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June 1, 1984

THE 67th ANNUAL MEETING OF THE  
FLORIDA ENTOMOLOGICAL SOCIETY  
FIRST ANNOUNCEMENT

The Florida Entomological Society will hold its 67th Annual meeting on 24-27 July 1984 at the Holiday Inn, 6515 International Drive, Orlando FL 32809; telephone—1-(305)-351-3500. Room rates will be \$58.00, for single, double, triple, or quadruple.

Questions concerning the local arrangements should be directed to:

FREDERICK L. PETITT, Chairman  
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Florida Entomological Society  
Walt Disney World-Epcot Center-The Land  
P.O. Box 40  
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Phone: 1-(305)-827-7256

To present a paper, the tear out sheet must be postmarked and sent no later than 15 MAY 1984, to:

JAMES A. REINERT, Program Chairman  
Ft. Lauderdale Research and Education Center  
University of Florida  
3205 S.W. College Avenue  
Ft. Lauderdale, Florida 33314 USA

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 3 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. Awards will be \$125.00, 75.00 and 50.00.

The 3 student display presentations judged to be the best on content and preparation will also be awarded monetary prizes during the meeting. Student authors *must* be Florida Entomological Society Members and *must* be registered for the meeting. Awards will be \$125.00, 75.00 and 50.00.

Registration Schedule<sup>1</sup> for Annual Meeting:

	<u>Preregistration</u>	<u>Registration On Site</u>
Full & Sustaining Members	\$35.00	\$40.00
Student <i>not</i> in Student Contest	18.00	20.00
Student <i>in</i> Student Contest	13.00	15.00
Each Extra Banquet Ticket	10.00	10.00

<sup>1</sup>Each fee includes one banquet ticket.

PAPER SUBMISSION  
Deadline:  
*15 May 1984*

## SLIDE POLICY FOR ANNUAL MEETINGS

The following slide policy will govern slide presentations at the Annual Meetings. Only Kodak Carousel projectors for 2 x 2 slides will be available. However motion picture projectors will be available by special request to the Local Arrangements Chairman prior to the date of the meeting.

Authors should keep slides simple, concise, and uncluttered with no more than 7 lines of type on a rectangle 2 units high by 3 units wide. All printed information should be readable to an audience of 300 persons.

A previewing room will be designated for author's use. A projectionist will be available in the previewing room at least one hour before each session. Authors are expected to give the projectionist their slides in the previewing room prior to each session. Slides will be returned to the authors after each session in the meeting room.

Authors are expected to organize their slides in proper order in their personal standard Kodak Carousel slide tray (no substitution, please). Only a few slide trays will be available in the previewing room from the projectionist for hardship cases. Slides in the tray should be in correct order starting with slot #1 of the tray and positioned correctly (position of slides to go into tray: 1. upside down, and 2. lettering readable from this position upside down and from right to left). A piece of masking tape should be placed on the slide tray by the author and the following information should be written on the tape: 1. author's name, 2. session date, and 3. presentation time.

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

Deadline for Paper  
Submission is 15 May 1984

Author's Name \_\_\_\_\_

Title of Paper \_\_\_\_\_

Affiliation and Address \_\_\_\_\_

of the First \_\_\_\_\_

(Presenting) Author \_\_\_\_\_

Time Required for Presentation (Max. 10 min.) \_\_\_\_\_

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

Suggestion for Evening Bull Session \_\_\_\_\_

\_\_\_\_\_

GOURMET INSECT BEHAVIORAL ECOLOGY:  
STALKING THE WILD SPECULATION

JAMES E. LLOYD\*

"Bold ideas, unjustifiable anticipations, and speculative thought, are our only means for interpreting nature: our only organon, our only instrument, for grasping her."

(Karl Popper, quoted in Beveridge 1980)

Insect Behavioral Ecology is a new and thriving discipline within Entomology. What is it that is new, and different from S. W. Frost's admirable insect natural history or bionomics? (Lloyd 1980). Whereas the discipline known as exobiology—the study of life on other planets and in outer space—has been called a science without a subject, insect bionomics might have been called a subject without a science—science is far more than the collection of facts and the arrangement of them into convenient but more or less arbitrary patterns. An historian of Newton said that "The naturalist is indeed a trained observer, but his observations differ from those of a gamekeeper only in degree, not in kind; his sole esoteric qualification is familiarity with systematic nomenclature." Actually this was a case of science snobbery, the subject Mayr (1982) was discussing when he passed this quotation along, but it helps me get to my point. It is Darwin's theory (and improvements on it) that is primarily responsible for raising our study of insects above what has gone before, and that gives us an "esoteric qualification." Now if used creatively, more than merely giving insight to explain the adventures of favorite animals and old problems, it can lead to the discovery of new and useful biological questions and generalizations at several levels in the explanation hierarchy. You would be asked, and then badgered, were you fortunate enough to be in one of Dick Alexander's classes, "What are the 10, exactly 10, no more no fewer, what are the 10 most important concepts in [some subject area]." Well then, it is 18 past Williams (1966), do you know where your conceptual progeny are? Do you know how to make an innovation or tickle an inspiration out of the right side of your brain?

"The creative mind is able, as Schopenhauer has stated it, 'to think something that nobody has thought yet, while looking at something that everybody sees.' Imagination, thus, is ultimately the most important prerequisite of scientific progress."

(Ernst Mayr 1982)

The process of going from original observation, to disciplined observation (see Altmann, this Symposium), to testing and "proof" requires imagination. Imagination is the critical and certainly the most intellectual element of the hypothetico-deductive method (see Ghiselin 1969, Mayr 1982, and Thornhill, this Symposium.) Some people have it. Perhaps some don't. Some seem to have more of it than others, but can be helped with training and practice (Adams 1979, Beveridge 1980, Daitzman 1980). The first step is to ignore those who remain of the opinion that speculation

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("trivial and stupefying natural philosophy," H. Kolbe, see Van't Hoff 1967) should be bridled or eschewed entirely, for they will only be helpers at the nest—show me a biologist who can't appreciate a good just-possibly-so story and I'll show you a technician (see Mayr 1983). A colleague recently sent me a paper in which, after presenting pages of data, he submissively and apologetically tendered the notion that there was "scope for profitable speculation in some instances." However, he noted that functional interpretations were a minefield for the incautious! Who is going to get blown up by whose mines for trying to narrow the search for meaning in the obese hog of Baconian trivia that fattens at granting agency troughs?, but, alas, I see I have answered my own question. Even the most unimaginative know or feel that an idea that explains their technical output makes them eunuchs (are we all merely Darwin's retainers?), so perhaps they favor a system that cuts off the potential seminal contributions of others. I think we have all sensed more than once that the castration of imagination is part of the rite of passage in "peer" review. But, when an idea is published everybody can think about it, develop it, juxtapose it with others, store it for future use or reference, use it to get to a better alternative, or constructively shoot it down. When an idea is censored all are poorer, except the reviewers and they are anonymous—and regardless of what you would prefer to believe, ideas are pirated from reviewed manuscripts and research proposals (more on this later; see Broad and Wade 1983). "Wild speculation"? From my experience this means that the accuser is too unimaginative, short-sighted, or unknowledgeable to understand it, where it might lead, or how to profit from it (e.g. see Van't Hoff 1967). I will eventually illustrate this in detail in the case history of a reviewer who referred to a suggested (shared) working hypothesis that grew out of and explained an aggregate of more than 60 years of observation as "wild speculation," though he himself had just proposed an explanation that was not merely pre-Darwinian, but, in fact, pre-Lamarckian and invoked a species spirituality. Now *that's* his kind of wild. Mine is the spice that completes the process of turning the study of insects into an epicurean delight and a scientific accomplishment.

Beveridge (1980) discussed several ways to put your full brain to work, in the search for innovation, new concepts, generalizations, and theories, and I cannot possibly do him justice here. (I enthusiastically recommend Beveridge's book—use it for a seminar text, and a source of numerous references on the subject.) The obvious first way is critical thinking. This is disciplined thought that is directed by one's consciousness. It follows logical pathways and stops lines of thought that are inconsistent with known facts and accepted theories. This is the supposed basic *modus operandi* of science, and all of us are trained in it and inhibited by it to some degree. Another is imaginative thinking. This is not usually consciously directed and is often subjective, and is what psychologists call associative flow. It is a way of avoiding the use of words, which are the material of critical thinking but a hindrance to imaginative thinking. Visual not verbal symbols are used. For example, you might imagine yourself to be a parasite looking for a host, or a sperm in a race in the female reproductive track. Who are you to argue or chortle—Einstein did it!

And then there is wild thinking. Wild thinking goes the next step, and breaks out of the restrictions imposed by the limits of ingrained in-

hibitions that will still be present in the unaided imagination of the previous method. In wild thinking, aids to the imagination are used. For example, you might go to the hardware store and look at every item on the shelves and force yourself to figure out how each could be used to solve the problem, or could be analogous to part of the biological mechanism you can't understand. (I suppose if you are researching mating biology you should visit the "Sex Toys" store, reported to be on Bourbon Street, New Orleans). To get in condition for this sort of thing, try what is called mental jogging (Daitzman 1980). For example, as your assignment, list seven changes that would or could be made at "Wendy's (Where's the beef?)" fast food restaurants if humans had hypognathous heads, piercing mouth-parts, and parthenogenesis. But even this will not be enough, for remember what J. B. S. Haldane said about Nature—its not only queerer than we suppose, it's queerer than we can suppose.

"Everything about which I thought or read was made to bear directly on what I had seen or was likely to see; and this habit of mind was continued during the five years of the voyage. I feel sure that it was this training which has enabled me to do whatever I have done in science."

(Charles Darwin, ca. 1876, in Barlow 1969)

A less *avant-garde* form of inspirational activity makes use of the fact that a fertile union is often made at the interface of two sciences, subjects, or different disciplines within a science. A classic example is that Gregor Mendel not only knew his peas but his mathematics as well. In these Symposia we are trying to have some papers that are right on insect behavioral ecology (wherever that is, Lloyd 1980), and others that run to the side, at another level, or across the grain, and that might make a neural bridge in the gray matter of someone who hears or reads the proceedings. Toward that connection, let us now begin with the papers at hand.

But first, I thank the Executive and Program Committees of the Society for their enthusiastic support and cooperation and I also thank the following individuals for reviewing and making helpful suggestions on manuscripts and for technical assistance: John Alcock, Tim Forrest, Barbara Hollien, Dick Johnston, Ngo Dong, John Sivinski, John Strayer, Tom Walker, Susan Wineriter, Dan Wojcik, and Lewis Wright. Symposium—'83 was made possible by contributions from Carl Barfield, IFAS through the efforts of Dan Shankland, and the Society.

Symposium—'84 will be held at the annual FES meeting at Orlando in July 1984. Florida Agricultural Experiments Station Journal Series No. 5473.

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Symposium Participants. Back row, l to r: Awinash Bhatkar, Carl Barfield, John Sivinski, Franz Huber, Randy Thornhill. Front row: Howard Seliger, Mary Jane Angelo, Brian McNab, Eric Charnov, Jim Lloyd. Photographed by Frank Mead, FADCS-DPI. 11 August 1983, Clearwater Beach, Florida.

# ENTOMOLOGICAL SOCIETY



## EVOLUTION OF HOST SELECTION AND CLUTCH SIZE IN PARASITOID WASPS

ERIC L. CHARNOV AND SAMUEL W. SKINNER\*

### SYNOPSIS

This paper discusses the evolution of host selection, including superparasitism, and the evolution of clutch size in non-solitary parasitoids. First, we review the natural selection (as opposed to proximate mechanism) approach to understanding life-histories. We discuss this approach specifically in reference to parasitoids, reviewing previous work. Then we build a simple or first order model for a primary parasitoid's clutch size; this is tested against lab/field data for two parasitoids (*Trichogramma*, *Nasonia*). The model fails to account for the data, but the failure is in a very particular way. This leads us to revise the theory, adding factors left out of the first order approach. This new theory building is not *ad hoc* as the factors added are very natural and general considerations. We then consider the problem of superparasitism, the two key questions being, when should it be expected to happen, and what clutch size ought the superparasite have? Finally, we make some general remarks on the natural selection approach to evolutionary ecology.

### INTRODUCTION

All organisms pass through a series of physiological and behavioral stages over the courses of their lifetimes. Sometimes these stages of life are reflected in profound changes in the form: for instance, a butterfly begins life as an egg, hatches into a larva, and goes through a pupal stage before emerging as an adult. Other creatures undergo less drastic physical changes.

The study of life histories takes as its subject these general patterns in the lives of individual organisms. It is a powerful tool with which to understand the compromises that organisms have evolved to deal with the many physical and biological factors that affect them during their lives.

Most of the important concepts in the study of life histories can be framed in terms of trade-offs. For example, Pacific salmon of the genus *Oncorhynchus* spend two to three years of rapid growth at sea and then travel up a river or estuary to spawn, after which they die. Trout, of the genus *Salmo*, are closely related to salmon and also come in from the sea to spawn in many of the same streams. But trout do not die after a single spawning; they return to the sea and breed again the next year. Assuming that these two patterns were produced by natural selection operating upon the reproductive advantages to an individual organism, why should any fish die after one spawning? Why not return, as trout do, to spawn many times?

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\*Eric L. Charnov first began working on evolutionary ecology when he was a graduate student with Gordon Orians at the University of Washington, in the early 1970's. His personal discovery of natural selection constitutes the only religious experience of his life. Currently at the University of Utah, he is a Professor in the departments of Biology, Psychology and Anthropology. His current research concerns human social development, human hunter-gatherer ecology; and sex allocation in plants and animals especially barnacles and coral reef fish.

Samuel Skinner completed a Ph.D. in Biology at the University of Utah in 1983. Presently he is an NIH Postdoctoral Fellow with James F. Crow at the University of Wisconsin. His interests include sex ratio and clutch size evolution. Current addresses: Charnov, Dept. of Biology, Univ. of Utah, Salt Lake City 84112. Skinner, Laboratory of Genetics, Univ. of Wisconsin, Madison 53706.

In this case, there is a trade-off which relates to the fact that a fish must reduce the number of eggs it produces during a single spawning if it is to have enough energy to return to the sea and survive until the next spawning season. Trout produce fewer eggs each year than they would if they invested all their energy in reproduction and died soon after spawning. With salmon, this trade-off is made differently—they put all of their energy into reproduction and in this way increase the chances that more of their offspring will survive. Just why the tradeoff is resolved differently in trout versus salmon is unclear.

The concept of fitness—an organism's genetic contribution to future generations—is central to analyses of such problems. Almost all current models use as a criterion for fitness the reproductive success of an individual, that is, the number of its offspring that survive to reproduce. But reproductive success is in turn determined by several different factors.

The general problem was first clearly posed by Darwin in 1871:

“Thus the fertility of each species will tend to increase, from the more fertile pairs producing a larger number of offspring, and these from their mere number will have the best chance of surviving, and will transmit their tendency to greater fertility. The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of more power and the greater risks run by the parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size, or less vigorous, or subsequently not so well nurtured. To strike a balance in any case between the disadvantages which follow from the production of a numerous progeny, and the advantages (such as the escape of at least some individuals from various dangers) is quite beyond our power of judgment.”

The balance spoken of by Darwin is the basis of current life history theory. For example, there is often a trade-off between a parent's reproduction and its survival; helping offspring to survive reduces the chance that the parent will survive to reproduce again. A simplified representation of this trade-off is shown in Figure 1. The exact form of the trade-off curve depends on the species and its particular environment. To determine this form, one must know the extent to which producing more eggs or providing more care for offspring reduces the parent's chances of reproducing in the future. Given such a trade-off, the theory of natural selection allows us to calculate the point on the trade-off relation which provides greatest reproductive fitness (illustrated on the curve).

For parasitoid wasps (and many other insects), the production of offspring involves at least two general components: host selection (including the habitat searched for hosts) and determination of clutch size. For this discussion, we will generally ignore a third important component, the sex ratio (reviewed for parasitoids in Charnov (1982) and discussed in a previous symposium by Frank (1983)). The parasitoid and general insect literature shows two rather different approaches to host selection problems. The first, well illustrated by the recent reviews of Vinson (1976) and Vinson and Iwantsch (1980), is the *proximate mechanism* approach. Clearly offspring production involves the factors of (1) habitat selection (where does the female parasitoid search for hosts?), (2) the detailed search for hosts,

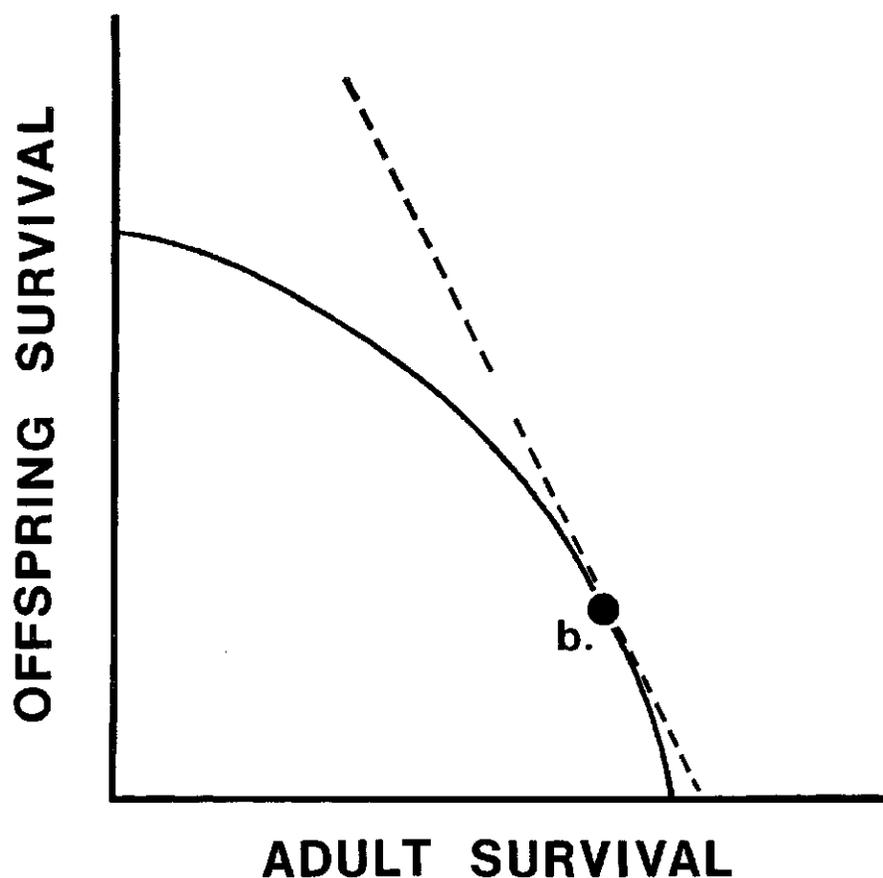


Fig. 1. An assumed tradeoff between the mother's yearly survival and the survival to adulthood of the single offspring born each year leads to an intermediate for both being favored by selection. Population genetic techniques (for example, Charnov 1982) show that the equilibrium is at point *b*, where a line of slope minus two is just tangent to the tradeoff curve.

(3) the acceptance or rejection of "hosts" found and (4) the suitability of the chosen hosts for offspring growth and survival. All of these must be mediated by various cues (chemical, tactical, etc.) and a great deal of research has been devoted to sorting them out. Thus, one attempts to understand in great detail the *immediate or proximate mechanisms* involved in the process of offspring production. This approach is rather different from the *natural selection* approach where we calculate the fitness-maximizing alternative from among those possible in a trade-off situation. This natural selection or proscriptive approach says what the beast ought to do, not how it arranges to do it. Of course, both approaches are useful and interesting; it's just that they ask different questions. That is the two approaches are not alternatives, but are complementary.

The natural selection approach is the newer of the two, although sex ratio decisions (Charnov 1982) enjoy a large literature. Let us briefly mention previous work, with parasitoids or related (life-history-wise)

insects. Two important early papers are Klomp and Teernik (1967), on optimal clutch size in *Trichogramma*, and Mitchell (1975) for the same applied to a bean weevil. More recent work on *Trichogramma* applies precise adaptational models to clutch size and sex ratio (Charnov 1982, Waage and Ming 1983, Waage and Lane 1983). Green (1982) has similarly considered the coevolution of host choice and sex ratio for solitary parasitoids. Chew and Robbins (1983) have reviewed oviposition decisions in butterflies from both the proximate and natural selection viewpoints. Weis, Price and Lynch (1983) have modeled clutch size for a gall making Dipteran. Finally, Skinner (1983a) and Parker and Courtney (1983) have discussed some general adaptational models for several aspects of insect oviposition. Our work discussed here is in the spirit of these last two papers.

#### LACK'S THEORY FOR BIRD CLUTCH SIZE . . . APPLIED TO WASPS

In the 1940's, the great British ecologist, David Lack, became interested in the factors affecting clutch size in birds. Why did some sea birds attempt to rear but a single offspring, while some titmice produced a dozen? And why did clutch size within a species alter from year to year or with latitude? His approach to the determinants of clutch size consisted of asking the *ultimate question* of the consequences on the parents' fitness of rearing a clutch of a particular size. The fundamental idea was quite simple. Suppose that the survivorship to adulthood of each offspring declined with increasing clutch size (perhaps due to less food available for each child), as shown in Figure 2. This figure is simply illustrative, as the survival decline may well not be linear. Disregarding clutch size influences on parental survival, this survival decline would mean that some intermediate clutch size would be the value which resulted in the largest number of surviving offspring, a fairly good measure of parental fitness. As a first order theory, we might ask if the clutch size of a primary parasitoid, *for each single host*, obeys a rule like Lack's hypothesis. Do female parasitoids lay a clutch which maximizes the number of offspring surviving to adulthood?

The application of these ideas to parasitoids is, however, a bit more complicated than for birds, for one simple reason. Birds have determinate growth and same-sex adults of a given species are roughly all the same size. Insects have no such constraints and size variation among reproductive adults may be several-fold. Thus immatures growing up in a crowded host may simply emerge as small adults. Thus crowding may cause immature survival to decline and/or adult size to decrease. Adult body size may have large effects on adult fitness, altering both life span and egg production (cf. Charnov et al. 1981). Figure 3 shows data from the parasitoid literature which illustrate these notions. In 3a larval crowding (for a bruchid weevil attacking beans) results in a linear decline in survival. In 3b, data from Salt's (1940) work on the parasitoid *Trichogramma* shows how larval crowding lowers the resulting adult size. Figure 3c is a hypothetical relation between female adult size and lifetime egg production, a measure of lifetime fitness for an offspring. If these data were available for one parasitoid in a specified host, we could easily calculate the total fitness through offspring (here restricting our calculations to female offspring) a mother would realize through a given clutch size. This value ( $W_f$ ) would be the product of:

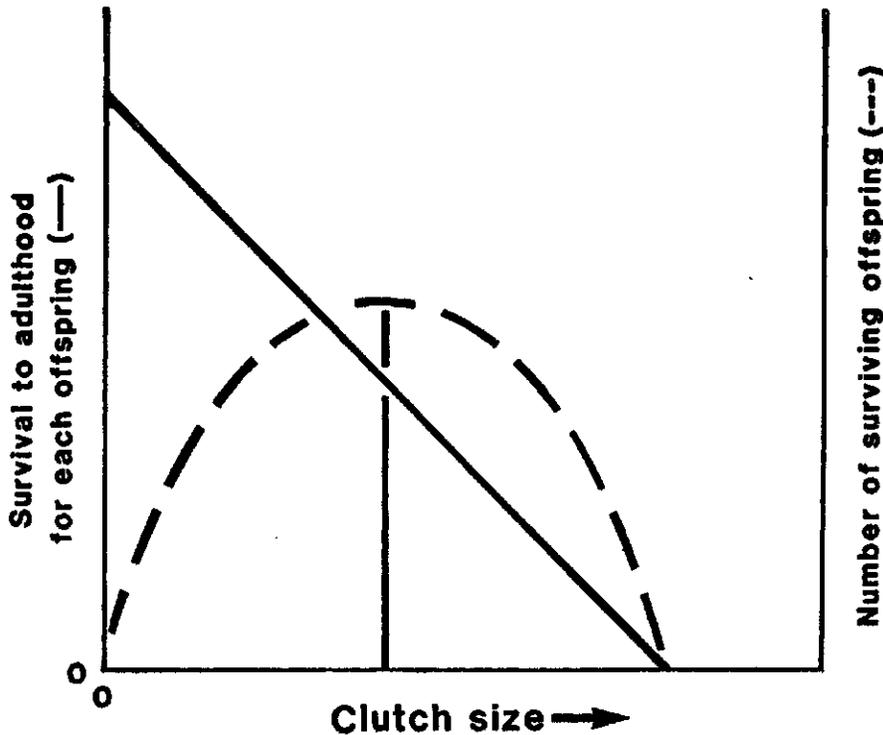


Fig. 2. Lack's hypothesis for clutch size. As clutch size increases, the survival to adulthood of each offspring declines, resulting in an intermediate clutch size which maximizes the number of surviving young. All else equal, this is the size favored by selection (Charnov and Krebs 1975).

$$W_t = (\text{clutch size}) \times (\text{proportion of offspring surviving to adulthood}) \times (\text{size of offspring}) \times (\text{lifetime egg production for offspring of this size}) \quad (1)$$

Under Lack's hypothesis applied to parasitoids, natural selection would favor the clutch size which maximizes  $W_t$ . Let us now apply this theory to two parasitoids.

A. *Trichogramma embryophagum*

Clutch size and sex ratio (from a natural selection view) have been studied in several species of egg parasitoids of the genus *Trichogramma* (Charnov 1982, Waage and Ming 1983, Waage and Lane 1983, Klomp and Teerink 1967). Here we briefly review the classic work of Klomp and Teerink (1967). For the species *T. embryophagum*, they studied clutch size in hosts of a wide size range (100-fold range, although five of the six host species were in a 10-fold size range). As expected, the wasp's clutch size increased with host size. For three of the hosts (two large, one small) they determined the effect of clutch size on offspring survival and final adult size.

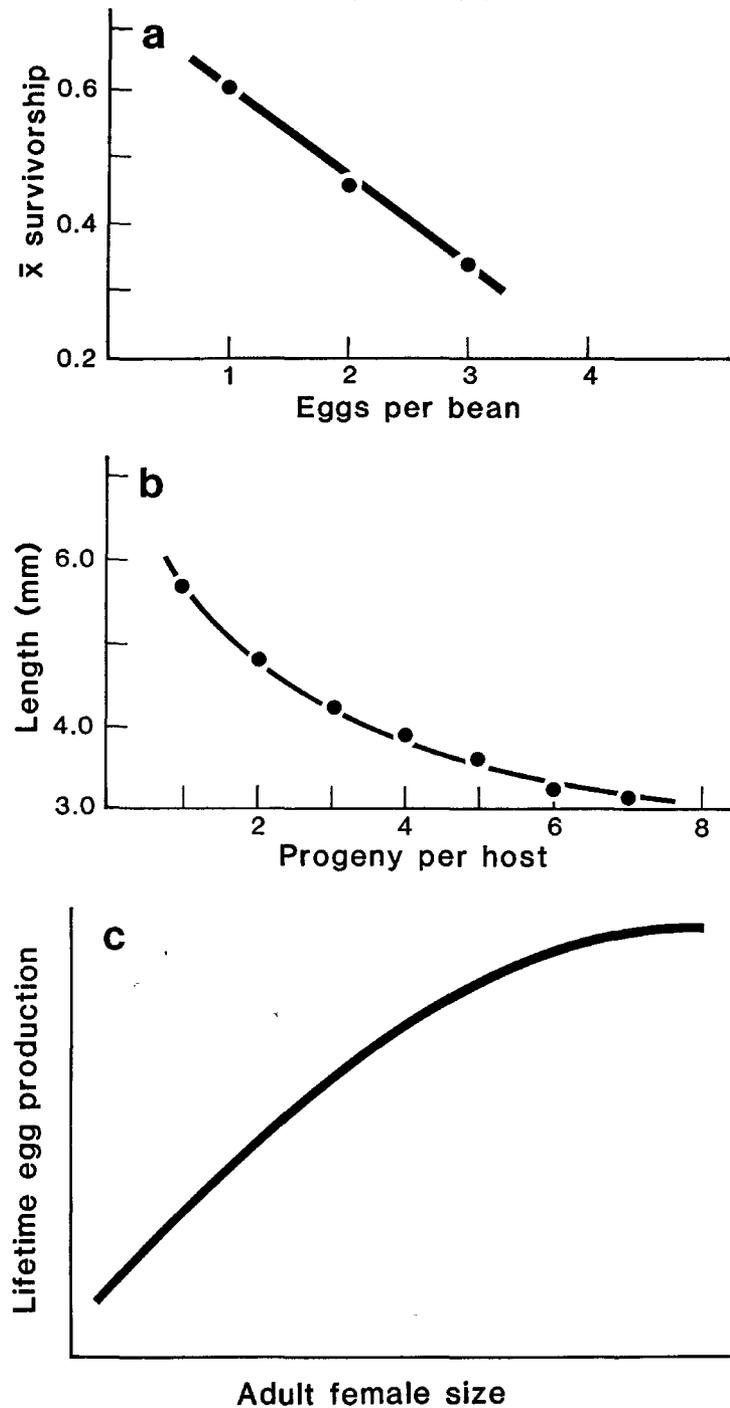


Fig. 3. Clutch size tradeoffs for parasitic insects. *a.* A bruchid weevil attacking beans; immature survival declines with clutch size (data from Mitchell 1975). *b.* The wasp *Trichogramma*; in crowded hosts, the adults emerge at a smaller size (data from Salt 1940). *c.* A hypothetical relationship between adult size at emergence and the adult's lifetime fecundity. These 3 relations allow one to calculate mom's fitness (through offspring from a single host) for a specified clutch size, and thus to derive the insect parasitoid analogue of Figure 2.

In Figure 4a, we show the survival effect for the small and one large host type. Both show declines, but as expected the smaller host goes down fastest. Figure 4b shows a similar plot for clutch size versus resulting adult size. Adult size clearly declines with clutch size. Under lab conditions they also determined the lifetime fecundity for female wasps as a function of female size. Figure 4c shows the resulting relation. While the data showed a fair bit of scatter (and the lab may not represent the field), as a first approximation we may take Figure 4c to translate female size into lifetime fecundity. Figures 4a-c provide sufficient data to calculate  $W_f$  versus clutch size for two host sizes (actually three since we omitted from Figure 4 the other large host). Figure 5 shows such a plot, with the hosts labeled. The most productive clutch sizes for the three hosts (in increasing order) are four, seven, and nine eggs respectively. From the lab data on oviposition, the parasitoid laid the following ranges of eggs in these three host species: 1-2, 5-8, 5-8. As can be seen, in general *the parasitoid laid a smaller clutch than that predicted by Lack's hypothesis.*

#### B. *Nasonia vitripennis*

*Nasonia vitripennis* is parasitic on the pupae of numerous cyclorrhaphous Diptera, particularly in the families Calliphoridae and Sarcophagidae (Whiting 1967). The ones attacked are largely carrion feeding flies, although one genus utilized by *Nasonia* (*Protoalliphora*) is parasitic on nestling birds. The wasp has been the subject of extensive laboratory research and its general biology is well known (see reviews by Whiting 1967 and Cassidy 1975). The treatment of the data presented here is from Skinner (1983b).

*Nasonia* attacks several fly species, which in our study sites range 12-fold in body volume. *Phormia regina* is the most abundant host. Under less than severe larval crowding, *Nasonia* shows no increased larval mortality. However, the size of emerging adults declines with crowding. Figure 6a shows data on this for 4 host sizes of *Phormia*. For each of the four there is a significant linear decline in wasp size with increasing clutch size. Figure 6b shows lab data on the number of oocytes in a female as a function of her head width. There is an almost perfect linear regression which suggests that females with heads of width .5 mm or less will have zero fecundity. Unfortunately, we have no data relating oocyte number to lifetime female fitness; thus here we will make the simple assumption that oocyte number is proportional to lifetime fitness. If we combine this with the last two figures, we can calculate  $W_f$  versus clutch size for the four host sizes. These calculations are shown in increasing order (a to d) in Figure 7. Now . . . how do the predicted "most productive clutches" (as a function of host size) compare to the clutches found in nature? Figure 8 shows field data for *Nasonia* clutch size versus host volume. The \* associate the "Lack clutch size" with its appropriate host volume (for the four host volumes of Figure 6a). Again, most all the clutches found in nature are smaller than those predicted by the Lack hypothesis. Indeed, here the hypothesis predicts rather well the maximum clutch size observed.

