Sons. XXIV + 524 pp.
- THOMPSON, C. R. 1980. *Solenopsis (Diplorhoptrum)* of Florida. Unpublished Ph.D. dissertation, Univ. Florida, Gainesville.
- THOMPSON, C. R. 1982. A new *Solenopsis (Diplorhoptrum)* species from Florida. (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.* 55: 485-488.
- TRAGER, J. C. 1984. A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the Continental United States. *Sociobiology* 9: 49-162.
- TRAGER, J. C. AND C. JOHNSON. 1984. A slave-making ant in Florida: *Polyergus lucidus* and its host, *Formica archboldi* (Hymenoptera: Formicidae). *Florida Entomol.* 68: 261-266.
- VAN PELT, A. F. 1958. The ecology of the ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae). Part II. Annotated list. *American Midl. Natur.* 59: 1-57.
- WALKER, J. 1983. The soldier caste and colony structure in the ant *Camponotus (Colobopsis) impressus*. Unpublished Ph.D. dissertation, Univ. California, Davis.
- WARD, P. S. 1985. The Nearctic species of the genus *Pseudomyrmex*. *Quaest. Entomol.* 21: 209-246.
- WATKINS, J. F., II. 1976. The identification and distribution of New World army ants (Dorylinae: Formicidae). Baylor University Press. 102 pp.
- WILSON, E. O. AND A. FRANCOEUR. 1974. Ants of the *Formica fusca* group in Florida. *Florida Entomol.* 57: 115-116.
- WHITCOMB, W. H., H. A. DENMARK, W. F. BUREN, AND J. F. CARROL. 1972. Habits and present distribution in Florida of the exotic ant, *Pseudomyrmex mexicanus* (Hymenoptera: Formicidae). *Florida Entomol.* 55: 31-33.
- WILSON, E. O. 1964. The ants of the Florida Keys. *Breviora* 210: 1-14.
- WOOD, S. L. 1977. Introduced and exported American Scolytidae (Coleoptera) Gt. Basin *Natur.* 37: 67-74.
- WOODRUFF, R. C. 1973. Arthropods of Florida and neighboring land areas. 8. The scarab beetles of Florida. Gainesville, Florida Dept. Agric. Consum. Serv. Div. Plant Indust. iv + 220 pp.

DESCRIPTION OF THE MALE OF *ACROSTERNUM ISTUM*
(HEMIPTERA: PENTATOMIDAE)

D. A. RIDER

Department of Entomology
Louisiana Agricultural Experiment Station
Louisiana State University Agricultural Center
Baton Rouge, LA 70803

ABSTRACT

Figures and a description are given of the previously unknown male of *Acrosternum istum* Rolston. New locality records from Costa Rica and Panama are listed.

RESUMEN

Se dan figuras y una descripción de los machos anteriormente desconocidos de *Acrosternum istum* Rolston. Los nuevos records de localidad de Costa Rica y Panamá están listados.

In his revision of the New World species of *Acrosternum* Fieber, subgenus *Chinavia* Orian, Rolston (1983) described the species *A. istum* from a single female specimen from Panama. Since that time, a series of 13 males and 5 females from Panama and a single male from Costa Rica have been collected. To further characterize this species, a description of the male is given (numbers in parentheses represent measurements for females), and intraspecific variation is indicated.

Acrosternum (Chinavia) istum Rolston
(Fig. 1-5)

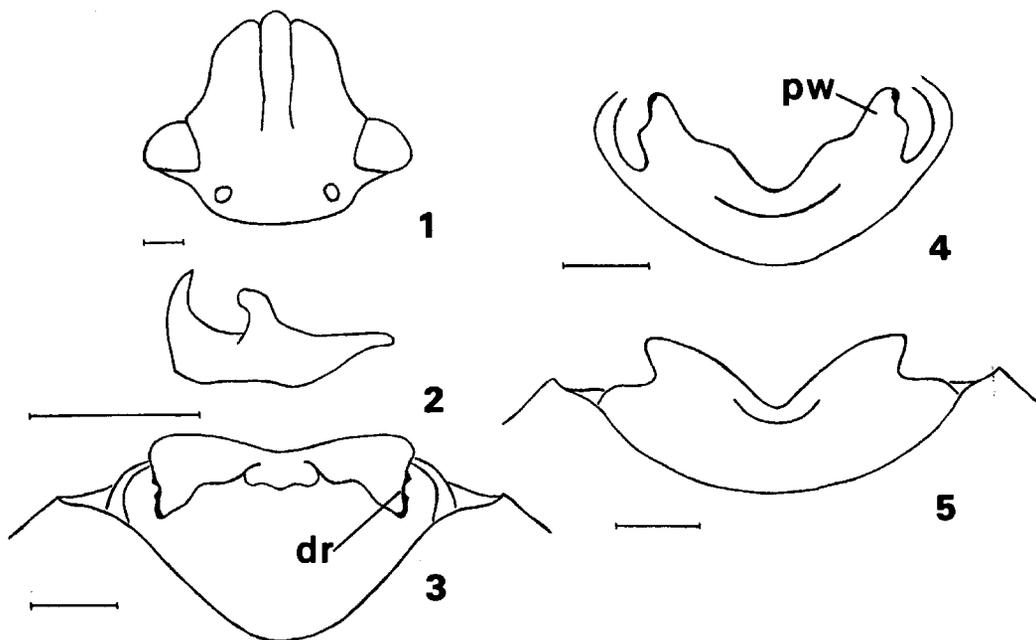
Acrosternum (Chinavia) istum Rolston, 1983: 121-122, fig. 49.

Description. Medium to dark green above; medium green below, usually pale mesially, abdominal spine and surrounding area of supporting abdominal segment often pale to dark brown. Lateral margins of juga, pronotum, connexiva, and bases of coria bordered dorsally and ventrally with yellow-orange. Dorsal punctation dark green, dense on head, less dense on pronotum, scutellum, and coria. Length 12.1-13.8 (13.7-16.2) mm.

Head narrowly rounded apically, jugal margins slightly concave before eyes, nowhere parallel (Fig. 1). Length of head 2.3-2.4 (2.4-2.7) mm, width across eyes 2.9-3.1 (3.0-3.4) mm. Each antenna green, distal one-third of segment 3, distal one-fourth of segment 4, and distal one-half of segment 5 pale fuscous to black; length of segments 1-5 about 0.5-0.6 (0.5-0.7), 1.2-1.4 (1.3-1.4), 1.4-1.7 (1.5-1.8), 1.9-2.2 (2.0-2.2), 1.9-2.1 (2.0-2.2) mm.

Pronotum 7.1-8.1 (7.8-9.5) mm wide at humeri, mesial length 2.4-2.9 (3.0-3.2) mm. Each humeral angle narrowly rounded, slightly produced beyond base of coria. Anterolateral margin of pronotum straight or slightly convex. Cicatrices not marked with black.

Scutellum 4.4-5.2 (5.0-6.0) mm wide at base, mesial length 4.9-5.9 (5.9-6.5) mm; base void of any pale or black markings. Coria rounded apically, reaching beyond middle of sixth (fifth visible) abdominal segment, rarely reaching seventh (sixth visible) abdominal segment. Connexiva with posterolateral angles black, with some black on posterolateral angle of laterotergites.



Figs. 1-5. *A. istum*. Fig. 1. Head. Fig. 2. Paramere. Fig. 3. Genital cup, dorsal view; dorsal rim of posterior wall (dr). Fig. 4. Pygophore, caudal view; posterior wall (pw). Fig. 5. Pygophore, ventral view. Dimensional lines equal to 0.5 mm.

Rostral segments 2-4 about 1.6-1.8 (1.8-1.9), 1.2-1.3 (1.3-1.4), 1.0-1.1 (1.1-1.2) mm long, pale green to pale brown, apex of segment 4 piceous, terminating between metacoxae. Each ostiolar ruga about three-fourths distance from mesial margin of ostiole to lateral thoracic margin. Abdominal spine compressed, usually reaching slightly beyond anterior margin of metacoxae, sometimes not quite reaching anterior margin of metacoxae. Posterolateral angles of sternites black. Each spiracle pale brown, not on callous, sometimes surrounded by small bright green spot. Legs green.

Pygophore with dorsal wall well-developed, expanded dorsolaterally forming a deep v-shaped emargination at each posterolateral angle (Fig. 4-5); posterior margin from ventral view with broad, deep, slightly sinuous, v-shaped emargination mesially (Fig. 5); from caudal view mesial emargination distinctly sinuous, v-shaped (Fig. 4); from dorsal view posterior margin of pygophore slightly emarginate mesially; lateral margin of posterior wall nearly parallel to longitudinal axis of body, dorsal rim black with 2-3 small denticles anteriorly (Fig. 3). Ventral surface of pygophore with semi-circular carina paralleling posterior margin of pygophore. Paramere as in Fig. 2.

Distribution. The holotype has the following locality data: PANAMA: Panamá Province, Altos de Maje, Chepo, 14-15-V-1976, D. Engleman, at lights. The two new locality records are: PANAMA: Coclé Province, Cerro Gaital, 10-12-VI-1985, E. Riley & D. Rider; COSTA RICA: Alejuela Province, San Juan de Grecia, Rio Sarchí, 11-VIII-1981, E. Barrera & H. Brailovsky.

Comments. Specimens of *A. istum* show variability for certain characters, especially the length of the abdominal spine. The length of the abdominal spine is fairly constant in most species of *Acrosternum*; however, in *A. istum* it ranges from reaching the middle of the metacoxae to almost attaining the posterior margin of the mesocoxae. Those specimens in which the abdominal spine does not surpass the anterior margin of the metacoxae will key to *A. marginatum* (Palisot de Beauvois) in the revision by

Rolston (1983). *Acrosternum istum* does seem to be related to *A. marginatum*, as the female genitalia are similar in both species; the basal plates have a posterolateral projection. The male genitalia, however, are distinctive, and in both sexes the dorsal punctation is much less dense in *A. istum* than in *A. marginatum*. The holotype specimen of *A. istum* was examined.

The Panama specimens were collected while beating and sweeping plants in the family Convolvulaceae.

ACKNOWLEDGEMENTS

I would like to thank T. J. Henry, National Museum of Natural History, for arranging the loan of the type specimen of *A. istum*. I would also like to thank J. B. Chapin, J. A. Moore, and L. H. Rolston, Louisiana State University, for reviewing an early draft of the manuscript.

REFERENCES CITED

- ROLSTON, L. H. 1983. A revision of the genus *Acrosternum* Fieber, subgenus *Chinavia* Orian, in the Western Hemisphere (Hemiptera: Pentatomidae). *J. New York Entomol. Soc.* 91(2): 97-176, 232 fig.

THE NEOTROPICAL SPECIES OF *PHAENOBEZZIA* (DIPTERA: CERATOPOGONIDAE)

GUSTAVO R. SPINELLI

Instituto de Limnología "Dr. Raúl A. Ringuelet," Casilla de Correo 55,
1923 Berisso, República Argentina. Carrera del Investigador Científico (CONICET)

AND

WILLIS W. WIRTH

Cooperating Systematic Entomology Laboratory, USDA; Research Associate,
Florida State Collection of Arthropods, Florida Department of Agriculture and
Consumer Services, Gainesville, Florida 32602, USA.

ABSTRACT

The genus *Phaenobezzia* Haeselbarth is recorded for the first time from the Neotropical Region, and a key is given for the 3 Neotropical species: *P. fulvithorax* (Malloch) from northern Mexico, *P. astyla* n. sp. from Colombia (type locality) and Ecuador, and *P. maya* n. sp. from Belize (type locality) and ranging from southern Texas to Panama.

RESUMEN

Se cita por primera vez al género *Phaenobezzia* Haeselbarth para la Region Neotropical, y se ofrece una clave para la identificación de las 3 especies Neotropicales: *P. fulvithorax* (Malloch) para el Norte de Mexico, *P. astyla* n. sp. para Colombia (localidad tipo) y Ecuador, y *P. maya* n. sp. para Belice (localidad tipo), registrándose esta última desde el Sur de Texas hasta Panamá.

Rolston (1983). *Acrosternum istum* does seem to be related to *A. marginatum*, as the female genitalia are similar in both species; the basal plates have a posterolateral projection. The male genitalia, however, are distinctive, and in both sexes the dorsal punctation is much less dense in *A. istum* than in *A. marginatum*. The holotype specimen of *A. istum* was examined.

The Panama specimens were collected while beating and sweeping plants in the family Convolvulaceae.

ACKNOWLEDGEMENTS

I would like to thank T. J. Henry, National Museum of Natural History, for arranging the loan of the type specimen of *A. istum*. I would also like to thank J. B. Chapin, J. A. Moore, and L. H. Rolston, Louisiana State University, for reviewing an early draft of the manuscript.

REFERENCES CITED

- ROLSTON, L. H. 1983. A revision of the genus *Acrosternum* Fieber, subgenus *Chinavia* Orian, in the Western Hemisphere (Hemiptera: Pentatomidae). *J. New York Entomol. Soc.* 91(2): 97-176, 232 fig.

THE NEOTROPICAL SPECIES OF *PHAENOBEZZIA* (DIPTERA: CERATOPOGONIDAE)

GUSTAVO R. SPINELLI

Instituto de Limnología "Dr. Raúl A. Ringuelet," Casilla de Correo 55,
1923 Berisso, República Argentina. Carrera del Investigador Científico (CONICET)

AND

WILLIS W. WIRTH

Cooperating Systematic Entomology Laboratory, USDA; Research Associate,
Florida State Collection of Arthropods, Florida Department of Agriculture and
Consumer Services, Gainesville, Florida 32602, USA.

ABSTRACT

The genus *Phaenobezzia* Haeselbarth is recorded for the first time from the Neotropical Region, and a key is given for the 3 Neotropical species: *P. fulvithorax* (Malloch) from northern Mexico, *P. astyla* n. sp. from Colombia (type locality) and Ecuador, and *P. maya* n. sp. from Belize (type locality) and ranging from southern Texas to Panama.

RESUMEN

Se cita por primera vez al género *Phaenobezzia* Haeselbarth para la Region Neotropical, y se ofrece una clave para la identificación de las 3 especies Neotropicales: *P. fulvithorax* (Malloch) para el Norte de Mexico, *P. astyla* n. sp. para Colombia (localidad tipo) y Ecuador, y *P. maya* n. sp. para Belice (localidad tipo), registrándose esta última desde el Sur de Texas hasta Panamá.

Haeselbarth (1965) proposed the genus *Phaenobezzia* for *Probezzia pistiae* Ingram and Macfie (type-species) and 11 other African species. Remm (1974) considered *Phaenobezzia* to be a subgenus of *Bezzia* Kieffer and included 1 species *B. rubiginosa* (Winnertz), in the fauna of the USSR. Wirth did not record the genus (or subgenus) in his catalogs of the Oriental (1973) and Neotropical (1974) Regions. More recently, Wirth & Ratanaworabhan (1981) gave a key to 5 species occurring in Southeast Asia and Wirth & Grogan (1982) revised the 3 North American species. The purpose of this paper is to record the genus for the 1st time from the Neotropical Region with the description of 2 new species, and to record a North American species from Mexico.

Good diagnoses of the genus *Phaenobezzia* may be found in the papers by Haeselbarth (1965), Wirth & Ratanaworabhan (1981) and Wirth & Grogan (1982). For general terminology of the Ceratopogonidae see Wirth et al. (1977) and Downes and Wirth (1981). The holotypes of our new species and most of the paratypes are deposited in the National Museum of Natural History in Washington, D.C. Paratypes will be deposited in the following collections: British Museum (Natural History), London; Canadian National Collection, Agriculture Canada, Ottawa; Florida State Collection of Arthropods, Florida Department of Agriculture, Gainesville, Florida; Museo de La Plata, La Plata, Argentina; and Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Key to the Neotropical Species of *Phaenobezzia* Haeselbarth

1. Females 2
- Males 4
2. Eyes broadly separated, by diameter of 5-6 ommatidial facets; apex of last flagellar segment bluntly rounded, not tapering *fulvithorax* (Malloch)
- Eyes narrowly to moderately separated, by diameter of 1-3 ommatidial facets; apex of last flagellar segment tapering 3
3. Antenna short, segment 11 1.5 as long as segment 10, antennal ratio 1.08; 5th tarsomere with 4-5 pairs of ventral, sharp-pointed spines *maya* n. sp.
- Antenna elongated, segment 11 1.4 as long as segment 10, antennal ratio 1.00; 5th tarsomere with 3-7 pairs of sharp-pointed spines *astyla* n. sp.
4. Eyes broadly separated, by diameter of 5-6 facets *fulvithorax* (Malloch)
- Eyes narrowly to moderately separated, by diameter of 1-3 facets 5
5. Dististyle absent; sensilla chaetica forming the antennal plume stout . *astyla* n. sp.
- Dististyle present but reduced; sensilla chaetica forming the antennal plume slender *maya* n. sp.

Phaenobezzia astyla n. sp.

(Fig. 1)

Female. Wing length 2.02 (1.81-2.21, n = 10) mm; breadth 0.70 (0.59-0.79, n = 10) mm.

Head: Brownish, eyes separated for a distance equal to diameter of 1 ommatidial facet. Antenna (Fig. 1a) relatively long and slender, entirely brownish; lengths of flagellar segments in proportion of 17-14-14-14-14-14-14-16-22-22-21-22-30; length of segment 11, 1.4 x length of segment 10; antennal ratio 1.00 (0.99-1.03, n = 10); apex of last segment tapering. Palpus (Fig. 1b) with lengths of segments in proportion of 5-10-14-8-10; palpal ratio 3.00 (2.80-3.25, n = 10); 3rd segment with scattered sensilla. Mandible with 6-7 teeth.

Thorax: Brownish, mesonotum without anterior spine. Legs yellowish, knees darkish. Ventral palisade setae absent on foretarsus, in 1 row on tarsomeres 1 and 2 on mid

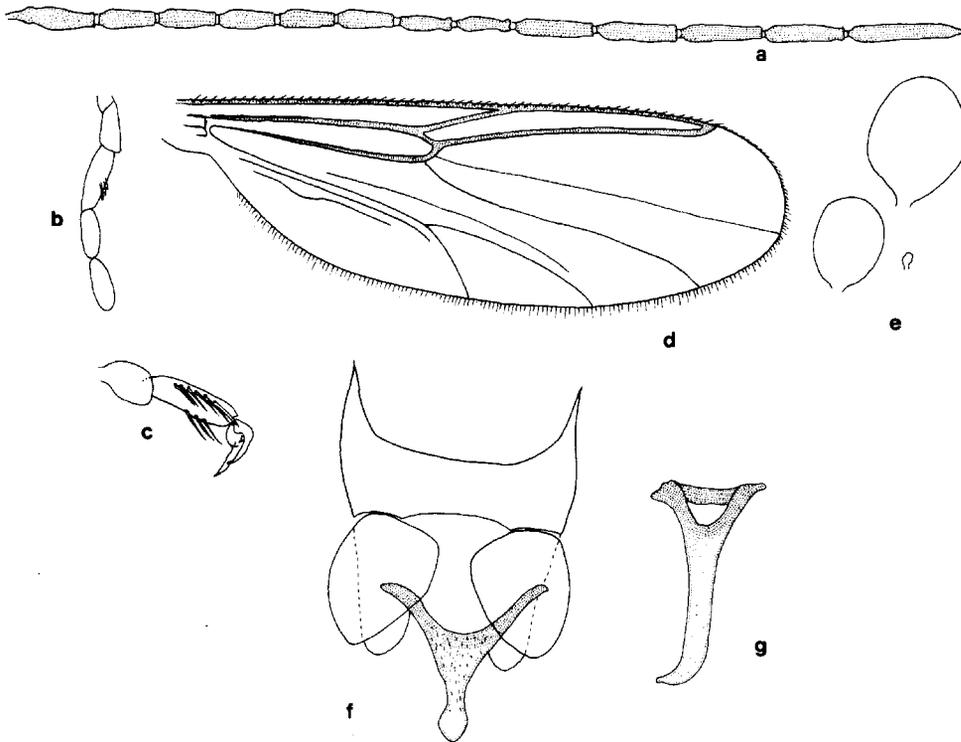


Fig. 1. *Phaenobezzia astyla*; a-e, female; f-g, male: a, antenna; b, palpus; c, 4th and 5th tarsomeres and claws; d, wing; e, spermathecae; f, male genitalia, parameres omitted; g, parameres.

leg and tarsomere 3 on hind leg, in 2 rows on tarsomeres 1 and 2 on hind leg; 5th tarsomere (Fig. 1c) with 3-7 pairs of strong, long, sharp-pointed ventral spines; hind tarsal ratio 2.50 (2.35-2.55, $n = 10$); claws not very curved, each with internal basal tooth. Wing (Fig. 1d) slightly infuscated, with costa extending to 0.88 (0.87-0.89, $n = 10$) of total length; venation as figured. Halter brownish.

Abdomen: Brownish; 5 pairs of well-sclerotized gland rods; spermathecae (Fig. 1e) ovoid with short necks; unequal, measuring 0.76 by 0.053 mm, and 0.053 by 0.041 mm; rudimentary 3rd spermatheca present.

Male.—Wing length 1.22 mm; breadth 0.43 mm; costal ratio 0.80. Similar to female with usual sexual differences; antenna with lengths of flagellar segments in proportion of 18-15-13-13-12-12-12-11-14-15-15-17-26; antennal ratio (12-15/3-11) 0.60; plume formed by strong sensilla chaetica. Genitalia as figured (Fig. 1f); basistyle short and stout; dististyle absent. Aedeagus with broad basal arch extending to 0.4 of total length, basal arms slender, distal portion tapering to slender process with expanded, capitate tip. Parameres (Fig. 1g) with caudal process long, dorsally bent at apex.

Distribution: Colombia, Ecuador.

Types: Holotype female, Rio Raposo, Valle, Colombia, III-1964, V. H. Lee, light trap; allotype male, same data except 1-VII-1964. Paratypes, 2 males, 33 females, as follows COLOMBIA: Rio Raposo, VIII-1963, V. H. Lee, light trap, 2 females; same data except XII-1963, 2 females: II-1964, 1 female: III-1964, 5 females; 15-IV-1964, 7 females; V-1964, 1 female: 28-VII-1964, 1 female; VIII-1964, 3 females: XII-1964, 1 female; VI-1965, 1 female; VII-1965, 1 male; VIII-1965, 2 females. ECUADOR: Puyo, Pastaza Prov., II-1976, P. J. Spangler, at light, 1 female; Pichincha, 47 km s San

Domingo, Rio Palenque, 28-VII-1976, J. Cohen, 4 females, 1 male, at light; Pichincha, 113 km via Puerto Quito (2700'), 20-VIII-1976, J. Cohen, 1 female, CDC trap; Esmeralda, La Chiquita, 11 km se San Lorenzo, 20-VIII-1976, J. Cohen, 1 female, CDC trap.

Discussion: This species can be distinguished from the other Neotropical species by the large number of ventral spines on the 5th tarsomere in the female, and by the stout sensilla chaetica in the male antennal plume, as well as the absence of dististyle in the male genitalia.

Phaenobezzia fulvithorax (Malloch)

Probezzia fulvithorax Malloch, 1915: 354 (male, female; Illinois).

Phaenobezzia fulvithorax (Malloch); Wirth and Grogan, 1982: 185 (redescribed; combination; distribution).

New Record: MEXICO: Nueva Leon, Linares, Rio Camacho, 21-VI-1965, O. S. Flint, 1 female.

Phaenobezzia maya n. sp.

(Fig. 2)

Female. Wing length 2.00 (1.77-2.45, n=10) mm; breadth 0.71 (0.63-0.83, n=10) mm.

Head: Dark brown, eyes separated for a distance equal to diameter of 2-3 ommatidial facets. Antenna short (Fig. 2a), dark brown, narrow bases of flagellar segments paler (entirely dark brown in some specimens); lengths of flagellar segments in proportion of 20-13-12-12-12-12-12-14-23-23-24-24-26; segment 11, 1.5 as long as 10; antennal ratio 1.08 (0.96-1.18, n=10); apex of last segment tapering. Palpus (Fig. 2b) with lengths of segments in proportion of 6-10-16-10-10; palpal ratio 2.88 (2.65-3.20, n=10); 3rd segment with sensilla. Mandible with 7-8 teeth.

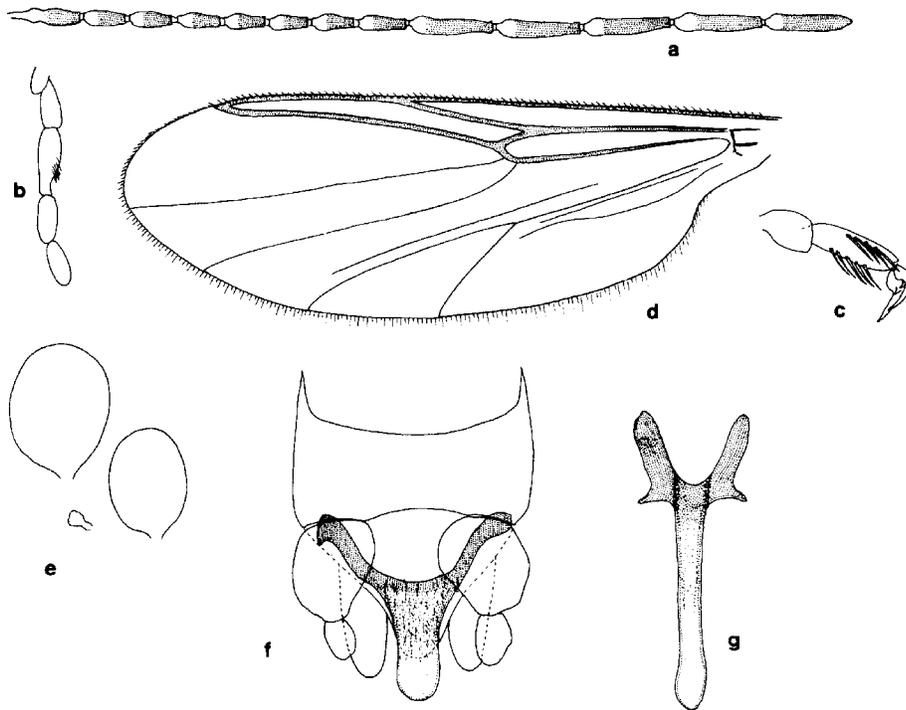


Fig. 2. *Phaenobezzia maya*; a-e, female; f-g, male; a, antenna; b, palpus; c, 4th and 5th tarsomeres and claws; d, wing; e, spermathecae; f, male genitalia, parameres omitted; b, parameres.