#### WHY DOES THE HYPOTHESIS FAIL?

Rather than predicting the average clutch size, the Lack hypothesis ap-

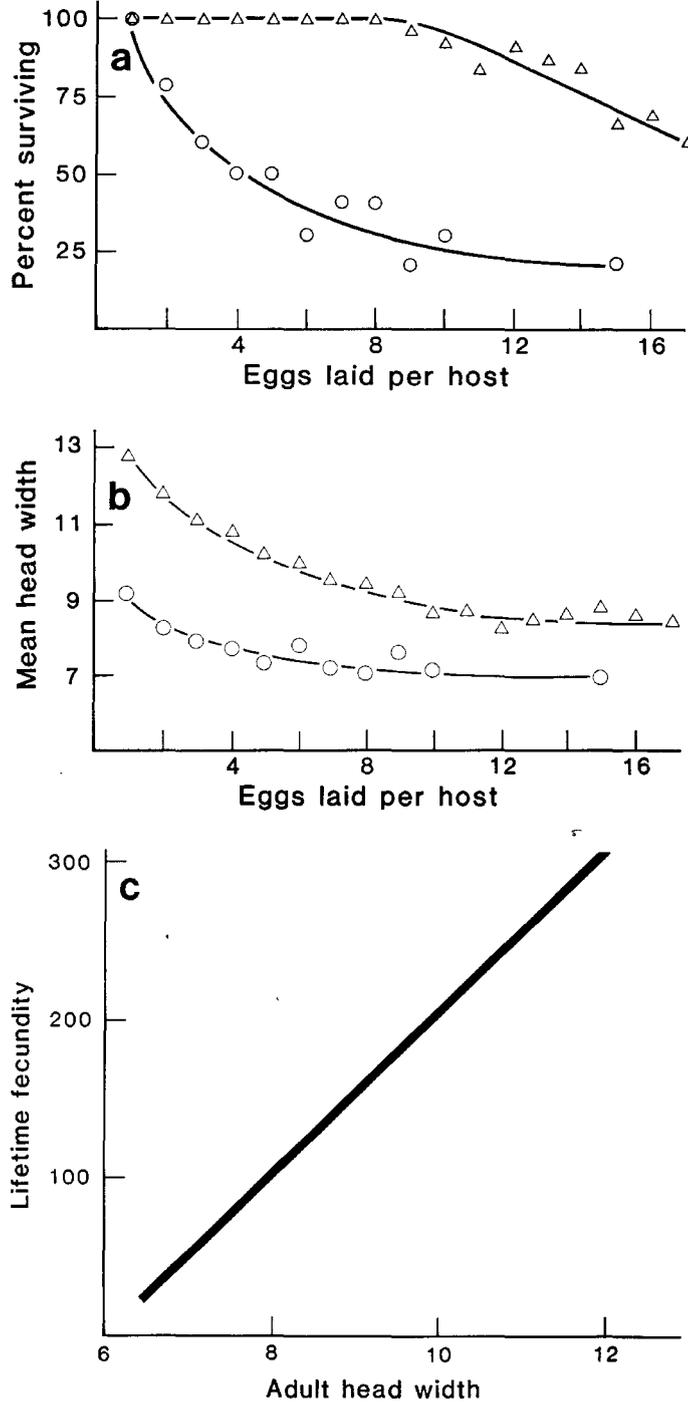


Fig. 4. Progeny fitness for the wasp *Trichogramma*. *a*. Immature survival as a function of clutch size for a large ( $\Delta$ ) and small (O) host species. See Figure 5 for host key. *b*. Emerging adult ( $\varphi$ ) size versus clutch size for the same two hosts. *c*. Lifetime female fecundity (total number of eggs produced) versus female size in laboratory experiments. (Data from Klomp and Teerink 1967)

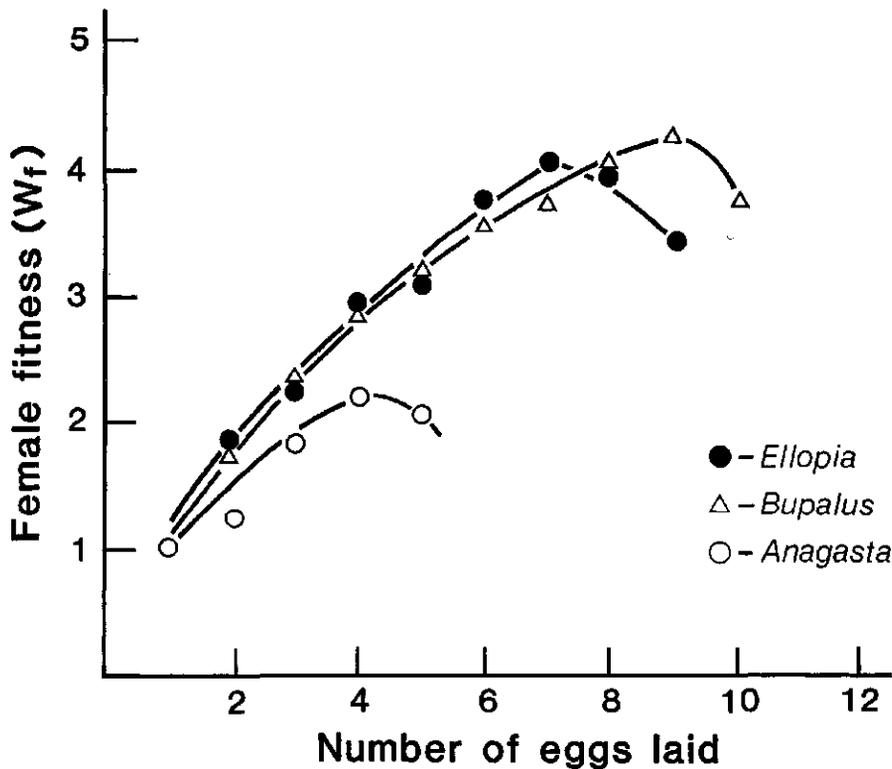


Fig. 5. Data from Figure 4 allow us to plot the mother's fitness (through offspring on a host) versus clutch size. Shown here are plots for 3 host species (2 of them from Fig. 4). See text for further discussion.

pears, in the case of both species, to be predicting clutch sizes just a bit larger than typically observed. The hypothesis fails. But why? We could at this point simply give up the natural selection approach to clutch size but such a decision seems very premature. There are at least three very natural life history factors which we ignored in equation 1, either in the original hypothesis or in its application to the wasps. Actually, we (i.e., we two authors) did not ignore these factors in our theory making (we built a large range of selection models at the beginning of the research), but for this exposition chose to present the simplest model and use its confrontation with data to suggest what to do next. The three factors we have so far ignored are:

- (1) A possible negative correlation between increasing clutch size and the mother's adult survival (or a negative relation between the rate of egg production and mother's survival).
- (2) The possibility that our measure of offspring fitness (i.e., their lifetime egg production) is incomplete.
- (3) The possibility that offspring production per host (that is, the mother's fitness through the offspring she produces in each host) is an incomplete measure of maternal fitness.

*Factor 1:* It is interesting to note that several years of applying Lack's hypothesis to birds showed a pattern similar to the wasps; the clutch sizes

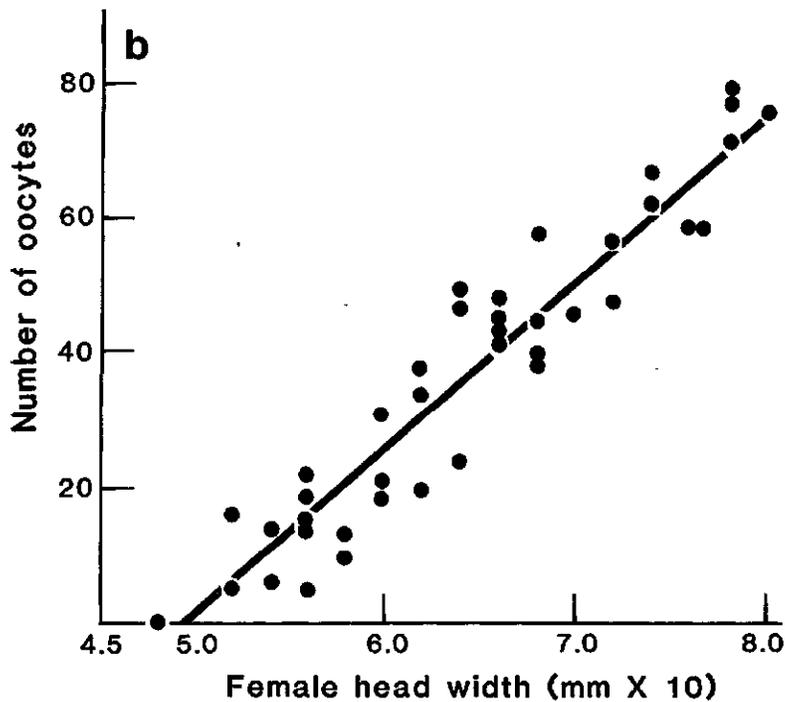
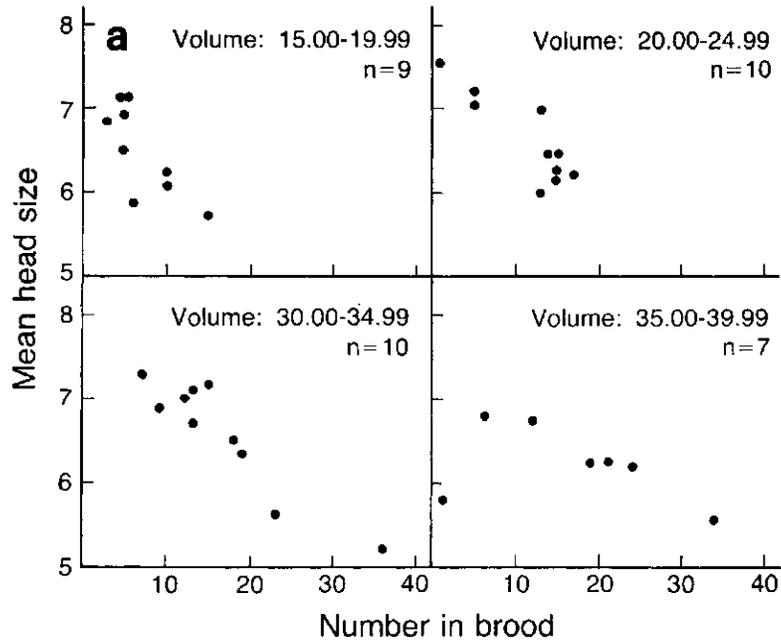


Fig. 6. *a.* In the wasp *Nasonia*, increased larval crowding typically results in smaller emerging adults, illustrated here for four host sizes of the fly *Phormia*. Immature survival did not decline with increasing clutch size. *b.* Larger females have more oocytes and presumably greater lifetime fitness (data from O'Neill and Skinner).

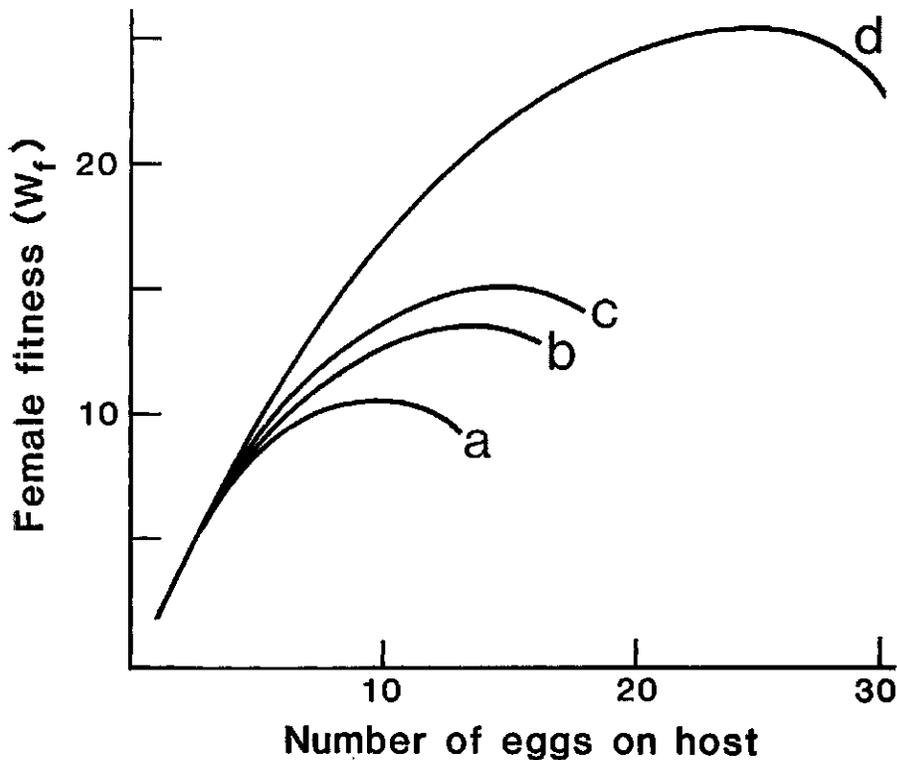


Fig. 7. Relative *Nasonia* adult fitness (through offspring production) as a function of clutch size for the four host sizes of Figure 6 (under the assumption that oocyte production is proportional to lifetime egg production).

observed in nature were generally smaller than the theory predicted. A decade ago Charnov and Krebs (1974) suggested that this might still follow from the natural selection model if adult yearly survival decreased with increasing clutch size. While supporting data are scant, the theoretical effect is real. There are several ways in which "egg production rate" might be negatively related to the parents' survival rate. Since natural selection is concerned with "lifetime adult fitness", such a correlation would mean that "fitness" would often be maximized at a smaller than Lackian clutch size (the math details will be published elsewhere).

Consider (2): in the *Nasonia* calculations we assumed that lifetime offspring (daughter) fitness was *proportional* to oocyte production. This is the same as assuming that each female lays the same proportion of her potential brood. Clearly, this need not be the case; a likely possibility is that larger wasps have relatively longer lifespans and thus lay relatively more eggs. If so, then small wasps are penalized more than the proportional assumption allows; then the "true" Lack clutch size is smaller than our calculated one. The same might apply to the *Trichogramma* data if the field is harsher on small females than the lab tests suggest (see also Waagø and Ming 1983).

Now consider (3): Begin with a simple question—which of these two situations produces greater maternal fitness? (Assume offspring survival and size are the same for both.):

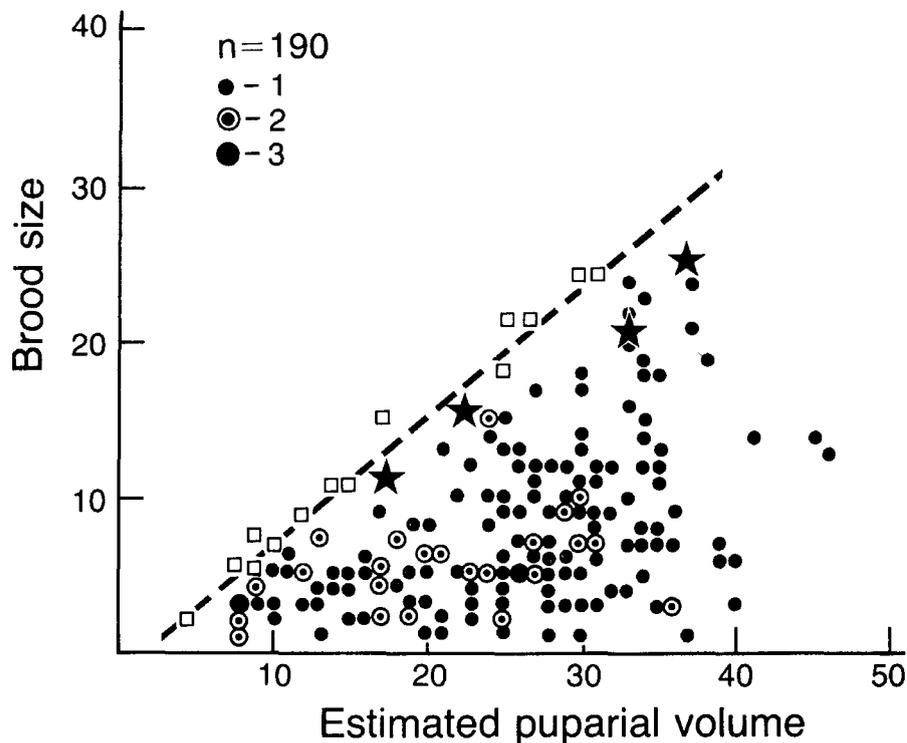


Fig. 8. Field clutch size data for *Nasonia* (*Phormia* hosts). The dotted line, through the  $\square$  points, shows the *maximum observed clutch sizes*, as a function of host volume. The four stars (\*) are the calculated "Lack clutch size" from the two previous figures. Note that the Lack hypothesis predicts fairly well the largest clutches, but certainly not the average clutch sizes (see Skinner (1983b) for more details).

a) 20 eggs per host, 40 minutes to find and handle each host

b) 30 eggs per host, 65 minutes to find and handle each host

Clearly, *b* provides greater maternal fitness under the Lack hypothesis (that is, greater fitness through the offspring produced in *each host*), but (*a*) provides greater maternal fitness *per unit time* since each host requires relatively less time to find and attack. The latter can be written as:

$$\frac{\text{Total fitness through offspring/host}}{\text{Total time per host}} \quad (2)$$

We have studied several population genetic models on these clutch size problems and this latter *rate measure of fitness* is usually a better indication of the direction of natural selection. (See also Parker and Courtney (1983) and Skinner (1983a).) And this *rate measure* applies even if the other two considerations do not (indeed its use often depends on the assumption that clutch size and mother's survival are uncorrelated). We now consider the implications of this alteration of the Lack hypothesis.

#### ON USE OF THE RATE DEFINITION OF FITNESS

To use the rate definition of fitness, we must first translate clutch size into

time. Upon encountering a host at least two sorts of time might be involved in producing a particular clutch size: time to mature the eggs and time to lay them. The first of these may be related to the general nutritional condition of the mother, or perhaps the time since the last oviposition. Considering both times (called here oviposition time) should allow us to associate with a given clutch size a particular time to get it into a host just discovered. If this is known, then the clutch size or X-axis of Figures 2, 5 or 7 can simply be rescaled into oviposition time. We have done this, for a hypothetical example, in Figure 9a. Such a plot gives us the mother's fitness through the offspring produced on a host as a function of time at the host. But the total time per host includes the search time between hosts, and this is also indicated on the graph. For simplicity, we limit this discussion to a single kind of host. Note that the "Lack clutch size" is the time which gives the greatest maternal fitness per host; i.e., the peak of the curve. However, the *rate* hypothesis says that selection favors the clutch size which maximizes the fitness gained per unit time (Equation 2). To find this, note the following on Figure 9a. We graph the time between hosts (the search time) *increasing to the left* of the oviposition curve. Now, if we draw a line from the search time ( $t_s$ ), the line has a slope which is in units of  $W_f/(t_s + t)$ , which is equivalent to Equation 2. Thus, we can find the optimal clutch size (here, optimal oviposition time) by finding the line through the specified search time which intercepts the  $W_f$  curve at the highest point possible. This is illustrated in 9a. In 9b we illustrate the effect of increasing search time, while holding the  $W_f$  curve (the oviposition relation) constant. Here the predicted clutch increases in size (from  $t_2$  to  $t_1$ ). We note here that only if search time is large is the predicted clutch size as big as Lack's hypothesis would predict. Otherwise, the clutch size favored by natural selection is smaller than the Lack size. This is exactly what the parasitoid data show—the Lack size is an outer bound and most clutches are smaller. This rate hypothesis makes two other sorts of predictions. First is that shown in 9b. Increasing search time should increase the clutch size. The second is that the oviposition relation may be sensitive to the rate at which eggs can be matured. It includes at the minimum the time to lay the eggs; if this is all it includes, then the faster they are laid the steeper the  $W_f$  curve rises, and the closer the optimum clutch is to Lack's. By manipulating maternal nutrition, one ought to be able to alter the oviposition relation, and see if the clutch laid alters accordingly. Unfortunately, we know of no data which bear on these issues. (Nor do we know of any data which bear on whether maternal survival is itself negatively related to the egg production rate (Factor 1). Such a correlation would similarly favor a smaller clutch size, as previously discussed.)

We now turn to a second general question for parasitoids, that of which hosts to attack in the first place.

#### HOST SELECTION

A vast literature documents that parasitoids of a given species "prefer" some host types to others. It seems reasonable to conceptualize this choice in the same fitness terms as the clutch size problem. This is not a new suggestion; models of optimal foraging (patch choice, food item choice, etc.) have long been used to view insect (including parasitoids) diet choice

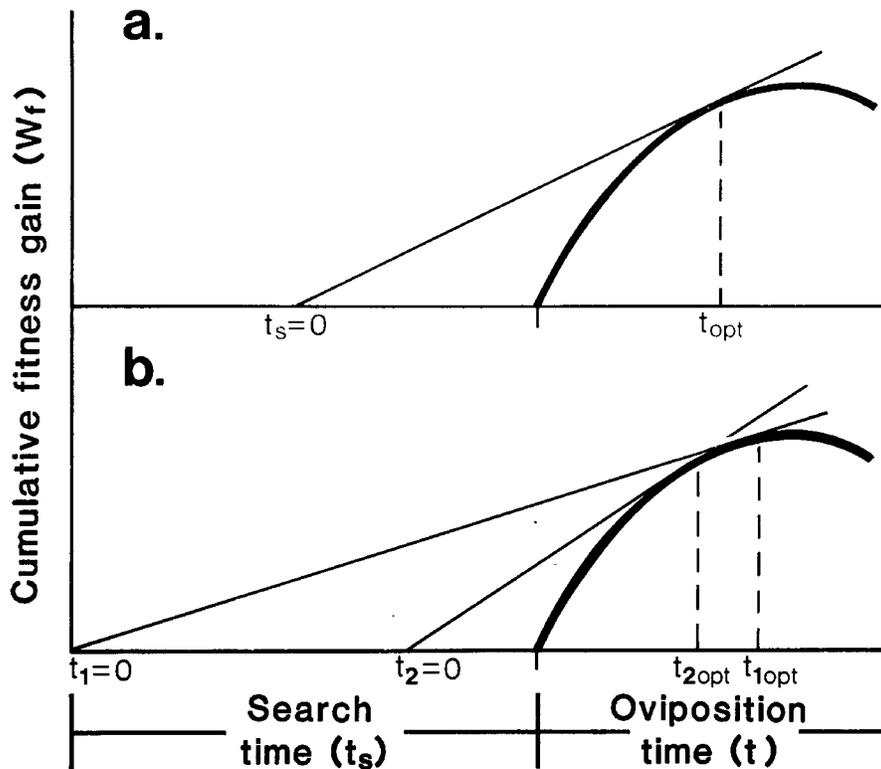


Fig. 9. Natural selection should favor the maximum rate of fitness production through offspring (all else equal), rather than the maximum per host (Lack's hypothesis). *a.* This figure shows how to calculate that clutch size, as a function of the search time between hosts ( $t_s$ ), the oviposition time once a host is encountered ( $t$ ) and the parent's fitness through offspring ( $W_f$ ); related to clutch size, thus to the time ( $t$ ) to deposit a clutch of a given size). The clutch size (= oviposition time) favored under Lack's hypothesis is at the peak of the curve. *b.* If the search time between hosts increases ( $t_2 \rightarrow t_1$ ), the most fit clutch size increases. The limiting or largest clutch is Lack's.

(e.g., Waage 1979, Green 1982, Charnov 1976a,b, Charnov and Orrians 1973). We will not review this literature here but instead will view one new problem: superparasitism. Superparasitism, where a host already attacked by a member of species Z is then further attacked by a second individual of Z, is widely described in the parasitoid literature as a "screw up", a mistake on the part of the second individual (van Lenteren 1981). Recently, Alphen and Nell (1982) suggested that superparasitism may sometimes be an advantageous (adaptive) response for the second individual. Independently, we reached the same conclusion through treating the host population as two separate kinds of prey (unattacked and attacked) and simply asking when the mother *should* include the poorer, already attacked hosts in those she attacks. In general, the answer to this optimal foraging question turns on factors such as how abundant the good hosts are, how easy eggs are to produce, how poor the already attacked hosts are for offspring pro-

duction, and so forth. In Figure 10, we show graphically how to answer the question of whether superparasitism ought to occur or not, using our previously defined oviposition relation. If superparasitism happens, there is the further question of the respective clutch sizes for the 1st and 2nd parasite. Such clutch size questions are beyond the technical scope of this paper and the reader is referred to the work of Parker and Courtney (1983).

IN CONCLUSION

We close this paper with the simple observation that our natural selection perspective has focused attention upon specific variables (e.g., search time, maternal survival, offspring survival and size related to brood host) seemingly important in understanding host utilization in parasitoids; variables which become part of a comprehensive and integrated approach to the problem. Of importance to us is not the present lack of answers, but the host of new questions, ones which readily suggest tests in lab and field. The natural selection approach also raises questions about the nature of the proximate mechanisms involved with the adaptations.

ACKNOWLEDGEMENTS

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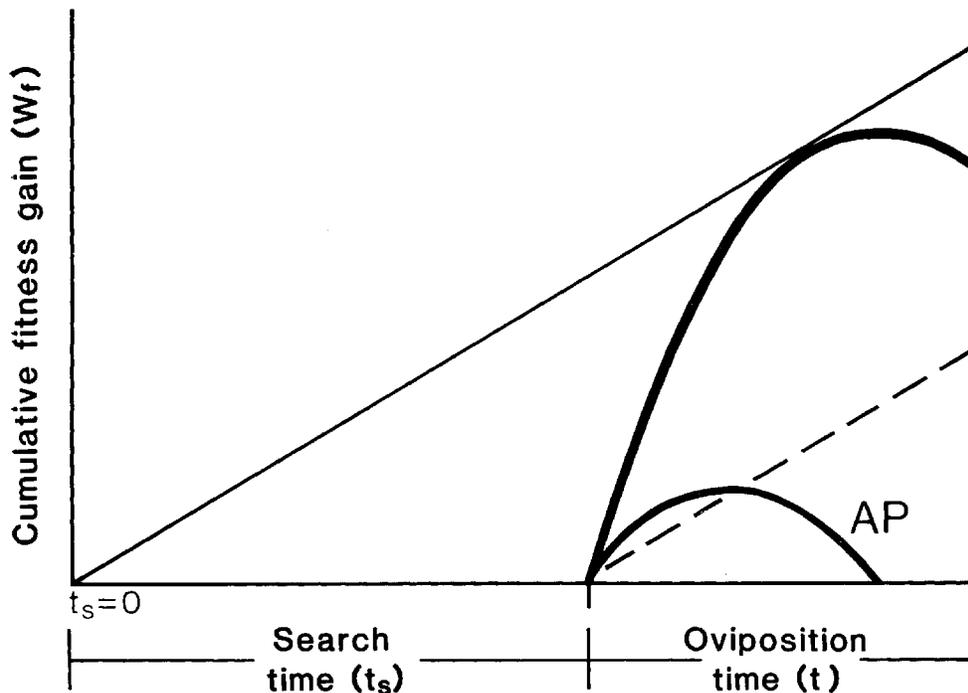


Fig. 10. When is it advantageous to superparasitize? The upper curve is a non-parasitized host, and the tangent argument from Fig. 9 shows the optimal oviposition time (in the absence of superparasitism). The *AP* curve shows the mothers fitness gain for attacking an “already parasitized” host. The dotted line is *parallel* to the upper tangent line. If it passes through the *AP* curve, as it does here, superparasitism is favored. (Argument from Charnov 1976a,b.). Optimal clutch sizes under superparasitism are treated in Parker and Courtney (1983).

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BODY BUILDING BY INSECTS: TRADE-OFFS IN  
RESOURCE ALLOCATION WITH PARTICULAR  
REFERENCE TO MIGRATORY SPECIES

MARY JANE ANGELO AND FRANK SLANSKY JR.\*

SYNOPSIS

Individuals of many species of insects inhabiting transient habitats exhibit migratory behavior and thereby escape deteriorating environmental conditions and colonize sites with favorable conditions. Limited food availability is one cue that may serve to induce migration, either by stimulating the adult to undertake migration, and/or by stimulating the larva to alter its resource allocation to "build" a migratory-form adult. Such changes in resource allocation often involve changes in lipid storage, body size, proportioning of wing size and body weight, and reproduction.

Detailed study of four species of presumed migratory noctuid moths indicated that the larvae retain the ability, when starved from various days in the last larval stadium, to pupate and metamorphose into adults. These adults have reduced body weights (from 12 to 24% of the weight of adults from fully fed larvae), and significantly lower wing loading ratios (i.e., body weight/wing area) than would be expected based on the predicted allometric relationship between body weight and wing area. We propose that this altered allocation of food to body weight and wing area is an adaptive response producing individuals with low wing loading ratios that presumably exhibit less energetically costly flight. This hypothesis is consistent with principles of flight energetics.

"The earth-bound early stages built enormous digestive tracts and hauled them around on caterpillar treads. Later in the life-history these assets could be liquidated and reinvested in the construction of an essentially new organism—a flying-machine devoted to sex." (C. M. Williams 1958)

". . . the central problem of evolutionary biology: to provide a general explanation for the design of organisms." (S. C. Stearns 1982)

INTRODUCTION

The liquidation and reinvestment of "assets" by insects during metamorphosis, mentioned in Williams' quote above, involves the allocation of acquired resources to building and maintaining the adult body. In addition, energy and nutrients are necessary for adult activities, including defense, dispersal and reproduction (Townsend and Calow 1981). We are in particular interested in the trade-offs of resource allocation among body-building, dispersal and reproduction.

Differences in resource allocation may be evident both among and within

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species. For example, an insect with a high-powered, hovering type of flight exhibits differently proportioned body and wings compared to an insect with a low-powered, gliding type of flight (Kammer and Heinrich 1978, Casey 1981a). Within a species, resource allocation may vary between generations. For example, individuals of certain seasonally migratory species respond to changing environmental conditions (e.g., photoperiod, food quality and quantity, and larval density) by altering their allocation of resources to body and wings, with consequent effects on fecundity (see below).

It is one goal of nutritional ecology to achieve an understanding of the patterns of resource allocation by species (Slansky 1982a, 1982b; see also Stearns 1982). In this paper we examine resource allocation to body building in insects, with particular reference to migratory species. Using data from the literature and our own unpublished data, we investigate the trade-offs among body weight, lipid content, wing size and reproduction. Our discussion is framed within the contexts of alteration of resource allocation in changing environments and the principles of flight energetics. In addition, we identify areas where more research is needed.

#### RESOURCE ALLOCATION TO BODY SIZE, PROPORTIONS AND COMPOSITION

Within a given environment, there will be some optimal adult body size (or sizes) for the individuals of a particular species that yields their maximal fitness. Selective forces acting at different times during an insect's life determine the evolution of optimal adult body size (Roff 1981, Ricklefs 1982). Such forces involve an individual's size-dependent relationships with food (Enders 1976, Wasserman and Mitter 1978, Mattson 1980), enemies (Hespenheide 1973, Enders 1975), competitors (Pearson and Stemberger 1980, Eberhard 1982) and the physical environment (Sweeney and Vannote 1978, Roff 1981), as well as the size-dependency of life history variables such as developmental time, fecundity and dispersal behavior (Dingle et al. 1980, Derr et al. 1981, Hinton 1981, Roff 1981, Ricklefs 1982, Stearns 1982).

Resource allocation to body building involves not only achieving a certain optimal size, but also, within the limits of that size, partitioning the resources among the various organs, structures and biochemical components of the body such that the insect will achieve its best performance (Calow 1977). One important feature of resource partitioning that is responsible for the different proportions of the various organs and structures to the body as a whole is allometric growth, whereby some tissues in the body grow at faster rates than others (Huxley 1972). Concentrations of the various biochemical components of the body (i.e., proteins, lipids, carbohydrates, amino acids, salts, etc.), also important to insect performance, result from the complex relationships of assimilation, anabolism, catabolism and excretion (Wigglesworth 1965, Gordon 1972, Rockstein 1978).

#### ADAPTIVE ALTERATION IN RESOURCE ALLOCATION: MIGRATORY INSECTS

Individuals of many species in habitats that can become adverse for reproduction or survival exhibit migratory behavior (Southwood 1977, Wellington 1980). These individuals can thereby escape deteriorating habitats and colonize favorable sites (Dingle 1978). The decision to migrate may be made either during the adult or larval stage.

Adult insects may initiate a migratory response based on their evaluation

of environmental cues such as photoperiod, temperature, and food quality and quantity (see Slansky 1982a). Induction of reproductive diapause commonly is associated with the decision to migrate. The integration of reproductive and flight behaviors occurs at the neurohormonal level (DeWilde and DeLoof 1973, Rankin 1978) and involves the investment of resources in the flight system and its metabolism rather than in reproduction (Slansky 1980, Heinrich 1981).

The flight system is energetically costly to maintain and operate: metabolic rate during flight may be increased 50-100 times that at rest, and over 50% of an insect's resting metabolism may result from the metabolism of the resting flight muscles (Kammer and Heinrich 1978, Heinrich 1981). However, the extent to which metabolic costs of flight may divert energy away from other behaviors, and thus reduce reproduction and survival probability is not clear. Significant negative effects of flight duration on reproduction and survival have been found in tethered flight studies of only some of the species studied (for review see Slansky and Scriber 1984). Perhaps tethered flight techniques do not put as great a metabolic demand on a flying insect as does free flight. In addition, although there are few data available, insects may exhibit adaptations that reduce the potential negative effects of flight. For example, adequate storage of lipid reserves prior to long flight may satisfy the energetic demands of the flight muscles, such that sufficient energy stores remain for reproduction and survival; also, post-flight increases in food consumption may occur (see Slansky 1980). Reduction of metabolic costs may result from histolysis of flight in muscles in some situations where the flight system is no longer needed by the insect, such as after the mating flight in termites and when certain scolytid bark beetles have dispersed to and colonized a host tree (Atkins and Farris 1962, Johnson 1973; see also Solbreck and Pehrson 1979).

Whereas adults of some species may themselves decide to migrate, adults of other species may, under certain circumstances, produce offspring destined to exhibit migratory tendencies as adults. Larval (or nymphal) response to environmental cues also may influence adult migratory behavior. Because these responses occur before the adult stage, differential allocation of food during the larval and pupal stages may result in migratory forms being produced that differ from non-migratory adults in the size, proportions and biochemical composition of their body, as well as in other aspects of their biology (Johnson 1976, Wellington 1980; Table 1). Among the most dramatic examples of this phenomenon are aphids and locusts (see Dingle 1980).

Several species of aphids display alary polymorphism associated with an alteration between sexual and parthenogenetic generations (Dixon 1973). Production of the alate (winged) form may occur in response to dietary influence (Mittler and Sutherland 1969) or population density (Dixon 1973) and may depend upon the population age structure (MacKay and Lamb 1979). Differences in food consumption and fecundity between alate and apterous forms (Table 1) indicate further differences in resource allocation. In migratory locusts, individuals of the gregarious phase, produced in response to increased density, differ from solitary phase individuals in morphology and reproductive and migratory behavior. They are migratory throughout their lives, first as nymphs "marching" across the terrain en

TABLE 1. DIFFERENCES IN PERFORMANCE AND BODY STATE (SIZE, PROPORTIONS AND COMPOSITION) BETWEEN PRESUMED MIGRATORY AND NON-MIGRATORY INDIVIDUALS (REVISED FROM SLANSKY AND SCRIBER 1984).

Orders/Species	Performance/Body State Differences	References
Coleoptera <i>Dendroctonus pseudotsugae</i>	Individuals with higher lipid content show greater dispersal activity	Atkins (1966)
Diptera <i>Aedes taeniorhynchus</i>	Migrant phase lighter in dry weight with lower wing loading ratio and % lipid	Nayar and Sauerman (1969)
<i>Drosophila melanogaster</i>	Larger individuals of both sexes show greater probability of dispersal	Roff (1977)
Hemiptera <i>Oncopeltus fasciatus</i>	Higher % lipid and cytochrome c oxidase activity in migratory strain; delayed oviposition associated with increased flight	Holmes <i>et al.</i> (1979); Dingle (1968)
Homoptera <i>Acyrtosiphon pisum</i>	Alatae with longer preoviposition period, longer oviposition period, lower fecundity than apterae; same lifespan	MacKay and Wellington (1975)
<i>Aphis fabae</i>	Alatae less fecund than apterae but have higher reproductive rate	Dixon (1972)
<i>Cicadulina</i> sp.	Shorter body length associated with greater flight ability, less feeding and lower fecundity	Rose (1972)
<i>Drepanosiphum dixonii</i>	Macropterous alatae less fecund than brachypterous alatae	Dixon (1972)
<i>Myzus persicae</i>	Alate morph consumes more food	Raccah and Tahori (1971)

Orders/Species	Performance/Body State Differences	References
Lepidoptera		
<i>Choristoneura fumiferana</i>	Smaller moths have lower wing-loading ratio; exhibit greater flight activity	Sanders and Lucuik (1975)
<i>Epiphyas postvittana</i>	Presumed migrants smaller with lower body length forewing length <sup>-1</sup> ratio	Danthanarayana (1976)
<i>Parnara guttata</i>	Fall season individuals have high tethered-flight activity, lower fecundity, longer preoviposition period	Ono and Nakasuji (1980)
<i>Pieris brassicae</i>	Adults from crowded larvae lighter in fresh weight with lower wing loading ratio	Long (1959)
<i>Plusia gamma</i>	Adults from crowded larvae lighter in fresh weight with lower wing loading ratio	Long (1959)
<i>Plutella xylostella</i>	Presumed migrants larger with longer forewings, greater fecundity	Yamada and Umeya (1972)
<i>Spodoptera exempta</i>	Crowded larvae with higher % lipid; presumed migrants have longest wing lengths	Matthee (1945); Aidley and Lubega (1979)
Orthoptera		
<i>Locusta migratoria</i>	Longer wings, higher % lipid; lower fecundity in migratory phase.	Matthee (1945); Norris (1950)
<i>Pteronemobius taprobanensis</i>	Macropterous form with longer preoviposition period, lower fecundity, greater survival during starvation compared to micropterous form	Tanaka (1976)

masse, and then as adults forming large swarms that are carried for long distances by prevailing winds (see Rainey 1978).

Differences in lipid content, wing size, body weight and fecundity between presumed migratory and non-migratory individuals also occur in Coleoptera, Diptera, Lepidoptera and other insects (Table 1). Although these differences are generally less extreme than the examples cited previously, they nonetheless similarly indicate that alterations in the consumption and allocation of food have occurred during the "building" of the various adult forms.

Insect flight involves different channels of power output or cost (Figure 1). In simplified terms, the energy actually utilized for flight provides the mechanical power output; the remaining power input is lost through muscle inefficiency as heat. Of the mechanical power output, some is used by the insect to accelerate and decelerate its wing mass (i.e., inertial power) whereas the remainder is used to do work on the surrounding air (i.e., aerodynamic power). The three aerodynamic power output components of a flying insect are profile power, which overcomes the drag on the surface area of the wings, induced power, which is used to accelerate air across the wings at a velocity sufficient to overcome the force of gravity and parasite power, which is necessary to overcome the drag on the body (Figure 1; Casey 1981a, 1981b). The design of the adult, in particular the ratio

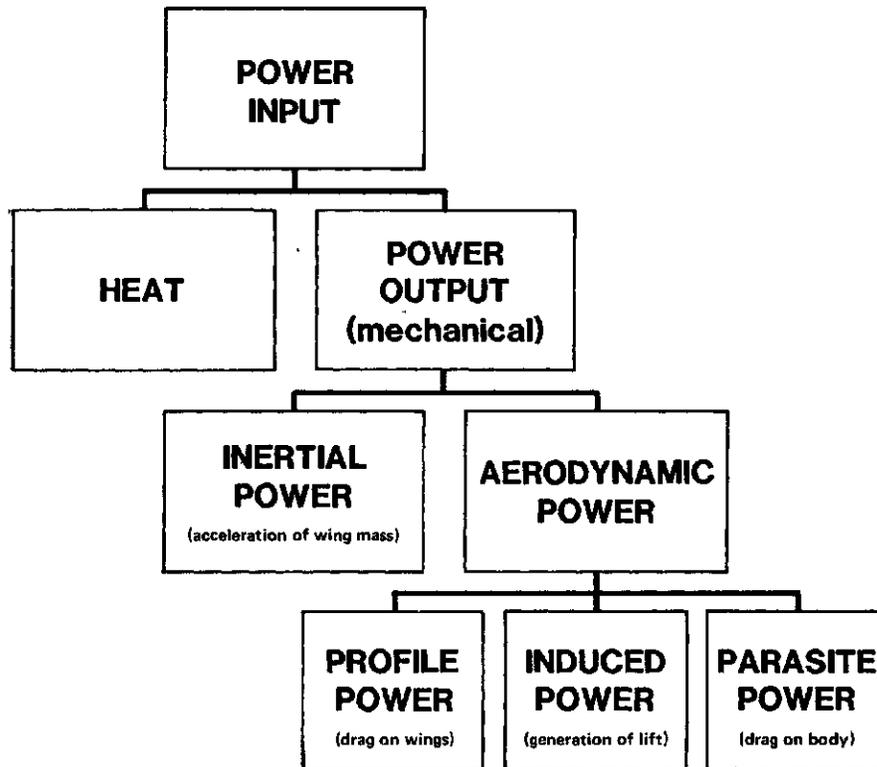


Fig. 1. Energy demands for power in flying insects (modified from Casey (1981b); see text for explanation).

between body weight and wing area (i.e., wing loading ratio), along with wing beat frequency and flight speed, in large part determine these power output demands.

A low wing loading ratio (i.e., large wing area relative to body weight), when coupled with a relatively slow wing beat frequency, would tend to minimize the power output demands of flight. Many insects presumed to be migratory exhibit low wing loading ratios compared to non-migratory individuals (Table 1), and many of these species seem to utilize air thermals and upper air currents to aid in their dispersal, thus presumably reducing the power output demands of their flight (Johnson 1969, Danthanarayana 1976, Gibo 1981).

#### RESOURCE ALLOCATION IN "LESS THAN IDEAL" ENVIRONMENTS

Associated with the strongly determinant relationship between an individual's body size, proportions and composition (i.e., its body state), and its fitness, are adaptations that may allow the insect to attain its optimal body state under less than ideal environmental conditions. For example, a larva may alter its food intake in response to changes in the nutrient content of its food, consuming more of a food with a reduced nutrient content and thereby achieving a body weight and composition similar to that of a larva consuming a more nutrient-rich food (Slansky and Feeny 1977). Increased catabolism and excretion also may be exhibited in response to a nutrient imbalance in the food (Gordon 1972, Horie and Inokuchi 1978, Rockstein 1978). Another food-related response involves the induction of detoxication enzymes upon consumption of potentially toxic allelochemicals (Brattsten 1979). These compensatory responses may incur various costs that could reduce fitness (e.g. energetic costs of increased feeding, catabolism and detoxication, and increased exposure to predators and parasitoids while feeding). Thus, the "success" of a compensatory response will be determined by the extent to which its benefits outweigh its costs. Compensatory success, when defined as the degree to which the actual body state approaches the optimal body state) varies among individuals, situations and species, and may reflect different adaptive strategies (Scriber and Slansky 1981, Slansky 1982b). However, more research is necessary to determine the benefits and costs of compensatory responses and the extent to which compensatory ability reflects adaptive strategies.

The frequent occurrence of prolonged larval development (in some cases including an increase in the number of instars) under conditions of "poor" food quality or reduced food quantity (for references see Scriber and Slansky 1981) may be another response by which larvae attempt to get as close as possible to their optimal body state with minimal costs. If feeding conditions improve within a relatively short period of time, then the larva may be able to closely approach its optimal body state with only a short delay in the timing of pupation. However, the success of this response may be tempered, for example, by the subsequent delay in onset of reproduction resulting from the prolonged development. Thus in certain circumstances, rather than exhibiting a compensatory response, larvae may be "making the best of a bad situation", prolonging their development in order to achieve not their optimal state but their minimal state necessary to survive metamorphosis and produce a reproductively competent adult.

Minimal-weight-values, below which a starved immature insect does not

undergo successful metamorphosis to an adult, vary considerably among species (Table 2), but similar to the situation of the compensatory abilities discussed above, we have little understanding of the ecological and evolutionary relationships between minimal-weight-values and adaptive strategies. Questions such as "Are adults at the minimal weight reproductively competent?" and "Have species subject to frequent food limitation (e.g., because of the ephemeral nature of their food in relation to the duration of the larval stage) evolved as an adaptation minimal-weight-values that are a low percentage of their presumed optimal weights (e.g., *Drosophila melanogaster*, Table 2, and certain species of tree-boring Coleoptera; see Andersen and Nilssen 1983)?" remain to be answered.

A further adaptation involves the utilization of environmental cues by insects to facilitate their avoidance of or escape from a deteriorating environment. Poor food quality and starvation, as well as other environmental factors, may serve as cues to larvae of many species to produce migrant-form adults (see above) and as cues to adults to stimulate migratory flight behavior (Dingle 1968, 1978, Mittler and Sutherland 1969, Elsey 1974, Sanders and Lucuik 1975, Solbreck and Pehrson 1979, Duelli 1980). These inductive responses (Slansky 1982a) involve changes in resource allocation that alter the optimal body state of the non-migratory form to produce the optimal body state of the migratory form. As discussed above, this commonly involves changes in body size and weight, and in wing size.

#### LARVAL STARVATION AND RESOURCE ALLOCATION IN NOCTUID MOTHS

Assuming that changes in body weight and wing area with body size follow some theoretical relationship, then significant differences from this relationship should indicate that resources are being differentially allocated to body weight and wing area at different body sizes. By relating this differential allocation of resources to the flight behavior and other aspects of a species' lifestyle, one can infer whether this differential allocation has adaptive value.

We investigated resource allocation in four presumed migratory species of noctuid moths in response to larval starvation (Angelo and Slansky in prep.). Larvae were experimentally starved from various days of their last instar, and measurements were made of the body weight, wing area and lipid content of newly emerged adults. Because area is the square and weight is the cube of linear dimensions, a log-log plot of these as length changes yields a straight line with a slope of 0.67 (indicating that area and weight do not change in proportion to each other; if they changed proportionately, the slope would equal 1). We compared the slope values between body weight and wing area for the four species with the 0.67 value, as well as among themselves, in an effort to demonstrate differential allocation of resources during starvation. Furthermore, we related the observed changes to aspects of these species' lifestyles.

Use of such theoretical allometric relationships is common in comparisons of organism performance (e.g. metabolic rate) across a range of species with different body sizes; both the slope of the line and the extent to which the performance value for a particular species lies off the line have been used to draw conclusions of biological significance (Schmidt-Nielson 1970, Blueweiss et al. 1978, Greenstone and Bennett 1980). However, there seems to have been considerably less use of comparisons between predicted

TABLE 2. THE MINIMAL WEIGHT AT WHICH LARVAE WILL PUPATE WHEN SUBJECTED TO STARVATION, EXPRESSED AS A PERCENTAGE OF THE MAXIMAL WEIGHT ATTAINED WHEN FULLY FED. WHEN SUBJECTED TO STARVATION BELOW THIS MINIMAL WEIGHT, LARVAE STARVE TO DEATH. (REVISED FROM SLANSKY AND SCRIBER, 1984).

Orders/Species	Sex	Minimal weight (% of maximal)	References
<b>Diptera</b>			
<i>Drosophila melanogaster</i>	♂	12% <sup>1</sup>	Beadle <i>et al.</i> (1938)
	♀	12% <sup>1</sup>	
	♂	19% <sup>1</sup>	Bakker (1959)
	♀	18% <sup>1</sup>	
<b>Hemiptera</b>			
<i>Oncopeltus cingulifer</i>	♀	44% <sup>2</sup>	Blakley and Goodner (1978)
	♀	38% <sup>2</sup>	
<i>O. fasciatus</i>	♀	51% <sup>2</sup>	Nijhout (1979)
	♂	53% <sup>2</sup>	
<i>Rhodnius prolixus</i>		25-43% <sup>3</sup>	Friend <i>et al.</i> (1965)
<b>Lepidoptera</b>			
<i>Anticarsia gemmatalis</i>	♀	18% <sup>1</sup>	M. J. Angelo and F. Slansky (unpubl.)
	♂	12% <sup>1</sup>	
<i>Bombyx mori</i>		60% <sup>4</sup>	Lees (1955)
<i>Choristoneura conflictana</i>	♀	32% <sup>2</sup>	Beckwith (1970)
<i>Danaus chrysippus</i>		23% <sup>1</sup>	Mathavan and Muthukrishnan (1976)
		36% <sup>4</sup>	
<i>Galleria mellonella</i>		36% <sup>4</sup>	Lees (1955)
<i>Heliothis zea</i>	♀	14% <sup>1</sup>	M. J. Angelo and F. Slansky (unpubl.)
	♂	23% <sup>1</sup>	
<i>Lymantria dispar</i>		25% <sup>2</sup>	Kopec (1924)
		45% <sup>4</sup>	Lees (1955)
		50-60% <sup>2</sup>	Nijhout (1975)
<i>Manduca sexta</i>		36-47% <sup>2</sup>	Higgins and Pedigo (1979)
<i>Plathypena scabra</i>		26% <sup>1</sup>	Mukerji and Guppy (1970)
<i>Pseudaletia unipuncta</i>	♀	19% <sup>1</sup>	M. J. Angelo and F. Slansky (unpubl.)
	♂	24% <sup>1</sup>	
<i>Spodoptera frugiperda</i>	♀	19% <sup>1</sup>	M. J. Angelo and F. Slansky (unpubl.)
	♂	20% <sup>1</sup>	

<sup>1</sup>Dry weight.

<sup>2</sup>Fresh weight.

<sup>3</sup>Minimal blood meal promoting molting in various instars.

<sup>4</sup>Time spent feeding in last instar.

and actual allometric relationships in interpreting differences in performance values among the individuals within a species (see, for example Casey 1976), and as a consequence, the significance of deviations of actual data from "expected" relationships is not as well understood. Nonetheless, we believe our logic is a good "first step" in interpreting the significance of

differential changes in body weight and wing area among the individuals within a species. In addition, we believe that between-species' comparisons of regression slopes for within-species' allometric relationships (such as that between wing area and body weight) can suggest meaningful differences between species (see, for example, Casey's (1976) study on sphinx moths) in how they respond to changes in their environment, as indicated in the following discussion.

The first species studied, the velvetbean caterpillar (VBC) *Anticarsia gemmatalis* is a presumed migratory insect that appears to fly northward each summer from overwintering sites in south Florida and elsewhere (Buschman et al. 1977, Greene 1979). When starved from various days in the last stadium, larvae of the VBC produce adults that are lighter in weight and have reduced wing area compared with fully fed larvae; the slope for these data (0.52) is significantly different from the theoretical value (Figure 2). Thus, as body weight is decreased due to starvation, moths are produced with significantly lower wing loading ratios than would be expected if the theoretical relationship is applicable. Smaller moths carry less weight per unit wing area than do larger moths, and the energetic cost of their flight is presumably reduced (Casey 1981a, Casey and Joos 1983; also see above).

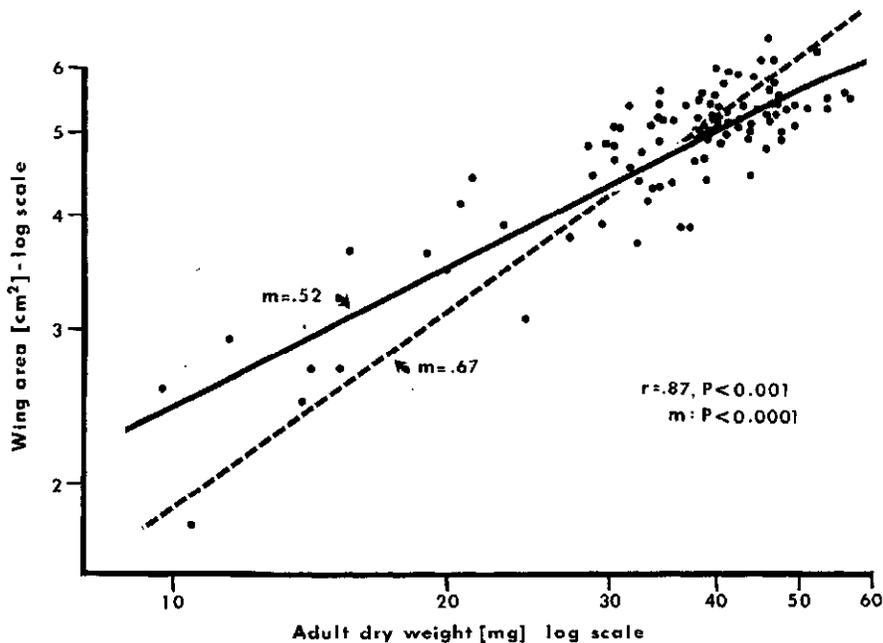


Fig. 2. Relationship between log wing area and log dry body weight. Dashed line: expected relationship based on area = the square and mass = the cube of linear dimensions. Solid line: actual relationship found for adult velvetbean caterpillar moths (both sexes) subjected to different durations of starvation during the last larval instar; regression is significant ( $p < .001$ ). The slope of the VBC line ( $m = 0.52$ ) is significantly different from the slope of the expected line ( $m = 0.67$ ;  $t$  test,  $p < .0001$ ), indicating that as body weight is reduced a relatively larger wing area is exhibited. Thus, smaller VBC moths have a lower than expected wing loading ratio (WLR = body weight/wing area) (from Angelo and Slansky in prep.).

Adult VBC, and many other species of insects, are presumably "passive" migrators, which, although maintaining active flight, are carried for long distances by upper air currents (see Rainey 1978, Rabb and Kennedy 1979, Walker 1980); a lower wing loading ratio may facilitate this type of movement (see above).

Migratory ability of VBC may have evolved to allow escape from seasonally unfavorable and/or food-depleted habitats, and colonization of seasonally favorable habitats containing suitable food. This ability to colonize and rapidly exploit new food sources undoubtedly contributes to its current status as a severe pest of soybean fields (see Barfield and O'Neil, this Symposium). In soybean fields (and perhaps when feeding on wild foodplants as well), starvation of VBC may frequently occur, especially due to high larval densities at certain times of the year (Herzog and Todd 1980, Linker 1980). If a relatively low minimal weight is an adaptation to frequent starvation as discussed above, then the low minimal-weight-values for VBC (Table 2) would further suggest the occurrence of frequent starvation in the field. If this is the case, then the lower than predicted wing loading ratio of the moths produced by starved larvae, involving a change in the allocation of food to body and wings, may be an adaptive response facilitating less costly flight in search of new larval foodplants.

Consistent with the reasoning above are the results from a similar starvation experiment with three other species of noctuid moths: the fall armyworm (FAW), *Spodoptera frugiperda*; the corn earworm (CEW), *Heliothis zea*; and another armyworm (SPLAT), *Spodoptera latifascia*. The FAW apparently has no diapause mechanism to allow survival during extended periods of low temperature, and therefore in the United States it is restricted to overwintering (with continuous generations) in subtropical areas of Florida and Texas (Mitchell 1979). Each spring and summer, FAW adults disperse throughout much of the United States as far north as Canada (Luginbill 1928). Adults of the CEW are also capable of dispersing over long distances (Phillips 1979). However, this species has a pupal diapause enabling it to survive cold winter temperatures throughout much of North America as far north as Canada (Hardwick 1965). Virtually nothing is known about the life history of SPLAT (Kovitvadhi 1969).

The wing area to body weight relationships for VBC, FAW and SPLAT yield very small slopes (0.35, 0.22 and 0.22, respectively; Figure 3), consistent with the hypothesis that these migratory moths should achieve lower than theoretically predicted wing loading ratios at reduced body weights to facilitate less costly flight in search of new larval foodplants. The slope for CEW (0.59; Figure 3) also is smaller than the theoretical slope of 0.67, but it is substantially larger than that of the other species, suggesting that the CEW has evolved a somewhat different strategy of resource allocation than the other three species. This is further indicated by the substantially different slope of the relationship between % lipid and dry weight for the CEW (0.25) compared to those of the VBC and FAW, which are similar (0.52 and 0.57, respectively; Figure 4). The slope for SPLAT (0.15; Figure 4) is surprisingly more similar to that of the CEW, from which it differs in the wing area to body weight relationship, than to those of the VBC and FAW, to which it is very similar in the wing area to body weight relationship (Figure 3). Like the VBC, these three species exhibit relatively low minimal weights (Table 2).

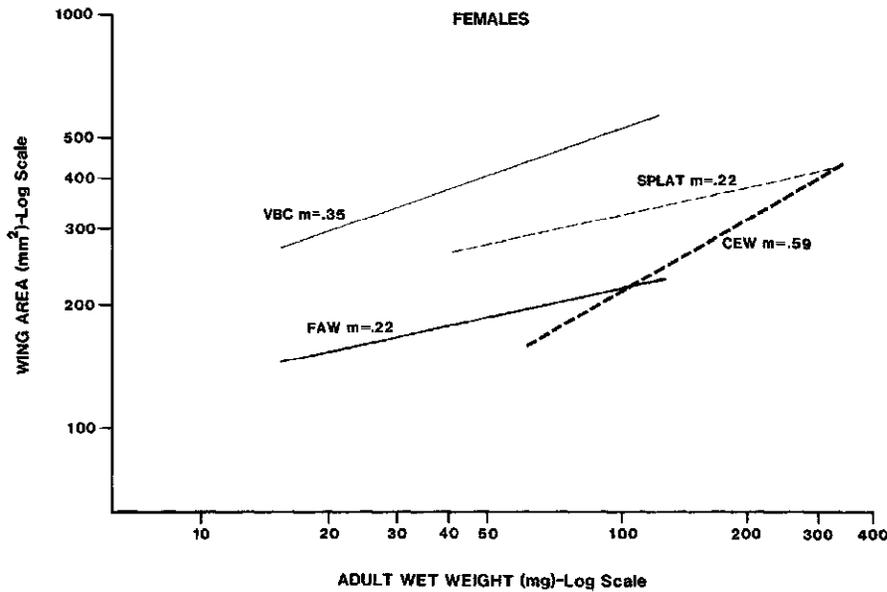


Fig. 3. Relationship between log wing area and log fresh weight for four species of noctuid moths subjected to different durations of starvation during the last larval instar. VBC = velvetbean caterpillar ( $n = 24$ ), FAW = fall armyworm ( $n = 27$ ), CEW = corn earworm ( $n = 18$ ) and SPLAT = the armyworm *Spodoptera latifascia* ( $n = 25$ ). Linear regression lines and slopes ( $m$ ) are presented for females only; males were similar. Analysis of covariance indicated significant differences between some of the slopes (from Angelo and Slansky in prep.).

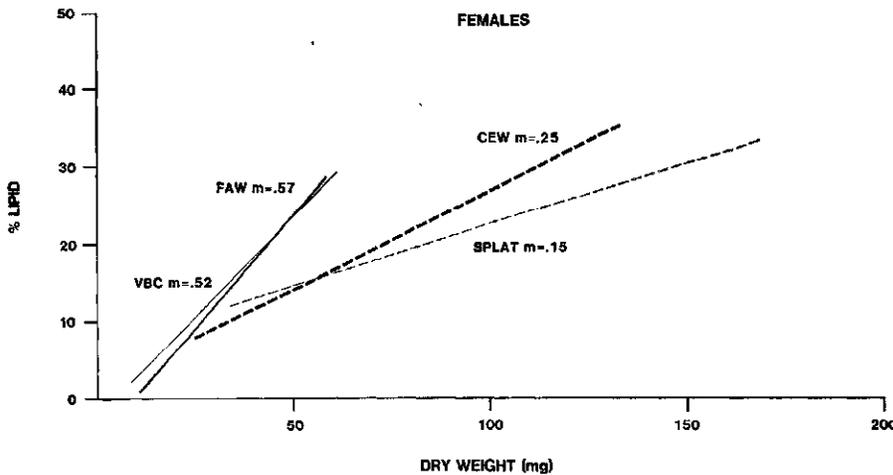


Fig. 4. Relationship between % lipid (dry weight) and dry body weight for four species of noctuid moths (see Figure 3 for explanation of abbreviations). Linear regression lines and slopes ( $m$ ) are presented for females only; males were similar. VBC ( $n = 31$ ), FAW ( $n = 28$ ), CEW ( $n = 18$ ) and SPLAT ( $n = 25$ ). Analysis of covariance indicated significant differences between some of the slopes (from Angelo and Slansky in prep.).

CEW (and SPLAT) thus exhibit less reduction in lipid when starved as larvae compared with VBC and FAW. Perhaps it is important for larvae of the CEW to maintain a relatively high lipid content (i.e., a relatively high metabolic fuel reserve) throughout their last instar in the event an overwintering pupal diapause is required. For VBC and FAW, however, which apparently lack an overwintering diapause, to be able to produce adults with reduced wing loading ratios, facilitating less costly flight in search of more favorable habitats, seems to take precedence over maintaining their lipid content. When starved, individuals of SPLAT substantially reduce their wing loading ratio and maintain a relatively high lipid content, but how this relates to their biology in the field is unknown.

In addition, the maintenance of a relatively high lipid content by CEW may provide it with the metabolic fuel source for a more highly powered migratory flight. The relatively high wing loading ratio and steeper slope for the wing area to body weight relationship for CEW compared with the other three species (Figure 3) could indicate that CEW does undergo a more highly powered flight. Although more energetically costly per unit time, perhaps the high wing loading ratio of a high-powered flier would allow greater flight speed with the cost of transport (energy cost per unit distance travelled) actually being similar to that of a more passive flier with a lower wing loading ratio. Because cost of transport is dependent on both the metabolic cost and the speed of flight, it would seem possible that a migratory insect could reduce its cost of transport by reducing the former or increasing the latter. Use of upper air currents by many migratory insects (see above) may increase their speed of flight with little or no increase in metabolic cost, thus reducing their cost of transport.

Much more research is needed to critically evaluate these hypotheses. Laboratory studies indicate apparent differences in flight behavior among these noctuid moths, with VBC and CEW exhibiting greater degrees of nocturnal activity than FAW (Leppa et al. 1979); adults of SPLAT also seem relatively sedentary in the laboratory (N. C. Leppa, personal comm.). However, the extent to which these species differ in their flight behavior, both when searching within a habitat for adult food, mates and larval food-plants and when migrating between habitats remains to be determined. The similarity in body weight between the small-sized adult VBC produced in our experiments by larval starvation and the smallest field caught specimens (Angelo and Slansky in prep.) suggests that we are dealing with adults within the natural size range in our experiments and that the small adults are at least flight-worthy. However, whether these small-sized adults are reproductively competent, and whether they exhibit migratory flight are interesting questions that remain to be answered. In addition, we lack detailed information on how flight behavior, metabolic costs of flight, longevity and reproduction vary as a function of body size, and on the impact of flight behavior on fitness.

#### CONCLUSIONS

The way in which the individuals of a species allocate their resources is intimately associated with the evolved lifestyle of the species. Some of the more evident differences in resource allocation are manifested in the variety of sizes, shapes and colors of different species of insects. Differences in the relative abundance of different species also are often very obvious

(e.g. the extremely numerous larvae of a particular moth species defoliating much of a crop versus that "rare" species still absent from a devoted lepidopterist's collection) and may reflect interspecific differences in resource allocation to production of offspring and defense from enemies.

Less obvious but nonetheless important differences in resource allocation appear in the different body compositions, proportions of body parts, and behaviors of species. As research progresses, we are finding that insects differ in how they respond, through changes in resource allocation, to changes in environmental conditions. Two significant features of the environment that frequently exhibit changes are the quality and quantity of food. Obtaining a sufficient quantity of adequate quality food seems to be a common dilemma among animals (White 1978), and for insects flight is a common means of dispersal in search of food. Some species exhibit dramatic shifts between wingless and winged forms depending on the environment; individuals of other species are always winged, but they may exhibit alterations in the relationship between body weight and wing area (i.e., wing loading ratio), among other changes.

Of the four species of noctuid moths that we studied, all altered the allocation of their resources under larval starvation to produce adults with relatively larger wings and low wing loading ratios, even lower than the presumed theoretical prediction (i.e., the slopes of the relationship between wing area and body weight were all less than 0.67). This response seems to have adaptive value, associated with the apparent "passive" mode of long distance dispersal of these species, whereby individuals are blown along by upper air currents while maintaining active flight.

In contrast to the above species, some animals with a more energy-demanding flight, such as hummingbirds and euglossine bees, exhibit relatively small wings and high wing loading ratios, even at low body weights. This is indicated by values for the slope of the relationship between wing area and body weight that are greater than 0.67 (the slope for hummingbirds is 0.75 (Greenewalt 1962) and for euglossine bees is about one (Casey et al. 1984)). For animals like these with high-powered flight (i.e., relatively high wing beat frequency), a strategy of producing relatively larger wings at smaller body weights (i.e., reducing wing loading ratio like the noctuid moths studied here), would undoubtedly increase, rather than decrease, the energy cost of their style of flight due in part to the increase in drag over the surface of the wings as they became larger (see Kammer and Heinrich 1978, Casey 1981a).

Support for this hypothesis of increased energy requirements associated with larger wings in species with a high-energy-demanding mode of flight comes from data for two species of sphinx moths, *Manduca sexta* and *Hyles lineata*. Individuals of these species exhibit a very energy-demanding mode of flight, both because they have relatively high wing loading ratios (ranging from approximately 5 to 80 times those found for the noctuid moths in our study) and because they exhibit hovering flight (Casey 1976). The slope of the relationship between log wing area and log body weight for these two species is *negative*, indicating that individuals lighter in weight have larger wings (on an absolute scale) than heavier individuals. Associated with this is a greater weight-specific power requirement for the moths that are lighter in weight (Casey 1976). Why these species produce larger (rather than smaller) wings at reduced body sizes is not clear.

Before the adaptive significance of the various alterations in resource allocation seen among species in response to environmental changes can be understood, more information on the consequences of such alterations is required. Thus, questions pertaining to the significance of interspecific differences in ability to achieve optimal weights, in minimal weight values, in changes in wing loading ratio and so forth must be answered within the context of the species' lifestyle in nature, in terms of trade-offs between reproduction, dispersal and mortality. This is a difficult task requiring detailed behavioral observations and quantitative measurements; it is clear that considerable research in nutritional ecology remains to be done.

In addition to the goal of understanding the evolution of species' lifestyles, there is a pragmatic side to research in nutritional ecology. If the factors influencing the behavior (including resource allocation) of insect pests, both in terms of their relative impact and their mechanisms of action are understood, then better methods of altering the behavior of pest species to their detriment may be devised (see Barfield and Stimac 1980). For example, many insect pests apparently exhibit long distance migration, as well as dispersal between and within crops (Stinner et al. 1983). Field-level control measures often overlook this fact; successful pest management must include a broader view of pest behavior, in this case attempting to identify "source areas" and influence the pest in these before it moves into the crop fields (see Barfield and O'Neil, this Symposium). Thus it can be seen that research on resource allocation is a valuable approach to understanding flight behavior and other features of insect lifestyles that have a significant bearing on crop production.

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## IS AN ECOLOGICAL UNDERSTANDING A PREREQUISITE FOR PEST MANAGEMENT?

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### SYNOPSIS

Comparison between the principles and real world practices of integrated pest management (IPM) reveals severe discrepancies. The cotton agricultural system is a problem with a long and sad history, and illustrates what not to do. But, examination of IPM relative to the mobile pests of polycultures in the southeastern USA would suggest that "here we go again?"

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Integrated pest management (IPM) is the current paradigm for dealing with pests; thus, it is prudent to inquire whether IPM will have a higher probability of long term success than other approaches which have failed. This paper is an attempt to compare the principles of IPM to the current control practices and to examine management approaches in two cropping systems. Primary objectives are to show that agriculturists are far from implementing programs that will solve pest problems and that such solutions will arise only from an ecologically sound foundation.

### PRINCIPLES OF IPM

The concept of integrated pest management (IPM) is well documented (e.g., Rabb and Guthrie 1970, Metcalf and Luckmann 1975, Apple and Smith 1976, Smith et al. 1976, Smith and Pimentel 1978, Bottrell 1979, Barfield and Stimac 1980); however, Bottrell (1979) appears to be the first to state explicitly the principles underlying IPM.

1. **POTENTIALLY HARMFUL SPECIES WILL CONTINUE TO EXIST AT TOLERABLE LEVELS OF ABUNDANCE.** The objective of IPM is to lower pest populations below economically important levels; eradication is not the objective.
2. **THE ECOSYSTEM IS THE MANAGEMENT UNIT.** The boundaries of and the couplings among components of the system must be identified before design and implementation of an IPM program.
3. **THE USE OF NATURAL ENEMIES IS MAXIMIZED.** An understanding of how natural enemies work in the system must be acquired so that optimal use can be made of their impact on target pest populations.
4. **ANY CONTROL PROCEDURE MAY PRODUCE UNEXPECTED AND UNDESIRABLE CONSEQUENCES.** An ecologically based management strategy is less likely to result in "negative effects" within the system being managed.

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5. AN INTERDISCIPLINARY SYSTEMS APPROACH IS ESSENTIAL. The assumption is that information collected by various scientists can and will be integrated.

Implicit in Bottrell's principles is the concept of monitoring. Design or evaluation of an IPM program demands monitoring of relevant aspects of the system. Thus, any IPM program must have well defined and utilized monitoring schemes.

An examination of currently used IPM programs for a variety of crops and pests (see Bottrell 1979, Barfield and Stimac 1980, Huffaker 1980, Flint and van den Bosch 1981 for general reviews) reveals that instead of IPM programs having the above six characteristics, most existing programs have the following:

1. There is virtually no appreciation for the boundaries and characteristics of the system being managed. Target pests are dealt with as if sessile, and individual fields as though they are independent of the agroecosystem.
2. Mortality from natural enemies is poorly understood, even totally ignored.
3. Most "IPM programs" are not integrated, but are actually four unilateral efforts—one each for weeds, insects, pathogens, and nematodes. Farmers must do the integrating, if any is to occur. Potentially useful integrative tools (e.g., systems models) have not been incorporated into the mainstream of agricultural thinking.
4. The level at which a pest population is considered to be economically important is usually considered static, not a function of changes in the system being managed.
5. Monitoring is not often a part of field activities. Sampling plans are often inadequate and do not allow estimation of pest population levels with precision or accuracy.

While some programs have been deemed successful, others have not (see Barfield and Stimac 1980). Assessing why a program fails is often difficult. To evaluate the applicability of IPM as an approach, we must first delineate "true" IPM programs from the plethora of programs that are called IPM. Determining whether IPM will lead to more solutions to pest problems than other approaches requires a historical perspective. For illustration, two approaches to boll weevil (*Anthonomus grandis*) management are compared, with respect to their spatial and temporal utility. The amount of ecological information incorporated into particular programs is the primary focus. The thesis is that ecologically based programs will be effective, but programs that ignore significant components of pest ecology will not. Following the boll weevil example, a description of the complex of noctuids typical of polycultural systems in the southeastern USA is given. This second system forces the question "are the same mistakes still occurring?"

#### THE COTTON WEEVIL: A MODEL FOR IPM

After entering the United States (ca. 1892) and spreading throughout most of the range of its cotton host plant, the boll weevil caused radical changes in the way cotton was cultivated (Adkisson and Bottrell 1977, Bottrell 1983). The numerous approaches that were attempted to manage the weevil mirrored developments in Economic Entomology in the 20th

century (see Perkins 1982). To a varying degree, weevil management relied on a knowledge of pest biology and ecology. Two management approaches can be contrasted for their long term utility in space and time (robustness). PRE-INSECTICIDE ERA. Since little was known about the boll weevil prior to its introduction, early workers had to investigate weevil ecology before they could develop even a preliminary management program. Significant constituents of early management programs were strategies that maximized within- and between-season mortality (Adkisson and Bottrell 1977, Bottrell 1983). Within seasons mortality was identified primarily to be a function of two components: (1) natural enemies and (2) host plant responses to weevil infestation (Hunter and Hinds 1904; 1905, Pierce et al. 1912, Fenton and Dunnam 1929). Natural enemies were studied extensively (see Pierce 1908, Pierce et al. 1912). Of particular interest was the interaction between host plant and insect parasitoids. Since weevil immatures (eggs to pupae) developed inside the cotton floral buds (weevils also attack fruits, but prefer buds—called “squares”), parasitoids had to search buds for suitable hosts. In response to weevil attack, the plant abscised infested buds. Most buds fell to the soil surface, but some remained on the plant. These were referred to as “hanging squares”. It had long been noted that parasitism rates in hanging squares consistently were higher than in fallen squares (Hunter and Hinds 1904; 1905, Pierce et al. 1912, Fenton and Dunnam 1929). To maximize parasite efficacy, Pierce et al. (1912) suggested that farmers refrain from destroying hanging squares and that a “hanging square” variety of cotton should be developed and used in production.