Thorax; Brownish to dark brown, mesonotum with a very short, blunt, anterior spine (not visible in the holotype.). Legs yellowish brown, knees darkish, hind tibia slightly infuscated in some specimens. Ventral palisade setae sparse on tarsomeres 1-3 on mid leg, dense on tarsomeres 1-3 on hind leg; 5th tarsomere (Fig. 2c) on all legs with 4-5 pairs of strong, sharp-pointed ventral spines; hind tarsal ratio 2.50 (2.30-2.65, n=10); claws moderately long and curved, each with internal basal tooth. Wing (Fig. 2d) slightly infuscated, with costa extending to 0.85 (0.84-0.87, n=10); of total length; venation as figure. Halter brown.

Abdomen: Brownish to dark brown; 5 pairs of dorsal gland rods, but only the posterior pair and the anterior margin of the tergum on which they are borne sclerotized dark brownish to blackish; spermathecae (Fig. 2e) ovoid with slender and short necks; unequal, measuring 0.064 by 0.053 mm, and 0.049 by 0.041 mm; rudimentary 3rd present.

Male. Wing length 0.97 mm; breadth 0.34 mm; costal ratio 0.72. Similar to female with usual sexual differences; antenna with lengths of flagellar segments in proportion of 14-10-9-9-8-8-8-10-12-13-15-18-24; antennal ratio (12-15/3-11) 0.79; plume formed by slender sensilla chaetica. Genitalia (Fig. 2f) as figured; basistyle short and stout, length equal to basal breadth; dististyle about 0.5 as long as basistyle. Aedeagus with broad basal arch extending to 0.33 of total length, basal arms slender and well sclerotized, distal portion with stout tip. Parameres (Fig. 2g) with basal arms elongated, well sclerotized and directed mostly cephalad; caudal process long and slender, slightly expanded distally, with somewhat pointed tip.

Distribution: Belize, Costa Rica, El Salvador, Honduras, Mexico, Panama, U. S. A (Texas).

Types: Holotype female, allotype male, Belize, Cayo District. Western Hwy MP66, VI-1969, W. & D. Haase, light trap. Paratypes, 77 females, 18 males, as follows: BELIZE: same data as types, 46 females, 9 males; same data except 12-VII-1969, 2 females, 1 male; Augustine, 1-VII-1968, W. L. Haase, 1 female, black light; Nattievile, Western Highway, 7/8-VII-1968, W. L. Haase, 3 females, black light; same data except 8-VII-1968, 2 males, light. COSTA RICA: 10 mi. N.W. Liberia, 25-VII-1965, P. J. Spangler, 1 female, 1 male. EL SALVADOR: San Vicente, Santo Domingo, XII-1966, F. S. Blanton, 1 female; same data except VIII-1967, 1 female. HONDURAS: 5 mi. W. Jicaro-Galant Jct., 9-VII-1965, P. J. Spangler, 1 female, light trap; Comayagua, Rancho Chiquito, V/VI-1964, F. S. Blanton, 2 females, 1 male; Comayagua, Siguatepeque, IX-1964, F. S. Blanton, 1 female; same data except IX-1966, 2 females; same data except V/VI-1966, J. F. Matta, 1 female; Comayagua, Comayagua, 29-VII-1966, J. F. Matta, 2 females; same data except IX-1966, F. S. Blanton, 1 male; Copan, Santa Rosa, 15-VI-1966, J. F. Matta, 1 male; same data except X-1966, F. S. Blanton, 3 females. MEXICO: Veracruz, Catemaco, 9-VIII-1964, P. J. Spangler, 7 females, light trap; Morelos, El Salto Falls, 17-VI-1969, W. & D. Haase, 1 female, 2 males, light trap. PANAMA: Chiriqui, El Hato, 16-VI-1964, F. S. Blanton, 1 female. U. S. A.: Texas, Real Co., Garner St. Park, 23-V-1972, W. W. Wirth, 1 female, light trap.

Discussion: This species is closely related to the Nearctic species *P. opaca* (Loew), from which it can be distinguished by the shorter antenna (antennal ratio 1.08 in *P. maya*, 1.82 in *P. opaca*), by the presence of 4-5 stout bristlelike setae on 5th tarsomere (3-4 in *P. opaca*), and by the stout tip of the aedeagus.

The species is named for the Mayan Indians, early inhabitants of the area of the type locality.

REFERENCES CITED

- DOWNES, J. A., AND W. W. WIRTH. 1981. Chapter 28. Ceratopogonidae. pp. 393-421. In: McAlpine, J. F., et al., Eds. Manual of Nearctic Diptera. Vol. 1, 674 pp.

- Agric. Canada Res. Br. Monogr. 27. Ottawa.
- HAESSELBARTH, E. 1965. *Phaenobezzia* a new genus of biting midges (Diptera: Ceratopogonidae), with a review of the African species. Ztschr. Angew. Zool. 52: 297-324.
- MALLOCH, J. R. 1915. The chironomidae, or midges, of Illinois, with particular reference to the species occurring in the Illinois River. Bull. Ill. St. Lab. Nat. Hist. 10: 275-543, 23 plates.
- REMM, H. 1974. A review of species of the genus *Bezzia* Kieffer (Diptera, Ceratopogonidae) from the fauna of the USSR. I. (In Russian, English summary; Ent. Obozr. 53: 429-442.
- WIRTH, W. W. 1973. Family Ceratopogonidae (Heleidae). pp. 346-388. In: Delfinado, M. D., and D. E. Hardy, Eds. A Catalog of the Diptera of the Oriental Region. Vol. I. Suborder Nematocera. 618 pp. Univ. Press of Hawaii, Honolulu.
- WIRTH, W. W. 1974. A catalogue of the Diptera of the Americas south of the United States. 14. Ceratopogonidae. Mus. Zool. Univ. São Paulo 14: 1-89.
- WIRTH, W. W., AND W. L. GROGAN, JR. 1982. The predaceous midges of the genus *Phaenobezzia* in North America (Diptera: Ceratopogonidae). Mem. Ent. Soc. Washington 10: 179-192.
- WIRTH, W. W., AND N. C. RATANAWORABHAN. 1981. New species and records of predaceous midges (Diptera: Ceratopogonidae) from rice paddies in Thailand. Pacific Ins. 23: 396-431.
- WIRTH, W. W., N. C. RATANAWORABHAN, AND D. H. MESSERSMITH. 1977. Natural History of Plummers Island, Maryland. XXII. Biting midges (Diptera: Ceratopogonidae) I. Introduction and key to genera. Proc. Biol. Soc. Washington 90: 615-647.

PHANEROTA CUBENSIS AND *PHANEROTA BRUNNESSA*
N.SP., WITH A KEY TO THE SPECIES OF *PHANEROTA*
OCCURRING IN FLORIDA (COLEOPTERA: STAPHYLINIDAE)

JAMES S. ASHE
Division of Insects
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605

ABSTRACT

Phanerota cubensis Casey, previously known only from Cuba, is reported from Florida, and a new species, *Phanerota brunnessa* n.sp., is described and illustrations of distinctive features are provided. A key for identification of the 5 species of *Phanerota* occurring in Florida is provided, and diagnostic characteristics of the species are discussed. Species of *Phanerota* can be distinguished primarily by differences in color pattern, sculpture and secondary sexual characteristics of males. Structure of the male copulatory organ is very similar among species and offers unreliable distinguishing characteristics for some species. Similarity in aedeagal form among *Phanerota* species, in contrast to the interspecific diversity of form among other gyrophaenine staphylinids, suggests that study of these groups may provide insight into evolution of isolating mechanisms among species.

RESUME

Phanerota cubensis Casey, previamente conocida solo de Cuba, se reporta en la Florida, y una nueva especie, *Phanerota brunnessa* n. sp., es descrita y se proveen

- Agric. Canada Res. Br. Monogr. 27. Ottawa.
- HAESSELBARTH, E. 1965. *Phaenobezzia* a new genus of biting midges (Diptera: Ceratopogonidae), with a review of the African species. Ztschr. Angew. Zool. 52: 297-324.
- MALLOCH, J. R. 1915. The chironomidae, or midges, of Illinois, with particular reference to the species occurring in the Illinois River. Bull. Ill. St. Lab. Nat. Hist. 10: 275-543, 23 plates.
- REMM, H. 1974. A review of species of the genus *Bezzia* Kieffer (Diptera, Ceratopogonidae) from the fauna of the USSR. I. (In Russian, English summary; Ent. Obozr. 53: 429-442.
- WIRTH, W. W. 1973. Family Ceratopogonidae (Heleidae). pp. 346-388. In: Delfinado, M. D., and D. E. Hardy, Eds. A Catalog of the Diptera of the Oriental Region. Vol. I. Suborder Nematocera. 618 pp. Univ. Press of Hawaii, Honolulu.
- WIRTH, W. W. 1974. A catalogue of the Diptera of the Americas south of the United States. 14. Ceratopogonidae. Mus. Zool. Univ. São Paulo 14: 1-89.
- WIRTH, W. W., AND W. L. GROGAN, JR. 1982. The predaceous midges of the genus *Phaenobezzia* in North America (Diptera: Ceratopogonidae). Mem. Ent. Soc. Washington 10: 179-192.
- WIRTH, W. W., AND N. C. RATANAWORABHAN. 1981. New species and records of predaceous midges (Diptera: Ceratopogonidae) from rice paddies in Thailand. Pacific Ins. 23: 396-431.
- WIRTH, W. W., N. C. RATANAWORABHAN, AND D. H. MESSERSMITH. 1977. Natural History of Plummers Island, Maryland. XXII. Biting midges (Diptera: Ceratopogonidae) I. Introduction and key to genera. Proc. Biol. Soc. Washington 90: 615-647.

PHANEROTA CUBENSIS AND *PHANEROTA BRUNNESSA*
N.SP., WITH A KEY TO THE SPECIES OF *PHANEROTA*
OCCURRING IN FLORIDA (COLEOPTERA: STAPHYLINIDAE)

JAMES S. ASHE
Division of Insects
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605

ABSTRACT

Phanerota cubensis Casey, previously known only from Cuba, is reported from Florida, and a new species, *Phanerota brunnessa* n.sp., is described and illustrations of distinctive features are provided. A key for identification of the 5 species of *Phanerota* occurring in Florida is provided, and diagnostic characteristics of the species are discussed. Species of *Phanerota* can be distinguished primarily by differences in color pattern, sculpture and secondary sexual characteristics of males. Structure of the male copulatory organ is very similar among species and offers unreliable distinguishing characteristics for some species. Similarity in aedeagal form among *Phanerota* species, in contrast to the interspecific diversity of form among other gyrophaenine staphylinids, suggests that study of these groups may provide insight into evolution of isolating mechanisms among species.

RESUME

Phanerota cubensis Casey, previamente conocida solo de Cuba, se reporta en la Florida, y una nueva especie, *Phanerota brunnessa* n. sp., es descrita y se proveen

ilustraciones de rasgos distintivos. Se da una clave para identificar las 5 especies de *Phanerota* que ocurren en la Florida, y se discuten características diagnósticas de las especies. Especies de *Phanerota* pueden ser distinguidas principalmente por diferencias en el patrón de color, la escultura, y las características sexuales secundarias de los machos. La estructura del órgano copulatorio del macho es muy similar entre las especies, y en algunas especies ofrece características que no se pueden utilizar con confianza para distinguirlas. Similarmente, en la forma aedeagal entre las especies de *Phanerote*, en contraste a la diversidad interespecifica de forma entre gyrophaenine staphylinids, sugiere que estudios de estos grupos pudiera dar un discernimiento de la evolución del mecanismo de aislamiento entre las especies.

The genus *Phanerota* Casey is one of the most distinctive aleocharine staphylinids found on fresh mushrooms in North America. Among gyrophaenine aleocharines, members of this genus are immediately recognizable by their extremely large bulbous eyes which take up virtually the entire lateral margins of the head. In addition, they have a number of apomorphic characteristics which clearly separate them from members of the genus *Gyrophaena* to which they are closely related (Ashe 1984).

Phanerota is primarily a tropical group with species occurring throughout the world in the tropics and subtropics and a few species in more temperate areas. At least 14 species which should be assigned to *Phanerota* have been described in the New World fauna, mostly in the genus *Gyrophaena*. All New World forms are in the subgenus *Phanerota* (see Ashe 1984). Seevers (1951) recognized 3 of these species in America north of Mexico. Remaining species occur in Mexico, Central America, South America or the West Indies, where, in addition, undescribed species exist.

Of the 3 species recognized by Seevers (1951) in America north of Mexico, 2 species, *P. fasciata* (Say) and *P. dissimilis* (Erichson) are broadly sympatric across the eastern half of North America south of 45° N latitude. Along the Gulf Coast and throughout Florida these 2 species are sympatric with a 3rd species, *P. carinata* Seevers, which is limited to this region.

In 1973 I collected a single male specimen of a *Phanerota* from a wood rat nest on Upper Key Largo, Florida. This specimen did not agree in color pattern or details of body sculpture with any known North American species. Some time later I was able to identify it as *P. cubensis* Casey by comparing it to type material in the Casey collection at the United States National Museum. Recently, Dr. Howard Frank, Florida Medical Entomology Lab, Vero Beach, Florida, sent me a number of specimens of *Gyrophaena* and *Phanerota* from Florida for identification. Among these were additional specimens of *P. cubensis*. Finally, while searching for other specimens of *P. cubensis* among undetermined *Phanerota* in the collections of the Field Museum of Natural History, I discovered a number of highly distinctive dark brown specimens of *Phanerota* from Florida. Comparisons with specimens of all species of *Phanerota* described from the New World in the collection of the Field Museum showed it to be an undescribed species. This increases the known *Phanerota* fauna of America north of Mexico from 3 to 5 species, all of which are sympatric in Florida.

The purposes of this paper are to report the occurrences of the West Indian species *P. cubensis* in Florida, to provide diagnostic characteristics for recognition of this species, to report on the known distribution of *P. cubensis* in Florida and the West Indies, to describe a new species of *Phanerota* from Florida, and to provide a key to the 5 species of *Phanerota* known to occur in Florida. Specimens discussed are in the collections of the Field Museum of Natural History (FMNH) or the private collection of Dr. Howard Frank, Florida Medical Entomology Lab, Vero Beach, Fla., (HF).

Phanerota cubensis Casey

Phanerota cubensis Casey, 1906, p. 228. Leng and Mutchler, 1914, p.407. Seevers, 1951, p.747.

Gyrophaena cubensis (Casey), Fenyés, 1918-21, p.97. Bernhauer and Scheerpeltz, 1926, p.527. Blackwelder, 1943, p.541.

Diagnosis.—The description of *P. cubensis* provided by Casey (1906) within his key to the species of *Phanerota* is essentially correct in the characters he discusses. *P. cubensis* may be distinguished from all other North American *Phanerota* by the combination of: body flavate to rufo-flavate; head, posterior 0.50-0.75 of elytra and abdominal terga 5-10 (or 6-10) black to dark piceous; elytra rufo-flavate to testaceous in antero-lateral 0.50-0.25 to medial margin at, or slightly posterior to, scutellum; antenna and legs flavate; antenna with article 4 slightly elongate, 5-10 more or less quadrate; head with moderate reticulate microsculpture; pronotum slightly to obsoletely reticulate; elytra with reticulate microsculpture, slightly transverse in some specimens; abdomen moderately reticulate. Secondary sexual characteristics of male with posterior margin of tergum VIII broadly sinuate, lateral margins of sinuation more or less prolonged as blunt spines, sinuation internally with very slight (0.05 times length of lateral margins of sinuation) to slight (0.25 times length of lateral margins) broad lobe; some males with lateral margins of sterna III and IV very slightly thickened and slightly spiniform posteriorly and/or very slight broad elevation near apico-lateral margins of elytra (absent in most); aedeagus similar to that of *Phanerota fasciata* (Say) (Figures 9A,B, and Seevers 1951, p. 748, Figure 123). Female with apex of tergum VIII broadly, shallowly sinuate, sinuation without broad lobe medially.

Distribution in Florida.—Known in the United States from specimens from the following localities. FLORIDA, Dade County. Matheson Hammock, 22-XI-1975, Coll. M.C. Thomas (2) (HF); Monroe Co., Upper Key Largo, 24-III-1973, J.S. Ashe, berlese from wood rat nest (1) (FMNH).

Comments.—*Phanerota cubensis* is distinctive and easily recognized among North American *Phanerota* by the dark apical segments of the abdomen and more extensive dark areas of the elytra. All other North American members of *Phanerota* have at least the apex of the abdomen and medial margins of the elytra light.

Casey (1906) gives the known distribution of *P. cubensis* as Cuba (Cayamas). This distribution is repeated by Blackwelder (1943). In addition to the specimens from Florida noted above I have seen additional specimens from Cuba (FMNH) and from several localities in Jamaica (HF).

Phanerota brunnessa new species

(Fig. 1-7)

Length 1.8-2.3mm. Coloration of body brown to piceous-brown, many specimens with head, outer apical 0.5-0.3 of elytra and abdominal tergum VI, and, in a few specimens, terga V, VI and anterior margin of VII, darker, piceous-brown. Punctuation and setation throughout body very sparse, body subglabrous, shining; head with 12-14 large, widely scattered setigerous punctures in each half; punctures of pronotum small to minute, distant, widely scattered, microsetae very sparse and fine, pronotum subglabrous, macrosetae small to moderate in size; elytra with microsetae sparsely scattered, punctures moderate to fine, uniformly scattered; abdomen with punctures and microsetae very widely scattered and fine, subglabrous. Sculpture of head and pronotum without isodiametric reticulate microsculpture, integument smooth, markedly shining; elytral microsculpture various, moderately developed to obsoletely reticulate, reticulations slightly to moderately transversely elongated, a few specimens with reticulate

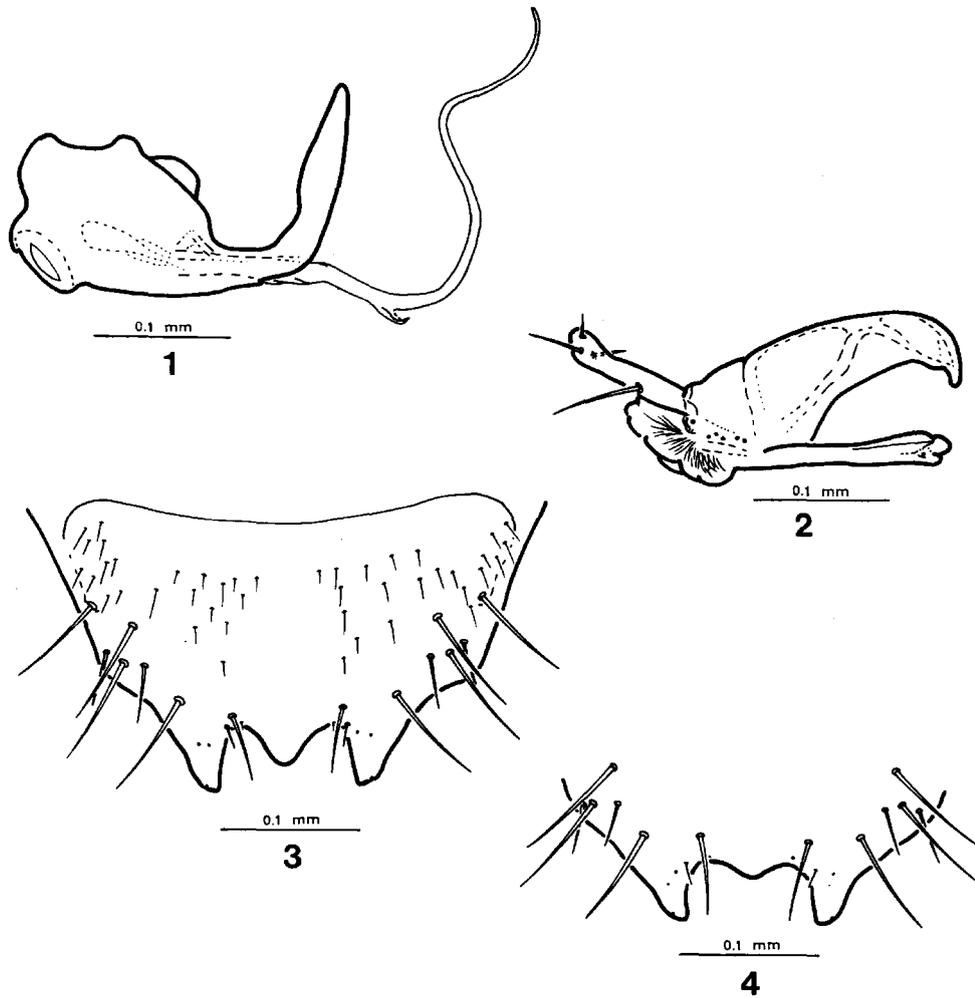


Fig. 1-4. *Phanerota brunnessa* n. sp. 1, aedeagus, median lobe, lateral aspect; 2, aedeagus, paramere, internal aspect; 3, male, abdominal tergum VIII; 4, male, distal margin of abdominal tergum VIII showing variant structure of secondary sexual characteristics.

microsculpture absent and integument strongly shining; abdomen with microsculpture obsolete to moderately developed.

Head, including eyes, 0.9-1.0 times as wide as pronotum; eyes typical of genus, very large, bulbous, occupying entire lateral margins of head from tempora to insertion of mouthparts; interocular width to total head width (including eyes) 0.52-0.54; infraorbital carina moderately developed, complete, forming ventral margin of eyes. Antenna (Fig. 5) with antennomeres 1-3 elongate, 4 about 1.3 times as long as wide, 5-10 about equal in length and progressively increasing slightly in width from basal to distal articles; antennomere 5 quadrate, about as long as wide; antennomere 10 slightly transverse, about 0.8-0.9 times as long as wide. Hind tarsus with tarsomere 1 about 1.3 times as long as 2. Abdomen with tergum VII broadly and very shallowly concave dorso-medially.

Male: (Fig. 1-4) Posterior margin of tergum VIII broadly emarginate medially, emargination flanked by broad blunt tooth on each side, emargination internally with slight (about 0.25 times length of lateral margins) to marked (about 0.85 times length lateral

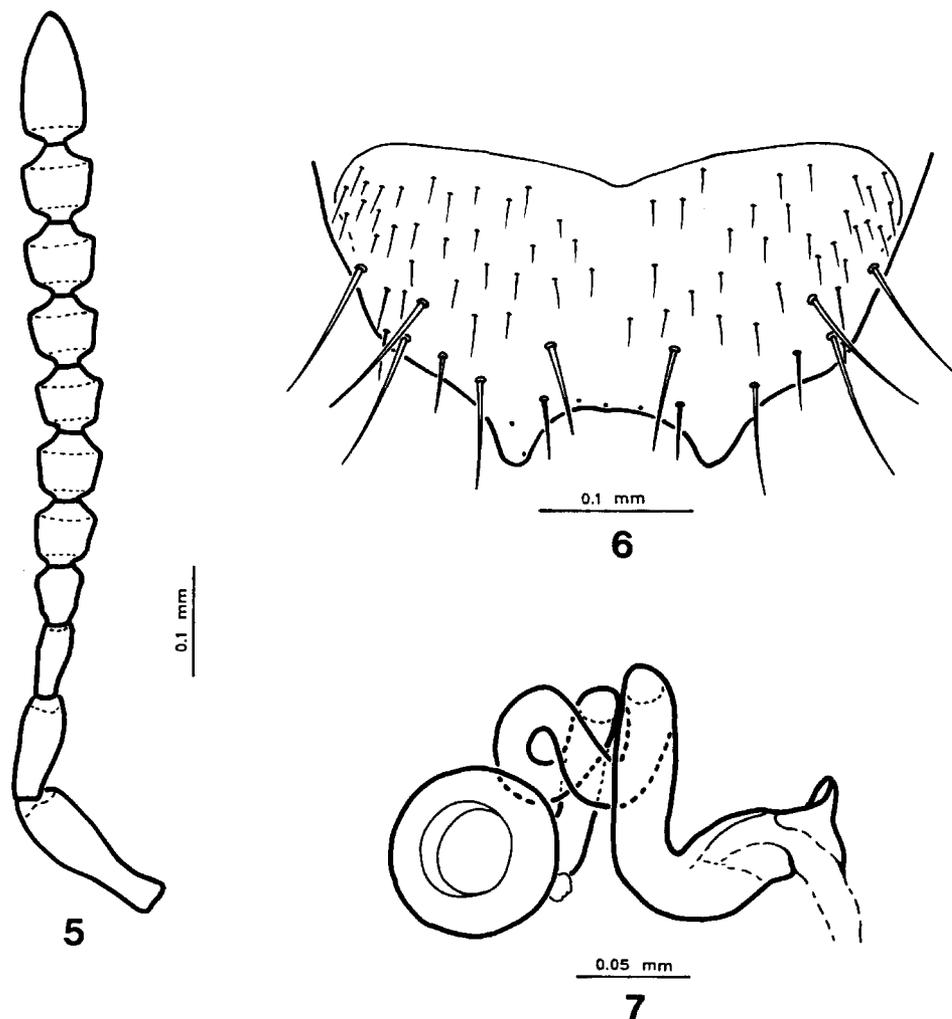


Fig. 5-7. *Phanerota brunnessa* n. sp. 5, antenna; 6, female, abdominal tergum VIII; 7, spermatheca.

margins) broad lobe medially, lobe broadly rounded to bluntly pointed apically (Fig. 3,4). Elytral punctures slightly to markedly asperate; some specimens with distinct, blunt, more or less elongate elevation in latero-apical third of elytra and smaller more flattened elevation in medio-apical third; elytral modifications absent in some and various among individuals from without elytral elevations to elevations prominent. Lateral margins of abdominal sternum III unmodified to postero-lateral margins thickened and slightly spiniform. Aedeagus distinctive; parameres as in Fig. 2, median lobe as in Fig. 1; median lobe markedly sclerotized, piceous-brown.