Abscission of infested squares also played an important role in weevil mortality. Squares that fell between rows were sunlit and dried more rapidly than those that fell in plant shade. Immature weevil mortality was found to be affected significantly by the location and subsequent drying time of fallen squares (Hunter and Hinds 1904; 1905, Fenton and Dunnam 1929, Folsom 1932). To take advantage of this source of weevil mortality, some authors suggested varying cotton row spacing (Mally 1901, Cook 1932).

Perhaps the most significant component of weevil ecology was identified to be the survivorship of overwintering weevils (Hunter and Hinds 1904; 1905, Pierce et al. 1912). Weevil adults overwinter in and around cotton fields under leaf litter and crop residue. To maximize adult mortality, two suggestions were made: (1) shorten the growing season to increase the time in overwintering sites and decrease the time suitable host material was available, and (2) destroy crop residue and other overwintering habitats (see Cook 1932).

Growers following these ecologically-based recommendations were able to produce an economically viable cotton crop for over 40 years (Adkisson and Bottrell 1977, Bottrell 1983). Although insecticides were available (e.g., calcium arsenate), they were used sparingly (Isley 1926, Folsom 1932). The advent of inexpensive, effective synthetic insecticides (e.g., DDT) led to major changes in boll weevil management—changes that ultimately led to disaster.

INSECTICIDE ERA. Following World War II, the incorporation of synthetic insecticides into cotton crop protection schemes led to a dramatic change in boll weevil management. The decimation of weevil populations following insecticide application allowed growers to maximize yields while minimizing damage (Newsom 1970, Reynolds et al. 1975). Preventative ap-

plications and "calendar sprays" (i.e., "ever so often, need it or not") were used widely, eliminating the "need" to determine whether weevil densities were above economically damaging levels (Adkisson and Bottrell 1977). With the widespread acceptance of a management plan based solely on insecticides, research on weevil ecology was de-emphasized. Eventually, this overreliance on insecticides led to widespread ecological perturbations and near economic collapse of the cotton agricultural system (Adkisson and Bottrell 1977).

Weevil resistance to organochlorine insecticides in the 1950's was followed quickly by analogous resistance to other compounds by both the weevil and other cotton pests (Newsom 1970, Adkisson and Bottrell 1979), and growers soon found that increased application rates could not provide needed control. Organisms not formerly pests became pests, and existing pests got worse. Cotton agriculture was out of control (Newsom 1970, Adkisson and Bottrell 1977), and several major cotton growing regions faced economic ruin.

What emerged from this disaster was an approach called IPM. IPM largely adopted the recommendations made by workers in the pre-insecticide era. Focus was again on maximizing overwintering weevil mortality, shortening the cotton growing season and judicious insecticide use (Bottrell 1983). Weevil management was fortunate at least to have had an ecological template. However, examination of how much remains to be learned about boll weevil shows that agriculturists are far from implementing a complete solution to the boll weevil problem.

Although early workers identified the importance of the plant's abscission of infested squares, just how this affects weevil dynamics or whether immature parasitoids also suffer from square drying mortality remains to be learned. Given the apparent increase in parasitization in handing squares, should parasitoids that prefer to search in this region of the plant's environment be released? There are many such questions. In addition, major elements of weevil biology and ecology are still being discovered. For example, despite intensive studies on adult overwintering, it was 1959 before diapause in adult weevils was discovered (Brazzell and Newsom 1959). By 1968, only four exotic natural enemies (see Clausen 1978) had been released against the weevil, a species which itself was introduced. As late as 1975, major alternative host plants were being found (Cross et al. 1975). In 1979, a closely related weevil (*Anthonomus hunteri*), and a potential clue to natural enemies, was described from the boll weevil's Central American aboriginal home (Burke and Cate 1979).

What has been shown here for the boll weevil is true of many other pests. Now, examination of a second system will reveal whether today's workers have profited from yesterday's experiences.

#### THE NOCTUIDAE

The southeastern USA contains a mosaic of agricultural production systems. Within these, a complex of pest organisms exists that appears to reinvade crops annually through migration and/or dispersal. Of particular concern in recent times is a complex of moths (mostly Noctuidae) that is suspected to overwinter in more southern latitudes and move northward each spring and summer. A number of recent reviews and symposia have addressed these insects and what is and is not known about them (e.g.,

Rabb and Kennedy 1979, Stinner et al. 1983). Others have reviewed and discussed the phenomenon of movement in great detail (Johnson 1969, Baker 1978, Gauthreaux 1980), theoretical evolutionary problems and selection models (Walker 1980), and movement of pests relative to the structure of agricultural systems (Stinner et al. 1983, Rabb and Stinner 1978, Johnson et al. 1975, Stimac and Barfield 1979). Inability to forecast when and where these mobile moths will occur and the reasons why also have been confronted (Barfield et al. 1980).

Current IPM strategies against these pests are similar to those for less mobile organisms—an individual farmer's field is scouted and the pest population treated (primarily chemically) when damaging density levels are suspected. These fields are treated as "islands," and there is virtually no consideration of the significance of the processes determining the timing and rate of influx. Though most agriculturists recognize that pest population levels are related to both the timing and magnitude of immigration, few measure influx rates and evaluate quantitatively the consequences of those influxes (see Rabb and Kennedy 1979). Research extended from the soybean plant growth model (see Wilkerson et al. 1983) is an exception to this generalization. Unless an understanding of the role movement plays in moth dynamics and "pest status" is acquired, agriculturists can not design robust management strategies against pests such as these (e.g., Stinner et al. 1983, Rabb and Stinner 1978, Barfield 1983, Barfield et al. 1980, Rabb and Kennedy 1979).

"IPM" programs against these noctuids could, over the long term, prove to be just as unstable as boll weevil management when it abandoned an ecologically based approach. Since the general attitude of the agricultural community currently is for "judicious use of pesticides," the polycultural systems of the southeastern USA may not suffer the catastrophe seen in cotton; however, that is not the point. The thesis is that what IPM needs is robustness—it needs to be based on ecological understanding sufficient to adapt to the dynamic nature of the system being managed and to work in space and time. For a proper noctuid IPM program, the following must be known (see also Stinner et al. 1983):

1. seasonal patterns of appearance and geographical distribution of both immature and adult stages
2. overwintering (quiescence or continuous breeding) habitats and associated environments
3. methods for differentiating local from migrant populations
4. weather patterns in a fashion meaningful for interpreting moth displacement trajectories and flight behaviors
5. physiological and behavioral attributes conducive to initiating, maintaining, and terminating non-trivial flight
6. relationships between relative density estimators (e.g., light traps) and absolute densities occurring in particular crops

These six investigative areas will yield information that is crucial for understanding the role movement plays in the occurrence of moths in space and time (see Stimac and Barfield 1979). In addition, there is need to be able to evaluate whether specific influxes cause economic damage (see Barfield et al. 1980). The agricultural community appears to be a long way from a sound ecological understanding of these mobile noctuids (see Rabb

and Kennedy 1979), hence a long way from implementing an IPM program against them.

#### THE REAL MESSAGE

Long term solutions to pest problems must have sound and broad ecological bases. Boll weevil history offers a dramatic example of what can happen with a unilateral approach that ignores the ecology of the system. Will the Noctuidae be a repeat? Not if ecological understanding of the system is a prerequisite for the design of IPM programs. This, of course, means a re-orientation of experimental emphases and academic education and training for crop protection practitioners (see Barfield and Jones 1979, Barfield and Stimac 1980, Strayer et al. 1983).

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## OBSERVATIONAL SAMPLING METHODS FOR INSECT BEHAVIORAL ECOLOGY

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### SYNOPSIS

Researchers who want to retain relevant behavioral and ecological settings and at the same time conduct scientifically rigorous studies have increasingly turned to non-experimental research design. By understanding the basis for wise data collecting decisions, and their consequences, the observer can choose appropriate methods. Using illustrations from insect behavior, this paper discusses some of the basic principles involved and two of the most useful ways of collecting behavioral data.

### INTRODUCTION

One of the most important needs in observational research is for sensitive, non-destructive methods of studying social processes (Barker 1963). A major way this need can be met is through use of what Schneirla (1950) called observation-selective (as opposed to manipulative) controls, including systematic behavioral sampling methods. Many experienced students of naturalistic behavior will be familiar with a number of well-established methods for observing and sampling the responses that they want to study systematically. What may be unfamiliar is the implicit rationale behind these observational sampling methods and the fact that for a particular research question, only particular sampling methods can provide the answers. I shall discuss below several behavioral sampling methods and their uses, singly and in combination. First, however, let us briefly consider those steps in research design that should precede the choice of sampling methods.

As is the case for most tasks, different jobs call for different tools. So, an unambiguous formulation of a behavioral question is critical to the choice of an appropriate sampling technique. For behavioral problems the differences among various questions often hinge on whether the duration of the behavior is significant, i.e. on whether the behavior can be considered as a momentary event, a "happening" of negligible or inconsequential duration, or whether it should be considered as an enduring state. In the latter case the onset and offset, or at least the duration of the behavior, is important, and, therefore should be sampled in an appropriate way. For example, it may be that some insect obtains about the same amount of energy from each flower it feeds from, so that we need only count frequency of visits to flowers per unit time in order to estimate relative energy intake. However, in the same insect, it may be that the expenditure of energy is a function of time spent in transit between food plants and that these are variable, in which case it is not the frequency of moves but rather the duration or cumulative durations that we need to measure.

Consider another example: a male wasp's reproductive success might be a function of the number of different mates he has, or it might depend on

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the length of time he spends guarding a female after mating. In the former case we would need a sampling method that provides unbiased estimates of rates or relative frequencies; in the latter, we need unbiased estimates of duration or time spent. In another situation, reproductive success may be a function of sperm count which, in turn, may be a function of the length of time since the male's previous mating. In that case we would need a continuous record that included the interval *between* occurrences of behaviors.

Many sampling methods are suitable for answering only frequency-based questions, others, only for questions based on time spent in an activity, and a few provide data for unbiased estimates of behavior durations or inter-behavior durations. It is therefore important either to know ahead of time which of these is the important parameter or, if this is not possible, to choose one or more techniques that will allow the observer to gather both kinds of information. Sometimes a pilot study will enable the researcher to decide that only one of these kinds of information is needed, in which case efficiency of data collection and analysis is often greatly enhanced.

In the first stage of formulating a research question about naturalistic behavior, one usually uses informal, *ad libitum* observations to gain a general understanding of the situation and to avoid totally meaningless and inappropriate research directions. Burk & Calkins (1983) point out the importance of this stage in the research on medflies. These early observations may even be sufficiently informative to allow choice of the important parameters, such as frequency (including relative or conditional frequency), interval duration, or time spent, as discussed above.

The background information that we have about our subjects may enable us to make other important sampling decisions. If, for example, we are interested in mating behavior and we know that it is somewhat variable, we might rotate our observations among a number of (preferably identifiable) adults in order to evaluate individual differences or to at least be sure that the data were from a representative sample of adults. Likewise, if we cannot rule out variability among nests in the behavior we measure, we might decide to rotate among a sample of nests in a systematic way. Decisions on whether to sample during all times of the day, week, month, season, will also need to be made, based on specificity of the problem, assumptions about variability within and between classes, and the extent to which the results will be generalized. All too often, such sampling decisions are made without the investigator realizing that he or she has made a choice. Of course, one does not thereby escape the consequences of the choice. To the extent that decisions become explicit we shall improve the chances that they are the most appropriate to our goals.

Much of traditional fieldwork never went beyond simple natural observations, or what I have called *ad libitum* sampling, and the findings were, consequently, subject to the biases caused by attention-attracting, dramatic events, by the individual biases of each observer, and so on. For reliable and valid results, however, we must turn to more systematic techniques. Two of the most useful and most commonly used ones will be discussed below. For an analysis of others in the literature, the reader is referred to Altmann (1974), which also contains a more in-depth treatment of some of the topics mentioned only briefly here. More complete recent algebraic treatment of

some techniques can be found in Kraemer (1979) and in Griffin & Adams (1983).

#### FOCAL-ANIMAL (CONTINUOUS) SAMPLING

I coined the term "focal-animal sampling" to refer to any sampling method in which (i) all occurrences of specified behaviors or interactions of an individual are recorded during each sample period, and (ii) a record is made of the length of each sample period and the amount of time during the sample period that the subject is actually adequately in view for recording those behaviors. Under some conditions and at least for some behaviors, one may reasonably assume that a complete record is obtained, not only of the focal animal's actions, but also of behaviors directed to it by others. Under other circumstances, it may be possible to record all acts by the focal individual, but not all those directed toward it by others (e.g. silent threats performed at moderate distances). Several factors will affect the extent to which the observers can reliably detect and record behaviors directed toward the focal subject. These include the density of animals, the frequency and attention-getting nature of the behaviors, and the number of behavior categories. It is critical that complete records of the target behaviors are obtained during the observation period. Thus, it is important that the observer not try to record more information than can be done consistently, even at the busiest times, or else much of the advantage of systematic sampling will be lost.

The importance of several temporal aspects of behavior has been increasingly recognized. Fortunately, the development of field-portable, electronic data recording devices, as well as good inexpensive digital time-pieces, have greatly increased field workers' abilities to collect time-based data and have eliminated the subsequent chore of hand-entering the data for computer analysis. If the duration of activities or the duration of periods between activities is important, these data can readily be included in a focal animal sampling scheme. In the desire to sample more animals in any day, observers will sometimes make each individual sample short, say five or ten minutes. One should be aware that if sampling intervals are short relative to the durations to be estimated, much poorer estimates will result. In addition, one always loses some amount of time to searching and to sample initiation between individuals; the ratio of this lost time to sample time may be appreciable if short sample times are used. These factors will have to be taken into account in making wise decisions about sample lengths. As always, research design decisions involve compromises.

Focal sampling will be the method of choice, perhaps the only appropriate method, for many problems. However, it is a very labor-intensive method, and it is not suitable for most questions about behavioral synchrony among individuals unless several observers are collecting data simultaneously or if the synchrony questions involve only animals that are spatially very close and thus simultaneously observable. Consequently, it is useful to consider a complementary technique, instantaneous sampling.

#### POINT (INSTANTANEOUS) AND SCAN SAMPLING

Point sampling is a technique in which the observer records, at pre-selected moments in time, an animal's ongoing activity. As such, it is a

sample of behavioral states, not events. It is particularly useful in studies of activity time budgets but not in answering questions based on frequency of occurrence. Instantaneous sampling can be used to obtain data from a large number of individuals, by observing each in turn. Moreover, if the behavior of each group member is sampled successively within a very short time period, the record approaches a simultaneous sample on all individuals, which we refer to as scan sampling. If such sampling is done frequently, data are obtained on the time distribution of behavioral states among a whole group of animals. Data on behavioral synchrony are thereby obtained, which are virtually impossible to obtain by almost any other sampling technique.

In an ideal instantaneous sample, each individual's state is instantly noted. In practice, however, the observation and classification of a state takes time, particularly if one is moving or scanning from one individual to another. The observer should try to scan each individual for the same brief period of time, for otherwise a scan sample is equivalent to a series of short focal-animal samples of variable and unknown durations—ones that may be inadvertently biased by the different characteristics of the various activities being recorded. In order to keep sampling time consistent and brief, and to score reliably all items in one's catalog, the categories that are recorded in this type of sampling should be easily and quickly distinguishable. For some animals this has meant that the technique is more suited to studies of non-social rather than social behavior or to studies in which social behaviors can be lumped into a few easily and rapidly identified categories.

If animals are close together and little time is lost in sampling one after another, scans offer an efficient means of gathering data on all group members over a short time span. The absence of information on occurrence, on durations, and on temporal patterning, will rule out scan sampling for some questions. The observer also will need to be sensitive to the effects of the order of individuals to observe, the frequency of the instantaneous samples (which will affect their independence), and the distinguishability of the behaviors, as discussed above. As is the case for planning any research design, there is no substitute for knowing one's animals and for having well-defined questions.

#### USE OF COMBINATIONS OF SAMPLING METHODS

Sampling decisions almost always involve tradeoffs. Consequently, it is particularly useful to consider the possibility of using combinations of techniques to capitalize on the advantages of each. Often one can thereby greatly increase the information gained in a study. I shall describe examples of how this can be accomplished with *ad libitum*, instantaneous, and focal sampling to give a sense of the possibilities that await the researcher's creativity.

For many studies, focal-animal (continuous) sampling proves to be the main technique of choice because it provides data for frequency-based questions, for bout and inter-bout durations, time budgets, and so on. However, under most observational conditions, one is restricted to collecting data on a single animal at a time. Moreover, it is sometimes difficult, even with modern electronic event recorders, to collect very detailed data on a large number of behavior types. As a consequence of this second limitation, one

might decide for some activities, to record only their occurrence, not their duration, if the latter information were not critical. However, for some other activity, say foraging, the more important information might be how much time is spent in the activity, or whether foraging is ongoing when a second activity, say predation, occurs. In this latter case, we would take instantaneous samples, perhaps at five-minute intervals, of the presence or absence of foraging, and do so again when predation occurs. Then we can answer the question of whether predation occurs disproportionately during foraging: an affirmative answer to this question would suggest that there are costs as well as benefits to foraging, and that the costs are not just the energetic ones involved in obtaining food.

Questions about synchrony of activities in a group can be addressed by taking scan samples of the group at the beginning and/or end of a focal sample. Questions of subgroups or social affinities in a group can be addressed by instantaneous samples of nearest neighbors or all neighbors within a specified distance at fixed intervals within a focal sample during which details of social interaction are being recorded continuously. Then one has the baseline data for asking whether the distribution of interaction partners is predictable from the amount of time that individuals spend near each other. Obtaining the latter from continuous records would have been much more laborious to gather and such records are not needed to answer this particular question.

While conducting focal samples, one is sometimes able to record some additional observations on an *ad libitum* basis. While such data will not be useful for any questions that require unbiased frequency estimates, they can be useful for some other purposes. Their heuristic value has already been mentioned. In addition, there are situations in which one is primarily concerned with the asymmetry of some relationship within a pair of individuals, such as who grooms whom, and for which one can reasonably assume that the *ad libitum* observations are not biased toward any direction of this asymmetry. The direction of food exchanges in insects may be of this sort, as are agonistic/dominance interactions in some species. Thus, although interaction matrices constructed from *ad libitum* data cannot be used to answer the question of who fights more often or to whom does an animal direct most of its aggression (because those questions require data that are unbiased in ways that are seldom the case with *ad lib* observations and that require the focal sample data), they can answer certain questions: for example, when animals A and B fight (or exchange food) with each other, which member of the pair is more likely to be the recipient of the aggression (or food)? Because much larger data sets are likely to accrue from such a combination of *ad libitum* sampling and focal sampling, with the data from each carefully separated, of course, many observers have found it a fruitful combination.

Finally, the student of insect behavior may occasionally find that one of the more specialized techniques is the best method for a particular problem. In sequence sampling, for example, the focus of observation is a particular interaction that can be identified even if the initial participants discontinue the activity and others join. A primate play group can be of this sort, as might insect nest-building, the fate of some food item that is passed among and processed by many individuals in succession, and so on.

Another technique is one-zero sampling, in which the observer records

the occurrence (or existence) of an activity within the sampling period, and not the frequency, duration, or any other such information about the activity. This sampling method was for a time one of the most commonly used in some areas of behavioral research and as a consequence much attention was devoted to attempts to relate these scores to measures of occurrence and time spent (e.g. Simpson & Simpson 1977, Rhine & Flanigan 1978). Although the technique is not a good one for estimates of those important parameters, or for any questions based on those parameters, just the presence or absence of a behavior may itself be important in some situations, in which case, one-zero sampling would be the appropriate method to use. Thus, the main determinant of a potential foundresses' success may be whether she mates at all (and not how often) within a fixed time after she leaves her old nest. This is a one-zero situation. Or an animal's survival may depend on whether it finds any food within a single day, the amount being fairly irrelevant or constant. This, too, would be a one-zero biological situation and would call for a one-zero sampling technique in which the sampling unit of time should be the biologically-important unit, not the arbitrary times units previously used for this technique. The point, as always, is to choose the technique that is most appropriate to the question.

#### CONCLUSION

It is in field situations that biological problems usually arise and it is to just such situations that we return to test our answers. This is often most immediately clear in applied areas of science where the real-world tests are eagerly awaited and where the successes and failures may be very much on view. These applied areas, perhaps even more than others, require a thorough blend of observational work, often in the field, and solid scientific methodology. They have much to gain from the increasing recognition that neither laboratory nor field, experimental nor non-interventive methodologies, has a monopoly on scientifically rigorous ways to answer questions (Schneirla 1950, Altmann 1974, Mertz & McCauley 1980; see Thornhill, this symposium).

A primary function of any research design is to maximize the validity of conclusions, that is, to minimize the number of alternative hypotheses that are consistent with the data. Having done so, actions that are taken based on these conclusions have a greater chance of being successful. Experimental methods and manipulative control of variables can sometimes contribute to this goal, and are the approaches most commonly pursued to this end. They are not the only means however, and often not the best methods. Experimental research design, and the appropriate statistical techniques for each design, have been the objects of extensive investigation. While some of the results can be applied directly to non-experimental design, much of it cannot. The study of quasi-experimental and non-experimental design (e.g. Webb et al. 1966) is increasingly recognized as an important one (see, e.g. Slater 1978, Lehner 1979) that now even receives treatment in introductory texts, but is still in its infancy. At times this may be frustrating to the researcher, but it is also challenging, and exciting as one plays the game "Eliminate the Alternatives!"

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## THE BEHAVIORAL ECOLOGY OF VERMIN

J. SIVINSKI\*†

### SYNOPSIS

Some topics in evolutionary biology might be of interest to medical entomologists, particularly those concerned with the dispersal of ectoparasites. These include:

*Sexual selection*—Male competition and female mate choice may influence the propensity to disperse, which hosts are chosen, and where parasites are located on an animal. Phoretic flies on beetles can serve as models for vertebrates and their vermin and illustrate some possible sexually selected patterns of distribution.

*The maintenance of sex*—There is a cost to sexuality best described as the cost of producing males. Plant, but not animal, ectoparasites commonly mitigate this cost through cyclic parthenogenesis. It is suggested that phenotypic variability produced by the immune system of vertebrates may select for genetically heterogeneous offspring, i.e. sexual reproduction.

*The extended phenotype*—The notion that "gene" activity may extend into the form and behavior of a symbiont suggests that symptoms of infection or infestation should be considered from the perspective of both the host and the parasite. Vertebrate pathogens may influence the movement of ectoparasitic vectors.

### INTRODUCTION

I am not a medical entomologist and I do realize there is a certain presumption in writing on topics outside one's field of study. However, the perspective of an outsider can sometimes include features overlooked by the specialist. With this somewhat arrogant apology in mind, I will present some behavioral and evolutionary themes that might be of interest to medical entomologists. These topics are sexual selection, the maintenance of sex and the notion of the extended phenotype, particularly as they pertain to ectoparasitic insects and what seems to me to be a central problem in medical entomology, the dispersal of insects both between and over the surfaces of host animals.

### SEXUAL SELECTION

Sexual selection results from the difference in male and female investment in offspring (Trivers 1972, Thornhill 1980). At its simplest, females invest in large gametes and their reproductive success is limited by their ability to make eggs and obtain the highest quality paternal genes for their offspring. Males make cheap gametes and their reproduction is limited by their access to females. Mate competition among low-investing males creates intrasexual pressures that commonly result in the evolution of fierce, fast, or sneaky males. Female choice of mates generates intersexual selection that

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can favor, among other things, male advertisement and greater female powers of discrimination.<sup>1</sup>

Intra- and intersexual selection influence the movement of ectoparasites. As a simple example, it can behoove males but not necessarily females to go from host to host to find as many mates as possible.<sup>2</sup> Among ectoparasites this is reflected by the winged males but flightless females of the bat infesting fly *Ascodipteron* spp. (see Hackman 1964).

Things get more complicated. In *Carnus hemapterus*, an acalypterate fly that feeds on the skin secretions of nestling birds, all females and two-thirds of the males shed their wings (Capelle and Whitworth 1973). Apparently among male *C. hemapterus* there are both searchers and stayers. Reasons for the difference are unknown but might include the probability of sharing the nest with females and how intimidating the local rivals are.

When the possibility of females foraging for the best possible mates is added, complexity is compounded. The tiny dung fly *Borborillus frigipennis* (Sphaeroceridae) is a kleptoparasite that lays its eggs in the dung stores of scarab beetles (Sivinski 1983). It bears a number of parallels to certain lice and fleas and the symbionts can serve as a kind of scale model of a vertebrate and its vermin. A fly often stays on a single host for 30% of its adult life, for it rides on beetles both underground and in the air, and important to any extrapolation, it mates upon the host. Like *Carnus*, *B. frigipennis* males are stayers or searchers. This is not obvious from wing polymorphisms but is seen in the way flies behave when they mount unoccupied scarabs. Some hop on and ride, others scurry over beetles, dismount and await another that they search in turn. However, in *B. frigipennis* female as well as male dispersion appears to be influenced by sexual motives.

The mean male/female sex ratio of beetle-back fly groups rises and then falls with the increasing size of the group. This pattern is actually due to a female's preference for sparsely and densely inhabited beetles (Sivinski, unpublished data). Females may like empty beetles because of the lower levels of competition their larvae are likely to face, and there is some evidence that females come to bigger groups in order to mate with the most competitive of a large sample of males (see Sivinski 1984). If so, these beetle-back aggregations are similar to what Richard Alexander calls resource based leks (Alexander 1975, Lloyd 1979). That is, females prefer certain resources not only because of their quality as food or oviposition sites, but also because of the sexual opportunities offered by associated males.

Among the more vagile ectoparasites, such as Hippoboscidae and Streblidae, perhaps further study will add sexual partners already on an animal to the list of qualities such as hair size, molting pattern, health, grooming, and body temperature that influence the suitability of hosts. If so, this will probably not be a universal criterion for host choice. Some species may typically occur in such large numbers that the differences among animal borne populations will be trivial. That is, if the sample of males on each host is very large then the between-host variance in male quality is apt to be low and animals will present a similar set of sexual partners. For example, such lack of between-site variance might explain the failure of yellow dung fly, *Scatophaga stercoraria*, females to choose dung pat oviposition sites on the basis of resident males (see the results of Borgia 1979).

The distribution on an animal's surface, as well as dispersal among

animals, can be sexually selected. A *B. frigipennis* perched on a beetle's horn is usually a male. Horns may be good lookouts from which to search for females. Among ectoparasites there are patterns of distribution where adults are separated by sex, or less widely dispersed than their immatures. Some of these may be reflections of mating strategies (see Table 1). For instance the biting louse of cattle (*Haematopinus eurysternus*) has an intriguing distribution. Females are broken up into adult and nymphal clusters. Adults in groups of up to 60 oviposit together on the back of the neck. Males occur on the sides of the neck, or are associated singly or in small groups with nymphal clusters (Craufurd-Benson 1941). There may be a complex sexual environment on backs of cattle where some males obtain mates by waiting for the immatures they guard to grow up, while others condense on mating grounds that are near but not in breeding sites, either to intercept migrating females or to form leks where females shop for the most attractive mates.<sup>3</sup>

THE MAINTENANCE OF SEX

While considering sex, it is worth noting its surprising ubiquity among very intimate insect ectoparasites, particularly lice. There is a cost to sexuality best described as the cost of producing males; generally, a lineage would increase twice as fast if it consisted of parthenogenetic females. Therefore, there must be a greater than 2-fold reproductive advantage in producing genetically variable offspring for sex to resist replacement by asexual mutants (see Bell 1982 for a lengthy discussion). Most conjectural

TABLE 1. EXAMPLES OF ECTOPARASITE DISTRIBUTIONS THAT MAY REFLECT MATING SYSTEMS.

Order Insect	Comments and References
Dermaptera <i>Hemimerius talpoides</i>	Adults more anterior on backs of rats (Ashford 1970).
Hemiptera Cimicidae	Aggregations of cimicids off hosts—bug trains (e.g., Lee 1955, Overal and Wingate 1976, Cheng 1973).
Phthiraptera <i>Haematopinus eurysternus</i> and <i>Damalinea bovis</i>	Adult and nymphas clusters on cattle (Craufurd-Benson 1941).
Diptera <i>Melophagus</i> spp.	Males congregate on hind parts of sheep (Graham and Taylor 1941).
<i>Mystacinobia zelandica</i>	Communal oviposition and adult clusters off bat-hosts (Holloway 1976).
<i>Joblingia schmidti</i> and <i>Trichobius yunkeri</i>	Swarm in bat caves (Wenzel et al. 1966).
Siphonaptera <i>Echidnophaga gallinacea</i>	Males on body, females on heads of chickens (Suter 1964).

advantages to sex suppose environmental heterogeneity selects against genetically homogeneous clones, and one of the most important sources of environmental heterogeneity is biotic, the unpredictable amalgam of predators, competitors, and symbionts (e.g., Hamilton et al. 1981). Relationships with hosts are certainly intense and it is easy to see why colonizing ectoparasites might be sexual products. But it is less clear why sex should continue once a compatible, relatively unutilized animal has been reached. It would seem that cattle backs should be more biotically homogeneous than the pasture in which they stand. There are very few records of predation on lice by animals other than the host, and little opportunity for, or direct evidence of competition (see however, Wenzel and Tipton 1966, and Hopkins 1949). Actually a few species of biting lice do what is expected of them; males become progressively more rare after an animal is colonized (all are Ischnocera, see citations in Marshall 1981). This type of reproduction is much more common, however, among the ectoparasites of plants such as aphids and scales (see Price 1980 for a discussion of parthenogenic parasites).

It is reasonable to ask how trees and cows differ as sexual substrates? Could the genetic scrambling of animal ectoparasites be an attempt to keep up with changes in host phenotype, a pace of change that is not matched in long-lived plants? This is not to say that plants do not respond to their parasites, but that animals defend themselves in ways that plants do not, such as by learning and employing a sophisticated immune system (see Smith 1983 for an example of plant response). It is well known that animals differ in susceptibility to infestation. For example, the body louse, *Pediculus humanus*, has been known to do well on one person, while refusing to feed on his brother (Riley and Johannsen 1938). The head louse, *Pediculus capitis*, while specific to humans, prefers women to men and European strains do not survive on blacks (citations in Marshall 1981). My impression is that the causes of such variances are not always well understood (e.g., Nelson et al. 1977). Certain individuals may carry compounds in their blood that are toxic to endosymbionts or, as in the case of the generally undrinkable blood of guinea pigs, have haemoglobins that crystalize and rupture the gut (see Krynski et al. 1952, Nelson et al. 1975); or perhaps they carry psychoactive compounds like a turn of the century French sailor whose blood caused body lice to fight each other with "apparently vicious intent" (Foot [1920] in Riley and Johannson [1938]; note that *Polybia* wasps will not sting a hand covered with underarm perspiration, suggesting "secondary chemicals" that protect humans against insects other than ectoparasites; see Young 1978). Some forms of defense are known to be acquired. A rise and then a fall in the number of lice, mites, and keds on an animal is a fairly common pattern (e.g., Nelson et al. 1977). For example, local vasoconstriction that leaves insects unable to feed is a major form of such an acquired resistance. This and other less understood reactions are apparently regulated by the immune system.

It is tempting to think that a louse never bites the same animal twice; that the defensive physiology of the host is sufficiently labile to force migration/sexual recombination or to select for genetic shuffling in the parasites that stay.

## THE EXTENDED PHENOTYPE

A third area of evolutionary thought with implications for medical entomology is the notion of the extended phenotype recently formalized by Richard Dawkins (1982). Its basic concept is that the expression of a genetic program commonly extends beyond the body walls, the traditional limits of gene activity. Few would argue that caddisfly cases and termite mounds have evolved through the differential reproduction of genes the constructions themselves do not contain, but these are only the most obvious extrusions of gene activity through an animals "skin". Dawkins (1982) has emphasized the possibility that animals have evolved means to physically or psychologically control each other and that nature may be a tangle of manipulative forces stretched among incompletely autonomous genomes. An outcome of extended phenotype thinking is heightened doubts about whose genes are controlling whose body in cases of parasitism. That is, do "symptoms" benefit the infector or the infected.<sup>4</sup>

Consider the dispersal of animal diseases. Only a few microbes seem to take a direct hand in their own contagion. For instance certain bacterial pathogens of arthropods luminesce and probably attract new victims or vectors to themselves (see Harvey 1952, also Sivinski 1981, 1982). But usually microbes would be best served by subverting their larger and more complex hosts into spreading them around (Holmes and Bethel 1972, Ewald 1980, Dawkins 1982).

Such manipulation does not have to entail prodigious intellectual or physical feats. One need only reflect on who benefits from sneezes associated with cold virus or the biting of rabid dogs.<sup>5</sup> An example closer to our theme is that of tse-tse flies, which when infected with *Trypanosoma brucei*, feed more often and more voraciously (Jenni et al. 1980). The trypanosomes are associated with mechanoreceptors in the labrum that function in a feedback loop to restrict probing. Probing is essential for transmission of the trypanosome. A "gene" that changes the site of infection in a vector thus can be better dispersed by undermining a fly's ability to determine how much biting is enough.

Does anything like this influence the movement of ectoparasites? The only case I know of is where a nematode that infects the flea *Spilopsyllus cuniculi*, apparently causing its victim to remain and mate on doe rabbits rather than moving onto their litters (Rothchild 1969). The purpose, if any, is obscure. But one can imagine obviously functional changes in the behavior of ectoparasitic vectors that might be worth searching for. As an example, it has been noted many times that some fleas and lice leave sick or disturbed hosts (see citations Marshall 1981). A pathogen that causes mild disease and could lower thresholds to cues ectoparasites use to monitor host health (e.g., body temperature), would be able to hijack a flea out of an environment eroded by antibodies. I know of no evidence for such hijacking, but it is worth noting that sucking lice that might be vectors sometimes appear to leave sick hosts more rapidly than certain biting lice that cannot be vectors (again see citations Marshall 1981). Be that as it may, as a general principle, it should be useful to keep in mind the options open to the protagonists in diseases.

## APPENDIX

<sup>1</sup>—While the major concern here is the sexual selection of parasite behavior, parasites themselves might provide opportunities for sexual selection to occur in their hosts. Hamilton and Zuk (1982) have argued that displays of male vigor and ability to grow and maintain extravaganzas of feathers or fur could be advertisements of resistance to parasites. Such a scheme is an improvement over traditional “good gene” models since coevolution of parasite and host might generate genetic variance that intersexual selection could not exhaust.

<sup>2</sup>—A related problem among the more vagile bloodsucking “micropredators” of veterinary importance is whether males should search for females on or near hosts. It seems curious for instance that one can be surrounded by large numbers of sanguinary female mosquitoes, but that no male mosquitoes are overhead taking advantage of the concentration. There are at least two determinants of male search strategy: 1) where are females most likely to be concentrated, i.e. encountered (see Sivinski and Stowe 1980), and 2) the value of females in the different locales they inhabit—in a monogamous species that normally mates upon emergence, subsequent concentrations on hosts are sexually useless to searching males. Parenthetically, where females mate more than once and the last ejaculate fertilizes most of the eggs, copulations just before oviposition are most valuable, and females aggregated around a host may not be attractive if the host is widely separated from oviposition sites (see Thornhill and Alcock 1983).