Female: Posterior margin of tergum VIII broadly emarginate medially, lateral margins of emargination not produced to prominent broad, blunt teeth (Fig. 6); emargination internally without medial lobe. Spermatheca as in Fig. 7.

Type.—Holotype, male and allotype, female, each with labels as follows: USA: Fla., Leon Co., Tallahassee, 8-IV-1976, mixed hardwood litter, C.W. O'Brien & Marshall/HOLOTYPE ♂ (on ALLOTYPE ♀.) *Phanerota brunnessa*, desig. 1985, J. S. Ashe. Both holotype and allotype are deposited in the collection of the Field Museum of

Natural History, Chicago, Illinois.

Paratypes. 22, Deposited in the collection of the Field Museum of Natural History, Chicago. FLORIDA, Leon Co., Tallahassee, 19-IX-1977, mixed hardwood litter, C. W. O'Brien et al, 1 male; Tallahassee, 8-IV-1976, mixed hardwood litter, C. W. O'Brien & Marshall, 4 males, 3 females (2 males, 1 female on microslides); Tall Timbers Research Sta., Woodyard Hammock, 31-V-1977, beech-magnolia litter, C. W. O'Brien and Wibmer, 1 female; Lafayette Co., 10 mi. NW Mayo, hwy. 27, 24-V-1977, mixed hardwood litter, C. W. O'Brien, et al, 3 males, 3 females; GEORGIA; Decatur Co., 4 mi. N Faceville, 28-II-1977, hardwood litter, C. W. O'Brien & Marshall, 5 males, 2 females.

Distribution.—This new species is only known from localities in northwestern Florida in Leon and Lafayette Counties and an adjacent locality in southwestern Georgia in Decatur County.

Habitat.—Specimens of this species have only been collected in relatively short series from litter associated with mixed hardwoods. All *Phanerota* for which adequate natural history information is available are known to be obligate inhabitants of fresh mushrooms (Ashe 1984). It seems reasonable to expect that members of *P. brunnessa* are likewise fungicolous, though this association requires confirmation. Specimens have been collected in February, April, May and September.

Etymology.—The name of this species is chosen to reflect the distinctive brown color of the body (from medieval latin, *brunneus* = brown).

Remarks.—Specimens of *Phanerota brunnessa* are easily distinguished from all other known North American *Phanerota* (and all described New World species) by the distinctive uniformly brown to piceous-brown color of the body. The median lobe of the aedeagus is also unusual among those of North American *Phanerota* because it differs from the relatively uniform structure of the aedeagus found among males of other species. Differences in the median lobe of the aedeagus of *P. brunnessa* in comparison to those of other species are slight but easily distinguishable. Distinctive characteristics include the dark brown and relatively heavily sclerotized nature of the median lobe, the more sharply upturned apical process (more nearly approaching a 90° angle with the basal bulb) without a recurved apex, and the slightly longer flagellum (compare Figures 1 and 9A).

Males show a great diversity of secondary sexual characteristics. Relative development of these characteristics appears to be correlated among most males; most males with a larger lobe in the emargination of tergum VIII usually also have more asperite elytra with more prominent apico-lateral elevations and modification of the postero-lateral margins of abdominal sternum III to slightly thickened and spiniform processes.

Key to the species of *Phanerota* occurring in Florida

Seevers (1951) gives keys and descriptions for four species of *Phanerota*, including *P. fasciata* (Say), *P. dissimilis* (Erichson) and *P. carinata* Seevers, all of which are found in Florida. The key presented here is a modification of his key to include other species and use additional distinguishing characteristics.

Discrimination of species of *Phanerota* is based primarily on differences in color pattern and sculpture. These features show little overlap among most species. Structure of the male copulatory organ is very similar among species of this genus and offers unreliable or difficult species discrimination in most instances. However, aedeagi are at least marginally useful for some species and can be used to eliminate some alternative choices even when aedeagal characteristics overlap broadly. Therefore, they are included in the key presented here.

1. Ground color of body brown to piceous-brown or testaceous 2
- 1'. Ground color of body rufo-flavate to flavate 3
2. Head microsculpture smooth, not reticulate; ground color of body brown to piceous-brown throughout with head, outer apical angle of elytra and abdominal tergum 6 (or 5-7) darker piceous-brown in some; aedeagus as in Figure 1 *P. brunnessa* new species
- 2'. Head microsculpture reticulate; ground color of body testaceous, with head, postero-lateral 0.7-0.5 of elytra and abdominal terga 5-9 dark; aedeagus similar to Figure 9A *P. dissimilis* (Erichson)
3. Head microsculpture moderately reticulate; ground color of body flavate; elytra dark in outer apical 0.7-0.5 to near scutellum medially; abdominal terga 6-10 (or 5-10) dark; elytra of males without distinct carina near apico-lateral margin (slight broad elevation may be present in some males); aedeagus similar to Figures 9A,B *P. cubensis* Casey.
- 3'. Head microsculpture smooth, or, at most obsoletely reticulate; ground color of body flavate to rufo-flavate; elytra dark in apico-lateral 0.5-0.3 to near postero-apical angles medially, or dark color not extended to medial margin; terga 7 or 6-8 dark; elytra of males with or without distinct carina near apico-lateral margin 4
4. Elytra of most males with distinct spiniform carina near apico-lateral border; aedeagus as in Figures 8A-C *P. carinata* Seevers
- 4'. Elytra of males without distinct spiniform carina near apico-lateral border (slight to distinct elevation may be present in some males); aedeagus as in Figures 9A-D *P. fasciata* (Say)

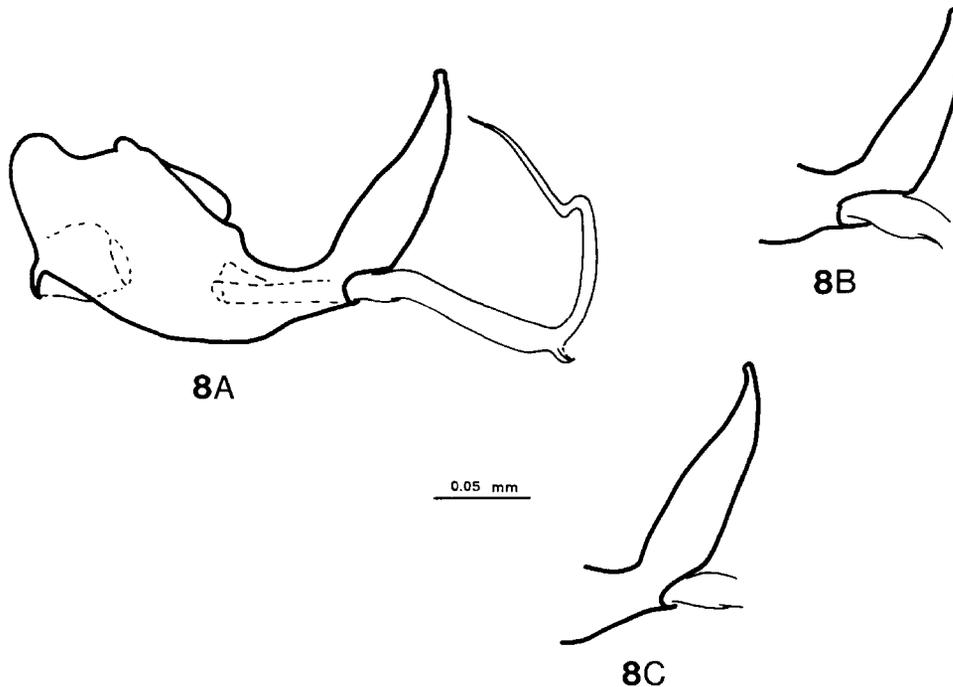


Fig. 8A-C. *Phanerota carinata* Seevers, aedeagus. 8A, medial lobe, lateral aspect; 8B-C, variant forms of apical process of median lobe.

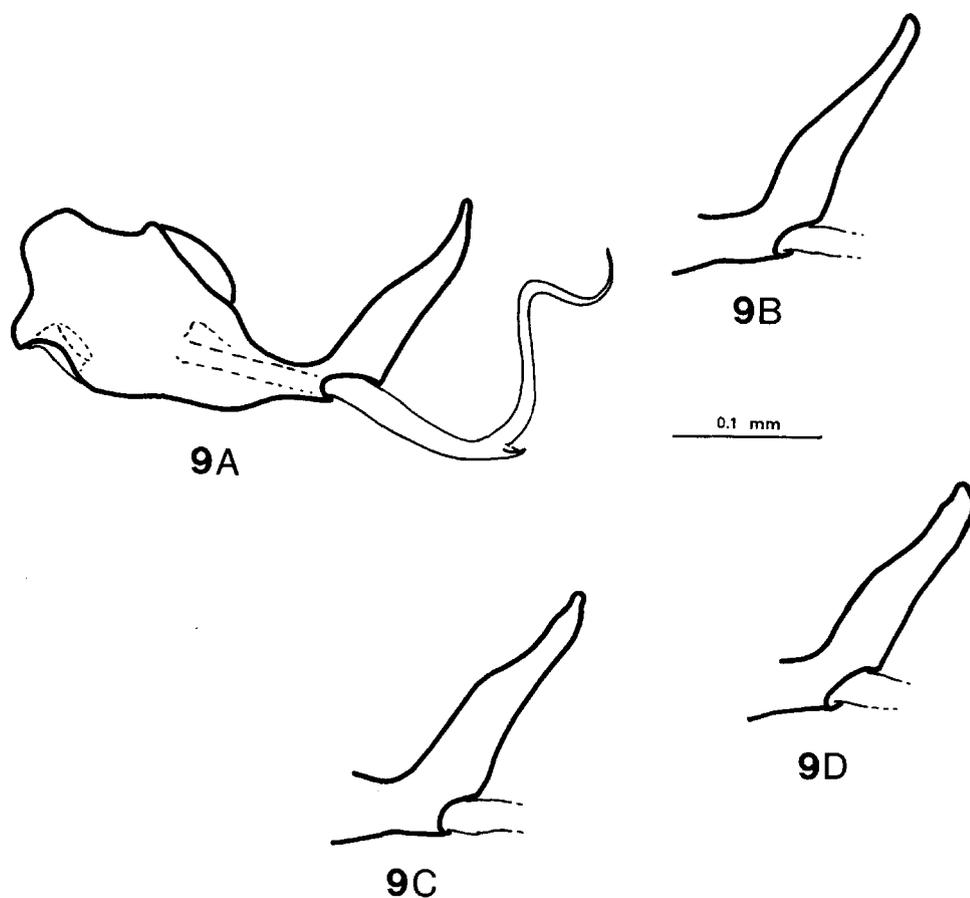


Fig. 9A-D. *Phanerota fasciata* (Say), aedeagus. 9A, median lobe, lateral aspect; 9B-D, variant forms of the apical process of the median lobe.

DISCUSSION

The addition of 2 species, *P. cubensis* and *P. brunnessa* to the *Phanerota* fauna of Florida increases the number of species known from that state to five, the maximum diversity of *Phanerota* of any area of America north of Mexico.

Members of *Phanerota* are unusual among gyrophaenine staphylinids because they must be distinguished primarily by differences in color pattern, sculpture and secondary sexual characteristics of males. The highly distinctive interspecific differences of the male copulatory organ, so characteristic of members of the closely related genus *Gyrophaena*, are not evident among species of *Phanerota*.

This paucity of reliable aedeagal characteristics is evident in the key provided above as well as in the treatment of *Phanerota* by Seevers (1951), and caused Seevers considerable uncertainty about whether some available morphs of *Phanerota* actually represented distinct species. Reexamination of material considered by Seevers as well as newly acquired material has revealed small, but distinguishable, variation in aedeagal structure among some species. For other species color pattern appears to be a reliable distinguishing feature.

Among the *Phanerota* of Florida, specimens of *P. brunnessa* are the most easily distinguished, both because of the brown or piceous-brown color pattern and because

of the relatively distinctive aedeagus. Males of *P. cubensis* and *P. dissimilis* have aedeagi which fall within the range of variation of those of males of *P. fasciata*. However, all specimens of these 2 species can be easily distinguished from those of other *Phanerota* and each other by the characteristics of color pattern and sculpture given in the key.

Separation of specimens of *P. fasciata* and *P. carinata* is a particular problem. Seevers (1951) noted that most males of *P. carinata* are readily recognizable from those of all other North American *Phanerota* by presence of a prominent carina near the apico-lateral border of the elytra. However, a few males lack this feature. Seevers also noted that most specimens of *P. carinata* have a slightly more rufous ground body color and somewhat more extensive dark areas on the elytra and abdomen; however, specimens of these two species overlap broadly in these characteristics and cannot be reliably distinguished by color. Under these circumstances, isolated females and non-carinate males of *P. carinata* may be impossible to identify.

Seevers did not recognize any differences in the median lobe of aedeagi of males of *P. carinata* and *P. fasciata*. However, reexamination of Seevers material shows that slight, but in most instances recognizable, differences exist (compare Figures 8A-C and 9A-D). Apical processes of aedeagi of *P. carinata* are relatively more robust and broader basally and lack the attenuate and recurved apex characteristic of those of *P. fasciata*. However, at the extremes of variation these are structurally very similar (compare Figures 8C and 9A). Therefore, it is not possible to identify all males of these 2 species based on aedeagus alone.

Sympatry of a number of species of *Phanerota*, all of which are distinct in external characteristics, but which can either not be distinguished or only marginally distinguished by differences in the male copulatory organ, suggests questions about the isolating mechanisms by which these species maintain their distinctness. Unfortunately, too little is known about habits and life histories of most *Phanerota* for this question to be addressed effectively at this time. Ashe (1982) documented a distinct separation of adults of *P. fasciata* and *P. dissimilis* on different host mushrooms which provided support for the hypothesis that these represent distinct species. In addition, after evaluating a number of possible isolating mechanisms, he suggested that isolation on different breeding hosts was implicated as a possible premating mechanism responsible for limiting interbreeding between members of these two species. However, other possible isolating factors could not be eliminated based on available information.

Host relationships of most species of *Phanerota* have not been investigated and information about other ecological factors that might have bearing on this problem are equally lacking. The problem of isolating mechanisms among species of *Phanerota* without marked divergence of aedeagal form is especially interesting since members of the very closely related genus *Gyrophaena* exhibit great interspecific variation in this structure, associated with little external structural diversification in many instances. These contrasts between apparent primary modes of modification in closely related groups provide excellent opportunity to investigate comparatively the factors responsible for development of different approaches to limiting hybridization between species.

ACKNOWLEDGEMENTS

I thank Dr. Howard Frank, Florida Medical Entomological Lab, Vero Beach, Florida, for loan of specimens of *Phanerota cubensis* as well as other gyrophaenines and for numerous other courtesies.

REFERENCES CITED

- ASHE, J. S. 1982. Evidence on the species status of *Phanerota fasciata* (Say) and *Phanerota dissimilis* (Erichson) from host mushroom relationships. Coleopt.

- Bull. 36(2): 155-161.
- ASHE, S. 1984. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of described subgenera and major features of evolution. *Questiones Entomologicae* 20(3): 129-349.
- BERNHAEUER, M. AND O. SCHEERPELTZ. 1926. *Coleopterorum catalogus*. Pars 82, Staphylinidae 6: 499-988.
- BLACKWELDER, R. E. 1943. Monograph of the West Indian beetles of the family Staphylinidae. U. S. Natl. Mus. Bull. 182: 1-658.
- CASEY, T. L. 1906. Observations on the staphylinid groups Aleocharinae and Xantholinini, chiefly of America. *Trans. Acad. Sci. St. Louis* 16: 125-434.
- FENYES, A. 1918-21. *Coleoptera*. Subfamily Aleocharinae. *Genera Insectorum* 173. Pasadena, Calif. 453 pp.
- LENG, C. W. AND A. J. MUTCHLER. 1914. A preliminary list of the Coleoptera of the West Indies as recorded to Jan. 1, 1914. *Bull. American Mus. Nat. Hist.* 33: 391-493.
- SEEVERS, C. H. 1951. A revision of the North American and European staphylinid beetles of the subtribe Gyrophaenae (Aleocharinae: Bolitocharini). *Fieldiana: Zoology* 32: 659-762.

LEG ABCISSION AND ADULT *DOLANIA* (EPHEMEROPTERA: BEHNINGIIDAE)

JANICE G. PETERS AND WILLIAM L. PETERS
Department of Entomology and Structural Pest Control
Florida A&M University, Tallahassee, FL 32307 USA

ABSTRACT

Legs of male imagos and female subimagos of *Dolania americana* Edmunds and Traver are described. Distal segments of meso- and metathoracic legs of males break during the subimaginal molt and remain in the cast exuviae. Leg abscission is probably a method to ensure rapid completion of the subimaginal stage in this short-lived mayfly.

RESUMEN

Se describen las patas de los imagos machos y los subimagos hembras de *Dolania americana* Edmunds y Traver. Los segmentos distales de las patas meso- y metatorácicas de los machos se rompen durante la muda subimaginal y permanecen en la exuvia. La abscisión de las patas es probablemente un método que asegura la conclusión rápida del estado subimaginal en esta efímera de vida de la mosca de mayo.

The descriptions of male imagos and female subimagos of *Dolania americana* Edmunds and Traver, the only North American member of the Behningiidae, have been published in parts. The wings, male genitalia, and female subimaginal head are illustrated in Edmunds *et al.* (1976), and the female abdomen and fore legs in Peters & Peters (1977). The only formal description of any adult behningiid is that for *Behningia lestagei* (?) Motas and Bacesco by Keffermüller (1959).

Herein, we describe the legs of subimagos and imagos of *Dolania*. Interestingly, the tarsi and claws of the meso- and metathoracic legs of the male imago are rarely attached

- Bull. 36(2): 155-161.
- ASHE, S. 1984. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of described subgenera and major features of evolution. *Questiones Entomologicae* 20(3): 129-349.
- BERNHAEUER, M. AND O. SCHEERPELTZ. 1926. *Coleopterorum catalogus*. Pars 82, Staphylinidae 6: 499-988.
- BLACKWELDER, R. E. 1943. Monograph of the West Indian beetles of the family Staphylinidae. U. S. Natl. Mus. Bull. 182: 1-658.
- CASEY, T. L. 1906. Observations on the staphylinid groups Aleocharinae and Xantholinini, chiefly of America. *Trans. Acad. Sci. St. Louis* 16: 125-434.
- FENYES, A. 1918-21. *Coleoptera*. Subfamily Aleocharinae. *Genera Insectorum* 173. Pasadena, Calif. 453 pp.
- LENG, C. W. AND A. J. MUTCHLER. 1914. A preliminary list of the Coleoptera of the West Indies as recorded to Jan. 1, 1914. *Bull. American Mus. Nat. Hist.* 33: 391-493.
- SEEVERS, C. H. 1951. A revision of the North American and European staphylinid beetles of the subtribe Gyrophaenae (Aleocharinae: Bolitocharini). *Fieldiana: Zoology* 32: 659-762.

LEG ABCISSION AND ADULT *DOLANIA* (EPHEMEROPTERA: BEHNINGIIDAE)

JANICE G. PETERS AND WILLIAM L. PETERS
Department of Entomology and Structural Pest Control
Florida A&M University, Tallahassee, FL 32307 USA

ABSTRACT

Legs of male imagos and female subimagos of *Dolania americana* Edmunds and Traver are described. Distal segments of meso- and metathoracic legs of males break during the subimaginal molt and remain in the cast exuviae. Leg abscission is probably a method to ensure rapid completion of the subimaginal stage in this short-lived mayfly.

RESUMEN

Se describen las patas de los imagos machos y los subimagos hembras de *Dolania americana* Edmunds y Traver. Los segmentos distales de las patas meso- y metatorácicas de los machos se rompen durante la muda subimaginal y permanecen en la exuvia. La abscisión de las patas es probablemente un método que asegura la conclusión rápida del estado subimaginal en esta efímera de vida de la mosca de mayo.

The descriptions of male imagos and female subimagos of *Dolania americana* Edmunds and Traver, the only North American member of the Behningiidae, have been published in parts. The wings, male genitalia, and female subimaginal head are illustrated in Edmunds *et al.* (1976), and the female abdomen and fore legs in Peters & Peters (1977). The only formal description of any adult behningiid is that for *Behningia lestagei* (?) Motas and Bacesco by Keffermüller (1959).

Herein, we describe the legs of subimagos and imagos of *Dolania*. Interestingly, the tarsi and claws of the meso- and metathoracic legs of the male imago are rarely attached

to the mayfly. They can be found in subimaginal exuviae, having broken off during the molt (parts of cerci may also break off). Fore legs are intact and functional in all stages. Descriptions of the reconstructed legs follow based on specimens in alcohol:

Male imago (Fig. 1-2). Prothoracic legs (Fig. 1-Im-I): tibiae a little longer than femora; tarsi one-segmented, sometimes with annulated appearance, a little less than 0.5 length of tibiae. Mesothoracic legs (Fig. 1-Im-II): tibiae a little shorter than femora; tarsi 2-segmented, segment one a little longer than tibiae, segment 2 about 0.25 length of segment 1. Metathoracic legs (Fig. 1-Im-III A): coxae well developed, elongated; tibiae small, less than 0.25 length of femora; tarsi 2-segmented, segment one 5-6 times length of tibiae, segment 2 about equal length of tibiae. Claws of all legs consisting of very small dactyl only (Fig. 2). Coxae, trochanters and base of femora of pro- and mesothoracic legs with well sclerotized areas, sclerotized rod along mid-line of coxae-trochanters of metathoracic legs weak in some specimens; femora of prothoracic legs with a well sclerotized macula at apex, remaining segments weakly sclerotized; femora and remaining segments of meso- and metathoracic legs variable, weakly sclerotized to membranous, tarsi and claws often flagellar, tarsi and claws usually separated from tibiae near base of tarsi; *if abscised*, tibiae and femora of mesothoracic legs and all remaining segments of metathoracic legs contracted, sometimes distorted to unrecognizable (Fig. 1-Im-III B).

Male subimago (Fig. 1-Sb). Legs similar to those of male imago except: tibiae and tarsi of prothoracic legs shorter, a membranous extension present on mesothoracic tibiae, and claws of meso- and metathoracic legs bulbous. All segments distinct and sclerotized to some degree.

Female subimago (Fig. 3). Coxae, trochanters, and femora of all legs similar to those of male imago; tibiae of prothoracic legs less than 0.25 length of femora, sometimes appearing fused with tarsi; tibiae of mesothoracic legs shorter than femora, membranous except at base, with apical membranous extension; tibiae of metathoracic legs less than 0.33 length of femora; tarsi of all legs membranous, flagellar, variable; claws absent or appearing as weak annulation at apex of membranous tarsi in some specimens.

Recent studies by Dr. E. L. Smith have homologized insect leg segments with those of other arthropods (Snodgrass 1935). Kukalová-Peek (1983, 1985) used this terminology for Paleodictyoptera and fossil mayflies; in fact, the patella was first discovered in fossil insects by Kukalová (1970, 1971). Some terms are applicable to recent mayflies, particularly the segmentation of the fused patello-tibia (commonly called the tibia). The separation of the male leg segments of *Dolania* occurs either at the patello-tibial suture or distal to the tibia (basitarsus is fused to tibia). Dr. Smith (pers. comm.) also notes that "claws" of male imagos and subimagos consist only of dactyls, and that annulations of the male prothoracic tarsi represent vestiges of tarsal segmentation.

We examined meso- and metathoracic legs of 324 male imagos collected in 8 samples on 6 days and found 5.6% ($5.7 \pm 4.6\%$) had one intact leg: 4 retained a mesothoracic leg and 14 retained a metathoracic leg, but none had more than 1. Quantitative exuvial results are not included because the exuviae of subimagos are fragile and many legs were broken off.