There are some data from the Diptera with which to test the later of these determinants; i.e., the principle of changing female value over space and time. Mosquitoes have distinct feeding and oviposition sites, and females generally copulate only once (Gillett 1972). Male mosquitoes would be predicted to concentrate their mating efforts at emergence sites, and as expected, males are only rarely found in the vicinity of hosts. However, I have found 13 species where males are located near hosts (the bizarre kleptoparasite of ants *Malaya leei*, Miyagi 1981; *Mansonina* sp., McIver et al. 1980; *Eretmapodites chrysogaster*, Gillett 1972; *Aedes aegypti*, Hartberg 1971; *A. albopictus*, Basio et al. 1976; *A. dominicii*, Bates 1949; *A. furcifer*, Jupp 1978; *A. pseudoscutellaris*, Horsfall 1955; *A. scutellaris*, Forbes and Horsfall 1946; *A. triseriatus*, Loor and DeFoliart 1970; *A. varipalpus*, Lee 1971; *A. vittatus*, Reeves 1951; *A. diantaeus*, Horsfall 1955). These exceptions are of interest because 11 out of the 12 haematophagous species develop in small containers, principally rot holes (compared to only 59% of 409 species of *Aedes* in Horsfall 1955). Such small, ephemeral, widely dispersed development sites may make it difficult for males to search for emerging mates. If so, they are “forced” to locate older females, ones less likely to be receptive, in the vicinity of hosts (note that several *Aedes* species are found both near animals and in the vicinity of their own emergence site, suggesting a dual sexual strategy).

A similar case occurs in horn fly, *Haematobia irritans*. Females mate once, both sexes are on cattle, and larvae develop in the ephemeral and dispersed medium of cattle dung (see Bruce 1964). In a close relative, the moose fly, *Lyperosiops alcis*, copulatory frequency is unknown but males are associated with hosts, and females have been found ovipositing on feces several inches up the rectum of freshly killed moose (Snow 1891).

A possibly contrary system to the proposal that males prefer to patrol emergence sites in female monogamous species and oviposition sites in polyandrous ones, is the multiple mating and male host occupancy of certain psychodids whose females feed on reptile blood (notably *Phlebotomus vexator*; see Chaniotis 1967). Larval substrates are undetermined but may consist of host feces. If so, the difficulty is mitigated since valuable last

matings before oviposition could be obtained by males stationed on the female. Males of ceratopogonid *Culicoides utahensis* wait in the ears of rabbits for feeding females (Downes 1969). Again, it is possible that larvae develop in the litter of the host's burrow. Likewise, in "bobos" (*Paraleucopis mexicana*) a chamaemyiid that laps fluids from the eyes of birds and reptiles, both sexes are found about hosts and larvae are thought to develop in the litter of birds' nests (Smith 1981).

Multiple inseminations and near-host male aggregations also occur in tse-tse (*Glossina* spp: Muscidae) (citations in Mulligan 1970, Tobe and Langley 1978). Peculiarities of tse-tse reproduction remove any difficulty. Unlike most Diptera, *Glossina* spp. are viviparous, so that zygote formation occurs long before deposition of offspring.

Male host occupancy occasionally occurs in other vertebrate-associated fly taxa. Lack of information on mating behavior and/or oviposition sites precludes analysis in these species: *Culicoides nebeculosus* (Ceratopogonidae) (Downes 1955); *C. variipennis* (Jones et al. 1977); *Lutzomyia vexatrix* (Psychodidae) (Chanotis 1967); *Tabanus auro-punctatus*, *Haemoptopota sewelli*, *H. pluvialis* (Tabanidae) (Bailey 1948); and *Wilhelmia equina* (Simuliidae) (Wenk and Schlorer 1963).

<sup>3</sup>The idea of lekking is particularly appealing when thinking about ectoparasites on large animals. Like lake-breeding mosquitoes or highly polyphagous tephritids, many ectoparasite populations look like they can be widely distributed over an extensive and fairly uniform "resource surface" (see Burk 1981 and Sullivan 1981 for discussions of the relationship between resource concentration and mating systems). An effect of uniformity can be unpredictability in locating sexual partners, and the result of this can be the evolution of true or nonresource-based leks where males aggregate and signal from an arena devoid of any special resources other than the males themselves (see Bradbury 1981 for recent consideration of lek evolution).

<sup>4</sup>As an illustration with some preliminary data, consider galls, "subcutaneous" parasites of plants. Galls are formed around a number of organisms including cynipid wasps and cecidomyid flies. One of their striking qualities is the breadth of their structural complexity and color. They range from green warts to objects that rival flowers. If color is treated as a symptom of infestation the extended phenotype question is: in whose interest, the plant or the insect, is the color produced?

To expand the metaphor of the flower, could these colors attract Hymenoptera, parasitic ones as opposed to pollinators? Up to 70% of galls are commonly parasitized (Russo 1979). Color and shape could be a flag that a plant raises over an infection to attract the macroscopic equivalent of an antibody. Gall formers of course would try to strike the colors down. Are some colors attractive to parasites? Yes. Catches of parasitoids are higher on gall-sized yellow balls (Tack-Traps® covered and hung in trees) than green or red ones (green 29 parasitoids, 9% of catch; red 21 parasites 7.6% of catch; yellow 67 parasites, 14.75% of catch; yellow > red, green  $p < 0.05$ ) (Sivinski, unpublished data).

Is yellow a common color on galls? Yes, of 525 oak-leaf galls, 20% are yellow or have yellowish tints at some point in their development. (This and following color data collected from the keys and descriptions of Felt 1918 and Russo 1979.)

Is there any reason to think that the presence of yellow is a signal? Perhaps. If we compare oak-root galls hidden underground to those visible on twigs and branches, a higher proportion of those that can be seen have the purported signal color (18% of 165 branch galls vs. 7% of 14 root galls).

Is color more common in situations where selection for parasite removal is strongest? Perhaps. Many gall-forming insects are weak fliers and poor dispersers, so perennial plants run the risk of reinfection by the offspring

of the previous seasons' parasites. Annuals however are less likely to survive their gall formers and in the absence of younger relatives to protect, should invest less in disinfecting. Yellow seems more common on perennial galls of compositoid plants (0 of 13 annuals and 12 of 107 perennials).

On the other hand, gall formers could benefit from gaudy houses. Many galls have defensive attributes such as spines or tannic acid levels of up to 65% that could be advertised by bright warning colors. It is interesting that galls formed by bacteria, fungi and mites, and presumably immune at least to parasitoids, are sometimes brightly colored.

Both or neither of these explanations may be correct, but they should illustrate the possibility that the appearance or behavior of an animal may not be the work of its own genes and that "symptoms" deserve being considered from both perspectives.

<sup>5</sup>The ability of a sick host to defend itself against vectors is considerably curtailed. Mosquitoes given a choice of feeding on a healthy or malarious mouse almost always suck from the infected animal (Day et al. 1983). It might be interesting to look for any differences in the ability of animals to discourage vermin when ill with diseases transmitted by and without vectors. Would the former be more listless, less able to brush away a fly?

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ENERGETICS: THE BEHAVIORAL AND ECOLOGICAL  
CONSEQUENCES OF BODY SIZE

BRIAN K. McNAB\*

## SYNOPSIS

The significance of body size for animal energetics is demonstrated by the seasonal behavior of the monarch butterfly and the fin whale. Both species in summer live in environments that are unacceptably harsh in winter; consequently, the butterfly and whale migrate in winter to hospitable environments at lower latitudes, which nevertheless are characterized by limited food supplies. As a result, both species in winter principally rely on stored lipids as their source of energy. The difference between the butterfly and whale in the time period over which starvation is tolerated can be accounted for by their differences in body mass and in their level of energy expenditure. The huge difference in body size between butterflies and whales does not necessarily mean that the solutions to environmentally imposed problems are different.

The one most important characteristic of animals is, above all, body size. It influences everything from the means of temperature regulation, type and amount of food consumed, and rate of locomotion to longevity, potential predators, and rate of reproduction. Size may be measured in many ways, including body length, wing spread, body volume, and body mass. Body mass is preferentially used as a measure of size in physiological studies because most functions depend on the amount of material reacting with the environment. For example, the rate of energy expenditure in animals normally is compared to their masses, and such a comparison has shown (Figure 1) that an individual's rate of metabolism (*i.e.*, the total rate) generally increases with body mass raised (approximately) to the 3/4 power (*i.e.*,  $m^{0.75}$ ). This pattern occurs both in ectotherms, *i.e.*, in animals that have body temperatures determined by ambient conditions, and in endotherms, animals that have temperatures that are determined mainly by high rates of chemical heat production (Hemmingsen 1960). It is somewhat disconcerting to note, however, that no adequate explanation for the  $m^{0.75}$  proportionality has ever been given.

At any particular body size, endotherms have rates of metabolism that are about 9 times those of ectotherms, assuming that endotherms have a body temperature of about 39°C and that ectotherms have a temperature of about 20°C, although endotherms can reduce energy expenditure somewhat by having an effective insulation. When body temperature in ectotherms is lower than 10°C, the metabolism-mass curve, although parallel to the endotherm and 20°C curves, is lower still (Figure 1): at 10°C rate of metabolism is only about 4% of that expected in endotherms. Another way of stating that total rates of metabolism are proportional to  $m^{0.75}$  is to note that mass-specific rates of metabolism are proportional to  $m^{-0.25}$ , which

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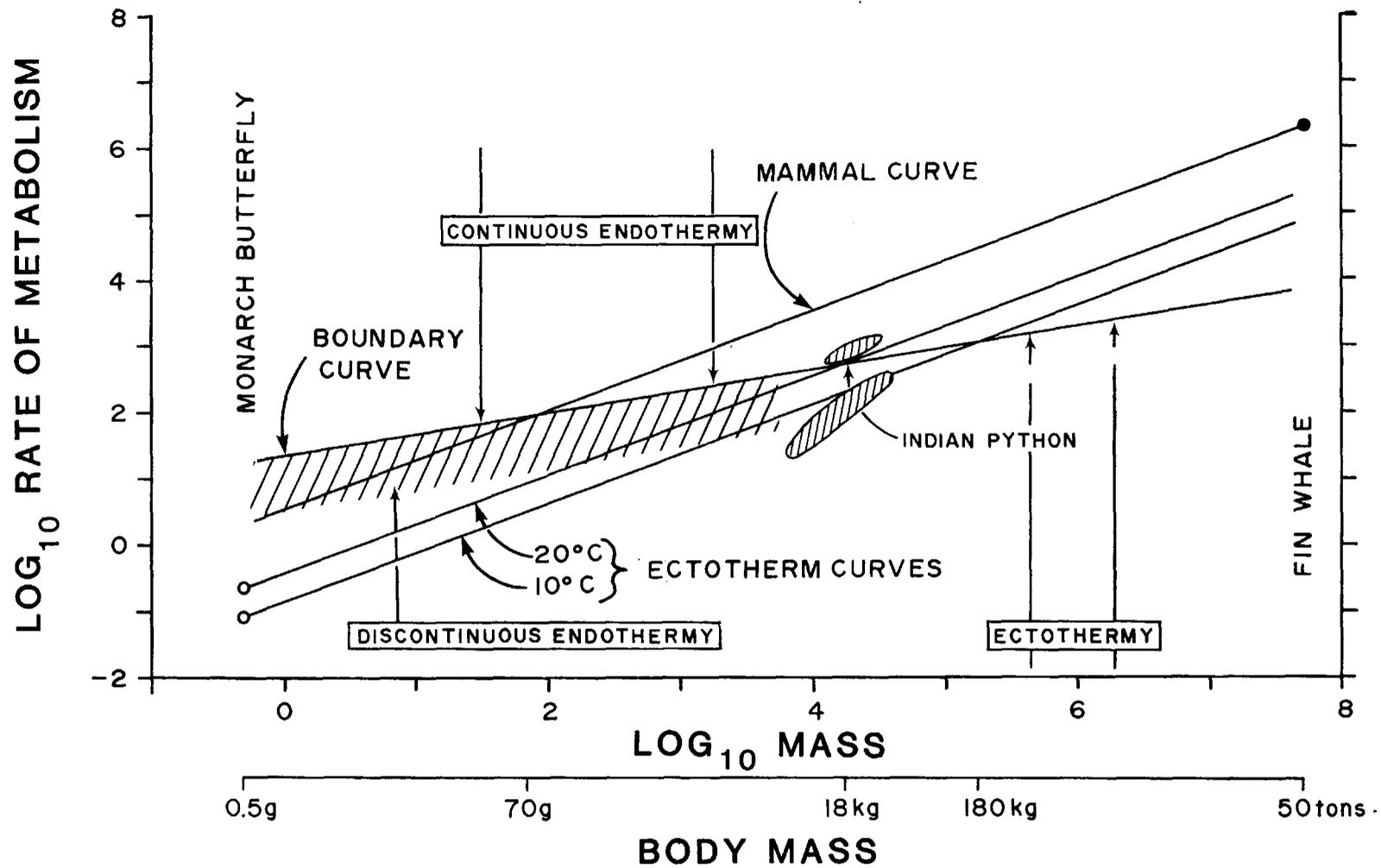


Fig 1. Logarithm of the standard rate of metabolism ( $\text{cm}^3\text{O}_2/\text{h}$ ) plotted as a function of the logarithm of body mass (g) for mammals (Kleiber 1932) and for ectotherms at 20 and 10°C (McNab 1983). The boundary curve was reported by McNab (1983). The shaded area below the boundary curve indicates endotherms that enter daily torpor. The data on Indian pythons were reported by Hutchison *et al.* (1966) and Van Mierop and Barnard (1978).

simply means that small animals have higher rates of metabolism per gram than large animals. As convenient as mass-specific units are, the ecologically relevant rates of energy expenditure are the total rates, because they describe the rate at which energy is used by an individual and the rate at which food must be harvested in the environment.

The only animals that had been considered to be endothermic, until recently, were birds and mammals. All animals other than these vertebrates were thought to be ectothermic. Within the last 20 years, however, many other animals have been shown to be endothermic to some degree. Among large vertebrates, some sharks and tunas are known to be endothermic (Barrett and Hester 1964, Carey and Teal 1969a,b), as are female pythons while incubating their eggs (Hutchison *et al.* 1966, Van Mierop and Barnard 1978); the leatherback turtle (*Dermochelys*) may also be endothermic (Frair *et al.* 1972). Among small animals, various insects, including some moths, hymenopterans, dragonflies, and beetles, are endothermic, at least during periods of activity (Heinrich 1974, May 1979). Periodic endothermy is of special interest because it is also found in mammals and birds that weigh less than 10 g, such as small mice and insectivorous bats, and all hummingbirds. In other words, the existence of continuous endothermy, itself, depends on body size.

At a small mass, animals, independent of taxonomy, can variously be continuously endothermic, discontinuously (periodically) endothermic, or completely ectothermic, depending on the level at which energy is expended (McNab 1983): rate of metabolism must be high to insure effective endothermy, ectothermy (as stated) is associated with low rates of metabolism, and discontinuous endothermy is characterized by intermediate rates (Figure 1). The transition between ectothermy, at one extreme, and continuous endothermy, at the other, also varies with body mass: compared to the standard mammalian relation, small animals must have high rates of metabolism to remain continuously endothermic, but animals weighing more than 70 g may have a low rate of metabolism without sacrificing continuous endothermy. These observations mean that another relationship between total rate of metabolism and body mass can be described, and it defines the boundary between continuous and periodic endothermy. This relationship, the so-called boundary curve for endothermy, is proportional to  $m^{0.33}$  (Figure 1); it is derived empirically from measurements on rate of metabolism in relation to body mass in those species of mammals, birds, fish, and snakes in which there is continuous endothermy.

At large masses, the resting rate of metabolism of an endotherm may be less than that of an ectotherm. For example, the mean boundary curve intersects the 20°C ectotherm curve at about 18 kg and the 10°C ectotherm curve at about 180 kg (Figure 1). These observations mean that the distinction between endothermy and ectothermy is not simply related to the level of energy expenditure. Unfortunately, there are few measurements of energetics in vertebrates at masses greater than a few kilograms, so the boundary between these states at large masses is unclear, and needs to be explored, especially in species with an intermediate form of thermal behavior. Nevertheless, the existence of the boundary curve at large masses is shown in the behavior of the Indian python (*Python molurus*): it raises its rate of metabolism sufficiently to exceed the boundary curve (Figure 1),

but it does not need "mammalian" rates of metabolism to assure effective endothermy (McNab 1983).

The impact of body mass on rate of energy expenditure can be shown by comparing the seasonal energetics of multicellular animals at the two ends of the size spectrum: a monarch butterfly (*Danaus plexippus*), which may weigh only 0.5 g, and a fin whale (*Balaenoptera physalus*), which may weigh up to 50,000,000 g. In spite of this great dissimilarity in mass, these species both migrate to wintering grounds on which they have a restricted food supply and intake. Monarchs winter in coastal California and in the highlands of central Mexico, while fin whales winter in tropical waters. There is evidence that neither the whale (Brodie 1975) nor the monarch (Chaplin and Wells 1982) feed much, or at all, on their wintering grounds. It is of interest here to compare the periods of time that these species live without eating, or at least with a highly restricted food intake, to see to what extent the observed periods can be quantitatively accounted for by comparing energy expenditures, as derived from the differences in their masses.

The amount of time that an animal can live without feeding is proportional to the ratio of the size of the energy store divided by the rate at which the store is consumed (Morrison 1960). If the size of the energy store is proportional to body mass, the time period for starvation would be proportional to  $m^{0.25}$  ( $= m^{1.00}/m^{0.75}$ ). For example, if two animals are compared, one the size of a monarch butterfly and the other the size of a fin whale, and if both have rates of metabolism that fall on the same metabolism-mass curve, then the ratio of time periods would be proportional to

$$\left(\frac{\text{whale mass}}{\text{monarch mass}}\right)^{0.25} = (10^8)^{0.25} = 100:1. \text{ Fin whales may not feed}$$

(much) for the half-year that they spend in tropical waters, which suggests that an animal the size of a monarch would be expected to tolerate starvation for about 1.8 ( $= 180/100$ ) days, but only if it conformed in rate of metabolism to the endotherm curve. If, however, a monarch were a continuous endotherm, it would have to follow the boundary curve for endothermy (see Figure 1), which at 0.5 g would raise the resting rate of metabolism by a factor of 8.4. That is, a continuous endotherm the size of a monarch could tolerate  $1.8/8.4 = 0.21$  days, or about 5 hours, by burning its fat stores. This graphically illustrates why animals the size of an insect cannot afford continuous endothermy. Actually, monarchs are not endothermic; their body temperature equals air temperature, as long as they are not exposed to the sun. In coastal California, monarchs face cool, cloudy weather in winter; mean body temperature is only about 10°C (Chaplin and Wells 1982). Measurements of oxygen consumption indicate that monarchs at 10°C have resting rates that are only about 3% of the value expected from the endotherm curve at 0.5 g. Consequently, the starvation time expected in monarchs is about  $1.8/0.03 = 60$  days. Chaplin and Wells estimate that monarchs in coastal California, given their fat stores, can tolerate starvation for about 60 days, a close agreement, seeing that here the estimate is derived from an extrapolation of the energetics of whales!

The difference in time period for starvation between monarch butterflies and fin whales, as absurd as this comparison might seem at first glance, can be accounted for by differences in body size, thermal behavior, and level of energy expenditure. In spite of all of these differences, both species

respond to the shortage of food and to seasonally harsh environments—such as cold temperatures in western North America (in the case of monarchs) and cold seas and winter storms (in the case of fin whales)—by the use of a similar response, namely, migration to benign environments, which nevertheless are characterized by a shortage of food and require the use of stored energy resources. Given their fixed energy reserves (dictated as they are by body size), these species reduce their rates of energy expenditure to extend the period over which starvation can be tolerated. In the endothermic fin whale, energy expenditure is reduced by living in warm water, that is, by retreating to the tropics. Time of starvation is extended to great lengths by a large body size, as is required to permit a polar-tropical migration on an annual cycle. Monarchs, being ectothermic, have to walk a thermal tightrope, because they have a reduced control over body temperature: they must avoid freezing temperatures, and must avoid warm temperatures that raise rate of metabolism, thereby reducing starvation time. It therefore is significant that wintering monarchs congregate in coastal California, where the environment in winter is cool and damp, and in the mountains of central Mexico, where monarchs cluster in forests at an elevation of 3100 m. Ambient temperatures encountered in Mexico generally fall between 3 and 12°C (L. Brower, personal communication), temperatures that are strikingly similar to those found in winter in coastal California.

This analysis suggests that many of the obvious differences between butterflies and whales are related to a striking difference in body mass, and when this difference is taken into consideration, a commonality is seen in their biology. Insects, by concentrating at the small end of the size spectrum, tend to be ectothermic, or if they are endothermic, are so only on a periodic basis. But as has been seen in the case of monarch butterflies, a small body size does not mean that the ecological problems faced, or even some of the solutions used, are necessarily different from those of large endotherms.

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## SCIENTIFIC METHODOLOGY IN ENTOMOLOGY

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## SYNOPSIS

Considerable research on insects is not directed by evolutionary theory. Fortunately, this is changing. The staggering diversity of insects will be rendered intelligible only by the explanatory and predictive power of the theory of evolution by natural selection. As an evolutionary understanding of insects increases, important clarifications and extensions of the basic theory probably will occur.

Entomologists that employ evolutionary theory should consider the basic nature of the hypothetico-deductive model of science and the four methods for applying it: lab experiments, field experiments, observational analysis and the comparative method. Here I outline the general model of science and the pros and cons of each of the four methods for applying it. I argue that the Popperian<sup>1</sup> view of science is useful because it causes scientists to consider predictions that may lead to elimination of hypotheses. An extreme interpretation of this approach, however, is inappropriate because it ignores the value of positive evidence for understanding nature. All four methods of applying the scientific model can lead to precise understanding of cause and effect in biology, especially when alternative hypotheses with mutually exclusive predictions are carefully considered. Lab and field experiments and observational analysis can provide answers to questions about the nature of selection presently acting on traits of organisms. But only the comparative method can yield answers to questions about evolved function (selective history) of traits.

There are evolutionists who argue that the comparative method is at best a method of obtaining correlative patterns that provide tentative hypotheses that must be subjected to experimental or observational tests in order to determine their value. But regardless of the method, the goal is to discover significant differences between sets of data that allow construction and refinement of correlations. I argue that scientific knowledge actually accumulates and science progresses toward understanding simply as a result of improving correlations between presumed cause and effect.

## INTRODUCTION

"For answering questions on function in biology, comparative evidence is more reliable than mathematical reasoning." (Williams 1975, p. 7)

"Only experiments can truly test theory." (Stearns 1976, p. 42)

"The only valid method by which the adaptive significance of a feature can be determined is by direct analysis which includes observing the animal in its natural environment and direct determination of the biological roles and selection forces." (Bock 1977, p. 79)

"There is no fundamental difference between the comparative method and the experimental method in biology." (Alexander 1978, p. 95)

". . . observation and comparison are methods in biological research that are fully as scientific and heuristic as the experiment." (Mayr 1982, p. 76)

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What is considered appropriate scientific methodology varies among areas of science, between disciplines of biology, and even among practitioners within a biological discipline. The above quotes by evolutionary biologists reveal that within this field of biology large differences in opinion exist about appropriate methodology. Some critics of the comparative method (e.g., Stearns 1976, Bock 1977, Reznick 1982) argue that experiments represent the only methodology that can yield an understanding of cause and effect. This view also is held by some biologists who are unfamiliar with evolution (e.g., many "laboratory" biologists) and by many physical scientists. On the other hand, some evolutionists state that the comparative and experimental methods are not fundamentally different in quality (e.g., Alexander 1978, 1979, Mayr, 1982) or imply this in their work (e.g., Darwin 1859, 1874, Williams 1975, Maynard Smith 1978, Alcock 1979, Clutton-Brock and Harvey 1979, Mayr 1982, 1983).

The view that the comparative method is inferior stems in large part from lack of recognition that each method has strengths and weaknesses and is consistent with criteria of the general model of science. I will argue in this paper that the comparative method is the only method we have for determination of the selection that has shaped characteristics of organisms (as opposed to the selection presently acting on traits) and it is as precise as any other method in science.

The study of the ultimate meaning of living things was brought into focus by Charles Darwin. Not only did he provide the general theory of life but he also gave us powerful methodology—comparative analysis—for examining and clarifying the theory. The profundity of Darwin's contributions was incompletely understood until recently. Hamilton's classic papers (1964 I and II) and Williams' book *Adaptation and Natural Selection: A Critique of Current Thinking in Evolution* (1966) had a revolutionary impact on biological investigation. They caused investigators in many biological disciplines to focus their thinking on reproductive competition between individuals and thus return to a Darwinian framework.

Like molecular biology (Lewin 1981) and certain other fields devoted to the study of life, entomology has generally lacked a strong evolutionary foundation. This is changing in molecular biology (e.g., Orgel and Crick 1980, Lewin 1981), and there is indication of such a shift within entomology as a result of efforts by several individuals, most notably Lloyd (see symposia volumes 1979-1982), but there is need for a stronger evolutionary basis in most insect studies. The lack of rigorous hypothesis testing in many areas of entomological research is a reflection of the absence of the powerful theoretical basis that evolution provides. Though I direct this paper primarily toward an entomological audience, the message I am trying to convey is general and applies to all areas of biology that do not presently rely on modern evolutionary analysis for research direction.

Undoubtedly, some of my entomological colleagues will reject my view of the current state of entomology. Such colleagues might point to some experimentally elegant piece of entomological research done in total absence of any understanding of evolution. However, the question is not how elegant research is in terms of control of confounding variables, or how clever the idea behind the work is, but, does the research yield a better general understanding of life? We see over and over again in the history of biology that specific results do not make any general sense until placed in the framework

of evolutionary theory (Dobzhansky 1973, Mayr 1982). An excellent example is the present attempt to couple molecular studies with evolutionary analysis (Lewin 1981). As Dobzhansky (1973) put it, "Nothing in biology makes sense except in the light of evolution."

#### CAUSATION AND THE GENERAL THEORY OF LIFE

The effects of interest to biologists are the traits or features of organisms. Biologists consider causation of any trait from two perspectives: proximate and evolutionary. Proximate explanations for the existence of biological traits deal with genetic, biochemical, physiological, developmental, social, or other immediate causes leading to the expression of the characteristics. Evolutionary explanations address causes that operated during evolutionary history to lead to present biological phenomena. The evolutionary approach focuses on the relationship between biological characteristics and the selective forces that produced them—that is, the contribution of traits to differential reproduction of individuals in the environments of evolutionary history.

Consider the warning coloration of the monarch butterfly. The colors of adults and juveniles are caused by genetic, biochemical, physiological, and developmental proximate factors. In terms of ultimate causation, the colors probably stem from a history of nonrandom differential reproduction of individuals in the context of avoiding visual predators. The two levels of explanation are complementary, but as discussed below, they are not alternatives.

It has been claimed by some that viewing traits in terms of evolutionary causation solely as the product of selection ignores the roles of agents other than selection in shaping them. For example, drift and mutation cause changes in gene frequencies from generation to generation (evolution). But, relative to selection, mutation and drift are impotent as evolutionary forces, because they act randomly with regard to fitness and thus are unlikely to bring about significant cumulative change (see Alexander 1979 for detailed discussion). Viewing features of life as shaped by selection provides the best general working hypothesis. Any other view is completely impervious to test, as critics of the selectionist approach admit (Lewontin 1978).

The selectionist approach is referred to as the ultimate approach because it is selection that accounts for the existence of proximate mechanisms. Thus, the two forms of causation are not alternatives in any sense. This means that there is really only one approach in biology and that it is the ultimate one. The theory of evolution by selection is not *a* theory of life, it is *the* theory of life. Charles Darwin did not invent the idea of selection; he discovered the process, as did Alfred R. Wallace independently at the same time. Selection has acted continuously on all living things throughout the history of life and continues to do so today. Thus selection is omnipotent. The features of life are what they are because of selection in the past, and thus all features of all living things are expected ultimately to promote reproduction or genetic propagation of individuals in evolutionarily relevant environments. This provides the foundation for scientific study of all life and tells the biologist how to proceed in order to gain further understanding of life through experiment, observation, and comparative analysis, regardless

of whether he is interested in molecules, behavior, physiology, morphology, proximate or evolutionary causation, or beetles or human beings.

This is not to say that study of proximate causation is unimportant. A complete understanding of any feature of life includes elucidation of both proximate and ultimate causation. I am saying that the theory of evolution by selection provides the best direction for investigating proximate causation. This approach has recently been used in the study of insect pheromones. Until recently, pheromone structure was approached only from a descriptive perspective, but now ideas are being developed regarding chemical composition of insect pheromones expected on the basis of sexual selection theory (Marshall 1982, Arnold and Houck 1982, Thornhill and Alcock 1983). Selection theory is being used successfully to predict the actual ingredients of insect pheromones (Marshall 1982, in preparation). In the sense I have outlined, the "evolutionary" in evolutionary biology is redundant. Biology is the scientific study of the evolution of life. No other definition of biology makes any sense.

#### THE GENERAL METHOD OF SCIENCE

Science is a very complicated endeavor, and definitions of science are probably as numerous as scientists. Although it is perhaps a waste of time to attempt a perfect definition of the enterprise, I like Peter Medawar's (1967) definition: the art of the soluble. Most scientists that I am acquainted with feel that things are ultimately knowable, and when we do not know, or only know incompletely, it is because we have not asked the right questions. The hypothetico-deductive method provides the way for scientists to ask questions and seek to answer them. The hypothetico-deductive model consists of the following stages: observation, hypothesis formation, identification of predictions, and testing predictions. The stages are interactive and all stages are creative. One can do science by generation and testing of hypotheses and/or by testing assumptions of hypotheses. These endeavors include locating errors in the observations, hypotheses, and tests of others, and for this reason science is often defined in terms of its repeatability and self-correcting nature (e.g., Simpson 1964).

An observation in the right hands leads to scientific inquiry. Hypotheses begin with speculation, a hunch about the cause of some effect of interest. Scientists should speculate. Without imaginative speculation there would be no hypotheses and thus no direction for seeking understanding (see Lloyd's discussion of speculation in this volume).

Gould (1978) and Lewontin (1978) have argued that evolutionary hypotheses are often ad-hoc (only specific to the trait in question and without sufficient generality to allow testing). They consider evolutionary hypothesizing the art of creating just-so stories the same way Rudyard Kipling did in explaining the leopard's spots, the camel's hump, etc. Ad-hoc arguments do not represent valid speculation. The initial speculations of the working biologist are post-hoc, not ad-hoc, and there is nothing wrong with using post-hoc leads for generating true hypotheses that are general enough for testing. As Clutton-Brock and Harvey (1979) have pointed out, post-hoc explanations represent an inevitable first step in any observational science. The suggestion that monarch butterfly coloration is an anti-predator trait can be used to generate a real hypothesis, which is testable by observational

analysis or experiments dealing with effects of the colors on predator preferences, or by comparative analysis across species of animals with and without warning colors.

For a hypothesis (or theory) to be scientific it must be testable. This means it must be *both* predictive and empirically falsifiable. The requirements for predictions are that they be logically derived from the hypothesis and be statements about the unknown. It has been argued that evolutionary theory is not truly predictive because it focuses on historical causes and not future events (Peters 1976). But, as numerous people have pointed out, prediction of future events is not a requirement of a scientific theory. Prediction of the unknown, whether past, present, or future, is the important issue.

A hypothesis that predicts everything imaginable is not within the realm of science because it cannot be falsified. That is, a hypothesis that explains everything explains nothing. The theory of evolution by selection erroneously has been called a nonfalsifiable theory because of this (Popper 1934). It is puzzling how Popper and others could read Darwin's work and conclude that the theory of evolution is nonfalsifiable. Darwin's writing reveals his care in identifying observations that would falsify his theory (for discussion see Ghiselin 1969, Alexander 1977). Popper (1934) is usually given credit for recognizing that in order for an idea to be considered scientific it must be falsifiable in principle (the criterion of demarcation), but this procedure is apparent throughout Darwin's work and in the research of other early scientists using hypothetico-deductive analysis (e.g., Mendel, Newton, Pascal, Pasteur).

One way to look at the value of the criterion of demarcation is in terms of what logicians call the fallacy of affirming the consequent. Consider a hypothesis and its derived predictions. Assume that the predictions are found to be true. Now consider the following argument: if the hypothesis is true, then the predictions must also be true; the predictions are true, therefore, the hypothesis is true. According to logicians the conclusion is not valid even if the hypothesis is correct. If the predictions of a hypothesis are confirmed, it is logically invalid to conclude that the hypothesis is correct, because some other hypothesis(es) might yield the same predictions. Thus, logicians argue that attempts to falsify hypotheses avoid this fallacy. It is logical to conclude that a hypothesis is false when its predictions are false.

But the major value of the criterion of demarcation is simply that it causes scientists to look for predictions that potentially can eliminate a given hypothesis rather than only evaluating predictions that, regardless of whether they are true or false, will support the hypothesis or multiple hypotheses. The importance of falsification of hypotheses to the advance of a science was eloquently stated by Darwin: ". . . false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness; and when this is done, one path towards error is closed and the road to truth is often at the same time opened" (C. Darwin 1874, p. 606). Envisioning empirical observations that would disprove hypotheses is vital for scientific advance. However, extreme applications of Popperian philosophy and the fallacy of affirming the consequent in scientific endeavors are inappropriate because they deny the significance

of positive evidence in the achievement of true understanding and promote the erroneous view that knowledge is an illusion (see below).

The strongest test of any hypothesis involves identification of competing hypotheses that predict mutually exclusive, empirically falsifiable outcomes. Such a test in its strongest form supports one hypothesis and falsifies the alternative hypotheses (see Platt 1964). Another aspect of strong scientific testing is that predictions be precise, which increases the likelihood of falsifying the hypothesis generating the predictions. A hypothesis that has passed many crucial tests involving precise mutually exclusive predictions from alternative hypotheses can be said to be corroborated (Popper 1934). The number of tests is not the important factor for evaluating the reliability of a hypothesis. Instead, it is the number of severe or crucial tests that determines our confidence in a hypothesis. The degree to which hypotheses are corroborated varies, and science can lead to a degree of corroboration appropriately labelled certainty.

The use of alternative causal hypotheses also avoids the natural tendency of investigators to become attached to a pet hypothesis. Of course, one can favor a pet hypothesis by setting up weak alternatives that have no chance of matching observation. But this will fail ultimately given the self-correcting nature of science.

By alternative hypotheses I mean alternative routes of causation, and not simply a test of a null hypothesis and its alternative, because only one causal hypothesis is identified in such a test.

Before outlining an example of the use of alternative hypotheses, I will address the view that knowledge is an illusion. That is, the notion that, given the necessity of employing the criterion of demarcation, we can never know anything with certainty (e.g., Harris 1982), which stems from extreme interpretations of the Popperian philosophy of science. An extreme Popperian accepts only negative results. With this view only falsified hypotheses are valuable; positive results do not count and certainly do not imply understanding, because to accept positive evidence commits the fallacy of affirming the consequent. This is where the actual practice of good scientists deviates from a Popperian perspective. Although one cannot actually prove a hypothesis to be true in the sense of *logical proof*, science can lead to proof of a hypothesis in the sense of meaningful understanding of natural phenomena. For example, the planets actually orbit the sun and not the earth, and the earth is roughly spherical and not flat. The hypotheses that the earth is the center of the universe and that the earth is flat turned out to be totally wrong. The notion of pangenetic inheritance is completely wrong. We now know that, barring cultural inheritance, genes (in interaction with environment) are responsible for parent-offspring correlations in similarity. The list of what we know for sure is long and growing. Any view of science that pretends we don't know for sure that insulin is produced in the isles of Langerhans, that bacteria and viruses can cause disease, that cells are the building blocks of higher organisms, that natural selection acts incessantly, that chromosomes house genes, etc. is nonsense.

#### TESTING ALTERNATIVE HYPOTHESES

In this section I provide an example from my own research of how useful alternative causal hypotheses with mutually exclusive predictions can

be. I use my own work because of my intimate familiarity with it. It deals with the nature of selection currently acting on a morphological feature of scorpionflies rather than the selection that has produced the structure; only the latter selection directly addresses the evolved function of a character. Later I discuss the distinction between selective maintainance and selective history and the methodologies for studying each of these categories of selection.

#### DORSAL CLAMP OF *Panorpa*: SPERM COMPETITION OR FORCED COPULATION

Sperm competition is competition between ejaculates of two or more males for the fertilization of eggs of a single female. That sperm competition can be a potent selective force leading to male morphologies and behavior was first discussed by Parker (1970). This now classic paper has led to many studies of sperm competition as the selective force that has molded male reproductive characteristics. However, sperm competition is the only context considered when many investigators study insect characteristics such as copulation duration, copulatory frequencies, interactions of males and females during copulation, and post and precopulatory interactions of females and males. There are alternative hypotheses to explain these characteristics, and they require examination.

I began work on scorpionflies (Mecoptera) in 1971, the year following the publication of Parker's seminal paper. The males have behavioral and morphological features that I initially interpreted as evolved in the context of reducing sperm competition. As my studies developed it became more and more difficult to accept this interpretation in all cases. This led to experiments beginning in 1977 designed to analyze alternative explanations of the traits.

There is a clamp-like structure on the dorsum of the male's abdomen in scorpionflies of the genus *Panorpa*. The dorsal clamp is formed from parts of the dorsum of the male's third and fourth abdominal segments. The clamp holds the female's wings during mating. Solitary males often attempt to disrupt copulating pairs and such males are occasionally successful. This led me initially to the interpretation that the clamp is important in preventing the female from being usurped and inseminated by an intruder, reducing the probability of the ejaculate of the usurped male being the fertilizing ejaculate. This interpretation was in keeping with Parker's (1970) view of male-grasping morphologies—he saw them as evolved to prevent "take-overs". (As it turns out, the dorsal clamp appears to be used for forced copulation; see below).

Male *Panorpa* exhibit three alternative forms of mating behavior that are present within the behavioral repertoire of each individual. Two alternatives employed by males to obtain copulations involve nuptial feeding—the male presents a food item to the female during courtship and the female feeds on it throughout copulation. (1) A male may secrete a salivary mass. After saliva secretion, males stand near their salivary mass and disperse distance sex pheromone. A female attracted by the pheromone feeds on the saliva. (2) A male may feed a female a dead arthropod. In this case a male locates a dead arthropod, feeds on it briefly, and then disperses sex attractant while standing next to it. (3) A male may employ forced copulation in which a male without a nuptial offering (dead insect or salivary mass) rushes toward a passing female and lashes out his mobile

abdomen at her. (Males engaging in forced copulation do not release pheromone.) If such a male successfully grasps a leg or wing of the female with his genital claspers, he then attempts to position her to secure the anterior edge of her right forewing in his dorsal clamp. Then the male attempts to grasp her genitalia with his genital claspers. The male retains hold of the female's wing with the dorsal clamp throughout copulation. Forced copulation in *Panorpa* is not an abnormal or "aberrant" behavior, but an aspect of the evolved behavioral repertoire of individual males that is widespread among species of the genus *Panorpa* (Thornhill 1980a, 1981, 1984a).

The behavior of females toward males with and without a nuptial offering is distinctly different. Females flee from males that approach without a nuptial offering but approach males that have nuptial offerings and behave "coily" toward them. Females struggle to escape from the grasp of forceful males, but do not resist copulation with resource-providing males.

I have shown in laboratory and field experiments and observations involving several species of *Panorpa*, that the extent of use of each of the three behavioral alternatives by males is related to the availability of dead arthropods, which is determined by absolute abundance of arthropods and by male-male competition for the arthropods. Individual males prefer to adopt the three alternatives in the following sequence: dead arthropod > salivary mass > forced copulation. That is, when males are excluded from dead arthropods via male-male competition, they secrete saliva if they can (a male's ability to secrete saliva is determined by his recent history of obtaining food), and males only adopt forced copulation when the other two alternatives cannot be adopted. A male's body size influences his ability in male-male competition, and large males tend to adopt the use of dead arthropods as nuptial gifts, medium-sized males most frequently use saliva, and forced copulation is adopted most frequently by small males.

The behavioral alternatives contribute differently to male fitness. The preference of alternatives employed by males is consistent with female choice, and thus with male mating success. Females prefer males with arthropods over males with salivary secretions and actively attempt to avoid force copulating males. Also, the alternatives appear to be associated with different male mortality probabilities. Relative to large and medium-sized males, small males tend to lose in the competition for food, and thus are forced to feed on dead arthropods in the webs of spiders, which results in high mortality. Finally, force copulators have relatively low reproductive success compared to resource-providing males because females lay few eggs following forced copulation (Thornhill 1980a, 1981, 1984a).

Lab experiments have revealed that the dorsal clamp is essential for forced but not unforced copulation (Thornhill 1980a, 1984a). In one experiment beeswax was used to cover the dorsal clamps of males that had been starved, which prevents them from secreting saliva. The dorsal clamp of starved control males was left functional. Treated and control males attempted copulation with equal frequency, but only control males succeeded. Treated males tried to reposition females so as to secure their forewing in the clamp, but the females escaped by struggling. In other experiments males with saliva or dead crickets were treated with beeswax. In these tests treated males readily copulated with females. Furthermore, insemination rates for treated males in unforced copulations was 100%.

The experimental results confirm predictions of the hypothesis that the dorsal clamp is important in the context of increasing the success of forced copulation attempts when sexual competition forces individuals into this alternative behavior. Yet, despite the apparent uselessness of the clamp in unforced copulation, the female's wing is placed in the clamp during both forced and unforced copulation. Could the dorsal clamp be important solely or in part in some other context? The experiments only superficially address this question. They were designed to test predictions of a forced copulation hypothesis. The predictions that were tested could be consistent with those stemming from an alternative hypothesis(es) for the role of the dorsal clamp.

A reasonable alternative was identified earlier. It views the dorsal clamp as important in the context of sperm competition—as a structure that prevents disruption of copulating pairs and the insemination of the female by an intruding male. Aspects of the reproductive behavior of male *Panorpa* are consistent with this hypothesis—pair disruptions by intruding males are not infrequent, disruptions sometimes result in the intruder copulating with the female, and the clamp is used in both forced and unforced copulations. Mutually exclusive predictions from the two alternative hypotheses are easily identified. If the clamp serves a male's reproduction by reducing the probability of the takeover of a copulating male's mate, one would expect treated males (dorsal clamp occluded with beeswax) to experience higher takeover rates than untreated males. But if the clamp is used solely for something else (i.e. is important in the context of forced copulation, or some other context consistent with the predictions examined earlier from the forced copulation hypothesis), one would expect the treated and untreated males to experience similar rates of takeover. If the former prediction (takeover highest when clamp functionless) is supported, the forced copulation hypothesis would be eliminated as the sole explanation of the selection presently acting on the dorsal clamp. If the latter prediction (takeover rate not influenced by clamp) is supported, the takeover hypothesis would be falsified. The predictions are strong in the sense that they offer potential for falsification.

The predictions from the two hypotheses were tested with a lab experiment. The results reveal that copulating males whose clamps were covered with beeswax had the same takeover rate as untreated copulating males (Thornhill 1984a). Thus, the clamp apparently does not presently aid a male's reproduction in the context of take-over attempts—i.e. there is no selection on the clamp in the context of take-over. If the experiment had shown that treated males experienced significantly higher take-over rates, the forced copulation hypothesis would remain potentially very important because of the findings from experiments described earlier.

#### DORSAL CLAMP OF *Panorpa*: OTHER HYPOTHESES

There are other alternative hypotheses that can be considered in an attempt to understand the selective maintenance of the dorsal clamp. Felt (1895) observed female *Panorpa debilis* palpating the dorsal clamp of males during courtship. I have observed palpation of the dorsal clamp during courtship by females of several *Panorpa* species. Felt concluded that the structure probably secretes a volatile oil that attracts the female to the male and primes her for mating. Felt's hypothesis is incorrect. I have

examined the histology of the dorsal clamp of several species of *Panorpa*, including *debilis*, and found no associated glandular tissue. The hypothesis is also inconsistent with experimental results. When the dorsal clamp of resource-providing males is covered with beeswax, presumably preventing any odors from being released, females mate readily with the males.

The dorsal clamp could be of value to males in species recognition. The dorsal clamp varies in morphology across *Panorpa* species. The examination (olfactory and apparently visual) by the female prior to copulation could reduce the probability of an interspecific mating error. This hypothesis must be examined because it has been, and still is, a widely used evolutionary explanation for species differences in courtship and mating behavior and associated morphological features. Darwin argued that sexual selection was the most important context for the evolution of sexual differences in sexual behavior and morphology, but Wallace identified species and sex recognition as the more likely contexts (see Thornhill 1980b). After Darwin and until recently, premating and mating behavior and associated morphological features have been generally viewed as functioning as reproductive isolating mechanisms—that is, as adaptations that prevent wasted reproductive effort by individuals in heterospecific interactions (Thornhill and Alcock 1983, West-Eberhard 1983). The theory of sexual selection appears to have far greater predictive power for understanding the diversity of these traits (Thornhill and Alcock 1983, West-Eberhard 1983). But the species' and sex identification hypotheses can serve as alternative hypotheses in studies of traits presumed to be important in the context of sexual selection or reproductive competition in general.

Although interspecific mating errors could potentially occur because of the co-occurrence of sexually active adults of several species of *Panorpa* in time, evidence indicates that females do not depend on cues from the dorsal clamp for species (or sex) discrimination. Male *Panorpa* produce species-specific sex pheromones that attract females from a distance and may also serve in close-range interaction (Thornhill 1979). Males exhibit species-specific courtship actions (wing and body movements). Also, when females approach a heterospecific male they do so to obtain a meal—i.e., they attempt to feed on the nuptial offering. Females never behave coyly toward heterospecific males as they always do toward conspecifics. Females of large species attempt to usurp, via aggression, the nuptial offerings of males of small species, and are sometimes successful. Resource-holding males behave aggressively toward heterospecific females that approach them. These considerations indicate that species and sex identity are discerned prior to close-range courtship by both sexes. Finally, the experiments discussed above are strongly inconsistent with the sex—and species—discrimination hypotheses. In these experiments the dorsal clamp was covered with opaque beeswax and thus it would not apparently emit normal visual (or olfactory) cues. Yet, females readily mated with treated males who offered nuptial gifts.

At this point in my research on the dorsal clamp of *Panorpa*, results suggest that this structure is maintained solely by selection in the context of forced copulation. The alternative hypotheses I have considered were either falsified (the sperm competition hypothesis and the pheromone-emission hypothesis) or inconsistent with existing evidence (the sex and species identification hypotheses). Only further tests would falsify the sex

and species identification hypotheses. The general point I want to emphasize is that alternative hypotheses should be impartially examined in relation to all available evidence. In a subsequent section I further consider the dorsal clamp in relation to comparative evidence that could provide the best understanding of its evolved function (as opposed to its selective maintenance).

#### METHODS OF APPLYING THE HYPOTHETICO-DEDUCTIVE MODEL

The hypothetico-deductive system for ascertaining cause and effect can be applied in four ways: lab experiments, field experiments, observational analysis, and comparative analysis. All four methods are equally valid scientific procedures: all four have strengths and weaknesses and they are based on different premises. The first three methods primarily yield information about present selection maintaining a trait of interest (i.e. about a trait's present contribution to reproduction), but only the comparative method can provide information about the selective history or evolved function of a trait.

#### EXPERIMENTATION

The essence of experimentation is manipulation. The experimental method involves some systematic variation of a variable of interest. But lab and field experiments represent very different scientific procedures. Lab experiments typically take the form of attempts to control all variables but one. Field experiments often do not involve control of variables that may confuse results; instead, all parameters except the manipulated one are allowed to vary naturally. Randomization of treatments in field experiments can produce limited control of confounding variables (e.g., site effects) but always many variables remain uncontrolled. Typically, one is less certain about the influence of other variables on the result with field experiments compared to lab experiments. Even with lab experiments, however, all potentially confusing variables cannot always be controlled. The number of confounding variables that could cause a given result is potentially infinite. Also, lab and field experiments are very different in that the lab is at best seminatural, and thus one can never be sure that lab results address nature.

A major problem with the experimental method is that manipulation effects often confuse results. It is always difficult to determine if one's result is due to the presumed cause, the manipulated variable, or is an experimental artifact unrelated to presumed causation. For example, it would seem from many lab and field experiments that nitrogen content of soil is a cause of plant growth and health (the effect). However, the correlation between nitrogen content and plant growth may be spurious (Grover 1982), because when nitrogen is added other changes occur (e.g., redox potential). These changes may be the actual cause of improved plant growth (effect). Other experiments will be necessary to control parameters that confuse the result.

Another problem with experimentation is the difficulty of determining the appropriate parameters to manipulate in order to yield biologically relevant information. It may take years of natural history observation on a biological system before an appropriate experimental procedure can be identified. For example, the availability of the limited resource (dead

arthropods) is a major determinant of the behavioral variation among male *Panorpa* (see above). Which alternative behavior is adopted by a male depends on his ability to obtain resources. Resource abundance for a male is a function of absolute abundance of dead arthropods in the habitat, sex ratio (number of competing males), and size of conspecific and hetero-specific male competitors (Thornhill 1981). It took several field seasons to obtain sufficient natural history information to identify the field and lab experiments that would provide results relevant to understanding *Panorpa* in nature, and it is my experience that biologists are often willing to initiate experimental work without a proper understanding of the natural history of the system they are interested in. Until recently experimental psychology was the epitome of such an approach. Elegant, elaborately controlled lab experiments were conducted with only repeatability in mind and without concern for the biological meaning of the results.

#### OBSERVATIONAL ANALYSIS

By observational analysis I mean the testing of predictions with observational data in the absence of manipulation or comparative analysis. The absence of manipulation is one of its strengths, but its weakness is a lack of rigorous controls. Confounding variables plague observational work. Some can be eliminated by refining observations via further observational analysis pertaining to some question about a trait (e.g., see Clutton-Brock and Harvey 1979 and Skinner and Charnov in this symposium volume for examples), but many problem variables will remain. Despite this problem, crucial tests can be conducted via observational analysis (i.e., tests involving mutually exclusive quantitative predictions from alternative hypotheses).

Parker's (1978) work on the dung fly *Scatophaga stercoraria* provides an example of observational analysis. Initial experimental research on sperm competition revealed that the longer a male mates the more eggs of his mate he fertilizes, up to 100 minutes of mating which results in all eggs fertilized. But the egg gain for the copulating male rapidly diminishes at about 40 minutes, a duration which yields 80% fertilization. With this information and an understanding of the average time necessary for a male to guard his mate from rivals until she lays her eggs, and then begin searching for another mate, Parker predicted that the optimal copulation time should be 41 minutes. This prediction is precise and thus easily disproved, and is logically derived from the hypothesis that males behave so as to maximize the number of eggs fertilized per minute. The actual average time in the field turned out to be 36 minutes. The prediction about copulation duration might be improved by considering the cost of extended copulation in relation to male size, rather than as an average for all males, because small vs. large male dung flies have different opportunities for access to multiple mates (see Borgia 1980).

Although explicit alternative hypotheses were not considered in the dung fly work they could be in future studies. It is not correct to argue that the use of alternatives is unnecessary because the prediction is precise enough to exclude a great many alternative hypotheses. Both the Bohr theory of the atom and the Schrödinger theory predict *exactly* the same Rydberg constant!

Observational analysis can be conducted in the same fashion as evolution-

ary comparative analysis (below). By using observational comparisons which by their nature and number randomize and thus control confounding variables, one can arrive at robust conclusions. A good example from everyday life is the work on the role of seat belts in preventing injury during automobile accidents (see Alexander 1979, p. 12). Another example is the research on the role of genetically inherited tendencies in criminal activity. With regard to the latter, sociologists have realized that with appropriate comparisons the quality of the result obtained is as good as in a rigorously controlled lab experiment (see Ellis 1982).

#### COMPARATIVE ANALYSIS

The comparative method involves species or population comparisons conducted so as to randomize the influence of confusing variables on the effect of interest (Alexander 1978, 1979). This method is based on convergent and divergent evolution. The former involves distantly related forms converging on an adaptation because of similar selection pressures. The latter pertains to closely related forms diverging in adaptation to some condition because of different selection pressures.

One real challenge in biology is understanding events of the distant past without which our understanding of evolutionary history would remain incomplete. The comparative method is analogous to a time machine, and with it we can ask what selective force operated to lead to the present expression of a characteristic of interest?

The comparative method randomizes the influence of confounding variables on a result in such a way that single presumed causal forces can be examined, though complete randomization is difficult, perhaps impossible. The difference between the comparative and experimental methods is not in controls, both methods include controls, but in the presence or absence of manipulation. Because manipulation effects can confuse results, the absence of manipulation in comparative analysis is one of its strengths.

With the appropriate comparisons, the comparative method can lead to results as precise as those obtained through other methods. Because life is incredibly diverse it provides vast numbers of appropriate comparisons for almost any question about the selective history of any biological characteristic. The ingenuity in use of the comparative method involves recognition of appropriate comparisons, i.e., those comparisons that because of their number and diversity are likely to randomize and thus control the influence of other variables on the result.

None of the methods I've discussed is perfect; all have inherent problems. Experiments designed to ascertain cause and effect are improved through time by investigators interested in a given cause-effect relationship. Experimenters strive for refinement; better controls and manipulations are created. Likewise, investigators using comparative analysis to elucidate a given cause-effect relationship make new and better comparisons. It is incorrect to suggest that a finding derived from the comparative method is less accurate than a finding derived from the experimental method. One's confidence in a given finding obtained by either method should depend only on the quality of controls employed.

The erroneous opinion that only experiment provides reliable results has led to inappropriate conclusions and research directions in biology. After

discussion of a few well documented cases of this in the history of biology, Mayr (1982, p. 856) said, "It would be interesting to go through the history of science and see how often a misplaced insistence on experiment has caused research to move into unsuitable directions."

It has been said that the comparative method can provide insights about general patterns in nature but cannot elucidate cause and effect (see Reznick 1982). That is, the comparative method can generate correlations but is not a method for examining causation; its results must be tested by other methods. This view is puzzling. All scientific findings are correlations. I don't mean that all scientific findings are represented by Spearman's or Pearson's correlation coefficients. I mean that all scientific knowledge is based on relationships between variables—presumed cause and effect relationships between variables. Regardless of whether we use experiments, observational analysis, or the comparative method to determine significance between sets of observations, and whether we use regression, t-test, etc., we are examining and attempting to construct and refine correlations.

#### *Examples of Comparative Method*

Two studies that should drive home the essence of comparative work are one dealing with the function of sexual reproduction and another with sexual dimorphism in vertebrates. Williams' (1975) analysis of the selective background of sexual reproduction is classic in this regard. Williams hypothesized that sex is a parental adaptation to the likelihood that offspring will face changed or unpredictable conditions. He made several predictions from this hypothesis about the occurrence and nature of sexual and asexual reproduction in organisms and tested these via the comparative method. One of the most important predictions he made was: in organisms that employ both sexual and asexual reproduction, sex should occur in the life cycle prior to changed or unpredictable conditions. This prediction was met. In effect he was attempting to randomize the influence of confounding variables on the timing of sex in life cycles of organisms with both modes of reproduction. In this analysis he examined the evolved function or selective history of sex. His analysis allows us to go back in time and begin to understand factors influencing differential reproduction of individuals as a result of variations in sexuality. His analysis is not the final answer, but it provides a beginning answer to an important question. Present attempts to elucidate the function of sex appropriately focus on tests of alternative hypotheses via comparative analysis (Bell 1982).

It has been assumed since Darwin that a positive relationship exists between adult sexual size dimorphism (with males larger than females) and degree of polygyny in vertebrate mating systems. Darwin reasoned that as the degree of polygyny increased, more and more males would be excluded from reproduction, which in turn would cause selection for male combative traits, including large body size. Comparative evidence suggested that the predicted relationship holds for birds and mammals, but no rigorous comparative analysis had been conducted until recently. The most rigorous tests have been done by Alexander and colleagues (1979), Clutton-Brock and Harvey (1977, 1979), and Payne (1983).

The approach is to make comparisons of vertebrates that differ in sexual dimorphism and breeding systems. If appropriate comparisons can be made the influence of confounding variables on the result can be controlled.

Alexander and colleagues found significant positive relationships between degree of sexual size dimorphism and degree to which breeding systems deviate from monogamy toward extreme polygyny in ungulates, primates, and pinnipeds. Closely related species diverged, and distantly related species, even across orders, converged in sexual dimorphism in relation to the extent of sexual competition in evolutionary history.

Clutton-Brock and Harvey analyzed 42 species of primates and found the same relationship that Alexander and colleagues found for this taxon. Clutton-Brock and Harvey's work is stronger in the sense that they used more species, carefully considered which taxonomic level should be used for analysis (e.g., species, genus, or family), paid careful attention to alternative hypotheses, and attempted to eliminate allometric effects, but their analysis is weaker because it did not cut across distantly related taxa, as did the analysis of Alexander and his coworkers. Payne's work on a diversity of bird taxa provides a comparative test of alternative hypotheses for the relationship between mating systems and sexual dimorphism; his results also support Darwin's hypothesis for sexual dimorphism.

The comparative method has made some sense out of seemingly chaotic natural variation but there is still unexplained variance in the correlations that have been discovered. The presence of unexplained variance in a significant relationship between two variables does not in itself mean that the relationship or the prediction behind the relationship are questionable. I know of no presumed cause and effect relationship in any area of science in which all the variance is understood. This is why statistical analysis is used to detect significant differences in results. Regardless of one's procedure—experimental, observational, or comparative—there are always exceptions to expected patterns.

#### *Other Applications of the Comparative Method*

I have focused my discussion of the comparative method on its value in studies of evolved function. This is where this method has been most successful. But Darwin, the inventor of the comparative method, used it to examine phylogeny, speciation, biogeography, soil formation by earthworms, and coral reef formation. Darwin even took a stab at community structure using the comparative method. Ghiselin (1969) and Gould (1982) address in detail the advances in the scientific study of historical phenomena that Darwin provided us with. The comparative method should be equally potent for studying all long-term events.

All methods need constant refinement, and it is likely that some considerations useful in analyzing evolved function will not work for biogeography or community structure and vice versa. Some of the problems that ecologists have encountered recently in attempts to apply the comparative method to community structure (Case and Sidell 1983 and references therein) may stem from not separating community organization into evolutionary and ecological components. The latter may change rapidly and lead to lack of fit between comparative predictions and pattern. The evolutionary component of community organization, perhaps synonymous with biogeography, is historical and thus subject only to comparative analysis. Clutton-Brock and Harvey (1977, 1979), Clutton-Brock (1982), Harvey and Mace (1982), and Jarman (1982) have provided some refine-

ments for use of the comparative method in study of evolved function which may be of value in analysis of other historical problems.

#### SELECTIVE HISTORY VS. SELECTIVE MAINTENANCE

Perhaps the most rigorous approach for examining a hypothesis is the use of critical tests involving all methods, because each method is based on different assumptions. When results from all methods point to the same conclusion, one usually achieves considerable confidence about cause and effect. But the combination of methods to examine a question must be done in a fashion that considers the relative potency of methods for ascertaining information about the role of selection in the history vs. the current maintenance of a trait.

Both experimental and observational analysis may cause one to reject a correct hypothesis about evolved function when predictions are not met because the tests are done in an evolutionarily novel environment. One may show via experiment or observation that a prediction from a hypothesis about the evolutionary history of some presumed adaptation is not correct, but one does not know if the validity of the hypothesis has really been examined.

Suppose a hypothesis predicts that the reproductive success of males of a species should be positively correlated with body size (e.g., the sexual dimorphism hypothesis discussed earlier). When one tests this prediction, no correlation is found. Thus, it seems that the hypothesis has been falsified. But is the hypothesis wrong or is the species living in an evolutionarily novel environment in which body size is not related to sexual access, despite the correlation between fitness and male size in the evolutionary history of the species. The novel environment might involve artificially high population numbers or very low food supply brought about by human activity. Under the former condition even the strongest and largest males may be unable to control the activities of other males that persist in copulation attempts. Under evolutionarily abnormally low food levels, large males may be too weak to fight for females or to intimidate males through display (because of the greater energetic cost associated with large body size). Sometimes the evolutionary novelty in the environment is apparent and research can be modified to take this problem into account (Jarvis 1974). But in most cases novel circumstances are unknown or incompletely understood.

Although novel environments may allow detection of counter selection on a trait—e.g., natural selection may reduce body size and sexual selection increase it—such circumstances present problems for testing functional hypotheses via experimental and observational methods. Furthermore, there is the difficulty of measuring fitness in a way that will provide meaningful answers via short-term and site specific experimental or observational analysis. On the other hand, observational and experimental results provide the only means of obtaining information about which selective force(s) is presently favoring a trait or if the trait is being selected against. This information is of great interest.

But only the comparative method can yield answers to questions about selection pressures that have led to present features of living things (also see Curio 1973 and Mayr 1982, pp. 855-6). If a functional hypothesis predicts a correlation between sexual size dimorphism and breeding system,

the more species that fit the assumptions of the hypothesis and also fit the prediction, the more one has confidence in the hypothesis. The more evidence for predicted convergence and divergence, the more assured the investigator is that the hypothesis is correct.

Thus the comparative method can corroborate results pertaining to possible evolved function obtained by other methods, but other methods cannot question results from comparative analysis. Observational and experimental studies can be coupled with comparative analysis in order to determine if a force presently favoring a trait is the same as the selection that produced it.

For these reasons, when possible in my own work on scorpionflies, I employ all methods in an attempt to examine major questions about specific traits (see Thornhill 1981). The experiments and observations I described earlier provide understanding of selection maintaining the dorsal clamp of male *Panorpa*. I consider the following prediction an important test for elucidating the evolved function of the dorsal clamp: the frequency with which males of the various species of *Panorpa* exhibit forced copulation should be positively related to the size of the clamp (or other morphological correlates of the effectiveness of the structure as a clamp). The alternative hypotheses pertaining to the dorsal clamp would not generate this prediction, but they would yield other mutually exclusive ones that could be tested against comparative data. *Panorpa* spp. and species in related genera exhibit considerable diversity in shape and size of the dorsal clamp (Byers and Thornhill 1983), but too little information is presently available for appropriate comparative work.

It is argued that the nature of selection that has shaped a trait can never be ascertained for sure because multiple selection pressures probably operated on the trait and in the same direction. This view is implicit in any attempt to rank selection pressures in importance in studies of the evolved function of biological characteristics. This argument is invalid. If two selection pressures are acting in the same direction, and one is stronger than the other, the degree of evolutionary modification of a trait will reflect the stronger of the two, because the organism cannot "feel" the weaker pressure. This holds regardless of number of selective pressures. It is highly unlikely that two selection pressures acting on a trait will be equally potent, but even if this does occur the degree of adaptive modification will reflect the strength of any one of them alone. See Curio (1973, p. 1046) for a full discussion of this. Any trait has many effects, some beneficial and others harmful to fitness, but only one fitness effect is its function—its reason for being (Williams 1966). This is why it is appropriate for biologists to attempt to locate a single evolved function for each trait they are interested in. Ecological phenomena, including selective maintenance of a trait, may have multiple causes, but a question about evolved function has only one causal answer.

#### SCIENTIFIC PROGRESS: IMPROVING CORRELATIONS

I think it is safe to say that there is no satisfactory account of how science progresses or accumulates knowledge. Some argue that science does not progress; that any impression of progress in understanding is an illusion. Others argue not only that science doesn't progress but that it changes in an arbitrary way. This stems from the view that, at any time,

the theories being examined in a science change like automobile styles. There is no right or wrong theory, only popular and unpopular theories. And some feel that the major determinate of popularity of an idea is cultural attitude. For example, when football and other sports are popular and during World Wars ecologists are expected to believe that competition is important as an organizer of community structure! Undoubtedly, our beliefs, which are culturally inherited from parents, friends, etc., influence how we view the world scientifically. This is especially apparent in the writing of scientists who adhere to Marxist philosophies, but is also present in more subtle form in the work of anyone who adheres to any strong ideology. But as Ruse (1982) has pointed out, ideas in science that stem from ideology, cryptic or blatant, are not necessarily bad, because they are subject to the same criterion as other ideas. When ideological perspectives are paraded as science they will eventually meet the criterion of demarcation and be eliminated if they are wrong.

I suggest that scientific progress ultimately has nothing to do with arbitrary popularity of ideas, but instead, advances happen via improved understanding of the relationship between variables—that is, by increased understanding of correlations between presumed cause and effect. Every scientific hypothesis (or theory) describes an expected correlation between a cause(s) and an effect. To elucidate the variance in such relationships via the hypothetico-deductive model is the occupation of scientists. In no case is all the variance understood, even for simple relationships. I'll take a relatively simple example from my own work to illustrate my view of scientific progress and the achievement of greater understanding in general.

I began work on female choice in the scorpionfly *Hylobittacus apicalis* in 1971. *H. apicalis* exhibits nuptial feeding: the male feeds a female a prey arthropod during courtship and throughout copulation. The sizes of prey carried by males vary. Initial observations led to the hypothesis, based on evolutionary theory, that females will value material and genetic benefits of males in mate choice. I assumed that the material benefits (nuptial prey size) and genetic benefits (offspring quality) a male could deliver to a female would be positively correlated. I examined two qualitative predictions from this hypothesis: 1) females will sometimes refuse to mate with males with small prey, and 2) the duration of mating will be positively related to nuptial prey size. The general correlation I sought to define and explain was choice behavior of females (effect) in relation to the prey size males possess (presumed cause).

Initial research revealed that the predictions were upheld (Thornhill, 1976, 1977). Many females refused to copulate with males with small prey (i.e., less than 16 mm<sup>2</sup> in surface area) and there was a positive relationship between mating duration and nuptial prey size. I also discovered that copulations involving large prey ( $\geq 16$  mm<sup>2</sup>) are terminated by males, whereas copulations involving small prey (when a female allows copulation) are terminated by the female. Furthermore, by interrupting lab copulations involving virgin females I found that in the first 5 minutes of copulation few or no sperm are transferred to the female. From 5 to 20 minutes there is a direct positive relationship between number of sperm transferred and mating duration, and beyond 20 minutes of mating no further sperm are transferred. Finally, studies revealed that females lay eggs and do not mate again following matings with males with large prey, but females

remain sexually receptive and do not lay eggs when they mate with a male with small prey.

The relationship between copulation duration and sperm transfer yielded the prediction that when females mate with males with small prey they will terminate copulation after 5 minutes; that is, at about the time when sperm begins to flow. This way a female obtains a brief meal but receives few or no sperm from inferior hunters. Field observations revealed that mean time of mating involving small prey was 5.8 minutes (Thornhill 1980c). Although this is close to the predicted 5 minutes there was still much variance in mating times when small prey were involved. But I was making progress in terms of understanding the initial relationship of interest to me. I now knew that 50% of the time females reject males with small prey and when females allow such males to mate they terminate mating on average at about the time sperm begins to flow from male to female. The correlation between female mate choice and male nuptial prey size was being improved.

At this point in the study I modified the hypothesis in an attempt to understand more variance in the relationship, but the modification did not change the general correlation I was studying. The modified hypothesis is: The relative value of material and genetic benefits for females in choice decisions depends on female conditions of body size, feeding history and mate availability. Basically, I was proposing that every female will strive to maximize material and genetic benefits received from males. But I need to clarify how I derived the modified hypothesis. Energetic cost of body maintenance is positively related to body size; the larger the animal the more nutrients required. Also, feeding history of females was expected to vary and thus some females should be more willing to mate with males with small prey. Mate availability should also influence female choice; the more males available the more choosy females might be.

The major predictions the modified hypothesis yielded were: 1) large females will be more likely to mate with males with small prey than will small females, 2) there will be a positive relationship between female body size and duration of matings involving small prey, 3) large females will behave like small females when fed prior to placing them with males possessing small prey, and 4) independent of female body size, females will become more choosy as potential mate availability increases.

I have begun testing these predictions. All four are supported. The first three are well substantiated, but the fourth will need more testing in order to clarify completely the role of male density in female mate choice (Thornhill 1984b). Thus, I have considerable understanding of the variance in the correlation between female mate choice and mate nuptial prey size. I do not have all the variation explained; there are still exceptions. But if I know a female's body size, her recent feeding history and the mate availability I can predict with considerable accuracy not only whether the female will mate with a male with small prey but also the duration of the mating if it occurs.

I emphasize that the the sequence my work followed is distinctly different from endeavors involving the addition of parameters that explain more and more variance in a data set. A common procedure in areas of social science and biology is to employ multiple regression analysis to determine the ability of presumably important parameters to explain variation. In some cases, parameters are added until most or all of the variance is ac-

counted for. This procedure involves ad-hoc explanation. It is not valid science to modify a hypothesis to account for unpredicted observations and then claim that the hypothesis is confirmed. Likewise, it is invalid to construct a model from data and claim that the model is confirmed. It is scientifically accurate, however, to use unpredicted observations to modify or eliminate a hypothesis and then test the predictions from the modified or alternative hypothesis with new observations (or simply suggest the direction that testing should involve).

I feel that the sequence of events the *Hylobittacus* work went through is the appropriate and typical sequence for scientific hypotheses and even general theories when they are successful. (See Skinner and Charnov's paper in this symposium volume for an additional example of this sequence.) Hypotheses other than the one outlined that I considered in my research sequence with *Hylobittacus* are discussed in Thornhill (1980c, 1984b). A particular sequence may involve only one or all methods of applying the hypothetico-deductive model. Also, a particular sequence may involve one or multiple investigators examining the same presumed cause-effect relationship. At any stage in a sequence a hypothesis (or theory) may be disproved and replaced by another hypothesis (or the original hypothesis modified) that attempts to account for the relationship.