From the description by Keffermüller (1959) and specimens we have seen, the abscission of the meso- and metathoracic tarsi and claws also occurs in male imagos of *Behningia* and may be a derived character of the family; however, imagos of a 3rd genus, *Protobehningia*, are unknown (Tshernova & Bajkova 1960). Leg abscission does not occur in males of most other genera of short-lived adult mayflies examined (*Homoeoneuria*, *Tortopus*, *Ephoron*, *Caenis*, *Brachycercus*, *Tricorythodes*) although segments of these legs are sometimes membranous and apparently non-functional. However, as mentioned by Needham & Murphy (1924), the meso- and metathoracic legs of males and females of *Campsurus* are reduced to stubs showing the "coxa, trochanter,

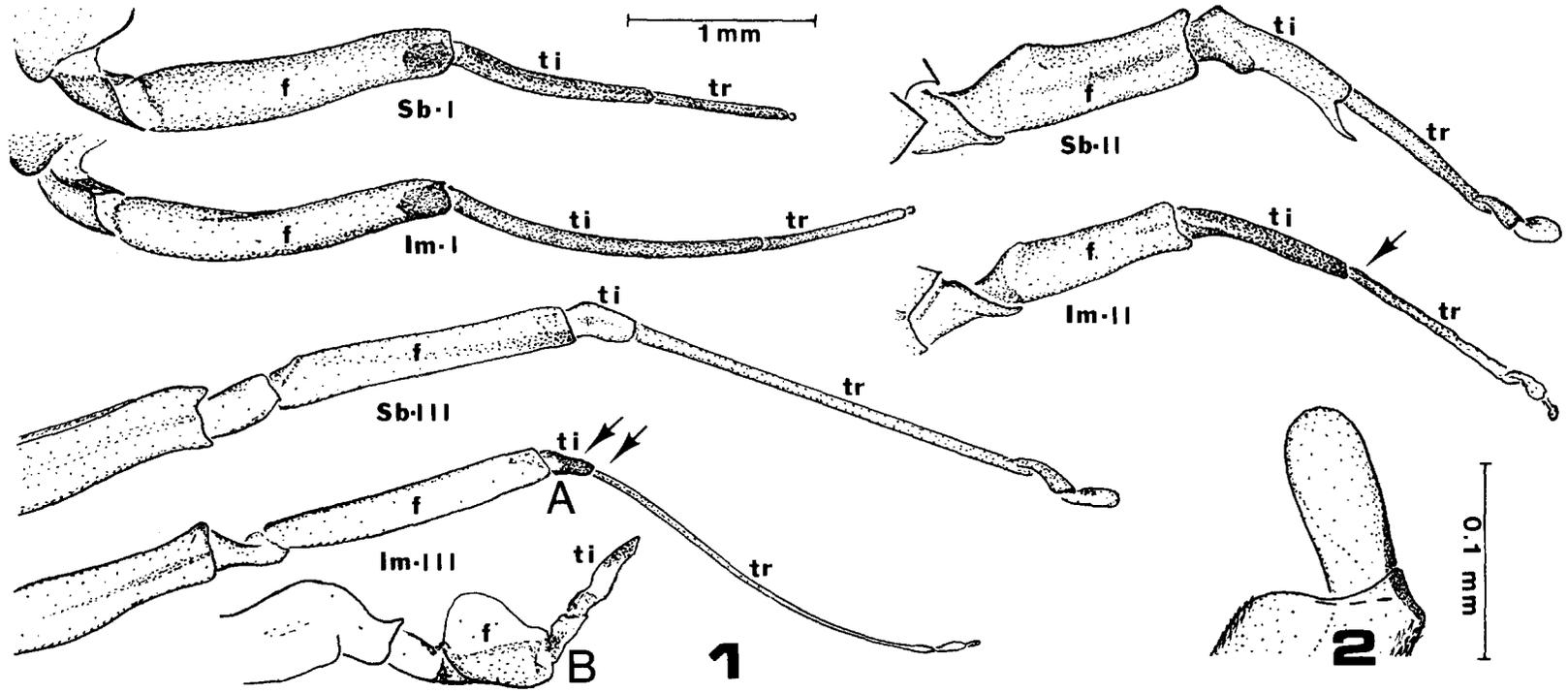


Fig. 1. Pro- (I), meso- (II), and metathoracic (IIIA without, IIIB with abscission) legs of male *D. americana*: Sb, subimago; Im, imago. Arrows mark points of abscission. Abbreviations: f=femur, ti=tibia, tr=tarsal segments.

Fig. 2. Fore claw of male imago.

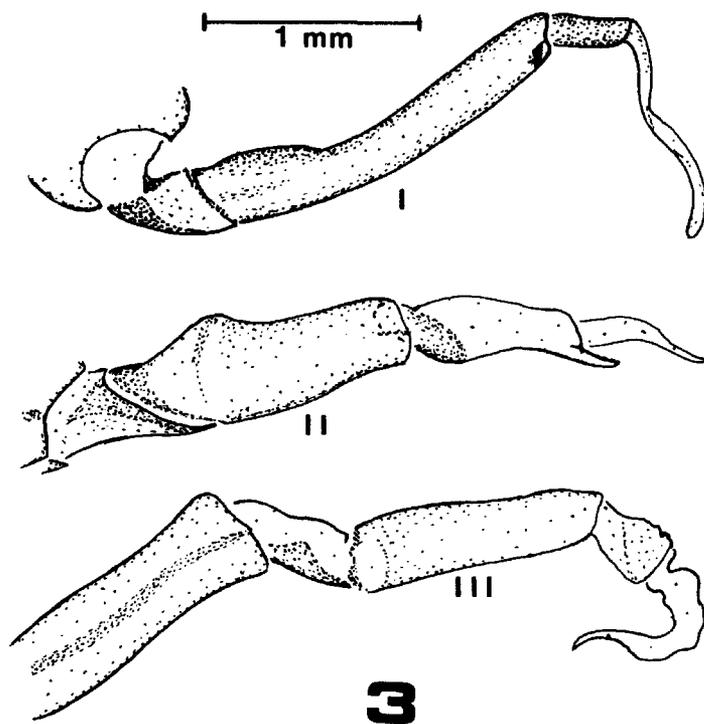


Fig. 3. Legs of female subimago of *D. americana*. Legend as in Fig. 1.

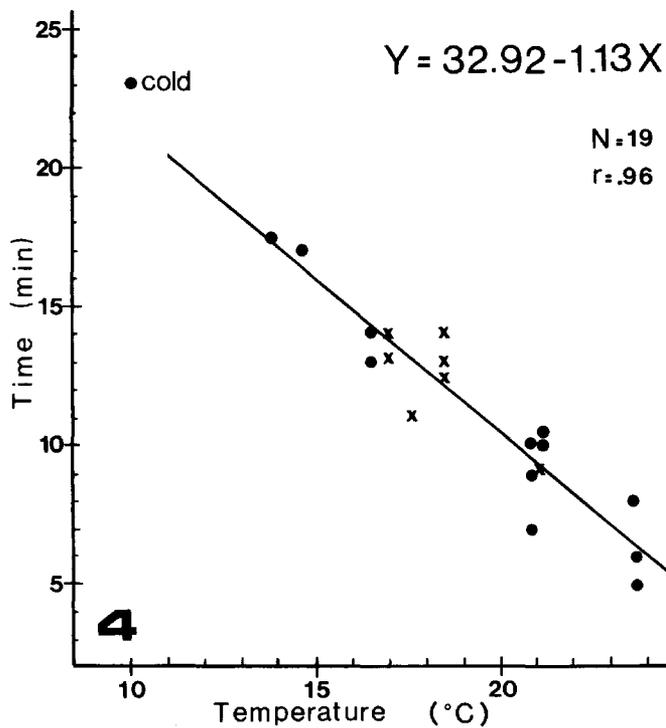


Fig. 4. Duration of male subimago of *D. americana*. Regression was computed from reared material (X) and 1983-1984 field-collected material (solid circles), except for molt labeled "cold" as discussed in text.

and a rudiment of the femur." The biology of *Campsurus* is little studied and it is not known if this condition results from abscission.

Functional segmented legs with full claws are the ancestral condition in mayflies (Kukalová 1968, Kukalová-Peck 1985). Legs of *Dolania* nymphs and female subimagos have either weak annulations at the apex of tarsi or no claws at all, and legs of females differ from those of nymphs mostly in the membranous condition of distal segments (Fig. 3). The fore legs of the male imago appear functional and all segments are present (tarsal segments fused); the male imago flies from completion of the subimaginal molt until death and has no apparent use for meso- and metathoracic legs however, we have no information on possible aerodynamic advantages resulting from abscission. Only the male subimago retains anything resembling the ancestral, functional, segmented leg.

The life span of subimagos is temperature dependent (Lyman 1944, Thomas 1969). The subimago of male *D. americana* lasts from 5 to 23 min. and is linearly correlated with temperature at temperatures above 11°C (Fig. 4). The regression line in Fig. 4 was computed for reared subimagos ("X" in Fig. 4) and for field-collected subimagos for 1983-1984 (solid circles) where temperatures were recorded by a thermometer with a small probe (accuracy $\pm 0.1^\circ\text{C}$) laid next to the molting mayfly and where specimens were not touched. Time was recorded from emergence to completion of the subimaginal molt, as measured as the time the imaginal wings came free from the exuviae. In general, the equation $[30 - X(\text{air temperature in } ^\circ\text{C})]$ will give duration of the subimago stage of males in minutes.

The molt labeled "cold" in Fig. 4 was not included in the regression line because molting success is greatly reduced at 10.2°C. Of 36 male subimagos observed, only 20 were able to complete the molt at that temperature. These males were on sand some distance from the river, the sand being warmer than the air (air temperature was 8°C). Another group of male subimagos (>70) attracted to light on wet sand at the shoreline molted successfully; there, the sand had been warmed by river water to 11.2 to >12°C.

Thus, in about 15 min. the male *Dolania* is in 3 life history stages. Male meso- and metathoracic legs progress from a derived nymphal state (no claws) to an ancestral subimaginal state (functional legs with claws) to a derived imaginal state (no legs). The retention of the ancestral condition in the intermediate instar suggests that functional male subimaginal legs are critical to the species. While the possibility of an in-flight molt for *Dolania* is not totally rejected (Peters & Peters 1977), it seems most improbable considering these morphological steps. Subimagos of most mayfly genera, except some Oligoneuriinae, must interrupt flight to molt (Edmunds 1956).

When reared in the laboratory, *Dolania* subimagos flew from the water surface to the nearest perch and remained there until the imaginal molt. A shortage of supporting field observations of subimagos on vegetation results from inadequate light for observation, the subimago living sometime between 1.5 to 0.75 h before sunrise. Some males do molt on the water, but this is less common and may be accidental.

Speculation on an in-flight molt resulted from observations of subimaginal exuviae on trailing caudal filaments of imagos. This occurs because the male takes flight as soon as the wings are free (the exuvia will eventually fall off) and reflects not on subimaginal, but on male imaginal behavior.

Reproductive stages of *D. americana* emerge synchronously and mate in the air in mass swarms. Although many mayflies are capable of parthenogenesis (Degrange 1960), only fertilized eggs of *Dolania* can develop (unpubl. rearing data). For the individual, the mass swarm increases chances of finding mates and reduces probabilities that any individual will be consumed by predators before mating and oviposition (Sweeney & Vannote 1982).

Females of *Dolania* do not molt but mate immediately after emergence with available males. Timing of the emergence of male subimagos anticipates that of females so

that most males complete the subimaginal molt before female emergence (Peters & Peters 1977). Males that are already imagos when females emerge presumably have the first and the greatest number of mating opportunities. In this situation, time is critical and males might be expected to dispense with neat molts and useless legs and to take flight as soon as physically able. Reproductive success favors the male that is ready, or "a male in the air is worth two in the bush." This strategy is beneficial to both sexes, according to Wiklund & Fagerstrom (1979) who modeled early male emergence in Lepidoptera: males maximize the number of matings and females minimize the time between emergence and oviposition.

ACKNOWLEDGMENTS

We sincerely thank Dr. G. F. Edmunds, Jr. and Mr. T. J. Fink, University of Utah, Dr. E. L. Smith, California Academy of Sciences, and Dr. M. D. Hubbard, Florida A&M University, for critical review and suggestions on the manuscript, and Mr. G. J. Wibmer for translation of the abstract. We gratefully acknowledge the cooperation and assistance of the Florida Game and Freshwater Fish Commission and the Florida Division of Forestry. The research was supported by a research program (FLAX 79009) of CSRS, USDA, to Florida A&M University.

REFERENCES CITED

- DEGRANGE, C. 1960. Recherches sur la reproduction des Ephéméroptères. Trav. Lab. Pisc. Univ. Grenoble 51: 7-193.
- EDMUNDS, G. F., JR. 1956. Exuviation of subimaginal Ephemeroptera in flight. Entomol. News 67: 91-93.
- EDMUNDS, G. F., JR., S. L. JENSEN AND L. BERNER. 1976. The Mayflies of North and Central America. Univ. Minnesota Press, Minneapolis.
- KEFFERMÜLLER, M. 1959. Nowe dane dotyczące jetek (Ephemeroptera) r rodzaju *Ametropus* Alb. i *Behningia* Lest. Poznanskie Tow. Przjy. Nauk., Biol. 19(5): 1-32.
- KUKALOVA', J. 1968. Permian mayfly nymphs. Psyche 75: 310-327.
- . (1970) 1969. Revisional study of the order Palaeodictyoptera in the Upper Carboniferous shales of Commeny, France.—Part II. Psyche 76: 439-486.
- . 1971. Morphology of the Paleozoic order Palaeodictyoptera. Proc. XIII Int. Congr. Entomol. (Moscow, 1968) 1: 263.
- KUKALOVA'-PECK, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. Canadian J. Zool., 61: 1618-1669.
- . 1985. Ephemeroid wing venation based upon new gigantic Carboniferous mayflies and basic morphology, phylogeny, and metamorphosis of pterygote insects (Insecta, Ephemera). Canadian J. Zool. 63: 933-955.
- LYMAN, F. E. 1944. Effect of temperature on the emergence of mayfly imagoes from the subimago stage. Entomol. News 55: 113-115.
- NEEDHAM, J. G. AND H. E. MURPHY. 1924. Neotropical mayflies. Bull. Lloyd Libr. 24, Entomol. Ser. 4: 1-79.
- PETERS, W. L. AND J. G. PETERS. 1977. Adult life and emergence of *Dolania americana* in Northwestern Florida (Ephemeroptera: Behningiidae). Int. Rev. Gesamten Hydrobiol. 62: 409-438.
- SNOGRASS, R. E. 1935. Principles of Insect Morphology. McGraw-Hill, New York.
- SWEENEY, B. W. AND R. L. VANNOTE. 1982. Population synchrony in mayflies: a predator satiation hypothesis. Evolution 36: 810-821.
- THOMAS, E. 1969. Zur Tagesperiodik des Schlüpfens von Ephemeropteren und Plecopteren. Oecologia (Berl.) 3: 230-239.
- TSHERNOVA, O. A. AND O. YA. BAJKOVA. 1960. [On a new genus of may-flies (Ephemeroptera, Behningiidae)]. Entomol. Obozr. 39: 410-416.
- WIKLUND, C. AND T. FAGERSTROM. 1979. Reply to Mr. S. R. Bowden's note "Protandry in butterflies." Entomol. Gaz. 30: 112-114.

NEW STATE RECORDS FROM THE SOUTHEASTERN
UNITED STATES FOR *AELIA AMERICANA*
(HEMIPTERA: PENTATOMIDAE)

D. A. RIDER

Department of Entomology
Louisiana Agricultural Experiment Station
Louisiana State University Agricultural Center
Baton Rouge, Louisiana 70803

The genus *Aelia* Fabricius belongs to the group of pentatomine genera which lack a spine or tubercle at the base of the abdominal venter and are keyed by Rolston and McDonald (1984). *Aelia* is holarctic in distribution, but *A. americana* Dallas is the only species known to occur in the western hemisphere. This is a very distinct species and can be readily identified by its elongate oval shape, intermediate size (8.5-9.0 mm), and characteristic coloration. The dorsal surface is striped longitudinally, alternating in pale white and dark brown.

Aelia americana is uncommon and is usually associated with grasses (McPherson 1982). It has been swept from wheat, rye, and barley and may cause some damage to the developing grain (Gates & Peters 1962, Smith et al. 1943). It has been collected also from apple trees in Missouri (Froeschner 1941).

McPherson (1982) gave extensive information on the distribution of *A. americana*, which he said "occurs from British Columbia south to Arizona, and east to Manitoba, Michigan, and Illinois." In the eastern United States there has been no record from south of the Ohio River. The easternmost records are Manitoba (Gibson 1914, Van Duzee 1904, 1917, Walley 1929), Michigan (McPherson 1970), Illinois (McPherson 1974, 1978, 1979, McPherson & Mohlenbrock 1976), and Missouri (Froeschner 1941).

In the spring of 1984, while sweeping various grasses, I collected one female specimen from Macon County, Alabama. Further collecting in the area yielded no more specimens. Simons (1969) reported collecting two female specimens of *A. americana* from neighboring Lee County, Alabama, but these specimens were not found in the Auburn University collection. The Alabama records represent a considerable range extension for the species.

There are also three specimens of *A. americana* representing two new state records in the Louisiana State University collection (LSUC). Two are from Washington County, Arkansas, and the other is from Alfalfa County, Oklahoma.

The label data is as follows: ALABAMA: Macon Co., 4 m. E. Shorter on I-85, 16-IV-1984, D. A. Rider, 1♀ (DAR). ARKANSAS: Washington Co., 18-II-1966, 1♀ (LSUC); 25-II-1966, 1♂ (LSUC). OKLAHOMA: Alfalfa Co., 10-VIII-1932, R. Dahms, 1♂ (LSUC).

I would like to thank Thomas T. Dobbs (Auburn University) for checking the Auburn University collection for specimens of *Aelia americana*. I would also like to thank Joan B. Chapin (Louisiana State University) for reviewing an early draft of the manuscript.

REFERENCES CITED

- FROESCHNER, R. C. 1941. Contributions to a synopsis of the Hemiptera of Missouri, Pt. 1. Scutelleridae, Podopidae, Pentatomidae, Cydnidae, Thyreocoridae. American Midland Natur. 26: 122-146.
- GATES, D. E., AND L. L. PETERS. 1962. Insects in Kansas. Kansas State Univ. Ext. Service B-94: 1-307.

- GIBSON, A. 1914. The entomological record, 1913. 44th Ann. Rep. Entomol. Soc. Ontario, pp. 106-129.
- MCPHERSON, J. E. 1970. A key and annotated list of the Scutelleroidea of Michigan (Hemiptera). Michigan Entomol. 3: 34-63.
- MCPHERSON, J. E. 1974. The first record in Illinois of *Aelia americana* (Hemiptera: Pentatomidae). Trans. Illinois State Acad. Sci. 67: 151.
- MCPHERSON, J. E. 1978. A list of the Scutelleroidea (Hemiptera) of southern Illinois. Great Lakes Entomol. 11: 159-162.
- MCPHERSON, J. E. 1979. A revised list of the Pentatomoidea of Illinois (Hemiptera). Great Lakes Entomol. 12: 91-98.
- MCPHERSON, J. E. 1982. The Pentatomoidea (Hemiptera) of northeastern North America with emphasis on the fauna of Illinois. Southern Illinois Univ. Press, Carbondale and Edwardsville, 240 pp.
- MCPHERSON, J. E., AND R. H. MOHLENBROCK. 1976. A list of the Scutelleroidea of the La Rue-Pine Hills Ecological Area with notes on biology. Great Lakes Entomol. 9: 125-169.
- ROLSTON, L. H., AND F. J. D. McDONALD. 1984. A conspectus of Pentatomini of the Western Hemisphere. Part 3 (Hemiptera: Pentatomidae). J. New York Entomol. Soc. 92: 69-86.
- SIMONS, E. E. 1969. The stink bugs (Pentatomidae) of Alabama. M.S. Thesis, Auburn University, Auburn, Alabama.
- SMITH, R. C., E. G. KELLY, G. A. DEAN, H. R. BRYSON, AND R. L. PARKER. 1943. Common insects of Kansas. Rep. Kansas State Board Agr., 440 pp.
- VAN DUZEE, E. P. 1904. Annotated list of the Pentatomidae recorded from America north of Mexico, with descriptions of some new species. Trans. Amer. Entomol. Soc. 30: 1-80.
- VAN DUZEE, E. P. 1917. Catalogue of the Hemiptera of America north of Mexico excepting the Aphididae, Coccidae and Aleurodidae. Univ. California Pub., Tech. Bull., Entomol. 2: 1-902.
- WALLEY, G. S. 1929. Hemiptera. In N. Criddle. The entomological record, 1928. 59th Ann. Rep. Entomol. Soc. Ontario, pp. 110-124.

RESPONSE OF *LARRA BICOLOR*
(HYMENOPTERA:SPHECIDAE) TO PARASITIZED AND
UNPARASITIZED MOLE CRICKET HOSTS
(ORTHOPTERA:GRYLLOTALPIDAE:SCAPTERISCUS)

JAMES L. CASTNER
Department of Entomology and Nematology
University of Florida
Gainesville, Florida 32611

Larra bicolor Fabricius (Hymenoptera:Sphecidae) parasitizes *Scapteriscus* mole cricket hosts (Orthoptera:Gryllotalpidae) (Castner 1984). When a female *L. bicolor* wasp encounters a suitable host, she performs a distinct sequence of actions terminating in the deposition of a single egg (Castner 1983, Williams 1928). Similar behavior has been recorded from other species of *Larra* (Smith 1935, Williams 1928). The parasitization process can be broken down into the following actions: 1) host is stung and immobilized, 2) wasp rubs tip of abdomen over site of egg attachment, 3) egg is attached between the prothoracic and mesothoracic legs on the ventral surface. The abdomen-rubbing by *L. bicolor* may serve both to locate the correct spot for oviposition, and to determine if a parasitoid egg or larva is already present. In this study, a comparison was made

- GIBSON, A. 1914. The entomological record, 1913. 44th Ann. Rep. Entomol. Soc. Ontario, pp. 106-129.
- MCPHERSON, J. E. 1970. A key and annotated list of the Scutelleroidea of Michigan (Hemiptera). Michigan Entomol. 3: 34-63.
- MCPHERSON, J. E. 1974. The first record in Illinois of *Aelia americana* (Hemiptera: Pentatomidae). Trans. Illinois State Acad. Sci. 67: 151.
- MCPHERSON, J. E. 1978. A list of the Scutelleroidea (Hemiptera) of southern Illinois. Great Lakes Entomol. 11: 159-162.
- MCPHERSON, J. E. 1979. A revised list of the Pentatomoidea of Illinois (Hemiptera). Great Lakes Entomol. 12: 91-98.
- MCPHERSON, J. E. 1982. The Pentatomoidea (Hemiptera) of northeastern North America with emphasis on the fauna of Illinois. Southern Illinois Univ. Press, Carbondale and Edwardsville, 240 pp.
- MCPHERSON, J. E., AND R. H. MOHLENBROCK. 1976. A list of the Scutelleroidea of the La Rue-Pine Hills Ecological Area with notes on biology. Great Lakes Entomol. 9: 125-169.
- ROLSTON, L. H., AND F. J. D. McDONALD. 1984. A conspectus of Pentatomini of the Western Hemisphere. Part 3 (Hemiptera: Pentatomidae). J. New York Entomol. Soc. 92: 69-86.
- SIMONS, E. E. 1969. The stink bugs (Pentatomidae) of Alabama. M.S. Thesis, Auburn University, Auburn, Alabama.
- SMITH, R. C., E. G. KELLY, G. A. DEAN, H. R. BRYSON, AND R. L. PARKER. 1943. Common insects of Kansas. Rep. Kansas State Board Agr., 440 pp.
- VAN DUZEE, E. P. 1904. Annotated list of the Pentatomidae recorded from America north of Mexico, with descriptions of some new species. Trans. Amer. Entomol. Soc. 30: 1-80.
- VAN DUZEE, E. P. 1917. Catalogue of the Hemiptera of America north of Mexico excepting the Aphididae, Coccidae and Aleurodidae. Univ. California Pub., Tech. Bull., Entomol. 2: 1-902.
- WALLEY, G. S. 1929. Hemiptera. In N. Criddle. The entomological record, 1928. 59th Ann. Rep. Entomol. Soc. Ontario, pp. 110-124.

RESPONSE OF *LARRA BICOLOR*
(HYMENOPTERA:SPHECIDAE) TO PARASITIZED AND
UNPARASITIZED MOLE CRICKET HOSTS
(ORTHOPTERA:GRYLLOTALPIDAE:SCAPTERISCUS)

JAMES L. CASTNER
Department of Entomology and Nematology
University of Florida
Gainesville, Florida 32611

Larra bicolor Fabricius (Hymenoptera:Sphecidae) parasitizes *Scapteriscus* mole cricket hosts (Orthoptera:Gryllotalpidae) (Castner 1984). When a female *L. bicolor* wasp encounters a suitable host, she performs a distinct sequence of actions terminating in the deposition of a single egg (Castner 1983, Williams 1928). Similar behavior has been recorded from other species of *Larra* (Smith 1935, Williams 1928). The parasitization process can be broken down into the following actions: 1) host is stung and immobilized, 2) wasp rubs tip of abdomen over site of egg attachment, 3) egg is attached between the prothoracic and mesothoracic legs on the ventral surface. The abdomen-rubbing by *L. bicolor* may serve both to locate the correct spot for oviposition, and to determine if a parasitoid egg or larva is already present. In this study, a comparison was made

between the behavior and actions of captive *L. bicolor* wasps offered both parasitized and unparasitized hosts.

Larra bicolor wasps were collected near Isabela (Aguadilla Province), Puerto Rico, during 13-14 June, 1983, using the techniques described by Castner (1983). Captured wasps were placed individually in glass test tubes stoppered with a cork. These were kept in an ice chest, except when fed or used in parasitization experiments, to minimize the amount of wasp movement. Parasitizations were obtained following the method of Williams (1928), by placing a mole cricket (*Scapteriscus vicinus* Scudder or *Scapteriscus imitatus* Nickle and Castner) in the test tube with a female wasp.

A total of 20 *L. bicolor* were initially given unparasitized mole cricket hosts (12 *S. vicinus* and 8 *S. imitatus*). Both species of hosts were obtained at electronic callers (Walker 1982); *S. vicinus* from Gainesville, Florida and *S. imitatus* from Isabela, Puerto Rico. On the day following the initial oviposition, 13 wasps were offered the same mole cricket now bearing their own egg and six were offered a mole cricket bearing the 1-day-old egg of another wasp of the same species. On the next day, 5 wasps that had been given their own parasitized hosts previously, were given the parasitized host of another wasp.

The responses of *L. bicolor* to parasitized and unparasitized hosts are presented in Table 1. All 20 wasps attacked their unparasitized hosts on the first day, and 19 successfully oviposited. Of the 13 wasps given mole crickets bearing their own egg on the 2nd occasion, 9 removed the egg and laid another, 2 laid a 2nd egg, and 2 appeared disinterested and refused to attack. Of the 5 wasps that had reparasitized the same mole cricket and were given hosts with foreign eggs on a 3rd occasion, 4 removed the egg and laid their own, while 1 laid its own without removing the other. In all cases reported, the removal of an egg was confirmed by searching the test tube until it was found.

The removal of another female's egg increases the chances that a wasp's own offspring will survive. It is doubtful if even a large mole cricket could supply enough food for two developing *L. bicolor* larvae. Also, unless the 2 ovipositions occurred near the same time, the older larva would kill the host before the younger could complete development. Premature death of the host causes death of the parasite (Castner 1983). A larger larva might also cannibalize a smaller one.

Larra bicolor may encounter the egg on a parasitized host while paralyzing it, or while rubbing the tip of the abdomen over the oviposition area. When an egg was detected, the wasps exhibited a fierce searching and biting behavior, firmly grasping the host's surface tissues between the mandibles and forcibly pulling outwards. Biting occurred over the host's entire body, but was always concentrated at the site of egg attachment. Biting and searching behavior usually persisted for 1-3 min, after which the wasp would again climb astride the mole cricket and use the tip of its abdomen to ascertain whether the egg had been removed. If the egg was still present and was again discovered, the biting behavior was reinitiated. One wasp repeated this action 6 times for a total of 18-20 min before finally removing the egg. In cases where the host began reviving, it was immediately restung and paralyzed.

Vision does not appear to play a major role in the detection of the egg, nor in its removal. The female wasp apparently locates the egg with tactile sensors in the tip of her abdomen, although the use of chemoreceptors cannot be ruled out. While biting, the wasp's labium could be seen flicking over the surface of the host. The labium may be used to detect hemolymph which would be present at the small wound resulting from removal of the egg. Identifying the presence of hemolymph, combined with tactile cues, may signal the wasp that the egg has been successfully removed. In none of the cases observed did a wasp go directly to an egg and remove it. A "hunt and peck" situation always prevailed, the female often going through 3-4 alternating phases of abdomen-rubbing and searching-biting before the egg was found and removed.

TABLE 1. RESPONSE^a OF *LARRA BICOLOR* TO PARASITIZED AND UNPARASITIZED MOLE CRICKET HOSTS.

Wasp	Host Status ^b		
	Not Parasitized	Parasitized With Wasp's Own Egg	Parasitized With Another Wasp's Egg
1	P	B,O	B,O
2	P	B,S	—
3	P	B,S	B,S
4	P	B,O	B,O
5	P	B,O	B,S
6	P	NA	—
7	P	B,O	2nd
8	U	—	—
9	P	B,O	—
10	P	B,S	—
11	P	B,S	—
12	P	2nd	—
13	P	NA	—
14	P	2nd	—
15	P	—	NA
16	P	—	B,O
17	P	—	B,S
18	P	—	B,S
19	P	—	B,O
20	P	—	B,S

- ^aP = Parasitized host immediately
 U = Attempted to parasitize host, but unsuccessful
 B = Biting and searching behavior exhibited
 S = Existing egg was removed and a new one laid near the same site
 O = Existing egg was removed and a new one laid opposite the original site
 NA = No attempt made to parasitize host and no egg laid
 2nd = Second egg was laid without removing first
 — = Not offered a host of that category

^bHosts for wasps 1-8 were *Scapteriscus imitatus* and for 9-20 *Scapteriscus vicinus*

The removal of its own egg 82% (9/11) of the time by *L. bicolor* when oviposition was attempted, indicates that the act is advantageous and increases the wasp's fitness. Preliminary field observations indicate that many *L. bicolor* females utilize the same locale when hunting for mole cricket hosts (Castner and Fowler, unpublished data). This increases the possibility that a captured mole cricket may have been previously parasitized, and justifies the egg-removal behavior exhibited by the female wasps. The absence of a mechanism allowing an individual female to recognize her own egg suggests that the chances of a given female encountering the same mole cricket more than once are minimal. This would appear to be a legitimate assumption since population densities greater than 70 mole crickets per square meter have been measured in heavily infested habitats.

I would like to thank Dr. Harry Fowler for assistance in collecting *L. bicolor* in Puerto Rico. Dr. Tom Walker and Dr. Reece Sailer reviewed the manuscript and made helpful suggestions. I also thank Janice Castner for typing the manuscript. This work was supported in part by USDA Cooperative Agreement 58-7B30-2-420. Florida Agricultural Experiment Station Journal Series No. 7247.

REFERENCES CITED

- CASTNER, J. L. 1983. Biology and ecology of the mole cricket parasitoid *Larra bicolor*. M.S. thesis, Univ. of Florida, Gainesville. 80 pp.
- CASTNER, J. L. 1984. Suitability of *Scapteriscus* spp. mole crickets (Orthoptera: Gryllotalpidae) as hosts of *Larra bicolor* (Hymenoptera: Sphecidae). *Entomophaga* 29(3): 323-9.
- SMITH, C. E. 1935. *Larra analis* Fabricius, a parasite of the mole cricket *Gryllotalpa hexadactyla* Perty. *Proc. Entomol. Soc. Washington* 37(4): 65-82.
- WALKER, T. J. 1982. Sound traps for sampling mole cricket flights (Orthoptera: Gryllotalpidae: *Scapteriscus*). *Florida Entomol.* 65(1): 105-10.
- WILLIAMS, F. X. 1928. Studies in tropical wasps—their hosts and associates. *Entomol. Ser. Exp. St. Hawaii. Sugar Plant. Assoc. Bull.* 19. 79 pp.

SPATIAL DISTRIBUTION OF CALLING FIELD CRICKETS, *GRYLLUS PENNSYLVANICUS* (ORTHOPTERA: GRYLLIDAE)

B. W. FRENCH, E. J. MCGOWAN, AND V. L. BACKUS
Biological Sciences, Brock University
St. Catharines, Ontario, Canada L2S 3A1

In this paper we report the results of a nearest-neighbour analysis of the spatial distribution of calling field crickets, *Gryllus pennsylvanicus* (Bigelow). To investigate the effects of habitat on spacing patterns three different habitats were sampled: a tall-grass field (ca. height = 1m), a short-grass field (ca. height = 0.1m) in St. Catharines, Ontario, Canada and a peach orchard including tall- and short-grass areas ca. 5 km west of St. Catharines. The study was conducted on 3 days in late September and early October 1984. Due to low nightly temperatures sampling took place from 13:00-16:00 h when males were expected to be calling (Alexander & Meral 1967). At each study site the position of calling males was marked with flags and when all calling males had been located, distance to the nearest neighbour for each male was determined.

The mean distance separating calling males was 7.7 m (SD = 3.7, Range 1.9-18.8) in the tall-grass field, 10.3 m (SD = 8.1, Range 2.9-32.4) in the short-grass field and 9.1 m (SD = 3.6, Range 2.2-17.0) in the peach orchard. Frequency distributions of distances separating nearest-calling males in the three habitat types are shown in Figure 1. Nearest-neighbour analysis using c , the standard variate of the normal curve (Clark & Evans 1954), revealed spatial distributions significantly different from random in the tall-grass field, the short-grass field and the peach orchard ($P < 0.01$, $c = 2.9$, -2.8 and 2.7 respectively). Calling males were distributed uniformly in the tall-grass habitat ($R = 1.23$) and the peach orchard ($R = 1.36$), however, calling males in the short-grass habitat were clumped ($R = 0.67$). The males in the short-grass habitat were found near the border of a contiguous old field and a within-clump statistic showed that the distribution was random ($R = 1.16$). Further study is necessary in order to determine the influence of border habitats on spacing patterns of calling field crickets.

Cade (1981) studied the spacing patterns in 3 species of field cricket, *Gryllus veletis*, *G. integer* and *Teleogryllus oceanicus*. Cade erred in his calculations of r expected by dropping the $2(2\sqrt{p})^{-1}$, from for all populations except *G. integer* 1-6 (William Cade pers. comm.). This error biased the results such that they showed more clumping of the males than actually existed. When corrected, Cade's results showed fewer clumped

REFERENCES CITED

- CASTNER, J. L. 1983. Biology and ecology of the mole cricket parasitoid *Larra bicolor*. M.S. thesis, Univ. of Florida, Gainesville. 80 pp.
- CASTNER, J. L. 1984. Suitability of *Scapteriscus* spp. mole crickets (Orthoptera: Gryllotalpidae) as hosts of *Larra bicolor* (Hymenoptera: Sphecidae). *Entomophaga* 29(3): 323-9.
- SMITH, C. E. 1935. *Larra analis* Fabricius, a parasite of the mole cricket *Gryllotalpa hexadactyla* Perty. *Proc. Entomol. Soc. Washington* 37(4): 65-82.
- WALKER, T. J. 1982. Sound traps for sampling mole cricket flights (Orthoptera: Gryllotalpidae: *Scapteriscus*). *Florida Entomol.* 65(1): 105-10.
- WILLIAMS, F. X. 1928. Studies in tropical wasps—their hosts and associates. *Entomol. Ser. Exp. St. Hawaii. Sugar Plant. Assoc. Bull.* 19. 79 pp.

SPATIAL DISTRIBUTION OF CALLING FIELD CRICKETS, *GRYLLUS PENNSYLVANICUS* (ORTHOPTERA: GRYLLIDAE)

B. W. FRENCH, E. J. MCGOWAN, AND V. L. BACKUS
Biological Sciences, Brock University
St. Catharines, Ontario, Canada L2S 3A1

In this paper we report the results of a nearest-neighbour analysis of the spatial distribution of calling field crickets, *Gryllus pennsylvanicus* (Bigelow). To investigate the effects of habitat on spacing patterns three different habitats were sampled: a tall-grass field (ca. height = 1m), a short-grass field (ca. height = 0.1m) in St. Catharines, Ontario, Canada and a peach orchard including tall- and short-grass areas ca. 5 km west of St. Catharines. The study was conducted on 3 days in late September and early October 1984. Due to low nightly temperatures sampling took place from 13:00-16:00 h when males were expected to be calling (Alexander & Meral 1967). At each study site the position of calling males was marked with flags and when all calling males had been located, distance to the nearest neighbour for each male was determined.

The mean distance separating calling males was 7.7 m (SD = 3.7, Range 1.9-18.8) in the tall-grass field, 10.3 m (SD = 8.1, Range 2.9-32.4) in the short-grass field and 9.1 m (SD = 3.6, Range 2.2-17.0) in the peach orchard. Frequency distributions of distances separating nearest-calling males in the three habitat types are shown in Figure 1. Nearest-neighbour analysis using c , the standard variate of the normal curve (Clark & Evans 1954), revealed spatial distributions significantly different from random in the tall-grass field, the short-grass field and the peach orchard ($P < 0.01$, $c = 2.9$, -2.8 and 2.7 respectively). Calling males were distributed uniformly in the tall-grass habitat ($R = 1.23$) and the peach orchard ($R = 1.36$), however, calling males in the short-grass habitat were clumped ($R = 0.67$). The males in the short-grass habitat were found near the border of a contiguous old field and a within-clump statistic showed that the distribution was random ($R = 1.16$). Further study is necessary in order to determine the influence of border habitats on spacing patterns of calling field crickets.

Cade (1981) studied the spacing patterns in 3 species of field cricket, *Gryllus veletis*, *G. integer* and *Teleogryllus oceanicus*. Cade erred in his calculations of r expected by dropping the $2(2\sqrt{p})^{-1}$, from for all populations except *G. integer* 1-6 (William Cade pers. comm.). This error biased the results such that they showed more clumping of the males than actually existed. When corrected, Cade's results showed fewer clumped

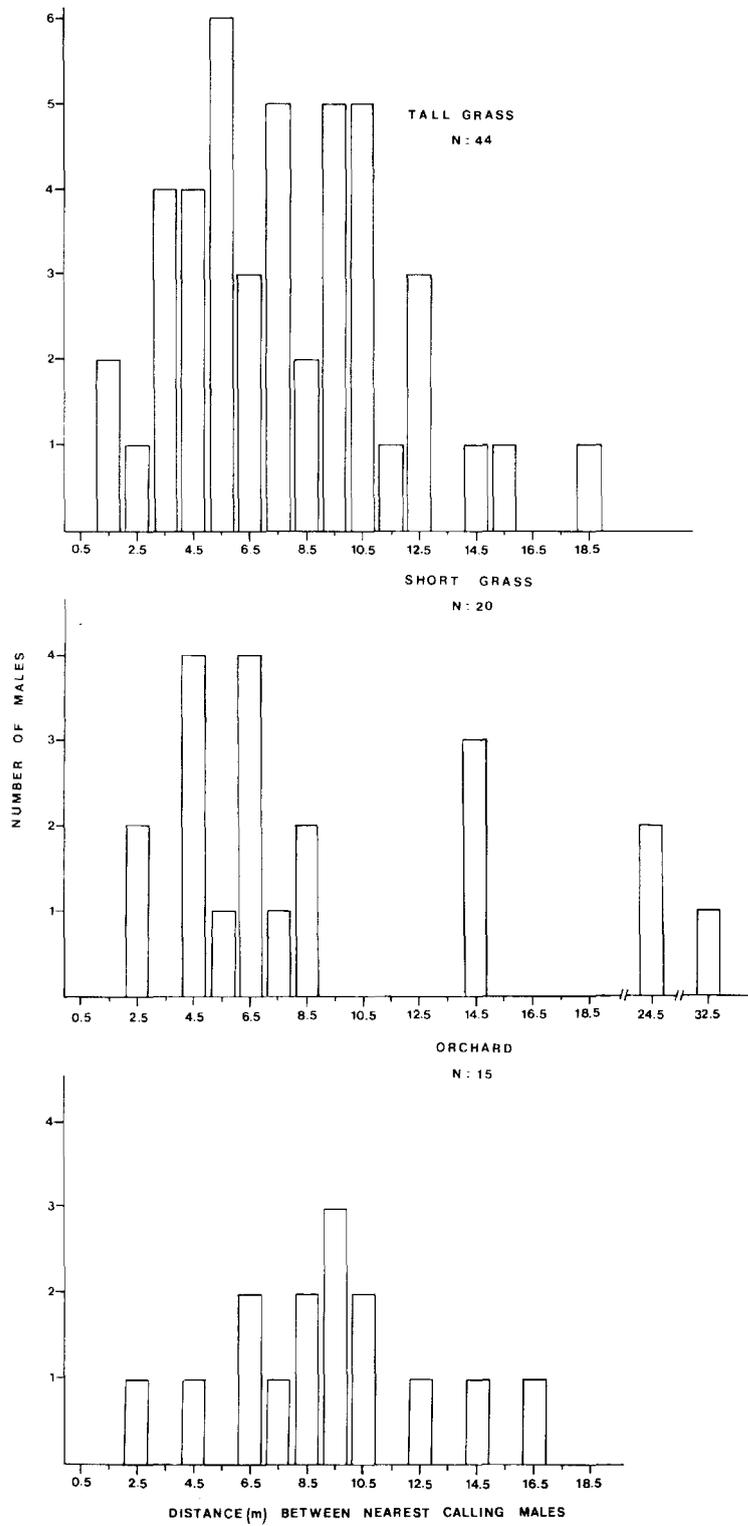


Fig. 1. Frequency distribution showing the distances separating nearest-calling males in the three habitat types surveyed.

and more random and uniform distributions (Byron Alexander pers. comm.). The spacing patterns found here for *G. pennsylvanicus* were consistent with Cade's (1981) findings when corrected.

We thank W. H. Cade for advice on data collection, R. D. Alexander, T. J. Walker and M. D. Greenfield for their comments on the manuscript. We also thank Byron Alexander for correcting Cade's (1981) results. The order of the authors was determined by a coin toss. V.L.B. is currently with the Department of Zoology, University of Vermont, Burlington, VT 05405. NSERC grant to W.H.C. (A6174) provided support for this research.

REFERENCES CITED

- ALEXANDER, R. D. AND G. H. MERAL. 1967. Seasonal and daily chirping cycles in the Northern Spring and Fall field crickets, *Gryllus veletis* and *G. pennsylvanicus*. *Ohio J. Science* 67: 200-209.
- CADE, W. H. 1981. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* 55: 365-375.
- CLARK, P. J. AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35: 445-453.

COMPARISONS OF CALORIC CONTENTS OF SOME AQUATIC INSECT EXUVIAE

G. SCOTT DESHEFY

New England Observatory of Animal Behavior
Uncasville, CT 06382

Aquatic insects of three taxa (*Belostoma flumineum* Say, *Libellula* sp. and *Lestes* sp.) were collected from the edge of Pendleton Swamp (Pendleton, SC) and were reared in the laboratory. Exuviae of *Belostoma flumineum* specimens were collected from second and succeeding instars, whereas exuviae of *Libellula* sp. and *Lestes* sp. were collected at final ecdysis. The samples were compacted, and the ash free dry weights of the exuviae were recorded. To determine whether caloric values of exuviae differed significantly among the three aquatic taxa occupying the same habitat, each sample was combusted with a Phillipson microbomb calorimeter (Richman & Slobodkin 1960, Phillipson 1964, Wissing & Hassler 1971) equipped with a 1.0 mv Honeywell Elektronik 196 recorder. Benzoic acid was used for calibration. Caloric values of exuviae were significantly different ($P < 0.05$, two-tailed t-test, Table 1) among the three taxa sampled. Exuviae of *Libellula* sp. exhibited the highest mean energy investment per unit ash free dry weight (29,140 joules (6.96 Kcal)/g; SD=1716, n=10). Damselfly exuviae (*Lestes* sp.) averaged lowest (19,259 joules (4.60 Kcal)/g; SD=879, n=18). Comparisons within *B. flumineum* further revealed that mean caloric investments (per gram) of third instar exuviae (22,064 joules (5.27 Kcal)/g; SD=753, n=8) were significantly lower ($P < 0.05$) than caloric values of second instar exuviae (24,534 joules (5.86 Kcal)/g; SD=1423, n=12), but significantly higher ($P < 0.05$) than those values obtained from *B. flumineum* fourth and fifth instars. I thank the Deshefy-Sekora family and the New England Institute of Animal Welfare in Uncasville, Connecticut.

and more random and uniform distributions (Byron Alexander pers. comm.). The spacing patterns found here for *G. pennsylvanicus* were consistent with Cade's (1981) findings when corrected.

We thank W. H. Cade for advice on data collection, R. D. Alexander, T. J. Walker and M. D. Greenfield for their comments on the manuscript. We also thank Byron Alexander for correcting Cade's (1981) results. The order of the authors was determined by a coin toss. V.L.B. is currently with the Department of Zoology, University of Vermont, Burlington, VT 05405. NSERC grant to W.H.C. (A6174) provided support for this research.

REFERENCES CITED

- ALEXANDER, R. D. AND G. H. MERAL. 1967. Seasonal and daily chirping cycles in the Northern Spring and Fall field crickets, *Gryllus veletis* and *G. pennsylvanicus*. Ohio J. Science 67: 200-209.
- CADE, W. H. 1981. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. Z. Tierpsychol. 55: 365-375.
- CLARK, P. J. AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

COMPARISONS OF CALORIC CONTENTS OF SOME AQUATIC INSECT EXUVIAE

G. SCOTT DESHEFY
New England Observatory of Animal Behavior
Uncasville, CT 06382

Aquatic insects of three taxa (*Belostoma flumineum* Say, *Libellula* sp. and *Lestes* sp.) were collected from the edge of Pendleton Swamp (Pendleton, SC) and were reared in the laboratory. Exuviae of *Belostoma flumineum* specimens were collected from second and succeeding instars, whereas exuviae of *Libellula* sp. and *Lestes* sp. were collected at final ecdysis. The samples were compacted, and the ash free dry weights of the exuviae were recorded. To determine whether caloric values of exuviae differed significantly among the three aquatic taxa occupying the same habitat, each sample was combusted with a Phillipson microbomb calorimeter (Richman & Slobodkin 1960, Phillipson 1964, Wissing & Hassler 1971) equipped with a 1.0 mv Honeywell Elektronik 196 recorder. Benzoic acid was used for calibration. Caloric values of exuviae were significantly different ($P < 0.05$, two-tailed t-test, Table 1) among the three taxa sampled. Exuviae of *Libellula* sp. exhibited the highest mean energy investment per unit ash free dry weight (29,140 joules (6.96 Kcal)/g; SD=1716, n=10). Damselfly exuviae (*Lestes* sp.) averaged lowest (19,259 joules (4.60 Kcal)/g; SD=879, n=18). Comparisons within *B. flumineum* further revealed that mean caloric investments (per gram) of third instar exuviae (22,064 joules (5.27 Kcal)/g; SD=753, n=8) were significantly lower ($P < 0.05$) than caloric values of second instar exuviae (24,534 joules (5.86 Kcal)/g; SD=1423, n=12), but significantly higher ($P < 0.05$) than those values obtained from *B. flumineum* fourth and fifth instars. I thank the Deshefy-Sekora family and the New England Institute of Animal Welfare in Uncasville, Connecticut.

TABLE 1. MEAN CALORIC CONTENTS OF AQUATIC INSECT TAXA COLLECTED FROM PENDLETON SWAMP, SOUTH CAROLINA. UNLESS INDICATED OTHERWISE, MEAN CALORIC VALUES FOR EACH GROUP ARE SIGNIFICANTLY DIFFERENT ($P < 0.05$). ASTERISKS DENOTE THOSE VALUES WHICH DO NOT DIFFER SIGNIFICANTLY ($P > 0.05$) FROM ONE ANOTHER.

Aquatic Insect	Number of Exuviae	Mean Ash-free Dry Weight of Exuvia (mg)	\pm SD	Mean Caloric Investment per Ash-free Dry Wt. (joules/g exuvia)	\pm SD
<i>Belostoma flumineum</i> (fifth instar)	11	5.26	0.25	20,766 (4.96 Kcal) *	1214
<i>B. flumineum</i> (fourth instar)	12	4.51	0.22	20,389 (4.87 Kcal) *	1004
<i>B. flumineum</i> (third instar)	8	1.89	0.34	22,064 (5.27 Kcal)	753
<i>B. flumineum</i> (second instar)	12	0.47	0.15	24,534 (5.86 Kcal)	1423
<i>Lestes</i> sp. (final ecdysis)	18	0.55	0.10	19,259 (4.60 Kcal)	879
<i>Libellula</i> sp. (final ecdysis)	10	2.58	0.31	29,140 (6.96 Kcal)	1716

REFERENCES CITED

- PHILLIPSON, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos* 15: 130-139.
- RICKHMAN, S. AND L. B. SLOBODKIN. 1960. A microbomb calorimeter for ecology. *Bull. Ecol. Soc. America* 41: 88-89.
- WISSING, T. E. AND A. D. HASLER. 1971. Intraseasonal change in caloric content of some freshwater invertebrates. *Ecology* 52: 371-373.

INSECT GROWTH REGULATOR (PRO-DRONE)
BAIT REMOVAL BY *SOLENOPSIS INVICTA*
(HYMENOPTERA: FORMICIDAE)

SHERMAN A. PHILLIPS, JR. AND HARLAN G. THORVILSON
Department of Entomology
Texas Tech University
Lubbock, Texas 79409

With the cancellation of Mirex in 1978, environmentally sound alternative methods of control have been sought for the red imported fire ant (RIFA), *Solenopsis invicta* Buren (Banks and Schwarz 1980). An alternative method for RIFA control is the use of insect growth regulators (IGRs). These compounds, many with juvenile hormone (JH) activity, influence RIFA fecundity, metamorphosis, and caste determination, while exerting a more selective effect on non-target organisms than conventional pesticides (Banks et al. 1983, Lofgren & Williams 1982, Robeau & Vinson 1976). One IGR with JH activity [1-(8-methoxy-4,8-dimethylnonyl)-4-(1-methylethyl) benzene], developed under the trade name Pro-Drone (Stauffer Chemical Company, Westport, Ct.), was field tested against the RIFA on ca. 53,000 ha in Chambers and Jefferson Co., Texas during 1983-1984. Herein, we report the rate of Pro-Drone removal by RIFAs under field conditions in these southeastern Texas counties.

Within the treated area, three disjunct sites, separated by 3-8 km, were located in improved pasture land. Approximately 5h prior to aerial application of Pro-Drone, all vegetation was removed from 18, 1m², randomly-selected plots (6 plots within each site). A standardized bait formulation of Pro-Drone (once-refined soybean oil + IGR incorporated into pregel, defatted corn grits) was aeriually broadcast at the rate of 11.86 g AI/ha on 21 October 1983. The number of bait particles falling within each cleared 1-m² plot was recorded. Colored pins were placed adjacent to each bait particle to mark its location. The rate of bait removal by foraging RIFA was monitored at 30-min intervals until all bait was removed. The bait removal rate was expressed as percent of total grits remaining through time. Site A was treated at 1230 h and a total of 383 grits (\bar{x} = 63.8) was located in the 6 plots. Since both sites B and C were treated at 1600 h by 9 aircraft, data from these two sites were combined and totaled 451 grits (\bar{x} = 37.6) in all 6 plots. Data obtained from all sites were analyzed by simple linear regression.