Even great theories like those of Darwin, Einstein, and Newton portray a relationship or correlation between variables. Darwin's theory is by far the most comprehensive theory in science in the sense that it is directed at explaining life, the most complex and diverse phenomenon known to humankind. But still even this theory rests on the relationship between the diversity of life (effect) and a history of differential reproduction of individuals (cause). Since Darwin, biologists have been attempting to understand the variance in this relationship. Biologists ask questions about the relation between imagined selection pressures and diversity in sexual dimorphism, life history, chromosome structure and number, mating behavior, etc. The imagined selection pressures of biologists serve as alternative hypotheses which succeed or fail to explain subrelationships of the general correlation Darwin's theory generated.

#### FOOTNOTE

<sup>1</sup>Karl Popper (1934), a philosopher of science, has argued that only falsifiable ideas are within the realm of science, and that tests of scientific hypotheses (or theories) should focus on attempts to falsify them. His ideas have been very influential in many areas of science, including biology.

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BOOLEAN MODEL OF THE COURTSHIP AND  
AGONISTIC BEHAVIOR OF *HENTZIA PALMARUM*  
(ARANEAE: SALTICIDAE)

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ABSTRACT

A behavior modeling technique based on Boolean algebra is developed and applied to the stereotyped courtship and agonistic behaviors of *Hentzia palmarum* (Hentz) males. A primary advantage of this type of alternative modeling technique comes from the precise relationship between cause and effect or stimulus and response inherent in Boolean algebra. In the present case, a preliminary model is developed that resolves the behaviors in question into overlapping, branching sequences of stereotyped behavioral units and sequential releasers.

RESUMEN

Un técnico de modelar basado sobre el álgebra booleana se elabora y se aplica al comportamiento estereotipado agonístico y de cortejeo de machos de *Hentzia palmarum* (Hentz). Una ventaja principal de este tipo de técnico alternativo de modelar viene de la relación precisa entre la causa y el efecto, eso es, entre el estímulo y la respuesta, inherente en el álgebra booleana. En el caso actual se elabora un modelo preliminar lo cual resuelve los comportamientos en cuestión en secuencias traslapados y ramificados de unidades de comportamiento estereotipado y disparadores consecutivos.

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Many behavioral systems diagrams (reviewed in Sustare 1978) give information concerning when particular events occur within complex sets of behaviors. Most such diagrams, however, are not suited to portraying clearly the precise relationship between stereotyped behaviors and their releasers. The result is that while such diagrams can be highly descriptive, they tend to offer little or no information as to causality. A systems diagram that incorporates elements of causality is much more useful for generating testable hypotheses and generalizations. The algebra of sets (Boole 1854), as adapted by Shannon (1938) and since developed as a major part of the logical foundation of modern digital electronics offers promise in respect to that limitation. Although no one appears to have made use of the technique previously, we have been impressed with the potential usefulness of Boolean algebra in depicting the roles of particular stimuli and pre-existing conditions in the release of complex stereotyped biological behaviors.

As a point of departure and to illustrate this approach, we have made use of a previously obtained set of observational data collected by the second author. Using these data, we have attempted herein to construct a

preliminary empirical Boolean model of the behavioral logic of males of the jumping spider *Hentzia palmarum* (Hentz) (Araneae: Salticidae) interacting agonistically with conspecific males and interacting in courtship with females.

#### METHODS

The spiders were observed in the laboratory, where individuals and pairs (2 ♂ or 1 ♂ + 1 ♀) of spiders were confined (1) in 10 cm dia glass petri dishes or (2) in clear plastic "shoe boxes" (40 x 27 x 16 cm). Graph paper with 1-mm squares was placed under the containers in order to facilitate the measurement of distances. We observed 36 agonistic (♂ vs. ♂) interactions involving the total of 12 adult males in different combinations, and 30 courtships (25 ♂ and 24 ♀). No more than 2 spiders were placed in a dish at a time. Encounters were initiated by placing the spiders, one after the other, into the test chamber. Solitary ♂ and ♀ also were observed for informal comparison, but their behaviors are not a specific part of the present paper.

#### TERMS AND ELEMENTS OF THE MODEL

Boolean algebra utilizes only 3 basic operators (AND, OR, and NOT), and 4 derived operators (NOR, NAND, INHIBIT, and the EXCLUSIVE OR) which will be briefly explained; those desiring more detail may check Bartee (1977), Mano (1972), or similar texts.

Boolean operators or "logic gates" resemble nerve axons in that they are binary devices: i.e., they have 2 distinct and contrasting states ("1" or "0", "+" or "-", "on" or "off"). We shall use "1" to indicate the presence and "0" to indicate the absence of a signal from detectors; within the model, "1" and "0" are merely contrasting states.

**AND:** (Fig. 1) requires a logical "1" on all of its 2-or-more inputs to yield a "1" output; if any input = 0, the output = 0.

**DETECTOR:** (Fig. 1) responds selectively to a particular simple aspect (pattern or intensity) of sensory data by sending an output to logic or motor circuits. (Maturana et al. 1960, Lewick 1967).

**DISENABLE:** Logical complement of "enable"; i.e., to cause the production of a logical "0" on the output of a Boolean logic gate.

**ENABLE:** To cause, by the proper input or combination of inputs, the production of a logical "1" on the output of a Boolean logic gate.

**EXCLUSIVE OR:** (Fig. 1) will produce an output of logical "1" only if a logical "1" is on 1 but not more of its inputs.

**INHIBIT:** (Fig. 1) the equivalent of an AND gate with a NOT gate affixed to 1 or more of its inputs. Such modified inputs are identifiable by a small circle interposed between the input lead and the body of the symbol. We also use this small circle as a convenient way of designating the NOT operation being performed on an input to an OR gate (Fig. 1).

**NAND:** (Fig. 1) the logical complement of AND.

**NOR:** (Fig. 1) the logical complement of OR.

**NOT:** (Fig. 1) the simplest operator—it simply inverts a signal; i.e., a logical "0" on its only input yields a logical "1" on its output, and vice versa. Also, see INHIBIT.

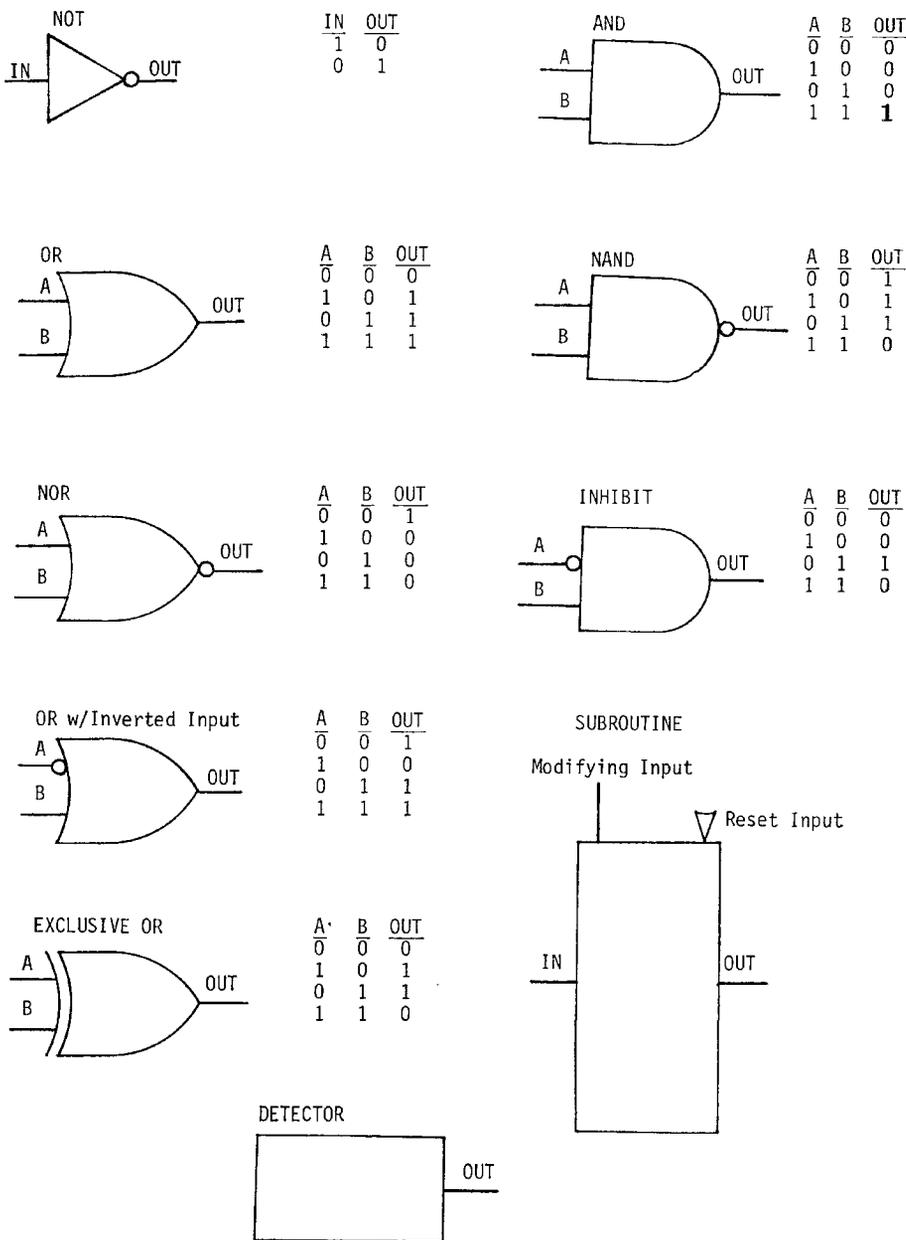


Fig. 1. Logic symbols and their truth tables. A, B, IN = inputs; OUT = output.

OR: (Fig. 1) has 2 or more inputs and a single output; it requires a logical "1" on at least 1 input to produce a logical "1" on the output.

THE MODEL

Maturana et al. (1960), working with frogs, and Lewick (1967), working with rabbits, discovered retinal information processors, or detectors, which

could respond to simple patterns in the animals' vision field. We reasoned that arthropods such as *H. palmarum* may also have such detectors which allow them to respond rapidly and selectively to many important and commonly encountered patterns of stimuli.

Accordingly, we included in the preliminary model appropriate hypothetical detectors (Fig. 2: RMD, LMD, SMD, AFD, PMD, PRD, PXD, CTD), the outputs of which are the external inputs of the model. Outputs of detectors PXD and CTD, respectively, terminate or prevent the activities of the respective behaviors (zig-zag approach and flutter approach) they affect; detector PXD also supplies an input into gate 13. Unidentified

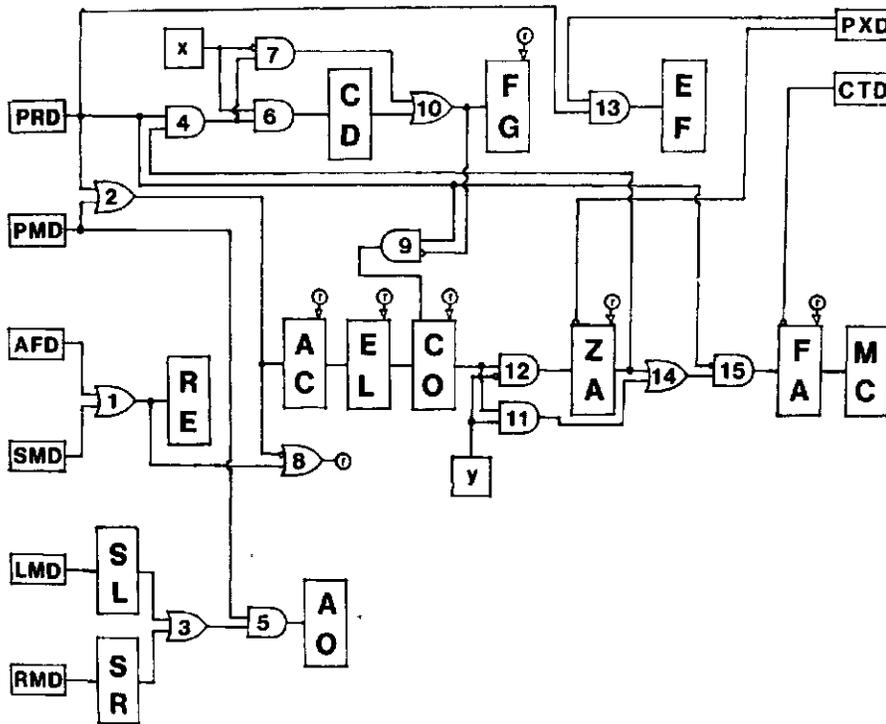


Fig. 2. Sequential and causal depiction of the courtship and agonistic behaviors of males of *Hentzia palmarum*. LMD = left motion detector; RMD = right motion detector; SMD = "superior male" detector; AFD = "aggressive female" detector; PMD = "potential mate" detector; PRD = "potential rival" detector; PXD = proximity detector; CTD = contact detector; r = reset impulse; x-y = unidentified stimuli; AC = abduct chelicerae subroutine; AO = align opisthosoma subroutine; CD = circle dance subroutine, CO = cock opisthosoma subroutine; EF = extend fangs subroutine; EL = extend legs subroutine; FA = flutter approach subroutine; FG = fang grappling subroutine; MC = mounting and subsequent copulation subroutines; RE = retreat subroutine; SL = swivel left subroutine; SR = swivel right subroutine; ZA = zig-zag approach subroutine; 1, 2, 3, 10, 14 = OR gates; 4, 5, 6, 11, 13 = AND gates; 8 = OR gate with 1 inverted input; 7, 9, 12, 15 = INHIBIT gates. Schematic conventions as in electronics.

stimuli (inputs x-y) were hypothesized to tend to inhibit (gate 7, 12) or enable (gate 6, 11) other gates.

The various behavioral units (in vertical rectangles: retreat, zig-zag approach, etc.) are depicted in the schematic as receiving a primary (enabling) input on the left, secondary (modifying) inputs on the ends, and producing an output at the appropriate time (usually at the completion of the execution of the behavior) on the right side of their rectangular symbols. The reset (r) signal produced by gate 8 is used to abort the behavioral sequence and return the affected units to their primal condition, once again responsive to an input.

In order to make the behavioral schematic (Fig. 2) more easily comprehensible, the Boolean logic of the following "Courtship" section is explained in detail in the text.

#### COURTSHIP

**ORIENTATION:** Detection of motion by the male triggers him to orient toward the source of motion. This centers the other spider in the field of his highly-developed anterior median eyes. In the first orientation movement, swivel, the male turns his prosoma toward the other spider while the opisthosoma remains stationary. This creates an angle between the prosoma and the opisthosoma. If the other spider is female, the next movement is alignment; there is no distinct alert phase, sensu Forster (1977). As in Forster (1977), alignment involves the moving of the opisthosoma into its normal position behind the prosoma. In interactions with other males (discussed subsequently), alignment is not performed. Thus, it appears that the male may be able to recognize the female spider's sex and presumed conspecificity almost immediately. Richman (1982) noted ready acceptance of other congeneric species as mates by *Hentzia* under laboratory conditions.

In designing a schematic representation (Fig. 2) of the events of orientation, we hypothesized that motion detectors (LMD, RMD) were responsible for triggering the swivel left (SL) and swivel right (SR) behaviors (or subroutines). The completion of either swivel is followed by the alignment of the opisthosoma if the other spider is a conspecific female (detector PMD). Thus, the output of either swivel unit can enable OR gate 3. AND gate 5 produces a logical "1" output (enabling the align opisthosoma subroutine) when it receives a "1" on both of its inputs (the outputs of OR Gate 3 and detector PMD).

**PREPARATION:** After orienting toward the other spider, the male executes several movements prior to advancing toward the other spider. The first 2 of these preparatory movements, abduction of the chelicerae and extension of the forelegs, are executed almost simultaneously. Cheliceral abduction is a lateral spreading of the chelicerae that exposes the fangs, abducted to the medial surface of the chelicerae. Foreleg extension straightens and moves the forelegs laterally such that they describe an angle of ca 100-130°. Typically, the chelicerae begin spreading before the legs are extended and become fully spread before the legs are fully spread. The male's forelegs are black—unlike its other legs, which are light colored. By fully extending the forelegs laterally, a black line running from the tip of one leg, across the clypeus to the tip of the other leg is presented to the female. This may aid the female in determining the male's size and species.

The next step, cocking of the opisthosoma, is a lateral (left or right) and rotational movement of the opisthosoma which creates an angle of ca.  $100^\circ$  between opisthosoma and the prosoma, increases the amount of body area being presented to the female, and discloses abdominal patterning. In courtship (but not in agonistic interactions), the abdomen may be cocked and returned to the midline several times during an approach.

In the model, preparation behaviors (Fig. 2: AC, EL, CO) are triggered via OR gate 2 by a "1" output from detector PMD or PRD. The unit producing the first of these behaviors, abduct chelicerae (AC), passes on the stimulus (logical "1") to the extend forelegs (EL) unit, the output of which triggers the cock opisthosoma (CO) unit. The output of INHIBIT gate 9 modifies the execution of cock opisthosoma in male-male agonistic interactions (the opisthosoma is kept cocked). A reset pulse (r) generated by OR gate 8, can abort the courtship behaviors if retreat (RE) becomes appropriate or if the output of OR gate 2 changes to "0" because the other spider is lost sight of. Note that a "0" output from OR gate 2 is felt as an enabling impulse at OR gate 8 due to the inverter (NOT gate) on that input.

**APPROACH:** This phase of the courtship begins with the zig-zag approach, which is characterized by the male walking a zig-zag path toward the other spider. During this approach, the male continuously faces the other spider, the prosoma is tilted successively to the left and right in phase with the alternating direction of lateral movement, the chelicerae are abducted, the forelegs are extended, and some males pause several times, cocking and returning the opisthosoma frequently. The numbers of pauses and of cocking motions varies directly with the duration of the zig-zag approach. This approach begins at 3-4 cm (Richman 1982) and continues until the male is 1-2 cm from the female. The zig-zag approach is not always performed in its complete form. Some males move in only one lateral direction until they get close enough to the female to begin a flutter approach; in some cases, the lateral movements (zig-zags) may not have much amplitude. Richman (1982) also noted that in a few cases *H. palmarum* mate after very little visual display.

Once the male is within 1-2 cm of the female, the zig-zag approach ends and the flutter approach begins. This change in behavior is probably a function of the proximity of the female. The flutter approach is characterized by the male walking directly toward the female while fluttering his forelegs rapidly up and down. The walk is hesitant, punctuated with brief pauses. The fluttering movements of the forelegs are continuous and of low amplitude (not touching the substrate), and the legs are extended immediately in front of the female's anterior median eyes. The zig-zag approach is sometimes omitted for reasons not yet discovered. In Fig. 2, this variability is depicted as being a function of an undefined factor,  $y$ . If  $y$  is a logical "1", it simultaneously disables INHIBIT gate 12 (note the inverter on the input) and predisposes the enablement of AND gate 11. This shunts the output of the cock opisthosoma subroutine around the zig-zag approach subroutine. If  $y = "0"$ , the condition of the AND gates is reversed, and the zig-zag approach is performed. The zig-zag approach is terminated when the male is sufficiently near the other spider to trigger an output from proximity detector PXD into the subroutine. In Fig. 2, divergence of courtship and male-male agonistic interactions sub-

sequent to the zig-zag approach is handled via the "0" output characteristic of the rival detector PRD in courtship. This "0" acts on AND gate 4 (to inhibit agonistic behaviors) and on the inhibit input of INHIBIT gate 15 (to predispose the enablement of that gate).

OR gate 14 is enabled by a "1" on either of its inputs. This "1" is passed through OR gate 14 and INHIBIT gate 15 (which has an "0" on its inverted input) and is felt at the input to the flutter approach subroutine, enabling it.

**CONTACT:** When the male becomes sufficiently proximate to the female, his fluttering forelegs touch her and their movement causes them to drum rapidly against her prosoma. In Fig. 2, contact detector CTD inhibits the further execution of the flutter approach and causes the production of a "1" output by the subroutine. The subsequent behaviors, mounting and copulation (MC), are not within the scope of the present paper.

On those occasions that the female raised her forelegs into the air (a threat display), the male either would retreat or would grapple with the female. In some cases, the female would approach a courting male or pursue a fleeing male. In the former case, the male would stop courting and retreat; captured males were bitten.

Virgin females ceased to be receptive to males if they were not mated within ca. the first 2 weeks of adult life. Conversely, females which had laid several clutches of eggs sometimes became receptive again. On some occasions, virgin females mated with up to 5 different males when the males were presented in rapid succession.

#### AGONISTIC INTERACTIONS

As in courtship, both males orient toward each other by performing a swivel (Fig. 2) which enables each to view the other with his anterior median eyes; the swivel is not followed by alignment of the opisthosoma, however. Swivels are performed toward any moving object, often at distances several times greater than 12 cm, especially if the moving object is large, but no swivels directed at other male *H. palmarum* occurred at distances greater than 12 cm.

Following the swivel, the preparation phase ensues, wherein both males spread their chelicerae and extend their forelegs laterally, as in courtship. These movements are performed simultaneously and are followed by a cocking of the opisthosoma to one side; unlike in courtship, the opisthosoma is held in this position until just prior to when the 2 males contact each other.

Next, the males mutually begin a zig-zag approach which differs in one major respect from the zig-zag approach of the courtship; the opisthosoma is not cocked repeatedly to either side, but is maintained in the cocked position. Subsequent to the onset of the zig-zag approach, but prior to actual contact, the fangs are extended; this activity seems to be primarily a response to the proximity of the opponent. Generally, when the males are 1-1.5 cm apart they initiate the circle dance. The circle dance resembles the zig-zag approach except that the prosoma is no longer tilted and the pattern described by the movement is that of an arc rather than a zig-zag line. The males move in opposition to each other, back and forth along short arcs around a central point until contact is made.

When the spread fangs of the opponents contact, fang grappling begins,

during which the males align their opisthosomas along the main body axis, extend their fangs far apart, make fang-to-fang contact with their opponent, and then push against each other's fangs—much like rival rams or bulls "butting horns". Occasionally, an attempt is made to close the fangs around those of the opponent in a pincher-like movement, but we have not seen this succeed. A jab made with 1 free fang was observed on 1 occasion, but for the most part fang grappling proceeds as a pushing contest. The loser of the contests (which may last from 3 to 30 s between males of similar size) invariably was the smaller of the 2 contestants.

Following fang grappling, the smaller male retreats. Retreat consists of 3 stages: backing away from the opponent, turning, and then running away. As the vanquished male backs away, he continues to face his opponent and keeps his forelegs extended laterally until he is sufficiently distant to turn and run away.

#### EXPERIMENTAL RESULTS VS. MODEL

The original data were not collected for analysis by the present method; a fact that stands in the way of precise validation of the preliminary model. We will, however, attempt an informal comparison of the model with the data. The incidences of particular behaviors (or subroutines) in the 30 observed courtships (with or without copulation resulting) were as follows: swivel and align, 23 (11 matings + 12 non-matings); abduct chelicerae, 28 (13 matings + 15 non-matings); extend forelegs, 30 (14 matings + 16 non-matings); cock opisthosoma, 26 (12 matings + 14 non-matings); zig-zag approach, 16 (7 matings + 9 non-matings); flutter approach, 10 (10 matings + 0 non-matings); contact female, 18 (14 matings + 4 non-matings); mount and copulate, 14. swivel and align subroutines were performed in all courtships, except when the male was initially oriented toward the female. Courtships resulting in mating tended to involve most or all subroutines: 3 were complete (swivel through copulate); 2 lacked only swivel and align; zig-zag or flutter approach was performed in all except 2 instances, and both were performed in 5 cases; of the 2 that lacked cock opisthosoma, 1 also was the only successful courtship without an observed abduct chelicerae subroutine. Aborted courtships broke off during or following cock opisthosoma (7 instances), zig-zag approach (5 instances), and contact female (4 instances). In 8 cases, extend chelicerae and extend forelegs were executed in such rapid succession that their respective sequencing was unclear or simultaneous; in 3 courtships, the forelegs appeared to have been extended first.

The align subroutine was not observed as a part of any of the 36 monitored agonistic interactions. This may indicate that the sex and species of the female is recognized almost immediately. Conversely, a stimulus from the other male may inhibit this behavior. Further investigation of this early dichotomy between courtship and agonistic interactions would be useful. Subroutines occurred in the 36 observed agonistic interactions in the following respective frequencies (both, winner only, loser only, neither): swivel (22, 3, 7, 4), abduct chelicerae (21, 9, 4, 2), extend forelegs (20, 9, 4, 2), cock opisthosoma (15, 13, 2, 6), zig-zag approach (13, 12, 2, 9), extend fangs (11, 1, 0, 24), circle dance (5, 0, 0, 31), grapple (7, 0, 0, 29), retreat (0, 0, 36, 0). Two interactions terminated with retreat after only swivel had

been performed. In 13 cases, both males performed the same number of subroutines prior to retreat; in most cases, these interactions contained almost all of the subroutines with both parties being very actively involved. In the 19 interactions in which (following swivel) different numbers of subroutines were performed by the 2 males, one male was active (performed all subroutines observed in the interaction), whereas the other was partially or uniformly passive. More pre-retreat subroutines were performed by the winner in 15 and by the loser in 5 interactions.

Because this is a preliminary model, we have left some items (e.g., unidentified stimuli *x* and *y*) in it for which we have no positive data. Stimuli *x* and *y* represent unexplained sources of variation to be determined in later research; as such they serve a function. Similarly, the detectors (RMD, etc.) that serve as the inputs to this model are not proven. Rather, they are presented as a challenge hypothesis for verification or replacement in models produced from subsequent research.

#### CONCLUSIONS

In courtship and in agonistic interactions, the behavior of males of *H. palmarum* consists of identifiable units, or behavioral subroutines, the execution of which is dependent on predisposing conditions and stimuli. Because these behavioral sequences need not always be executed in their full or "typical" form, it appears that the individual subroutines may have meaning by themselves. That some subroutines are common both to courtship and to agonistic interactions implies that males may communicate similar information to potential mates and potential rivals.

The major limitations we encountered in constructing the present illustrative model arose from the fact that we were using previously collected data that had not been gathered with this type of analysis in mind. Even with these constraints, we found Boolean logic schematics to be of great assistance (1) in defining and illustrating sequential and releaser-response relationships, (2) in refining and verifying our analyses, and (3) in comparing and contrasting the behavioral sequences. This method should also be useful in inter-species behavior comparisons. The clearly defined elements and organization of Boolean-type models facilitates the generation of unambiguous, testable statements about the workings of complex systems. The conspicuous and clear-cut relationship between releaser and response which is central to this technique gives it desirable predictive and analytical properties to supplement other modeling techniques. The expansion of this system to include multi-state, analog, and stochastic devices should extend its usefulness to the analysis and description of highly complex and variable behavioral systems.

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PSEUDOSCORPIONS FROM FLORIDA AND THE  
CARIBBEAN AREA. 12. *ANTILLOCHERNES*, A NEW  
GENUS WITH SETAE ON THE PLEURAL MEMBRANES  
(CHERNETIDAE)

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ABSTRACT

*Antillochernes* is described, with 5 new species from Florida and the Antilles. It is closely related to *Parachernes* Chamberlin from which it differs in the possession of setae on the pleural membranes of the abdomen. The new species are *A. bahamensis* from Grand Bahama Island and *A. biminiensis* from South Bimini Island, Bahamas, *A. floridensis* from Florida, *A. jamaicensis* from Jamaica, and *A. cruzensis* from St. Croix, U.S. Virgin Islands. *Parachernes muchmorei* Dumitresco and Orghidan from Cuba is transferred to *Antillochernes*.

RESUMEN

Se describe *Antillochernes*, con 5 especies nuevas de Florida y las Antillas. Se relaciona con *Parachernes* Chamberlin pero difiere por las setas sobre las membranas laterales del abdomen. Especies nuevas son *A. bahamensis* de Isla Grand Bahama y *A. biminiensis* de Isla South Bimini,

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Bahamas, *A. floridensis* de Florida, E.U.A., *A. jamaicensis* de Jamaica, y *A. cruzensis* de Isla Santa Cruz, Islas Virgenes. *Parachernes muchmorei* Dumitresco y Orghidan de Cuba se transfiere a *Antillochernes* igualmente.

The genus *Parachernes* Chamberlin (1931a) has long been recognized as a heterogeneous group of pseudoscorpions (Beier 1932b, Muchmore and Alteri 1974, Mahnert 1979). Though the group as a whole has not yet been critically analyzed, some closely related genera have occasionally been recognized and described (e.g. Beier 1932b, 1953, 1954, 1964a, 1976; Muchmore 1969, Mahnert 1979).

In the course of recent studies of pseudoscorpions of the Caribbean area, it has become apparent that some forms with all of the attributes of *Parachernes* differ from typical members of that genus in the possession of setae on the pleural membranes of the abdomen. Because these forms are mutually similar and because they occupy a discrete geographical range, they are here considered to constitute a separate genus.

Types of new species are deposited in the American Museum of Natural History, New York (AMNH) and the Florida State Collection of Arthropods, Gainesville (FSCA).

#### *Antillochernes* Muchmore, NEW GENUS

TYPE SPECIES: *Antillochernes bahamensis* Muchmore, new species.

DIAGNOSIS: A genus of the family Chernetidae Chamberlin. Of medium size for the family. Males and females similar, though females a little larger. With distinctive color pattern (Fig. 1); heavily sclerotized parts brown. Vestitural setae mostly denticulate to clavo-dentate. Carapace with or without transverse furrows; surface heavily granulate; center of posterior margin more heavily sclerotized than sides to form a distinct "keel" similar to that found in *Parachernes* (see Muchmore and Alteri 1974); 2 smooth eyespots; with 50-70 setae. Tergites and sternites distinctly divided; heavy sclerotization confined to center of each half tergite or sternite; surfaces granulate to scaly; middle tergites with 10-15 and sternites with 15-20 setae; 11th tergite with 2 and 11th sternite with 4 long, tactile setae; setae of anal plates denticulate; pleural membranes irregularly longitudinally striate and with 1 or more setae per segment. Male anterior genital operculum with central crescent of 6-8 long setae surrounded by 25-30 shorter ones; internal genitalia (where known) large and heavily sclerotized. Female anterior operculum with central cluster of small setae on a separate sclerite flanked posteriorly by a few setae on either side; spermathecae in form of 2 recurved sacs. Cheliceral hand with 5 setae, *b* and *sb* at least slightly denticulate, others long, acuminate; flagellum of 3 setae, distal one denticulate; galea slender, smaller in male, with 4-5 distal rami. Palps robust, no obvious sexual dimorphism; surfaces granulate, except chelal fingers; fixed finger of chela with only trichobothrium *et* located in distal half; movable finger with only *t* in distal half, *st* closer to *sb* than to *t*; venom apparatus well developed in movable finger, vestigial in fixed finger; marginal teeth small but well developed; accessory teeth present on each finger. Legs robust; tarsus of leg IV with slit sensillum near middle of dorsal margin and long tactile seta about  $\frac{2}{3}$  distance from proximal end.

DISTRIBUTION: From the species treated below, *Antillochernes* is known

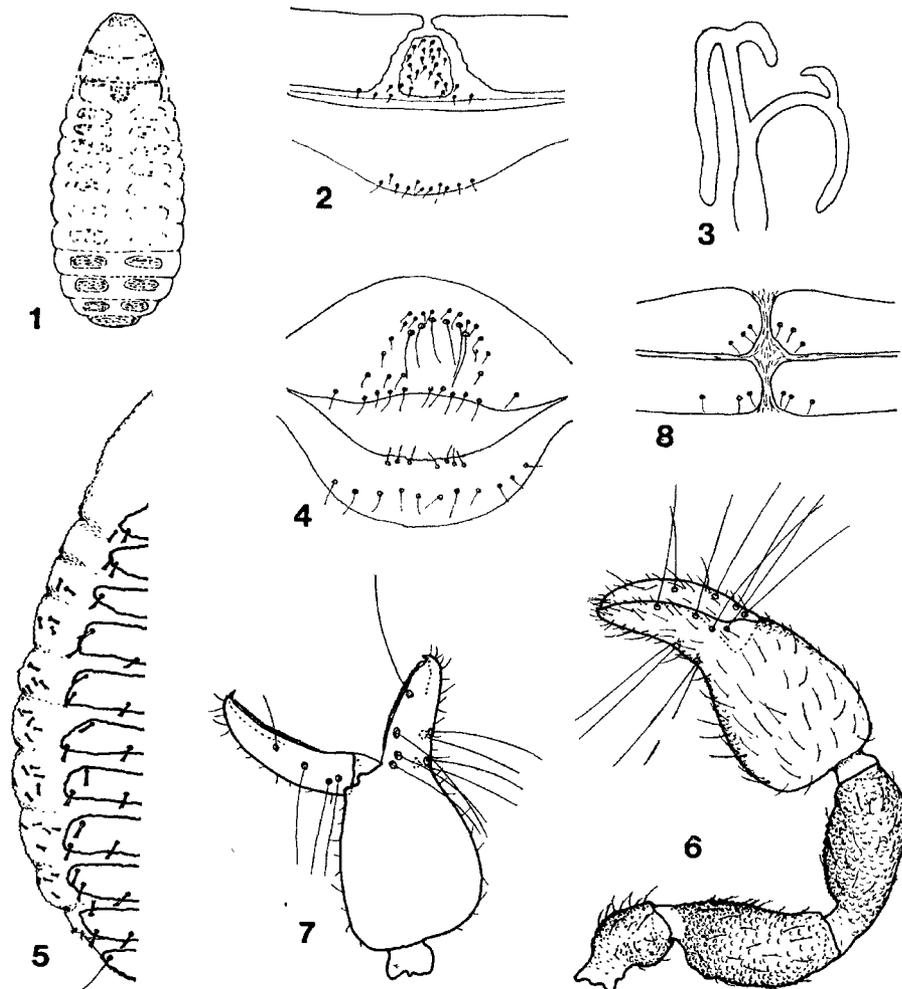


Fig. 1-8. *Antillochernes bahamensis* Muchmore, new species. 1) dorsal pattern of body, setae omitted; 2) genital opercula of female; 3) spermathecae of female; 4) genital opercula of male; 5) pleural membranes with setae; 6) dorsal view of right palp; 7) lateral view of left chela; 8) sternites 2 and 3 of tritonymph.

from the Bahamas, Florida, and the Greater Antilles, including Cuba, Cayman Islands, Jamaica, Puerto Rico, and St. Croix. Other representatives will certainly be found in other parts of the Caribbean area as more collecting is done.

**ETYMOLOGY:** The generic name is masculine and refers to the wide distribution of representatives in the Antilles.

**REMARKS:** *Antillochernes* is very similar to *Parachernes* in most respects, the obvious distinguishing difference being the presence of numerous setae on the abdominal pleural membranes of the former and their absence in the latter. The 2 genera are certainly closely related.

Only a few other genera of pseudoscorpions are known to include species with setae on the pleural membranes, namely *Garypus* L. Koch (see Lee

1979), *Anagarypus* Chamberlin (Muchmore 1982), *Elattogarypus* Beier (Beier 1964b), *Geogarypus* Chamberlin (Harvey 1981), and *Levichelifer* Hoff (Muchmore 1981). *Antillochernes* is the only known genus of the Chernetidae with this character. It is difficult to postulate a function for the pleural setae as the habits of these pseudoscorpions are so poorly known.