RIFAs removed ca. 50% and 70% of the IGR bait ca. 1 h after the 1230 h (early) and 1600 h (late) applications, respectively (Fig. 1). Four and one-half hours elapsed from the early application before 90% removal occurred, whereas 90% bait removal occurred within 2.5 h of the late application. Since higher ground and air temperatures existed at 1600 h (g = 27°C., a = 29°C) compared to 1230 h (g = 20°C; a = 23°C), greater numbers of foragers would be expected at that time. Therefore, the steeper negative

REFERENCES CITED

- PHILLIPSON, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos* 15: 130-139.
- RICKHMAN, S. AND L. B. SLOBODKIN. 1960. A microbomb calorimeter for ecology. *Bull. Ecol. Soc. America* 41: 88-89.
- WISSING, T. E. AND A. D. HASLER. 1971. Intraseasonal change in caloric content of some freshwater invertebrates. *Ecology* 52: 371-373.

INSECT GROWTH REGULATOR (PRO-DRONE)
BAIT REMOVAL BY *SOLENOPSIS INVICTA*
(HYMENOPTERA: FORMICIDAE)

SHERMAN A. PHILLIPS, JR. AND HARLAN G. THORVILSON
Department of Entomology
Texas Tech University
Lubbock, Texas 79409

With the cancellation of Mirex in 1978, environmentally sound alternative methods of control have been sought for the red imported fire ant (RIFA), *Solenopsis invicta* Buren (Banks and Schwarz 1980). An alternative method for RIFA control is the use of insect growth regulators (IGRs). These compounds, many with juvenile hormone (JH) activity, influence RIFA fecundity, metamorphosis, and caste determination, while exerting a more selective effect on non-target organisms than conventional pesticides (Banks et al. 1983, Lofgren & Williams 1982, Robeau & Vinson 1976). One IGR with JH activity [1-(8-methoxy-4,8-dimethylnonyl)-4-(1-methylethyl) benzene], developed under the trade name Pro-Drone (Stauffer Chemical Company, Westport, Ct.), was field tested against the RIFA on ca. 53,000 ha in Chambers and Jefferson Co., Texas during 1983-1984. Herein, we report the rate of Pro-Drone removal by RIFAs under field conditions in these southeastern Texas counties.

Within the treated area, three disjunct sites, separated by 3-8 km, were located in improved pasture land. Approximately 5h prior to aerial application of Pro-Drone, all vegetation was removed from 18, 1m², randomly-selected plots (6 plots within each site). A standardized bait formulation of Pro-Drone (once-refined soybean oil + IGR incorporated into pregel, defatted corn grits) was aeriually broadcast at the rate of 11.86 g AI/ha on 21 October 1983. The number of bait particles falling within each cleared 1-m² plot was recorded. Colored pins were placed adjacent to each bait particle to mark its location. The rate of bait removal by foraging RIFA was monitored at 30-min intervals until all bait was removed. The bait removal rate was expressed as percent of total grits remaining through time. Site A was treated at 1230 h and a total of 383 grits (\bar{x} = 63.8) was located in the 6 plots. Since both sites B and C were treated at 1600 h by 9 aircraft, data from these two sites were combined and totaled 451 grits (\bar{x} = 37.6) in all 6 plots. Data obtained from all sites were analyzed by simple linear regression.

RIFAs removed ca. 50% and 70% of the IGR bait ca. 1 h after the 1230 h (early) and 1600 h (late) applications, respectively (Fig. 1). Four and one-half hours elapsed from the early application before 90% removal occurred, whereas 90% bait removal occurred within 2.5 h of the late application. Since higher ground and air temperatures existed at 1600 h (g = 27°C., a = 29°C) compared to 1230 h (g = 20°C; a = 23°C), greater numbers of foragers would be expected at that time. Therefore, the steeper negative

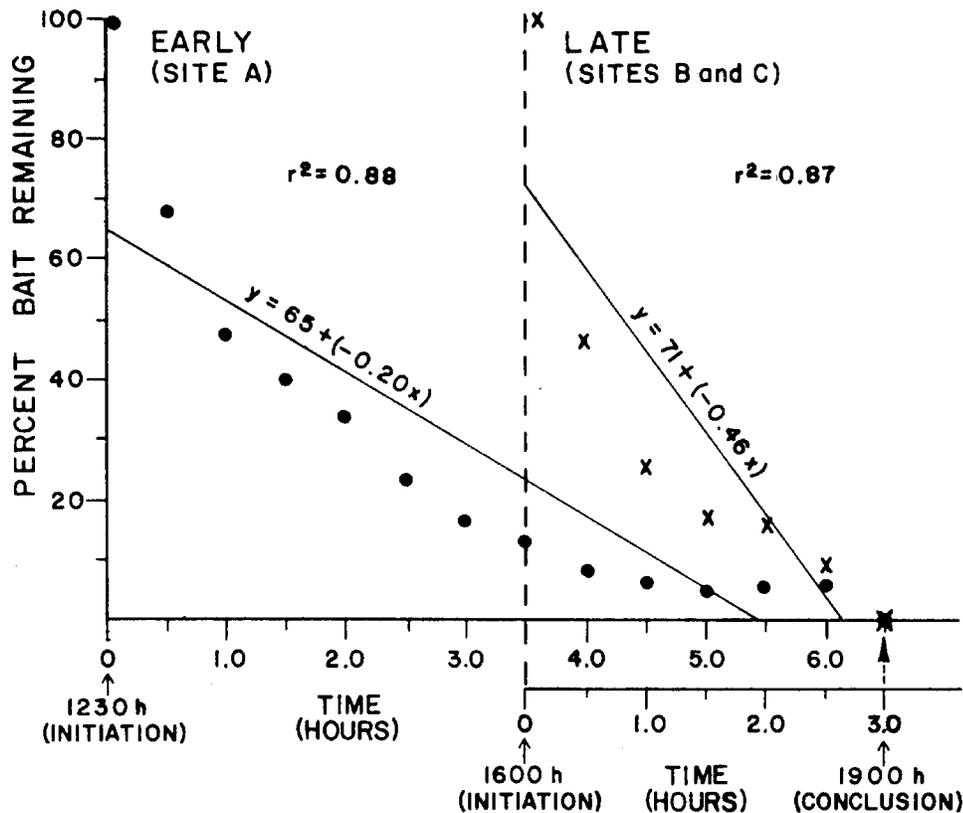


Fig. 1. Percent insect growth regulator (Pro-Drone) bait remaining every 30 min. at three disjunct locations in red imported fire ant, *Solenopsis invicta*, infested area, 21 October 1983 (data from sites B and C are combined—see text).

slope value (-0.46 as compared to -0.20) indicates greater foraging activity. Test for homogeneity ($t = 2.17$; $df = 17$) indicates that the slopes are significantly different ($p < 0.05$).

The high coefficients of determination (Site A: $r^2 = 0.88$; Sites B and C combined: $r^2 = 0.87$) indicate that the linear model describes the data well during both time periods. Therefore, these coefficients indicate that the RIFA was thoroughly "canvassing" the sites and that bait removal was a function of time.

Although using IGRs as control tactics is more selective than using conventional chemical insecticides, uncertainty remains as to the effect on non-target ants. Although Pro-Drone bait is formulated for RIFAs, other "oil-loving" ant species may be attracted to the bait. However, we observed no other invertebrate nor any vertebrate species foraging on the baits. Since all of the bait was collected by the foraging RIFA within a short time period, we suspect that at least a large majority of bait-formulated Pro-Drone reached the target organism. Contribution No. T-10-165, College of Agricultural Sciences, Texas Tech University (Mention of a commercial or proprietary product does not constitute an endorsement by Texas Tech University).

REFERENCES CITED

- BANKS, W. A., AND M. A. SCHWARZ. 1980. The effects of insect growth regulators on laboratory and field colonies of red imported fire ants. Proc. Tall Timbers

- Conf. Ecol. Anim. Control Habitat Manage. 7: 95-105.
- BANKS, W. A., L. R. MILES, AND D. P. HARLAN. 1983. The effects of insect growth regulators and their potential as control agents for imported fire ants (Hymenoptera: Formicidae). Florida Entomol. 66: 172-181.
- LOFGREN, C. S., AND D. F. WILLIAMS. 1982. Avermectin B_{1a}: Highly potent inhibitor of reproduction by queens of the red imported fire ant (Hymenoptera: Formicidae). J. Econ. Entomol. 75: 798-803.
- ROBEAU, M. R., AND S. B. VINSON. 1976. Effects of juvenile hormone analogues on caste determination in the imported fire ant *Solenopsis invicta*. J. Georgia Entomol. Soc. 11: 198-203.

EFFECT OF YARN ON ATTRACTIVENESS OF THE
WILLIAM TRAP TO *STOMOXYS CALCITRANS*
(DIPTERA:MUSCIDAE) ADULTS

J. M. TSENG

West Florida Arthropod Research Laboratory
Department of Health and Rehabilitative Services
P. O. Box 15277
Panama City, FL 32406-0277

AND

J. A. HOGSETTE AND R. S. PATTERSON
Insects Affecting Man and Animals Research Laboratory
USDA, ARS
P. O. Box 14565
Gainesville, FL 32604

The stable fly, *Stomoxys calcitrans* (L.), is an extremely noxious pest of man and livestock in Northwest Florida (Brown & Williams 1974 and Hogsette, et. al. 1981). Because of the economic impact of an invasion of these flies on the beach resorts along the Gulf Coast, the state routinely sprays the beaches with naled whenever flies reach a certain annoyance level (20 flies/man/minute, Brown personal communications). While this control technique is effective, alternative measures must be investigated to reduce the fly populations below an economic threshold.

A standard method, which has been used for years to monitor stable fly populations in N.W. Florida and throughout the world, is the Williams Trap (Williams 1973). The fiberglass panels (Alsynite™) reflect ambient light in a UV wavelength that is very attractive to stable flies (Agee & Patterson 1983). When the adhesive Tack Trap™ is applied to the fiberglass, it does not initially decrease the attractiveness of the panels to the flies, however, as flies accumulate on the panels, the traps' attractiveness is decreased. The Williams trap can be modified from a monitoring device to a control device by coating the fiberglass panels with various formulations of synthetic pyrethroids (Meifert et. al. 1978). While this technique is effective it has drawbacks because only technical material in acetone is effective for more than a few days. Formulated material, such as emulsifiable concentrates or wettable powders, does not adhere well to the impervious surface of the fiberglass, consequently, any heavy dews or light rains will wash off the chemical. A more recent modification, which has shown more promise, involves wrapping the fiberglass panels with white Orlon™ yarn which has been impregnated with 1% permethrin EC solution (Koehler & Patterson 1982).

- Conf. Ecol. Anim. Control Habitat Manage. 7: 95-105.
- BANKS, W. A., L. R. MILES, AND D. P. HARLAN. 1983. The effects of insect growth regulators and their potential as control agents for imported fire ants (Hymenoptera: Formicidae). Florida Entomol. 66: 172-181.
- LOFGREN, C. S., AND D. F. WILLIAMS. 1982. Avermectin B_{1a}: Highly potent inhibitor of reproduction by queens of the red imported fire ant (Hymenoptera: Formicidae). J. Econ. Entomol. 75: 798-803.
- ROBEAU, M. R., AND S. B. VINSON. 1976. Effects of juvenile hormone analogues on caste determination in the imported fire ant *Solenopsis invicta*. J. Georgia Entomol. Soc. 11: 198-203.

EFFECT OF YARN ON ATTRACTIVENESS OF THE
WILLIAM TRAP TO *STOMOXYS CALCITRANS*
(DIPTERA:MUSCIDAE) ADULTS

J. M. TSENG

West Florida Arthropod Research Laboratory
Department of Health and Rehabilitative Services
P. O. Box 15277
Panama City, FL 32406-0277

AND

J. A. HOGSETTE AND R. S. PATTERSON
Insects Affecting Man and Animals Research Laboratory
USDA, ARS
P. O. Box 14565
Gainesville, FL 32604

The stable fly, *Stomoxys calcitrans* (L.), is an extremely noxious pest of man and livestock in Northwest Florida (Brown & Williams 1974 and Hogsette, et. al. 1981). Because of the economic impact of an invasion of these flies on the beach resorts along the Gulf Coast, the state routinely sprays the beaches with naled whenever flies reach a certain annoyance level (20 flies/man/minute, Brown personal communications). While this control technique is effective, alternative measures must be investigated to reduce the fly populations below an economic threshold.

A standard method, which has been used for years to monitor stable fly populations in N.W. Florida and throughout the world, is the Williams Trap (Williams 1973). The fiberglass panels (Alsynite™) reflect ambient light in a UV wavelength that is very attractive to stable flies (Agee & Patterson 1983). When the adhesive Tack Trap™ is applied to the fiberglass, it does not initially decrease the attractiveness of the panels to the flies, however, as flies accumulate on the panels, the traps' attractiveness is decreased. The Williams trap can be modified from a monitoring device to a control device by coating the fiberglass panels with various formulations of synthetic pyrethroids (Meifert et. al. 1978). While this technique is effective it has drawbacks because only technical material in acetone is effective for more than a few days. Formulated material, such as emulsifiable concentrates or wettable powders, does not adhere well to the impervious surface of the fiberglass, consequently, any heavy dews or light rains will wash off the chemical. A more recent modification, which has shown more promise, involves wrapping the fiberglass panels with white Orlon™ yarn which has been impregnated with 1% permethrin EC solution (Koehler & Patterson 1982).

The purpose of this study was to determine the optimum yarn spacing, i.e. how much of the panel surface could be covered with yarn without significantly reducing the attractiveness of the fiberglass, and also to improve the yarn wrapping techniques designed by Koehler and Patterson.

The study was conducted in September and October of 1982 at Grayton Beach, Walton County, Florida, where high stable fly populations were present. The white Orlon yarn was wrapped in a continuous coil around the long axis of the panels. Panels were notched top and bottom for uniform yarn spacing at the desired intervals. After wrapping, panels and yarn were coated with Tack Trap and supported 90 cm above the ground on short wooden stakes. Four experimental yarn spacings were tested: 0.0, 0.64, 1.27, and 2.54 cm between strands. Standard Williams traps were used as checks. Traps were placed on the beach between the high tide mark and the dunes and arranged in a 5 X 5 latin square design. The distance between each trap was 6.1 m. Flies caught on each trap were counted at 24-h intervals. After each count, traps were cleaned with hexane, allowed to dry, and then recoated with Tack Trap in preparation for the next trapping interval.

The mean number of stable flies caught on the yarn wrapped panels (Table 1) were subjected to ANOVA and the means compared by Duncan's new multiple range test. The different distances between yarn strand wrappings on the Williams trap did influence the attractiveness for flies to the panels. Consequently, the more yarn strands wrapped on the trap, the fewer flies were caught. The greatest number of flies were caught when the distance between yarn strands was 2.54 cm. However, the Duncan's multiple range test shows that there is no significant difference when the distance between yarn strands is 2.54 and 1.27 cm. However, since the yarn is to be impregnated with permethrin, the 1.27-cm spacing increases the chances that flies attracted to the panels will contact the pesticide. In the field, no Tack Trap will be used to trap the flies. Therefore, without the accumulation of flies on the trap surface, the attractiveness of the traps will remain at a maximum at all times. Besides providing more impregnated yarn per unit area, wrapping the yarn around the panels in a continuous coil proved to be much more convenient than the criss-cross method suggested by Koehler and Patterson.

Field studies of this new design of yarn-wrapped panels for the control of stable flies at dairy farms have shown it to be as good as, if not better than, the one designed by Koehler and Patterson. This design saves considerable time and effort over the previous one and should be adopted for field control use.

This research was supported by Cooperative Agreement No. 28-7830-0-190 between the United States Department of Agriculture and the Department of Health and Re-

TABLE 1. NUMBER OF STABLE FLIES CAUGHT ON STICKY TRAP PANELS USING ORLON YARN STRANDS AT GRAYTON BEACH, FLORIDA.

Distance between each yarn strand (cm)	Number of flies caught on panels	Mean ¹
Check	1,846	369.1 a
2.57	1,154	230.7 b
1.27	1,127	225.5 b
0.64	414	82.7 c
0.00	185	36.9 c

¹Means followed by the same letter are not significantly different ($p < 0.01$).
F=11.85 df=4 MSE=7380.4

S of S=349687.9

habilitative Services, State of Florida. Mention of commercial or proprietary product does not constitute endorsement by the USDA or DHRS.

REFERENCES CITED

- AGEE, R. H., AND R. S. PATTERSON. 1983. Spectral sensitivity of stable, face, and horn flies and behavioral responses of stable flies to visual traps (Diptera: Muscidae). *Environ. Entomol.* 12(6): 1823-1828.
- BROWN, J. L. AND D. F. WILLIAMS. 1974. Dog flies in agricultural areas. Florida Cooperative Extension Service Circular, 391, 8 pages.
- HOGSETTE, J. A., J. P. RUFF, AND M. V. MCGOWAN. 1981. Stable fly integrated pest management (IPM) in northwest Florida. *J. Florida Anti Mosquito Assoc.* 52(1): 48-52.
- KOEHLER, P. G. AND R. S. PATTERSON. 1982. Stable fly control with fiberglass panels. IFAS, University of Florida, Cooperative Extension Service Livestock Protection Pointer, 14, 3 pages.
- MEIFERT, D. W., R. S. PATTERSON, T. WHITFIELD, G. C. LABRECQUE, AND D. E. WEIDHAAS. 1978. Unique attractant-toxicant system to control stable fly populations. *J. Econ. Entomol.* 71: 290-292.
- WILLIAMS, D. F. 1973. Sticky traps for sampling populations of *Stomoxys calcitrans*. *J. Econ. Entomol.* 66: 1279-1280.

PRESIDENTIAL ADDRESS

M. LEWIS WRIGHT, JR.
Wright Pest Control, Inc.
P.O. Box 2185
Winter Haven, Florida 33880

Members of the Florida Entomological Society, distinguished guests and participants from the Caribbean, ladies and gentlemen—I am pleased to address you this morning at the opening of the 68th Annual Meeting of the Florida Entomological Society.

Today marks a very important milestone in the history of the Florida Entomological Society. This Caribbean Conference is the culmination of a lengthy dream of very dedicated members who, in their long range planning and visions, have sought to conduct international meetings of Entomological interest in the Western Hemisphere. We have approached that moment in history when it has become essential that our profession must assemble periodically to share mutually our thoughts, accomplishments, and scientific approaches in entomology. Never before in the history of mankind have we been subjected to such a challenge to muster our efforts and deliver that which is expected of our profession. With the onset of increasing and overbearing regulations from our governing agencies; mounting pressures from the public and news media on activities involving our profession, directly or indirectly; the rapidly-growing worldwide populations; complex living conditions and worldwide transportation; and pest problems that continue to emerge in new areas—we as entomologists must unite to seek acceptable approaches in pest control. I challenge all fields of entomology to “put their best foot forward” and to make every effort through their contributions to meet these ever-growing impediments. To confront these obstacles we must intensify our efforts in arthropod physiology; ecology; genetics; so-called “new chemistry” as pheromones, growth regulators, and attractants; mechanical devices; behavioral patterns; toxicology; and many other branches of research. These Caribbean Conferences with their exchange of data will certainly be a contributing factor to this end. If the world of natural balance were permitted to lend itself to a few major insect outbreaks affecting the world food supply, it would not require much to throw millions of such people into catastrophic situations of starvation and famine. We must never permit this to occur! We must always have available safe and effective alternate means of control to supplement our present chemical control measures. Several unfortunate incidents involving Chlordane and Aldecarb occurring recently have evolved into very shocking reactions from the public in general, primarily instigated by the news media. These incidents could have been and must be approached with intelligent responses from our own profession with intelligent explanations to the public. This we have not properly addressed. The media releases have blown out of proportion the “facts”, the background data, and some of the reasons for these occurrences. These biased news reports to the public have left us with much to be desired. I again challenge the entomologists to organize public relations efforts and to establish a system of presenting releases periodically to the public through TV interviews, radio talks, editorials in newspapers, etc. We need to elevate our position as a profession in society. This image of Entomology was very ably expressed in A. C. White's Presidential Address before the 66th Annual Meeting in which he stressed the importance of the entomologist organizing and creating a new and important image, and his role in modern technology.

At this time I would like to project a few comments on the Society activities of the past year.

First of all, I wish to express very sincerely my thanks for the manner and attitude

with which the membership responded to my assignments and requests for both long standing and ad hoc committee work. There was no hesitancy from the members to carry out the responsibilities for each respective committee.

The Officers and Directors have fulfilled their job requirements diligently, and have been faithful in attending regularly held Directors' meetings as well as offering many suggestions to yield an exciting year.

Dr. Carl S. Barfield, with Co-Chairman Dr. David J. Schuster, have organized and presented the membership at this meeting a very outstanding program in which many scientists from our Western Hemisphere will be participating. This is a "First" for our Society and one that we can well be proud of. It is my sincerest hope that this will be the first in many periodic conferences which will be organized. As stated above, never in our history have we been in need of such a program. This year we have five Symposia, some running concurrently, and many submitted papers. These, along with the student papers, will total approximately 88 individual presentations at this meeting—the largest and most comprehensive FES program ever organized. I am very proud of the Program Committee's efforts, and wish to commend them highly.

Coinciding with the program organization was the outstanding effort of Dr. Strat H. Kerr, who chaired the committee to arrange for travel funds for those students participating in the student paper session of this meeting. He exerted much time in soliciting many industrial firms for their contributions for these funds. As a result of these efforts, we will have 15 student papers on this program. Those companies supporting the funds are listed on the inside front page of the program. Please take note and thank them when you see them. On behalf of the Society I wish to thank Strat and all of the contributors for their support.

Were it not for the advertisers we would have not been able to produce such a fine quality program for use by the membership and those attending this meeting. A word of appreciation is always due them.

During the past fiscal year we established a program in which our Florida Entomologist Journal and Editorship is on a self-paying basis. This program will be partly subsidized by our Society treasury funds. Dr. John R. McLaughlin and his Editorial Staff have performed an outstanding job this year with the Journal. I commend them all for their efforts.

Our Business Manger, Mrs. Ann Knapp, now has a full year of Society experience behind her and is to be praised for her untiring hours in keeping the Society's finances in superb order. For the first time in our history we are now able to extract from her computerized data specific items which our committees can utilize to facilitate their work. During the past fiscal year the Directors had several decisions to make with reference to the financial survival of our Society. One of these being a small dues increase which will be effective January 1st, 1986. This adjustment in our annual income projections will enable us to carry out in a financially sound manner many of the society projects which we have always taken pride in performing. Some of these include the awards committee work, student paper presentation awards at the annual meetings, scholarship awards, grants, and the like. We were very pleased that the membership realized this need and fully supports this increase.

Our membership, as indicated earlier, must be strengthened. I again challenge each of you to be a part of a membership campaign and make every attempt to bring in one member this coming year, regardless of the category. We need every one available as a member to accomplish in numbers the necessary reactions of Entomologists to the ever increasing regulations, adverse media statements, needs for research support, and the support of our public officials sympathetic to our cause. Let's all go out on a one-on-one basis and get a new member this year. I would suggest that we achieve a minimum of 10% net growth in our membership during this next year.

Through a program by Dr. Frank W. Mead, and his capable assistant Terry Green, our Directory of Florida Entomologists, which is over ten years old, is being updated and will be ready in the Spring of 1986.

Dr. William Peters and Dr. Michael Hubbard have agreed to work on the History of Entomology in Florida and update same. Its anticipated release to be sometime in the Summer of 1986.

I wish to thank sincerely Dr. David F. Williams for his untiring work as our Society Secretary for the past years. As a result of his work and reports, our Society and the Executive Committee have been kept advised on all the work carried out this past year. His prompt and accurate record keeping has been of inestimable value to all of us. Dave is retiring effective this meeting date. We will miss him and his contributions greatly, and do hope that he will continue to serve the society in other capacities in the future. My sincere thanks to you, Dave, for a job well done.

Several years ago the Society, under the direction of Dr. William L. Peters, organized an Ad Hoc Committee for a Past Presidents Breakfast to be held at each annual Society meeting. This year I understand that there will be approximately 20 past presidents attending this now annual affair. At the gathering this year the past presidents will participate in the breakfast program by contributing comments and suggestions for strengthening the Society as a whole. It is from this group of experienced members we gather many ideas for enhancing our organization.

In closing, may I again challenge each of you to "stand up and be counted" as an Entomologist in this technological world of science. Make every effort through the media to promote our image. Increase our membership and use our numbers to accomplish our goals and actions. Consider the possibility of having more and frequent Society/Caribbean Conferences in the future. Maintain a diversification of papers in our programs. Encourage the enlistment of more students in entomological programs. And, last of all—support your Florida Entomological Society.

Thank you for the honor of serving your Society, the best in the nation!

M. Lewis Wright, Jr., President
Florida Entomological Society
5 August 1985

EDITED MINUTES OF THE 68th ANNUAL MEETING
OF THE FLORIDA ENTOMOLOGICAL SOCIETY

(Copies of the complete minutes may be obtained from the Secretary.)

The 68th Annual Meeting of the Florida Entomological Society was held at the Ocho Rios Sheraton Hotel, Ocho Rios, Jamaica, West Indies, 5-8 August 1985.

The opening session was called to order by President M. Lewis Wright, Jr., Winter Haven, Florida, at 8:40 a.m., 6 August 1985. The invocation was offered by Dr. Howard V. Weems, Jr., Gainesville, Florida. The welcome was by Dr. Osmond Tomlinson, Custos, Ocho Rios, Jamaica. Dr. Hugh Popenoe, Director for the Center for Tropical Agriculture, IFAS, University of Florida, Gainesville gave the Keynote Address: "The international dimensions of Florida agriculture". An invitational paper was also presented by C. W. D. Brathwaite, Director, Inter-American Institute for Cooperation on Agriculture, Trinidad, Port-of-Spain.

REPORT OF THE BUSINESS MANAGER FOR YEAR JULY 1, 1984-JUNE 30, 1985.

Receipts:

Membership	\$10,375.00
Subscriptions	4,250.00
Annual Meeting	12,473.00*
Interest Earned	2,249.72
Back Issues	458.75
Refunds	(175.00)
Miscellaneous	32.90
Contributions	10.00
Student Travel	2,410.00**
	<hr/>
Total	\$ 32,084.37

Expenses:

Office Expense	\$330.54
Telephone	100.74
Postage	559.47
Contract Labor	
C.S. 900.00	
J.M. 300.00	
A.K. 3,900.00	5,100.00
Travel Expenses	125.70
Fla 4-H Foundation	600.00
Grants & Scholarships	1,700.00
Casual Labor	152.50
Journal Printing	9,351.19
Editing Expenses	860.84
Dues & Subscriptions	75.00
Bank Charges	118.40
Annual Meeting	12,488.06*
Miscellaneous	344.01
	<hr/>
Total	\$31,906.45

Gain \$177.92

*This figure contains deposit of \$4,960.00 made to and returned from Emmer Travel.

**This is shown as income but was distributed in July.

Petty Cash \$ 100.00
Cash in Bank \$16,273.68

Membership: Full 539
 Student 121
 Sustaining 48
 Total 708

The books are closed and have been audited for the fiscal year 1984-85. Our beginning balance in the checking account last year was \$1,214.00 plus a Certificate of Deposit of \$15,000.00. At the end of this year, we have total of \$16,274.18. The financial statement will be published in the *Florida Entomologist*. Hopefully, with the raise in dues and page charges we will begin to break even by next year.

A. C. KNAPP, Business Manager

REPORT OF THE FISCAL COMMITTEE

Two of 3 members of the Fiscal Committee examined the Society's financial records for the past fiscal year and found them in good order. We wish to compliment Ann Knapp on a job well done and thank her for her friendly cooperation throughout the year.

O. SOSA, J. M. BOSWORTH, AND R. J. BURGESS, Chairperson

REPORTS OF THE PUBLIC RELATIONS COMMITTEE

This committee did not submit any report to the Secretary during this year.

REPORT OF THE LONG RANGE PLANNING COMMITTEE

The FES Long Range Planning Committee proposes the following:

1. That the Society improve the balance of applied versus basic papers presented at annual meetings by:
 - a. Permanently installing concurrent sessions
 - b. Demanding more paper presentations by industrial reps who complain the most, yet defer with the old excuse of not being able to reveal "trade secrets"!
 - c. Establishing "Applied Seminars" to balance the preponderance of "Basic Seminars".
 - d. Encourage paper presentations not only from the agrichemical segment but also from the Florida Mosquito Control Association and from the Florida Pest Control Association.
2. That the Society's members be polled by letter as to what percentage of the Society's money be allocated to seminars, whether they be basic as is the current trend, or applied—hopefully, the future trend.
3. That the Society improve our public relations by:
 - a. Offering awards or recognition to those members who expound on entomology as a beneficial profession, to civic, governmental and school groups.

- b. Invite the press and TV media to attend our meetings and not just have press releases available.
 - c. Require that graduate students participate in this endeavor—they are our most convincing representatives!
4. That the Society increase our active membership by following through with Proposals No. 1, 2, and 3.
 5. That the Society foster involvement with other groups by:
 - a. Meeting with the ESA and/or SE Branch at opportune times.
 - b. Having contiguous or joint meetings with the Florida Weed Science Society, the Florida Pest Control Assoc., the Florida Mosquito Control Assoc., the Florida Horticulture Society, etc.
 - c. Polling the membership and deciding on future meetings with our southern counterparts.
 6. That the Society act on the previous proposal to establish an FES Committee on Common Names of Insects.
- T. W. DEAN, J. A. COFFELT, D. C. HERZOG, R. L. LIPSEY, C. S. LOFGREN AND E. A. MOHEREK, Chairperson

REPORT OF THE AMERICAS COMMITTEE

The activities of the Americas Committee during this past year have been directed towards (1) encouraging international attendance at the 1985 Annual Meeting which will take place in Jamaica, and (2) recommend future activities for the committee. Members of the committee personally contacted numerous entomologists, biologists, agronomists and others to inform them of the meeting in Jamaica. The committee suggested that a poster be sent to research stations, biology departments, etc., in the Caribbean to announce the meeting. A number of other committees are effectively handling matters that were originally initiated by the Americas Committee. The practice of including Spanish language abstracts for articles in the Florida Entomologist was originally conceived by the Americas Committee and is now handled by the Editors. A brochure about FES membership written in English, Spanish, and French is available from the Business Manager or the Public Relations Committee. The Long Range Planning Committee takes into account the desirability of increasing the presence of the FES in this hemisphere. Finally, the Caribbean Conference Committee has been very effective in stimulating the interest of entomologists from several countries in attending the meeting in Jamaica. Although these committees have effectively promoted the hemisphere-wide interest of the society, the Americas Committee has a continuing role to play in encouraging liaison between the FES and other institutions in the Caribbean. This includes preparation for future meetings outside of Florida, publishing mutually beneficial information in the Florida Entomologist, publicizing regional events, fostering interaction with other plant protection specialties, organizing activities at each annual meeting that have Caribbean-wide application, and documenting and evaluating the impact of FES involvement in the Americas.

C. O. CAULKINS, G. R. BUCKINGHAM, M. L. PESCADOR, N. C. LEPPLA, B. M. GREGORY, AND F. W. HOWARD, Chairperson

REPORT OF THE PUBLICATIONS COMMITTEE

The Florida Entomologist has published 366 pages through the June issue (68, No. 2). It appears that the committee's goal to get the 1985 issue out on schedule will be met. The December issue is full and papers are concurrently being assigned to March

86 issue. From August 1984 to August 1985 the editor has received nearly 150 scientific articles or notes to process (including symposia).

Florida Entomologist will have published 20 symposia articles, 51 scientific papers, and 32 scientific notes in volume 68. In volume 67, the corresponding values were 16, 50, 16, and for volume 66: 13, 34, and 14. It is a growing journal. The 1985 ESA Student Symposium will be published in the Florida Entomologist as well as numerous papers from the symposia at the 68th Annual Meeting.

The Committee would like to commend Dr. Musgrave for contributing in a very great way to the orderly transfer of the Editorship. Dr. Musgrave's continuing efforts in assisting with the timely assignment of manuscripts and her advice and support have been responsible for much of this year's success.

H. V. WEEMS JR., M. D. HUBBARD, F. W. HOWARD, O. SOSA, A. ALI, W. C. ADLERZ, W. W. WIRTH, A. C. KNAPP, J. R. McLAUGHLIN, Chairperson

REPORT OF THE AD HOC COMMITTEE ON FES OFFICER AND COMMITTEE CHAIRPERSON JOB DESCRIPTIONS

About half of the job descriptions for officers and committee chairpersons have been written. Some are complete, others are in various stages of review by select members who have held those positions previously.

H. L. DENMARK, W. L. PETERS, H. V. WEEMS, JR, D. H. HABECK, Chairperson

REPORT OF THE AD HOC COMMITTEE ON CONSTITUTION AND BY-LAWS

The committee has decided not to recommend any changes in the Constitution or By-Laws this year. The general feeling is that until the job Description Committee finishes its work and our status with the IRS is clarified, any further changes would be premature at this time.

F. W. MEAD, R. I. SAILER, D. H. HABECK, Chairperson

REPORT OF THE COMMITTEE ON SCHOLARSHIPS

The Committee on Scholarships has evaluated nine candidates for the \$500 scholarships to be awarded at the 1985 FES meeting. The top 3 candidates according to the combined vote of the committee are: J. L. Belwood, J. L. Castner, and M. G. Spofford. The results were revealed at the Annual Meeting in Jamaica.

A. R. SAPONIS, D. L. KLINE, R. F. BROOKS, D. L. SHANKLAND, Chairperson

REPORT OF THE STUDENT ACTIVITIES COMMITTEE

The Student Activities Committee normally has three projects: mini-grants, student paper contest, and student poster contest. Because of financial considerations, the only activity held this year was the student paper contest. Fifteen students participated and each received a \$15 reduction in the registration fee. Winners were:

- 1st Place (\$125.00)—Olusola Adeyeye
- 2nd Place (\$75.00)—Gregory Lanzaro
- 3rd Place (\$50.00)—W. Hargrove

Again, as a result of financial considerations and other commitments, none of the six members of the Student Activities Committee were able to attend this year's meeting. Without the help of Dr. Nan-Yao Su who presided over the contest and Drs. J. H. Frank, N. C. Leppla, R. F. Mizell, W. C. Peters, and R. M. Baranowski (the judges),

we would not have had a contest. The Committee would also like to thank Dr. S. H. Kerr for working so hard to obtain funding to help students attend this years meeting. E. GORDON; G. B. MARSHALL; J. M. BOSWORTH; P. M. GRANT; AND L. S. OSBORNE, Chairperson

REPORT OF THE HONORS AND AWARDS COMMITTEE

Tonight I have the privilege of presenting awards to 11 outstanding entomologists. But before I start I would like to thank those of you who submitted nominations. The number of nominations has increased substantially over the past 2 years and is deeply appreciated by the Honors and Awards Committee. Please keep up the good work in the years to come!

Certificate of Appreciation

Our first honoree received his B.S. & M.S. degree in Entomology from Kansas State University and his Ph.D. in Entomology from Oklahoma State University. He joined the University of Florida as an Assistant Professor in 1975 and is currently Professor of Entomology at the Gulf Coast Research & Education Center. His primary responsibilities have been to develop practical methods for managing arthropod pests of vegetables produced on the West Coast of Florida. He is presently serving as co-chairman of the conference committee for this meeting and in addition is responsible for the fine program. It is with pleasure, that we present this Certificate of Appreciation to Dr. David J. Schuster for services rendered to the Florida Entomological Society.

Our next honoree obtained the B.S. degree from East Texas Baptist College, the M.S. from Stephen F. Austin State University and his Ph.D. from Texas A & M University. He is Professor of Entomology at the University of Florida where he designs IPM strategies for field crops and teaches several courses.

As chairman of the Joint Program Caribbean Conference Committee, he has played a key role in this first out-of-the-state meeting of the Florida Entomological Society.

We are indeed pleased to present this Certificate of Appreciation to Dr. Carl S. Barfield for services rendered to the Florida Entomological Society.

The final recipient was born in New Orleans, Louisiana and raised in Biloxi, Mississippi. After completion of his B.S. and M.S. degrees at the University of Southwestern Louisiana, he received his Ph.D. in Entomology from the University of Florida in 1969. He served as assistant professor of Biology at Greensboro College from 1969-1971 and Research Entomologist at the State of Florida, Department of Health, West Florida Arthropod Research Laboratory from 1971-1974. From 1974-1977 he served as Location Leader and Research Leader at USDA, ARS, Federal Experiment Station, St. Croix, Virgin Islands where he received the USDA-ARS Certificate of Merit for work in the integrated technique for elimination of stable flies. Since 1977 he has been at Insects Affecting Man and Animals Research Laboratory in Gainesville, Florida as Research Entomologist on the Imported Fire Ant Project.

A member of several professional organizations, he has served as secretary of the Florida Entomological Society for the past three years. During this period he has been a model for those who will follow him.

It is with great thanks that we present this Certificate of Appreciation to Dr. David F. Williams for his years of service to the Florida Entomological Society.

Certificate of Merit

Our first honoree, Research Entomologist and Project Leader for plant resistance and sorghum insects at the Insect Biology and Population Management Research Lab-

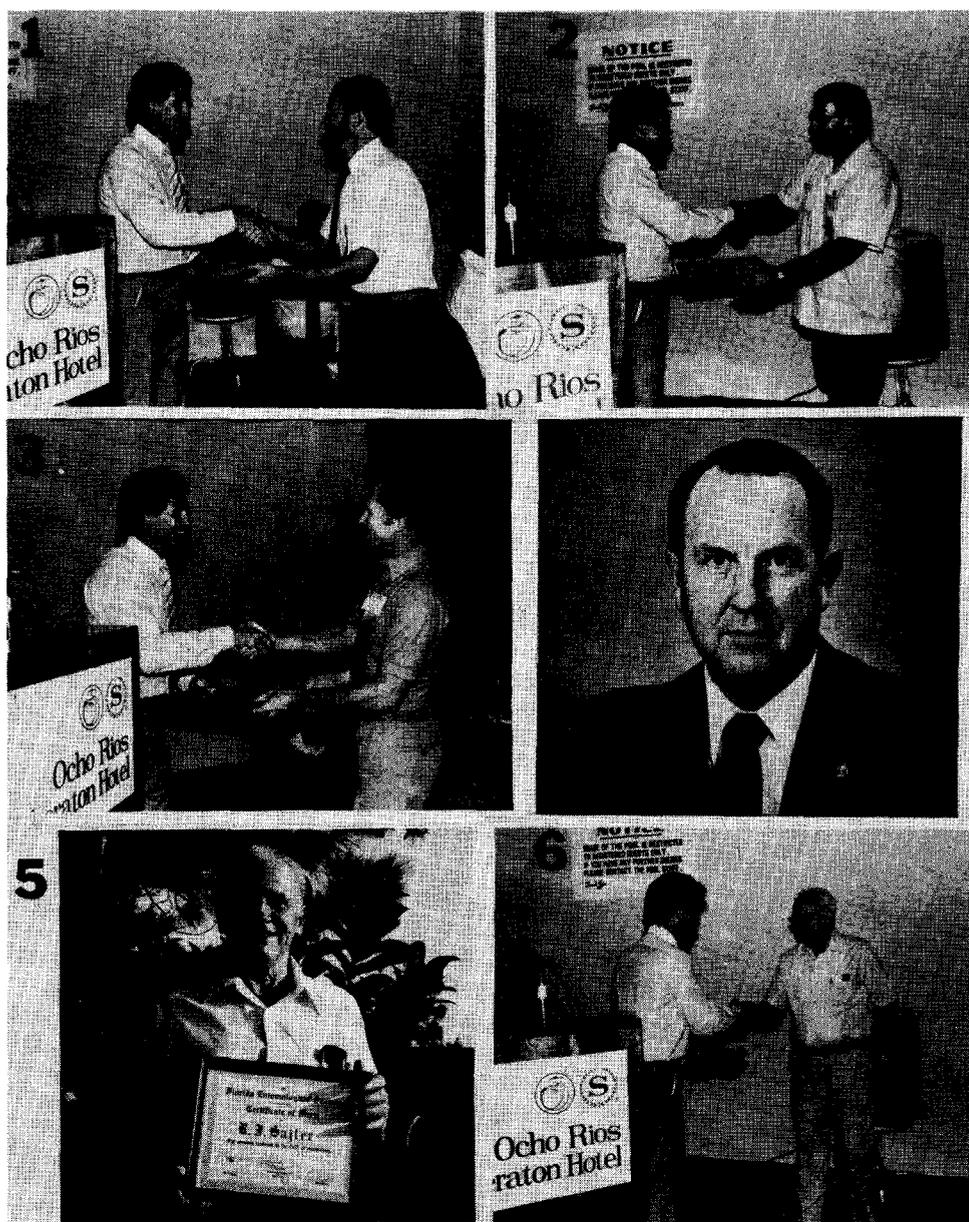


Fig. 1. David J. Schuster (right), Professor of Entomology, Univ. of FL, receives a Certificate of Appreciation from Van Waddill, Chairman, Honors and Awards Committee. (All photos except no. 4 by Frank W. Mead.); Fig. 2. A Certificate of Appreciation is presented to Carl S. Barfield (right), Professor of Entomology, Univ. of FL.; Fig. 3. A Certificate of Appreciation is presented to David F. Williams (right), Secretary of the Florida Entomological Society.; Fig. 4. Billy R. Wiseman, Research Entomologist, Insect Biology & Population Management Research Laboratory, ARS, USDA, Tifton, GA, was a recipient of a Certificate of Merit.; Fig. 5. Reece I. Sailer, Graduate Research Professor, Univ. of FL, with his Certificate of Merit.; Fig. 6. A Special Award is presented to Charles Poucher (right), Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Winter Haven, FL.

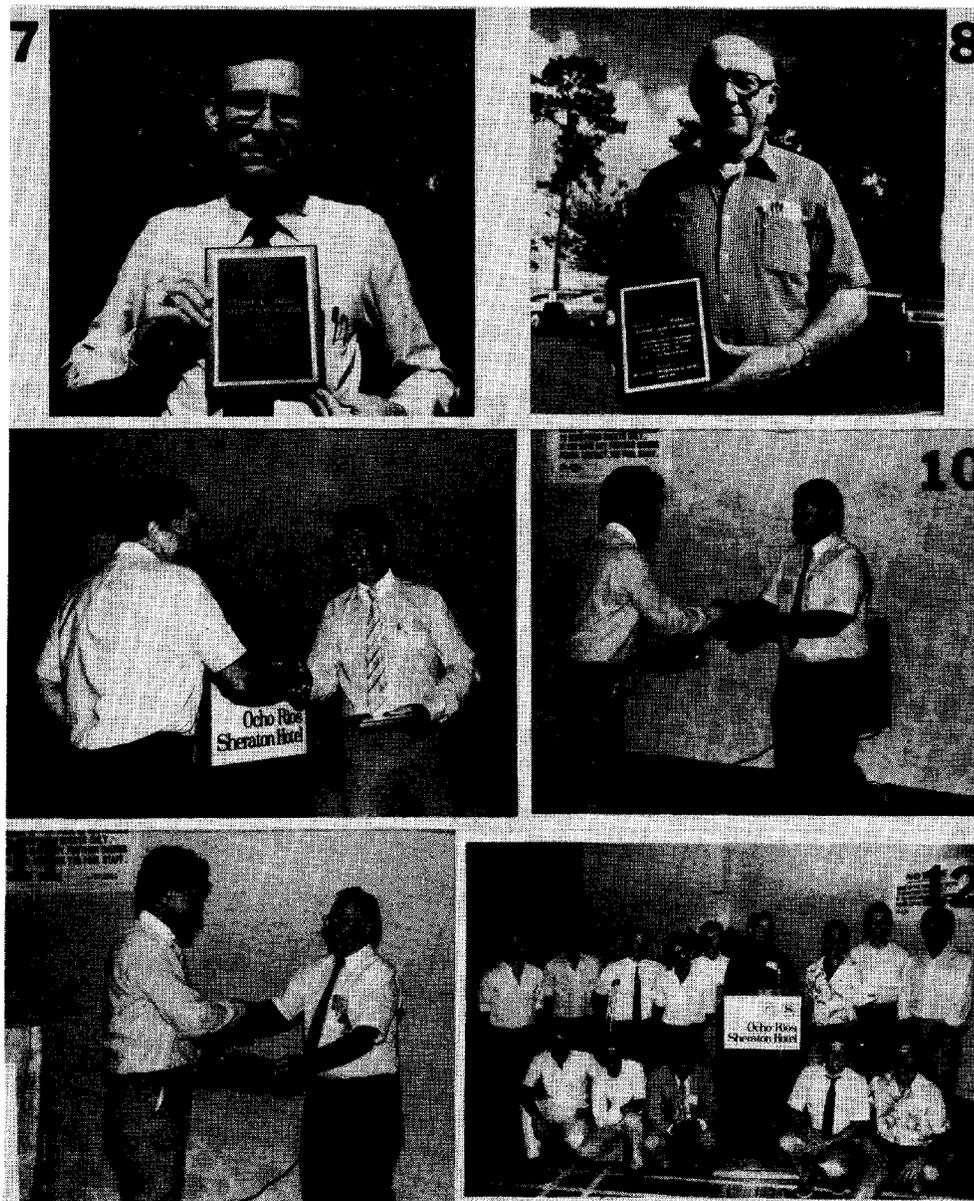


Fig. 7. James L. Nation, Professor of Entomology, Univ. of FL, was the recipient of the Annual Award for Teaching.; Fig. 8. Clifford S. Lofgren, Research Leader, Insects Affecting Man and Animals Research Laboratory, ARS, USDA, Gainesville, FL, was the recipient of the Annual Award for Research.; Fig. 9. Freddie A. Johnson (left), Professor of Entomology, Univ. of FL, receives the Annual Achievement Award for Extension and Industry.; Fig. 10. The Entomologist of the Year Award is presented to James A. Reinert (right), Resident Director, Texas A&M Univ., Research and Extension Center, Dallas, TX.; Fig. 11. M. Lewis Wright, Jr. (right), Outgoing President, receives a plaque for a job well done.; Fig. 12. Participants in the Student Papers Contest are (standing) (left to right): Jose Negron, Guy Mathurin, Andrew Gannon, Alberto Pantoja, Christopher Shea, Patrick Parkman, Greg Lanzaro (2nd Place), W. W. Hargrove (3rd Place), L. A. Salles; (kneeling) (left to right): John Vaughn, Kirti Patel, Olusola Adeyeye (1st Place), Brian Hagenbuch, Alan Gettman.

oratory in Tifton, Georgia, hails originally from Sudan, Texas. He received his B.S. degree from Texas Technical College, his M.S. and Ph.D. degrees from Kansas State University.

In over 18 years of service in USDA-ARS, he has authored or co-authored 127 referred scientific papers and numerous reviews, talks and presentations. He is an internationally recognized authority in the field of host plant resistance with special attention being given to resistance of corn and sorghum to insect attack. For the past 14 years he has taught two graduate courses in host plant resistance at the University of Florida. To prevent conflict with his USDA research, he has taught these courses on Saturdays, driving over 300 miles each Saturday.

It is with great pleasure that we award this Certificate of Merit to Dr. Billy R. Wiseman for many years of dedicated service to the field of Entomology.

The second Certificate of Merit goes to a man who had a distinguished career spanning 31 years with USDA before joining IFAS. Born in Roseville, Illinois in 1915, he attended the University of Kansas, receiving his AB degree in 1938 and Ph.D. in 1942. In 1942 he joined the staff of the Bureau of Entomology and Plant Quarantine as a taxonomist. From there he served as a field researcher in Alaska, as the officer in Charge of the USDA European Parasite Laboratory in Paris, as Assistant Chief, and later Chief, of the Insect Identification and Parasite Introduction Branch of the Entomology Research Division. Shortly before joining IFAS, he became Chairman of the Insect Identification and Beneficial Insect Introduction Institute. In 1973 he was appointed Graduate Research Professor in the Department of Entomology and Nematology at the University of Florida.

Throughout his career he has focused on the biological control of insects and other pests. Shortly after arriving at UF he initiated a bio-control project on the Mexican bean beetle, vowing to eat any beetles found alive in Alachua County in April and May, 1976. That year, at the annual meeting of the Florida Entomological Society, he only had to eat 14 beetles.

It is an honor to present this Certificate of Merit to Dr. Reece Sailer for many years of service to the profession of Entomology.

Special Award

Tonight we would like to pay special tribute to a man who has been a highly visible entomologist for many years. A graduate of the University of Florida in 1943, he has spent almost 40 years with the Division of Plant Industry. Starting as a Grove Inspector in 1946, he progressed through the ranks of Nursery Inspector, Special Inspector, Regional Inspector and Assistant Chief Inspector to his current position as Chief of Pest Eradication and Control. He has been an able spokesman in many pressure-cooker situations, including projects to eradicate the Mediterranean fruit fly.

It is a pleasure to present this Special Award to Mr. Charles Poucher for outstanding sustained contributions to Agricultural Entomology in Florida.

Annual Award for Teaching

Our honoree for the Teaching Award hails from Webster County, Mississippi. He obtained his A.A. from Sunflower Junior College and his M.S. from Mississippi State University. He received his Ph.D. from Cornell University in 1960. Shortly afterward he joined the faculty of the University of Florida and currently serves as a professor in the Department of Entomology and Nematology at UF. During his tenure there he has specialized in insect physiology, pheromone biology, nutrition and reproductive biology. He has been especially active in research dealing with fruit fly pheromones.

He is highly respected for his teaching and fairness. Perhaps this quote from the nominating statement sums it up best, "He is simply a good teacher and is concerned about his students. He is innovative in the area of physiology and creates a good atmosphere for all students."

The Teaching Award for 1985 is respectfully given to Dr. James L. Nation.

Annual Achievement Award for Research

The recipient of the Annual Achievement Award for Research has, since 1955, pursued a career with USDA. He received his B.S. from Gustavus Adolphus College in Chemistry, his M.S. in Entomology from the University of Minnesota and his Ph.D. from the University of Florida. He began his career with the Insects Affecting Man and Animals Research Laboratory in Orlando, Florida, where he conducted research on household insects. In 1957, he was selected to organize, staff, develop and supervise a research program for a new Methods Improvement Laboratory for the Plant Protection Division of ARS to support the Imported Fire Ant Control Program. In 1963 he rejoined the Insects Affecting Man and Animals Research Lab in Gainesville as Project Leader of the Area Control Section, later assuming direction of a new research program on imported fire ants. In 1977 he was assigned full-time responsibility for research on imported fire ants. He has been involved in research to develop means to control the spread of fire ants, including development of four new baits, Amdro, Pro-Drone, Logic and Affirm. Over the years he has received several awards for his research and has published over 200 papers.

It is with great pleasure that we award the Annual Achievement Award for Research to Dr. Clifford S. Lofgren.

Annual Achievement Award for Extension and Industry

Our honoree for the Annual Achievement Award for Extension and Industry is a Florida Cracker born in Jennings, Florida. He received his B.S., M.S., and Ph.D. degrees from the University of Florida and is currently professor of Entomology at the University of Florida. During the past 11 years he has become the most broadly knowledgeable entomologist in IFAS on insect problems in Florida and the Southeastern United States. He has written many extension publications and spoken extensively throughout the state. He is known for his communication skills, being able to present material at all levels and have it understood. In addition, he has the one quality essential to all good extension workers - he tells a great joke. His service as Principal Investigator on the Kellogg Grant, a grant that supported the development of the Florida Agricultural Information Retrieval System, allowed him to demonstrate his competence for leadership and provided a program that can usher in a major change in the means of conducting extension programs.

Dr. Freddie A. Johnson is this year's recipient of the Annual Achievement Award for Extension and Industry.

Entomologist of the Year Award

Our selection for Entomologist of the year award obtained his B.S. from Oklahoma State University and his M.S. and Ph.D. from Clemson University. He was Assistant, Associate and Professor of Entomology at the University of Florida's Agricultural Research and Education Center at Ft. Lauderdale from 1970-84. His research on arthropods associated with turfgrasses and ornamentals won him national recognition as

a first class researcher. In addition, he was asked to initiate a research program on the citrus blackfly when it was found in Florida in 1976. In the first phases of this program, he coordinated the University of Florida's research with programs of the USDA-SEA and with the regulatory efforts of the USDA-APHIS. This program ultimately lead to effective biological control of this destructive pest of citrus. He is presently Resident Director at Texas A&M's Research and Extension Center at Dallas.

It is with great pleasure that we name Dr. James A. Reinert Entomologist of the Year.

Recognition of the President

Finally we wish to recognize the outstanding job done by our outgoing President, Mr. M. Lewis Wright. He has provided enlightened leadership for the Society during this year which is culminated by our first out-of-the country annual meeting.

President Wright we are pleased to present you with this plaque as a token of an appreciation for a job well done!

Ladies and Gentlemen, fellow members, and honored guests, this completes the report of the Honors and Award Committee.

Respectfully submitted,
 JAMES KRING
 DAVID DAME
 VAN WADDILL, Chairman

FINAL BUSINESS MEETING

The final Business Meeting was called to order by President Wright at 12:11 p.m. Thursday, 8 August 1985. Thirty-seven members were present.

REPORT OF THE JOINT COMMITTEE, PROGRAM/CARIBBEAN CONFERENCE

There were 93 papers (32 foreign) and 5 posters (1 foreign) listed in the program. The actual numbers presented were 85 papers and 3 posters. There were 110 persons registered at this years meeting with 144 (147 tickets were sold) in attendance at the banquet. Six symposia were held and 15 student papers were presented this year.

S. H. KERR; H. M. NIGG; J. F. PRICE; J. E. LLOYD; R. M. BARANOWSKI; J. B. KRING; R. M. BENNETT; N. C. LEPPLA; W. H. WHITCOMB, Co-Chairperson; D. J. SCHUSTER, Co-Chairperson; C. S. BARFIELD, Chairperson

REPORT OF THE RESOLUTIONS COMMITTEE

Resolution No. 1

WHEREAS the 68th annual meeting of the Florida Entomological Society at the Ochos Rios Sheraton Hotel, Ocho Rios, Jamaica, has enjoyed excellent facilities and hospitality which had a significant positive impact on the success of the meeting,

AND WHEREAS Emmer Travel, Inc., Gainesville, Florida, provided outstanding services which contributed significantly to the successful travel plans of the Society's membership,

THEREFORE, BE IT RESOLVED that the Secretary of the Society be instructed to write letters of appreciation to the hotel and the travel agency management.

Resolution No. 2

WHEREAS the local arrangements committee provided excellent organization and

facilities for the 68th annual meeting of the Society under more difficult circumstances than usual,

AND WHEREAS the speakers who presented papers, both invited and submitted, shared their superior work and ideas with our Society,

AND WHEREAS exceptional symposia were organized by Janice Reid, James E. Lloyd, Herb N. Nigg, Everett R. Mitchell, Willard H. Whitcomb, Fred B. Bennett, Richard M. Baranowski, and Keith L. Andrews,

AND WHEREAS Carl S. Barfield, David J. Schuster and the Joint Program/Caribbean Conference Committee provided a first class, well-balanced program,

AND WHEREAS the Committee on Student Activities encouraged exceptional student participation in and contributions to our annual meeting,

AND WHEREAS other committees and individuals have provided immeasurable contributions of their time, ideas, and talents to our Society this past year,

THEREFORE, BE IT RESOLVED that the Society expresses its appreciation to these individuals.

Resolution No. 3

WHEREAS President M. Lewis Wright provided our Society with superlative leadership and invaluable service,

AND WHEREAS Ann C. Knapp has done an outstanding and selfless job and provided many hours of service in her position as Business Manager,

AND WHEREAS the other members of the Executive Committee have contributed exceptionally of their time and leadership to the Society,

AND WHEREAS John R. McLaughlin and the Associate Editors of the Florida Entomologist have performed a herculean job in maintaining the highest of standards for the Society's journal,

AND WHEREAS Frank W. Mead has contributed significantly over the years with his excellent photographs of the Society's activities,

THEREFORE, BE IT RESOLVED that the Society recognize these contributions and hereby expresses its appreciation to each of these individuals.

Resolution No. 4

WHEREAS members of industry and other businesses and organizations have continued to provide much needed financial support to the Society by means of Sustaining Memberships, contributions for student travel, advertising in the program, and in a myriad of other ways,

THEREFORE, BE IT RESOLVED that the Society recognizes the importance of these contributions and expresses its sincerest appreciation to these groups.

M. L. PESCADOR; D. H. VICKERS; AND J. E. EGER, Chairperson

NECROLOGY REPORT

Two of our members passed away during the last year or so. They are:

GERMAIN C. LABRECQUE (1922-1984). Retired USDA-ARS entomologist. Obituary, Florida Entomologist 68 (2): 362, June, 1985 and Bull. Ent. Soc. Amer. 31 (4): 55, 1985.

EUGENE G. KELSHEIMER (1902-1985). Retired University of Florida's Gulf Coast Experiment Station. Memoriam, Florida Entomologist 68 (3): 507, September 1985. Obituary, Bull. Ent. Soc. Amer. 31 (4): 54, 1985.

A few moments of silence were observed in tribute to the memory of these former colleagues.

D. H. HABECK, Necrologist

REPORT OF THE AD HOC COMMITTEE,
CARIBBEAN CONFERENCE EVALUATION

A preliminary survey of members attending the meetings in Jamaica indicating the following:

- 86% wanted to see more meetings of this type
- 53% favored these meetings to be held every 3 years while 40% favored every 5 years.
- 30% indicated the quality of the meeting to be good while 25% said the meeting was average.
- 66% said that the balance between symposia and submitted papers was okay.

A finalized report of the survey will be presented to the President and members of the Executive Committee.

D. GREEN; W. HOWARD; H. V. WEEMS, JR.; B. M. GREGORY, JR.; H. L. DENMARK;
AND S. S. FLUKER, Chairperson

REPORT OF THE NOMINATING COMMITTEE

The Nominations Committee reports that 106 ballots were cast for the respective society offices. Elections were officially closed at 5:00 p.m. on August 1, 1985. The results were as follows:

President-Elect	David Schuster
Secretary	Everett R. Mitchell
Member-at-Large	Joseph E. Eger, Jr.
Student Members	Guy Mathurin
	Al Gettman
Vice-President (Tied)	Larry Beasley & James Taylor

The Nominations Committee recommends that a run-off election for Vice-President be performed by mail-out ballot as soon as possible. The details for conducting the run-off election will be left to the discretion of President Dale Habeck.

W. L. PETERS; J. L. KNAPP; AND C. W. MCCOY, Chairperson

The new President, Dale H. Habeck, was escorted to the podium by R. M. Baranowski and J. B. Kring. President Habeck congratulated outgoing President Wright on a job well done. He then appointed a Nominating Committee consisting of Eger, Kring, Baranowski, and Wright (Chairman) to initiate a run-off election for the position of Vice-President. President Habeck announced that the next annual meeting will be held August 5-7, 1986 at the Sheraton Sand Key Hotel in Clearwater Beach, Florida. There being no further business, the 68th Annual Meeting of the Florida Entomological Society was adjourned at 12:34 p.m. 8 August 1985.

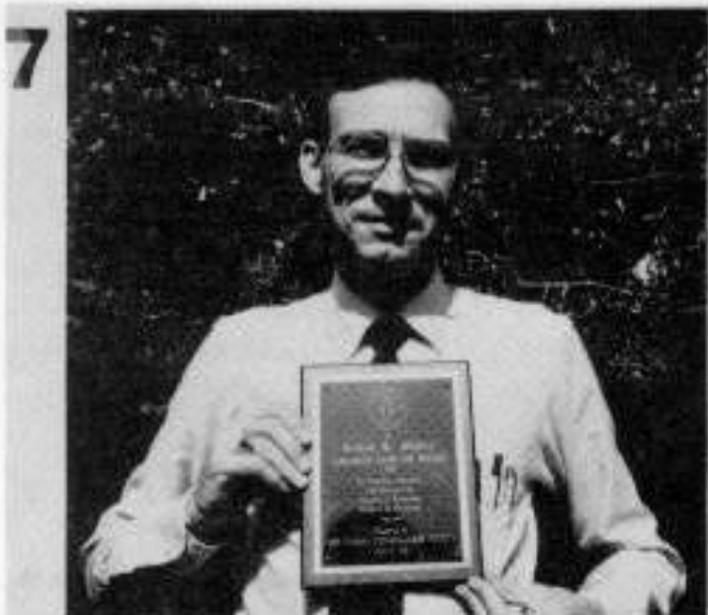
EXECUTIVE COMMITTEE MEETINGS
1984-1985

11 October 1984, Lake Alfred, Citrus Research Center
6 February 1985, Lake Alfred, Citrus Research Center
5 June 1985, Lake Alfred, Citrus Research Center
5 August 1985, Ocho Rios, Jamaica

Respectfully submitted,

DAVID F. WILLIAMS, Secretary







IN MEMORIAM

JOHN ANDREW MULRENNAN, SR.

1906-1985

Following a very brief illness, Dr. John A. Mulrennan, Sr. died on November 20, 1985 in Jacksonville, Florida. A native Floridian, he was born and brought up on a cattle and citrus farm in Hillsborough County, Florida. He left home in 1928 to attend the University of Florida where he earned a B.S. degree in 1932 in entomology. Upon graduation he worked as an entomologist for L. Maxey Inc., a large citrus company. After one year he accepted a position with the Rockefeller Foundation in Tallahassee, Florida working on malaria vector control. Thus began a unique career in public health which spanned almost 50 years and earned John A. Mulrennan a place in the annals of mosquito control not only in Florida but the nation. He left Florida in 1935 to work for the Texas State Health Department as a malariologist but returned in 1938 to the Rockefeller Foundation to work on mosquito control in Florida. In 1941, he was named Chief entomologist and director of the Bureau of Entomology of the State Board of Health (now Health and Rehabilitative Services). In cooperation with the U.S. Public Health Service, the Rockefeller Foundation and the County Health Departments; malaria control programs were established throughout the state. Since 1948 no indigenous malaria has been found in Florida due to this control effort. He created the present mosquito control system which has been so successful in Florida. This was done by writing two state laws which created state funds for mosquito control in counties and districts. Similar mosquito control projects and laws have been carried out in other states which were copied after Floridas' system. Since the 1953 State Aid Mosquito Control Law was enacted, tourist business in Florida has increased from less than one billion dollars annually from winter travelers to almost ten billion dollars from a year round industry. Salt marsh mosquitoes no longer scourge the public during the summer months in the coastal areas of the state.

He also had the foresight to realize that insecticides were not the long range solution to vector control. He persuaded the legislature to create two research centers, the Florida Medical Entomology Laboratory in Vero Beach, Florida and the West Florida Arthropod Research Center in Panama City, Florida. These laboratories work on the basic biology, physiology, genetics and ecology of mosquitoes, sand flies, midges and flies as well as new control techniques. Because of his tireless efforts in this field, Doctor Mulrennan Sr. is considered the father of Mosquito Control in Florida.

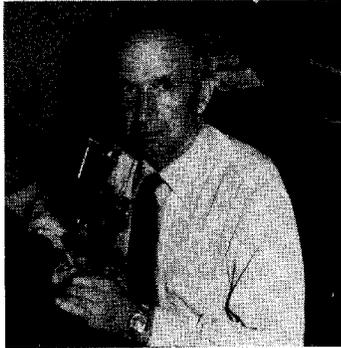
He also drafted the first state law in 1947 for regulation of the structural pest control industry and worked hard to upgrade this industry for the benefit of both the industry and the public. This law forced the unscrupulous individuals to leave the field and

upgraded the industry to the level of integrity it now enjoys in the state. The Florida Pest Control industry is one of the most progressive in the nation due to the guidance and regulations created by John Mulrennan. He was honored for his productive career in Entomology with a Doctor of Science degree in 1972 from the University of Florida. Although he retired as Director of the Bureau of Entomology in 1976, he continued to be actively involved in entomology through his work in professional societies. He was a member of the American Mosquito Control Association (Past President), Florida Anti-Mosquito Association (Past President and Secretary-Treasurer), the Florida Pest Control Association, Florida Public Health Association (Past President, and he was presented Meritorious Service Award 1971), Gamma Sigma Delta, Hyacinth Control Society, Phi Sigma and Alpha Zeta.

Dr. Mulrennan is survived by two sons, Dr. John A. Mulrennan, Jr., and Joseph P. Mulrennan, two daughters, Annie M. McCarthy and Sandra C. Jansen, 11 grandchildren and two great-grandchildren. He is also survived by four brothers, Joseph B., Michael M., Francis D., and Timothy C. Mulrennan; two sisters, Annie M. Mulrennan and Helen G. Young.

R.S. Patterson





IN MEMORIAM

GERD H. HEINRICH

Research Associate of the Florida State
Collection of Arthropods

Mr. Gerd Herrmann Heinrich, generally regarded as the world's leading authority on the subfamily Ichneumoninae, family Ichneumonidae, died 17 December 1984. All known Ichneumoninae are specialized parasites of Lepidoptera. Heinrich was the author of 6 major publications on Ichneumonidae, 4 popular travelogs, 97 smaller but significant publications on Ichneumoninae, 3 publications on European mammals, 3 publications on the biology of the birds of Angola, and 2 publications on the systematics of the birds of Angola coauthored with Dr. S. Dillon Ripley, formerly of Yale University and later Secretary of the Smithsonian Institution.

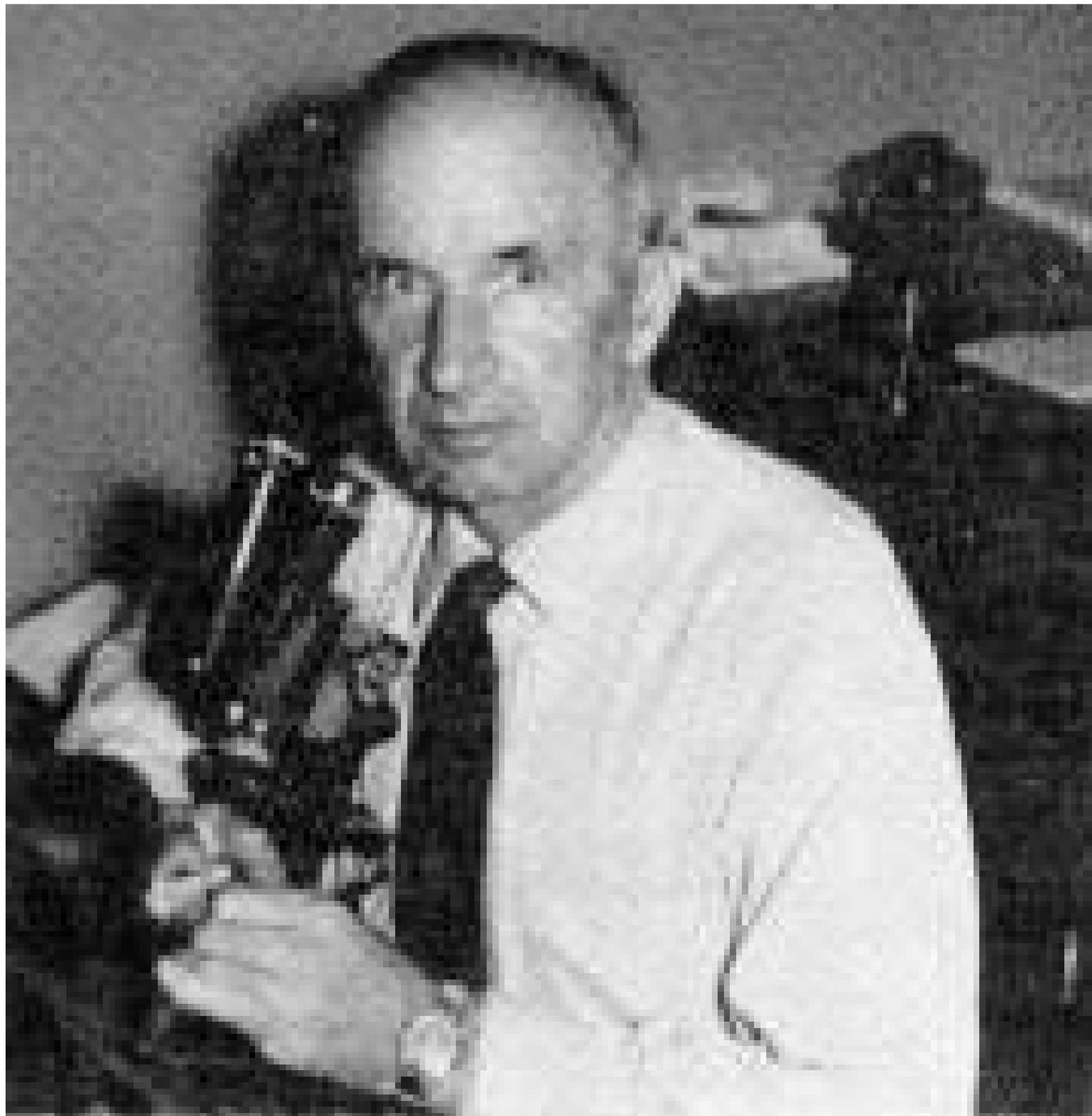
Heinrich's major publications were "The Ichneumoninae of Celebes" (German language, 1934, 265 pages, 7 plates of figures); "Les Ichneumonides de Madagascar" (French language, 1938, 139 pages, 6 plates); "Synopsis of Nearctic Ichneumoninae Stenopneusticae with particular reference to the Northeastern Region (Hymenoptera)" (English language, 1961-1962, 7 volumes, 886 pages, numerous illustrations); "Synopsis and reclassification of the Ichneumoninae of Africa south of the Sahara" (English language, 1967-1969, 5 volumes, 1,258 pages, numerous text figures; "Burmeseische Ichneumoninae" (German language, 1965-1980, 641 pages, 21 text figures); "Ichneumoninae of Florida and neighboring states (Hymenoptera: Ichneumonidae, subfamily Ichneumoninae), Arthropods of Florida and neighboring land areas" (English language, 1977, 1 volume, 350 pages, 77 text figures, 9 color plates). Heinrich described 1,479 species and subspecies of Ichneumoninae (Nearctic: 345, Africa: 408, Madagascar: 87, Celebes: 156, Palearctic: 1,083). Travelog books were about Heinrich expeditions, including 1 on the Celebes Island (1932), 1 on Burma (1940), and 1 on Persia (1933).

From early childhood, Gerd realized an interest in natural history. At the age of 15, through the influence of Professor Heymons, one of the custodians of entomology at the Museum für Naturkunde, this interest became concentrated on parasitic wasps of the family Ichneumonidae, a large, diverse, and at that time taxonomically poorly known group of insects.

Gerd Heinrich was born in Berlin, Germany on 7 November 1896, son of a physician, Dr. Herrmann Heinrich, and Margarethe von Tepper-Ferguson Heinrich, heir of a large agricultural estate in the German province (since 1918, Polish) of West Prussia. Gerd was educated at home by a tutor until his 9th year, graduated "primus omnium" from the Askanische Gymnasium in Berlin in 1914, at the age of 17, planning, like his father before him, toward a career in medicine. His education was interrupted by the declaration of war between Germany and Russia. He entered the German Army in the cavalry and subsequently became a pilot in the German Air Force. Following World War I, the family estate became a part of Poland where Gerd married and lived with his family. Poland was invaded by Germany in 1939, and World War II began. A series of bizarre incidences followed, during which both he and his wife were, for a time, on the "death list" of the Gestapo, but through the aid of a close friend from World War

I, who, meanwhile, had become a general in the German Air Force, he and his wife were rescued. Gerd, in an effort to survive, reentered the German Air Force over which the Gestapo had no authority. Near the end of World War II, leaving all that they owned in Russian-occupied Poland, he and his family escaped to West Germany under extremely dangerous circumstances. In 1951 they moved to the United States, and with the aid of Dr. Eric Cunliffe and Dr. Henry Townes, himself a world authority on ichneumonid wasps, became American citizens and settled on a little farm in Maine where his wife, Hildegard, continues to reside and where Gerd, assisted by his wife, continued his studies of Ichneumoninae of the world almost to the time of his death at the age of 88. His lifelong interest in ichneumonid wasps was one of virtually total commitment and dedication.

Howard V. Weems, Jr.
Taxonomic Entomologist and Curator
Florida State Collection of Arthropods
Division of Plant Industry
Florida Department of Agriculture and Consumer Services
Gainesville, FL 32602
17 February 1986



SUSTAINING MEMBERS, JANUARY, 1985

Abbott Labs—Chem & Ag. Products
Div.
Att: A. Crovetti, Dept. 912
14th & Sheridan Road
North Chicago, Ill 60064

Alert-Lear Pest Control
Att: N. Goldenberg
P.O. Box 381777
Miami, FL 33238

All American Termite & Pest
Control, Inc.
2809 Edgewater Drive
Orlando, FL 32804

Am-Mo Consulting, Inc.
Att: Dr. Emil A. Moherek
Rt. 1, Box 62
Clermont, Fl 32711

Biochem Products
Att: F. Van Essen
5014 NW 41 Street
Gainesville, FL 32606

Bio-Serv, Inc.
Attn: Clark F. Johnson
P.O. Box 450
Frenchtown, NJ 08825

Capelouto Termite & Pest Control
Att: Raymond Capelouto
700 Capital Circle N.E.
Tallahassee, FL 32301

Ciba-Geigy Corporation
Att: Haney B. Camp
P.O. Box 11422
Greensboro, NC 27409

Dow Chemical USA
Attn: Dr. Joe Eger
P.O. Box 22300
Tampa, FL 33622

Duphar B.V.-Corp Protection Div.
Att: A. H. Tomerlin
P.O. Box 695
Lake Mary, FL 32746

Florida Pest Control Association
Att: Toni Caithness
5104 N. Orange Blossom Trl.-
Suite 103
Orlando, FL 32810-1094

Gould Arborists
Att: J. Gould
P.O. Box 715
Sarasota, FL 33578

ICI Americas, Inc.
P.O. Box 208
Goldsboro, N.C. 27530

Martin Pest Control
Att: Michael D. Martin
P.O. Box 610605
North Miami, FL 33161

McCall Service Inc.
Att: Bryan Cooksey
P.O. Box 2221
Jacksonville, FL 32203

Nor-Am Agricultural Products Inc.
Field Station Florida
Att: George W. Bauta
P.O. Box 7
Cantonment, FL 32533

E. O. Painter Printing Co.
Att: S. Dick Johnston
P.O. Box 877
DeLeon Springs, FL 32028

Pesticide Chemicals, Inc.
P.O. Box 369
Fort Pierce, FL 33454

Pet Chemicals, Inc.
Att: Dr. Terry L. Couch
7781 N.W. 73 Ct.
Miami Springs, FL 33166

Plant Products Corporation
Att: Robert Geary
P.O. Box 1149
Vero Beach, FL 32960

Ratterman's Consulting Service
Attn: Clifford B. Ratterman
373 N. University Drive, Suite 44
Plantation, FL 33324

Rhone-Poulenc, Inc.
Att: Brian Tepper
6308 Hofstra Ct.
Ft. Myers, FL 33907

Robert G. Haines
The PLM Company
P.O. Box 733
Orange Park, FL 32073-0733

Rhom & Haas Company
Att: T. J. Stelter
224 Desota Road
West Palm Beach, FL 33405

Sandoz, Inc.
Att: Jeffrey R. O'Neill
2484 Wildflower Lane
Snellville, GA 30278

Southern Mill Creek Products Co.
Att: Herbert Friedman, Martin
Griffin
P.O. Box 1096
Tampa, FL 33601

Stauffer Chemical Company
Att: Tom W. Mills
1690 Raymond Diehl, Suite 2B
Tallahassee, FL 32308

Sun Refining & Marketing Co.
Att: Ms. E. A Winkeler
P.O. Box 1135
Marcus Hook, PA 19061-0835

Taylor & Turner, Inc.
Attn: David Turner
2520 N. Dixie Highway
Ft. Lauderdale, FL 33305

Truly Nolen
Att: Truly Nolen
5931 Hallandale Beach Blvd.
Hollywood, FL 33023

Union Carbide Corp.
Att: Thomas Minter
1700 Deleon Street
Oviedo, FL 32765

Uniroyal Chemical
Att: Keith H. Griffith
6233 Ridgeberry Court
Orlando, FL 32819

Van Waters & Rogers
Att: Norman R. Ehmann
2600 Campus Drive
San Mateo, CA 94403

Walt Disney World
Att: Jerry A. Hagedorn
P.O. Box 40
Lake Buena Vista, FL 32830

A. C. "Abe" White R.P.E.
817 W. Fairbanks Avenue
Orlando, FL 32804

Wright Pest Control
Att: M. L. Wright, Jr.
P.O. Box 2185
Winter Haven, FL 33880

Zoecon Corporation
Att: Dr. Kevin T. Short
5417 Colewood Place
Sarasota, FL 33582