*Antillochernes bahamensis* Muchmore, NEW SPECIES

Fig. 1-8

**MATERIAL:** *Holotype* ♀ (WM 4117.01006) from golf course, west end of Grand Bahama Island, BAHAMAS, 3-4-III-1967, A.M. Nadler. *Paratypes*: 3 ♂, 2 ♀, 5 tritonymphs, same data as holotype; 1 ♂, Freeport, Grand Bahama Island, 27-II-1967, A.M. Nadler; 1 deutonymph, Lucaya, Grand Bahama Island, 7-III-1967, A.M. Nadler. All types in AMNH.

**DESCRIPTION OF ADULTS:** Males and females similar. Body with characteristic pattern (Fig. 1); heavily sclerotized parts brown, other parts shades of tan. Carapace mostly well sclerotized, but thin laterally along posterior margin so that central thickened part (keel) is distinct; with 2 shallow, but distinct, transverse furrows; 2 large, smooth eye spots; surface, except for posterolateral corners, covered with smoothly rounded granules; with 50-60 rather short, denticulate to clavodentate setae. Tergites and sternites distinctly divided, with heavy, dark sclerites surrounded by light, membranous areas; surfaces scaly. Tergal chaetotaxy of holotype ♀ 8:12:11:13:12:12:11:12:11:12:T8T:2; sternal chaetotaxy 28:(2)10(2):(1)8(1):14:13:14:14:14:12:T2TT2T:2. Tergal setae clavodentate, sternal setae acuminate to finely denticulate; 11th tergite with 2 and 11th sternite with 4 long, acuminate tactile setae; setae of anal plates denticulate. Anterior genital operculum of holotype ♀ with central cluster of about 15 small setae on a separate sclerite and 5-6 posteriorly on each side, posterior operculum with a marginal row of 10 small setae (Fig. 2); spermathecae of 2 narrow, recurved sacs, each with a shorter side branch (Fig. 3). Anterior operculum of ♂ with a central crescent of 5-6 long setae, surrounded by about 30 shorter ones; posterior operculum with 2 groups of 3-5 small setae at anterior margin and a row of about 10 longer setae behind (Fig. 4); internal genitalia typical for the family, large and heavily sclerotized. Pleural membranes longitudinally, irregularly striate and bearing short clavodentate setae (Fig. 5).

Chelicera 1/3 as long as carapace; hand with 5 setae, *b* and *sb* finely denticulate, *es* long, acuminate; flagellum of 3 setae, the distal one denticulate; galea slender, with 3 small rami, smaller in ♂ than in ♀.

Palp robust (Fig. 6); palpal femur 2.25-2.4, tibia 2.15-2.45, and chela (without pedicel) 2.1-2.45 times as long as broad; hand (without pedicel) 1.1-1.35 times as long as deep; movable finger 0.8-0.9 as long as hand. Trochanter, femur and tibia heavily granulate, chelal hand lightly granulate, fingers smooth; setae terminally denticulate to acuminate. Trichobothria as shown in Fig. 7; on fixed finger only *et* distad of middle of finger, others grouped near base, with *it* near level of *ist* and *isb* at level of *ib*; on movable finger only *t* distad of middle, *st* nearer to *sb* than to *t*. Fixed finger with 38-43 and movable finger with 42-48 well-developed, contiguous marginal teeth; each finger with 6-8 external and 2-3 internal accessory teeth; venom apparatus well developed in movable finger, vestigial in fixed finger.

Legs rather robust; leg IV with femur 2.6-2.85 and tibia 3.4-3.5 times as long as deep. Tarsus of leg IV with prominent slit sensillum at middle of dorsal margin and long tactile setae  $2/3$  distance from proximal end.

**NYMPHS:** 5 tritonymphs and 1 deutonymph available for study are much like the adults in general features. Pleural membranes have up to 4 setae in segments 3-10 on each side. The carapace, like that in many *Parachernes* nymphs, is striking in that the portion bearing the posterior row of setae and including the keel is separated from the anterior portion by a narrow, lightly sclerotized band (=posterior furrow?). Because of reduced sclerotization of this posterior part, the keel usually appears as an isolated round sclerite. In tritonymphs, the 2nd sternite (=anterior genital operculum of adult) is divided, each half bearing 3-4 small setae near the medial edge; 3rd sternite also divided and with 3 setae on each side (Fig. 8).

**MEASUREMENTS OF ADULTS (mm):** Figures given first for holotype, followed in parentheses by ranges for the 6 paratypes. Body length 2.65 (2.0-2.65). Carapace length 0.75 (0.635-0.72). Chelicera 0.25 (0.215-0.26) long. Palpal trochanter 0.33 (0.30-0.33) by 0.18 (0.18-0.20); femur 0.62 (0.53-0.59) by 0.265 (0.22-0.245); tibia 0.585 (0.53-0.585) by 0.27 (0.22-0.265); chela (without pedicel) 0.96 (0.85-0.96) by 0.39 (0.38-0.445); hand (without pedicel) 0.57 (0.465-0.53) by 0.43 (0.39-0.46); pedicel about 0.09 long; movable finger 0.45 (0.41-0.48) long. Leg IV: entire femur 0.55 (0.48-0.54) by 0.19 (0.17-0.20); tibia 0.40 (0.36-0.41) by 0.115 (0.105-0.12); tarsus 0.30 (0.295-0.31) by 0.08 (0.075-0.08).

**TRITONYMPHS:** Ranges for 5 mounted specimens. Body length 1.95-2.15. Carapace length 0.555-0.605. Palpal femur 0.39-0.445 by 0.19-0.20; tibia 0.385-0.42 by 0.195-0.21; chela (without pedicel) 0.67-0.725 by 0.29-0.31; hand (without pedicel) 0.37-0.43 by 0.30-0.325; pedicel about 0.06 long; movable finger 0.33-0.355 long. Leg IV: entire femur 0.38-0.42 by 0.15-0.16.

**REMARKS:** Diagnostic features of *Antillochernes bahamensis* have been presented above in the description of the genus. So far, this species has been found only on Grand Bahama Island, though other, distinct species of the genus are present on Bimini Island and in Florida.

The distinct separation of the posterior part of the carapace in nymphs of this species (and others in *Antillochernes* and *Parachernes*) suggests strongly that the portion of the carapace behind the posterior furrows of adults is derived from a single segmental sclerite, contrary to the opinions of Chamberlin (1931b:59) and Beier (1932a:2). Further study of this phenomenon in these and other pseudoscorpions should be very interesting.

*Antillochernes jamaicensis* Muchmore, NEW SPECIES

Fig. 9-11

**MATERIAL:** Holotype ♀ (Hoff: S-2605.2) from St. Ann's Bay, St. Ann Parish, JAMAICA, 24-26-XII-1953, G. R. Proctor [in AMNH]. Numerous paratypes from JAMAICA: Discovery Bay, near Falmouth, Montego Bay, Negril, Christiana, Mt. Diablo, Port Henderson, Long Mountain, Kingston, Morant Point, Holland Bay, St. Ann's Bay, Unity Valley, collected by C. C. Hoff, A. M. Nadler, P. and C. Vaurie, P. F. Bellinger, P. W. Hummelinck [in AMNH and FSCA].

**DIAGNOSIS:** Variable in size (carapace length 0.63-0.87 mm), with generally stouter appendages than other species in the genus (palpal femur

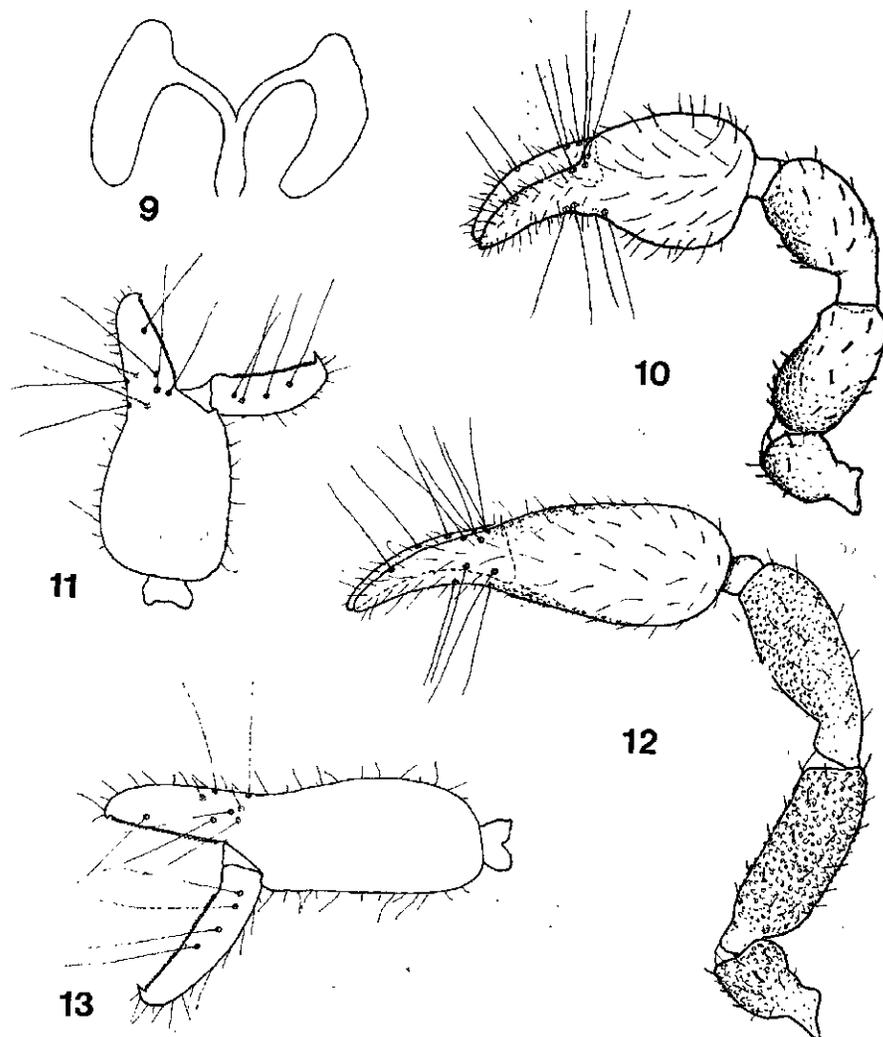


Fig. 9-11. *Antillochernes jamaicensis* Muchmore, new species. 9) spermathecae of female; 10) dorsal view of right palp; 11) lateral view of right chela.

Fig. 12-13. *Antillochernes biminiensis* Muchmore, new species. 12) dorsal view of right palp; 13) lateral view of left chela.

1/w = 2.0-2.3; femur of leg IV 1/d = 2.3-2.6), and with only 1 transverse furrow evident on carapace. Males have very distinctly clavate setae on dorsum of body and do not have long acuminate tactile setae on 11th tergite.

DESCRIPTION: Males and females similar in size and proportions. Body with characteristic pattern (see Fig. 1); with 1 shallow transverse furrow or none; 2 smooth eyespots; surface covered with smoothly rounded granules! with about 50 narrow clavodentate setae, shorter and heavier in ♂ than in ♀. Tergites and sternites distinctly divided, with lightly sclerotized borders; surfaces scaly to granulate; middle tergites with 11-14 narrowly clavodentate setae (shorter and heavier in ♂) and middle

sternites with 15-18 acuminate setae; 11th tergite of ♀ with 2 long, acuminate tactile setae, ♂ with long, clavodentate setae in corresponding positions; 11th sternite of both sexes with 4 long, acuminate setae. Pleural membranes longitudinally irregularly striate and bearing 2-7 clavodentate setae on each side in segments 3-10, and occasionally a seta in segment 2. Anterior genital operculum of ♀ with a central group of 12-15 small setae on a separate sclerite and 4-5 setae posterolateral to that; posterior operculum with a row of 8-10 setae near the middle of anterior margin; spermathecae of 2 recurved sacs expanded distally, as shown in Fig. 9. Anterior genital operculum of ♂ with a central crescent of about 8 long setae surrounded by 25-30 shorter ones; posterior operculum with 2 groups of 4-5 small setae at anterior margin and a row of 8 larger setae behind; genitalia of usual chernetid type, large and heavily sclerotized.

Chelicera 1/3 as long as carapace; hand with 5 setae, *b* and *sb* denticulate, *eb* long, acuminate; flagellum of 3 setae, the distal one dentate; galea of ♀ slender with 4-5 small rami, that of ♂ small with 1-2 tiny spinules.

Palp robust (Fig. 10); palpal femur 2.0-2.3, tibia 1.85-2.1, and chela 2.15-2.55 times as long as broad; hand 1.2-1.5 times as long as deep; movable finger 0.75-0.95 as long as hand. Surfaces except chelal fingers, distinctly but sometimes lightly granulate; setae short denticulate to acuminate. Disposition of trichobothria shown in Fig. 11. Fixed finger with 30-40 and movable finger with 35-45 contiguous teeth; each finger with 6-8 external and 1-2 internal accessory teeth; venom apparatus well developed in movable finger, vestigial in fixed finger.

Legs rather robust; leg IV with entire femur 2.3-2.6 and tibia 2.9-3.2 times as long as deep. Tarsus of leg IV with slit sensillum just proximad of middle and long tactile seta about 2/3 distance from proximal end.

**NYPHS:** The few nymphs available are quite similar to corresponding stages of *A. bahamensis*. As in that species, the posterior part of the carapace appears separate from the anterior part. Pleural membranes with 1-5 setae on each side in segments 3 or 4-10.

**MEASUREMENTS (mm):** Figures given first for holotype ♀, followed in parentheses by ranges for 36 paratypes. Body length 2.55(1.8-3.45). Carapace length 0.695(0.63-0.87). Chelicera 0.235(0.20-0.27) long. Palpal femur 0.50(0.45-0.70) by 0.24(0.21-0.30); tibia 0.48(0.44-0.65) by 0.245(0.22-0.32); chela (without pedicel) 0.82(0.77-1.10) by 0.36(0.325-0.49); hand (without pedicel) 0.47(0.44-0.635) by 0.35(0.33-0.52); Pedicel 0.065(0.06-0.08) long; movable finger 0.39(0.355-0.54) long. Leg IV: entire femur 0.52(0.42-0.65) by 0.215(0.18-0.25); tibia 0.36(0.31-0.46) by 0.125(0.105-0.15).

**REMARKS:** At hand is a ♀ taken from shrubs on Grand Cayman, CAYMAN ISLANDS, 21-V-1973, by P. W. Hummelinck. It is slightly smaller than any of the Jamaican specimens, but otherwise is similar. Until further material should prove otherwise, it must be considered a representative of *A. jamaicensis*.

*Antillochernes biminiensis* Muchmore, NEW SPECIES

Fig. 12,13

**MATERIAL:** Holotype ♀ (WM 5374.01001) from South Bimini Island, BAHAMAS, VIII-1951, C. and P. Vaurie [in AMNH].

**DIAGNOSIS:** A medium sized species (carapace length 0.755 mm) with,

for the genus, very slender appendages (palpal femur 2.95 and chela 3.3 times as long as broad); palpal hand no deeper than broad.

DESCRIPTION OF FEMALE (MALE UNKNOWN): Body with characteristic pattern (cf. Fig. 1). Carapace well sclerotized but thinner at posterolateral margins and with distinct keel; both transverse furrows shallow; 2 smooth eyespots; surface covered with large rounded granules, except posterolaterally; with 45-50 narrow clavodentate setae. Tergites and sternites distinctly divided; (tergal sclerites 7 and 8 on left side abnormally fused together) surfaces scaly; dorsal setae narrow clavodentate, ventral setae mostly acuminate. Tergal chaetotaxy 10:10:11:12:11:12:10:12:11:10: T6T:1; sternal chaetotaxy 31:(2)8(2):(1)6(1):15:15:15:14:13:14:T6T:1; anterior genital operculum with a loose cluster of 25 small setae on a separate central sclerite and 3 setae on each side posterior to this; posterior operculum with close-set row of 8 small setae at middle of anterior margin. Spermathecae not apparent (lost during preparation?). Pleural membranes with 1-5 clavodentate setae on each side in segments 4-10.

Chelicera about 1/3 as long as carapace; hand with 5 setae, *b* and *sb* denticulate, *es* long, acuminate; flagellum of 3 setae, distal one finely denticulate; galea rather short, with 3-4 small rami.

Palp rather slender for the genus (Fig. 12); femur 2.95, tibia 2.65, and chela 3.3 times as long as broad; hand 1.95 times as long as deep; movable finger 0.78 as long as hand. The depth of the palpal hand is slightly less than the width. Surfaces of trochanter, femur, and tibia heavily granulate, chelal hand with low, inconspicuous granules, fingers smooth; setae long clavodentate to acuminate. Trichobothria positioned as in others of the genus (Fig. 13). Fixed finger with 41 and movable finger with 46 marginal teeth; each finger with 6 external and 1 internal accessory teeth; venom apparatus in movable finger only.

Legs relatively slender for the genus; leg IV with entire femur 3.15 and tibia 3.75 times as long as deep. Tarsus IV with slit sensillum proximad of middle and long tactile seta 2/3 distance from proximal end.

MEASUREMENTS (MM): Body length 2.53. Carapace length 0.755. Chelicera 0.265 long. Palpal femur 0.635 by 0.215; tibia 0.62 by 0.235; chela (without pedicel) 1.08 by 0.325; hand 0.73 by 0.32; pedicel 0.08 long; movable finger 0.49 long. Leg IV: entire femur 0.58 by 0.185; tibia 0.41 by 0.11; tarsus 0.32 by 0.08.

*Antillochernes floridensis* Muchmore, NEW SPECIES

Fig. 14-16

MATERIAL: Holotype ♀ (WM 4963.01001) in *Myrica* at the St. Marks Wildlife Refuge, Leon County, FLORIDA, 17-VI-1975, J. Rey and E. McCoy [in FSCA].

DIAGNOSIS: *A. floridensis* is a medium-sized species (carapace length 0.77 mm) which can be distinguished from others in the genus by the shape of the palpal chela, which is relatively slender when viewed from above ( $l/w = 2.75$ ) but has the depth noticeably greater than the width (0.41 vs. 0.35 mm).

DESCRIPTION OF FEMALE (MALE UNKNOWN): Body with characteristic pattern (cf. Fig. 1), though both tergal and sternal sclerites more extensive than in other species of the genus. Carapace well sclerotized but with

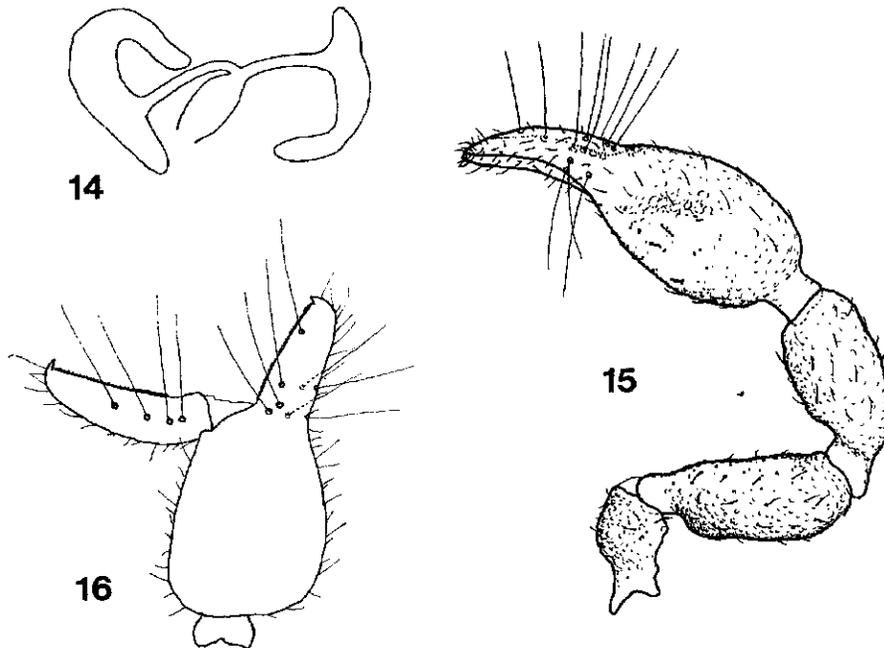


Fig. 14-16. *Antillochernes floridensis* Muchmore, new species. 14) spermathecae of female; 15) dorsal view of right palp; 16) lateral view of left chela.

distinct keel near middle of posterior margin; with distinct anterior furrow and faint posterior furrow; 2 smooth eyespots; in front of posterior furrow, surface covered with small rounded granules; behind posterior furrow, surface with low smooth elevations at center (on keel) but becoming smooth laterally; with about 50 narrow clavodentate setae. Tergites and sternites distinctly divided; surfaces scaly; dorsal setae narrow clavodentate, ventral seta mostly acuminate. Tergal chaetotaxy 9:12:11:12:14:12:13:12:12:12: T8T:2; sternal chaetotaxy 30:(2)12(3):(1)7(1):10:15:17:16:19:14: T3TT2T:2; anterior genital operculum with loose cluster of about 25 small setae at middle on indistinctly separate sclerite and 3-4 setae on each side posterolateral to this; posterior operculum with close set row of 12 small setae at middle of anterior margin. Spermathecae as shown in Fig. 14. Pleural membranes with 3-8 short clavodentate setae on each side in segments 3-10, and 1 on the right side in segment 2.

Chelicera about 1/3 as long as carapace; hand with 5 setae, *b* and *sb* denticulate, *es* long, acuminate; flagellum of 3 setae, distal one finely denticulate; galea slender, with 4-5 small rami.

Palp not as robust as in other species of the genus (Fig. 15); femur 2.45, tibia 2.25, and chela 2.75 times as long as broad; hand 1.25 times as long as deep; movable finger nearly as long (0.96) as hand. Trochanter, femur, tibia and chela covered with low, rounded granules, fingers smooth; setae denticulate to acuminate. Trichobothria positioned as in other members of the genus (Fig. 16). Fixed finger with 36 and movable finger with 41 marginal teeth; each finger with 9-10 external and 2 internal accessory teeth; venom apparatus in movable finger only.

Legs less robust than in other species of the genus; leg IV with entire femur 3.0 and tibia 3.5 times as long as deep. Tarsus IV with slit sensillum proximad of middle and long tactile seta  $2/3$  distance from proximal end.

MEASUREMENTS (MM): Body length 2.95. Carapace length 0.77. Chelicera 0.24 long. Palpal femur 0.59 by 0.24; tibia 0.56 by 0.25; chela (without pedicel) 0.96 by 0.35; hand (without pedicel) 0.51 by 0.41; pedicel 0.09 long; movable finger 0.49 long. Leg IV: entire femur 0.57 by 0.19; tibia 0.42 by 0.12.

*Antillochernes cruzensis* Muchmore, NEW SPECIES

Fig. 17-19

MATERIAL: Holotype ♀ (WM 5656.01001) in tunnel of wood borer in tree, Golden Grove, St. Croix, U. S. VIRGIN ISLANDS, 10-VI-1979, M. Ivie [in FSCA].

DIAGNOSIS: *A. cruzensis* is the largest known species in the genus (carapace length  $> 0.9$  mm), and has both transverse furrows on the carapace distinct.

DESCRIPTION OF FEMALE (MALE UNKNOWN): Body with characteristic pattern (cf. Fig. 1). Carapace mostly well sclerotized, but with distinct keel

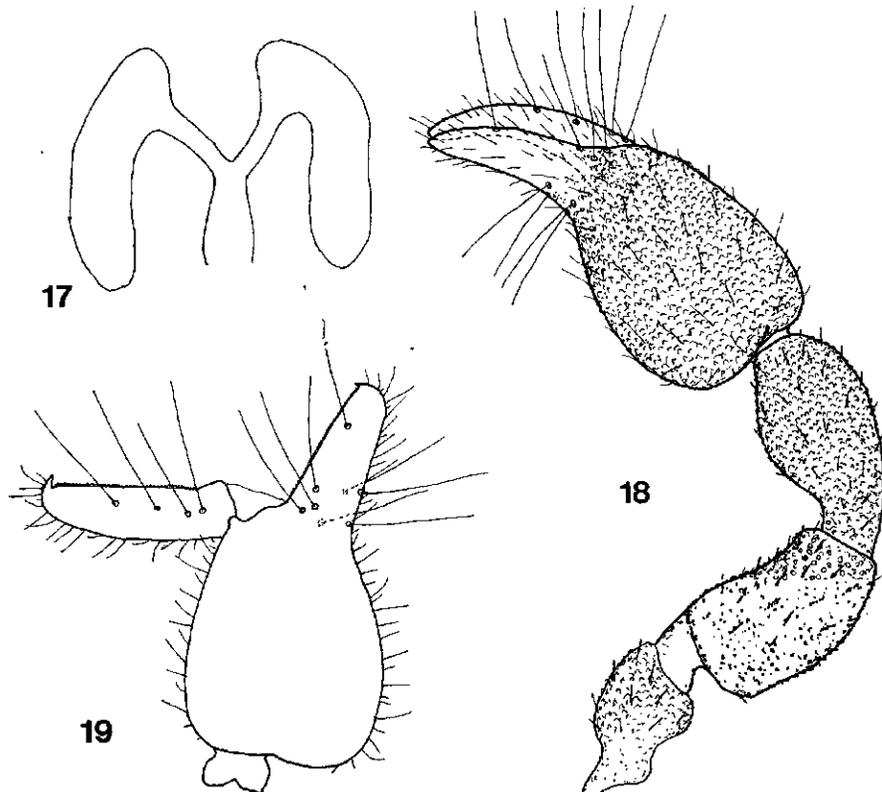


Fig. 17-19. *Antillochernes cruzensis* Muchmore, new species. 17) spermathecae of female; 18) dorsal view of right palp; 19) lateral view of left chela.

near middle of posterior margin; with 2 distinct transverse furrows; 2 smooth eyespots; surface covered with smoothly rounded granules; with about 65 short, clavodentate setae. Tergites and sternites distinctly divided, with heavily sclerotized area of each half tergite or sternite broadly bordered by thin membranes; surfaces scaly to granulate; setae of tergites clavodentate, those of sternites acuminate to denticulate. Tergal chaetotaxy 11:11:12:13:14:14:14:16:15:13:T10T:2; sternal chaetotaxy 30:(2)12(2):(1)9(1):14:13:16:19:22:16:T3TT4T:2; anterior genital operculum with 26 small setae clustered on a distinct central sclerite and 2 setae on each side of this; posterior operculum with a row of 12 small setae at the middle of the anterior margin. Spermathecae as shown in Fig. 17. Pleural membranes with 2-8 short, clavodentate setae on each side in segments 3-10.

Chelicera about 1/3 as long as carapace; hand with 5 setae, *b* and *sb* finely denticulate, *es* long, acuminate; flagellum of 3 setae, the distal one denticulate; galea slender, with 4-5 small rami.

Palp robust (Fig. 18); palpal femur 2.35, tibia 2.4, and chela 2.25 times as long as deep; movable finger 0.95 as long as hand. Trochanter, femur, tibia, and chelal hand heavily granulate, finger essentially smooth; setae clavodentate to acuminate. Trichobothria positioned as in other members of the genus (Fig. 19). Fixed finger with 44 and movable finger with 49 contiguous teeth; each with about 9 external and 3 internal accessory teeth; venom apparatus in movable finger only.

Legs rather robust; leg IV with femur 2.65 and tibia 3.3 times as long as deep. Tarsus IV with slit sensillum near middle and long tactile seta 2/3 distance from proximal end.

MEASUREMENTS (MM): Body length 3.65. Carapace length 0.925. Chelicera 0.29 long. Palpal femur 0.77 by 0.325; tibia 0.76 by 0.32; chela (without pedicel) 1.23 by 0.55; hand (without pedicel) 0.665 by 0.59; pedicel 0.11 long; movable finger 0.635 long. Leg IV: entire femur 0.72 by 0.27; tibia 0.53 by 0.16.

*Antillochernes muchmorei* (Dumitresco and Orghidan), NEW COMBINATION

*Parachernes muchmorei* Dumitresco and Orghidan 1977: 118-21, Fig. 16-9, 23, 24; types in the Institut de Spéologie "Emile Racovitza", Bucarest, Roumania.

Because it has all the characteristics of the genus *Antillochernes*, including, importantly, the possession of setae on the pleural membranes, this species must be considered a member of that genus.

DIAGNOSIS: Much like *A. floridensis* with relatively slender chela, as seen from above ( $l/w = 2.6$ ), but smaller (carapace length  $< 0.6$  mm) and with pleural setae apparently confined to segments 8-10.

REMARKS: According to Dumitresco and Orghidan (1977: 120), the holotype of *P. muchmorei* bears 2 or 3 setae on the pleural membranes of segments 8-10; presumably such setae do not occur farther anteriorly. While this situation is different from that in other species of *Antillochernes*, where setae occur opposite segments 3-10, the very presence of pleural setae here seems sufficient to remove this species from *Parachernes*. It should be noted that the statement of Dumitresco and Orghidan (loc. cit.) concerning the occurrence of setae in the pleural membranes of *Parachernes bisetus* (Muchmore and Alteri 1974) is incorrect; in fact, no such setae occur in *P. bisetus*.

Further, it appears that for part of their description of the female of *P. muchmorei*, Dumitresco and Orghidan were dealing with an abnormal individual or with a tritonymph misidentified as a female. The scanty sclerotization of the carapace (their Fig. 23), the small number of setae on the tergites (p. 121), and especially the chaetotaxy of the genital opercula (Fig. 19a) are all characteristic of tritonymphs, not adult females, of *Antillochernes* (and similarly for *Parachernes*). It is likely that the female is, in these characters, actually more like females of other species described above.

*Antillochernes* species

In the collection of the AMNH is a tritonymph belonging to this genus, taken at Lajas, southwestern PUERTO RICO, 13-III-1961, by A. M. Nadler. In view of our scanty information about nymphs in *Antillochernes*, no certain identification can be made; however, because of the large number of setae (up to 6 per segment) on the pleural membranes, it appears to represent an unnamed species.

KEY TO SPECIES OF *Antillochernes*

- 1. Setae on pleural membranes in abdominal segments 3-10 ..... 2
- 1'. Setae on pleural membranes in abdominal segments 8-10; from Cuba ..... *muchmorei* (Dumitresco and Orghidan)
- 2(1). Carapace length greater than 0.9 mm; from St. Croix, U. S. Virgin Islands ..... *cruzensis* Muchmore, n. sp.
- 2'. Carapace length less than 0.9 mm ..... 3
- 3(2'). Palpal chela with 1/w greater than 2.7 ..... 4
- 3'. Palpal chela with 1/w less than 2.7 ..... 5
- 4(3). Depth of chelal hand noticeably greater than width; from Florida ..... *floridensis* Muchmore, n. sp.
- 4'. Depth of chelal hand about equal to width; from Bimini Island, Bahamas ..... *biminiensis* Muchmore, n. sp.
- 5(3'). Carapace with 1 transverse furrow or none; from Jamaica ..... *jamaicensis* Muchmore, n. sp.
- 5'. Carapace with 2 distinct transverse furrows, from Grand Bahama Island, Bahamas ..... *bahamensis* Muchmore, n. sp.

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Contribution No. 571, Bureau of Entomology, Division of Plant Industry, Florida Department of Agriculture and Consumer Service, Gainesville, FL 32602 USA.

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PSEUDOSCORPIONS FROM FLORIDA AND THE  
CARIBBEAN AREA. 13. NEW SPECIES OF  
*TYRANNOCHTHONIUS* AND *PARALIOCHTHONIUS*  
FROM THE BAHAMAS, WITH DISCUSSION OF THE  
GENERA (CHTHONIIDAE)

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ABSTRACT

*Tyrannochthonius bahamensis* and *Paraliochthonius carpenteri* are described, from South Bimini and San Salvador islands, respectively. Diagnostic characters of the genera *Tyrannochthonius* and *Paraliochthonius* are compared.

RESUMEN

Se describen *Tyrannochthonius bahamensis* y *Paraliochthonius carpenteri*, nuevas especies, de las islas South Bimini y San Salvador, respectivamente. Se comparan caracteres diagnósticos de los géneros *Tyrannochthonius* y *Paraliochthonius*.

Though it was reported some time ago that pseudoscorpions occur in the Bahamas (Vaurie 1952), none from that area has been identified until very recently (Muchmore 1984).

Here are reported 2 new species of the family Chthoniidae from the islands of South Bimini and San Salvador.

Genus *Tyrannochthonius* Chamberlin, 1929

..TYPE SPECIES: *Chthonius terribilis* With, 1906: 69; from Island of Koh Chang and Lam Ngob, Siam (Chamberlin 1929: 74).

Representatives of *Tyrannochthonius* are apparently found around the world in tropical and subtropical areas. In the Caribbean region 8 species of the genus have been identified: *insulae* Hoff (1946) from Trinidad, *curazavius* Hummelinck (1948) from Curaçao, and *innoxius*, *callidus*, *proximus*, *imitatus*, *fastuosus*, and *lautus*, all described from Jamaica by Hoff (1959). Beier (1976a) reported *proximus* and *imitatus* from the Dominican Republic, and at the same time placed *fastuosus* and *lautus* in the synonymy of *imitatus*. Other as yet undescribed forms are present in the West Indies and in Florida (personal observation). A review of *Tyrannochthonius* is currently being prepared by D. R. Malcolm.

*Tyrannochthonius bahamensis* Muchmore, NEW SPECIES

MATERIAL: Holotype ♂ (WM 5373.01004) and 10 paratypes (6 ♂, 4 ♀)

from South Bimini Island, BAHAMAS, V-VII-1951, M. A. Cazier and C. and P. Vaurie. Types are in the American Museum of Natural History.

DIAGNOSIS: Much like *T. insulae* Hoff from Trinidad but with 6 setae, rather than 4, on tergites 4-10. In the key to Jamaican species of *Tyrannochthonius* (Hoff 1959: 38), *bahamensis* will key out to couplet 3; but it differs from both *callidus* and *innovius* in having the movable chelal finger much longer (1.75-1.95) than the hand.

DESCRIPTION: ♂ and ♀ very similar though ♀ usually a little larger. Carapace about as wide as long; epistome small, triangular, closely flanked by 2 setae which are very close to the edge of the carapace (Fig. 1); chaetotaxy d4d-4-4-2-2, the dwarf setae (d) lying anterior and ventral to the eyes; 4 corneate eyes, posterior ones less well developed than anterior. Coxa I medially with a prominent apical projection; coxal chaetotaxy 2-2-1:3-0:2-1-CS:2-3:2-2; each coxa II with a slightly oblique transverse row of 5-6 incised spines (CS) (Fig. 2).

Abdomen typical. Tergal chaetotaxy usually 4:4:4:6:6:6:6:6:6:4:T2T:0, but occasionally only 5 setae on tergite 4; sternal chaetotaxy of ♂ about 9: [4-4]:(3)10-10/8(3):(4)4(4):9:9:8:8:7:6:0:2, that of ♀ similar but posterior operculum with a row of 5-6 setae.

Chelicera about 7/8 as long as carapace; hand with 5 setae; flagellum of 7-8 irregularly pinnate setae; fixed finger with 8-10 teeth graded from large to tiny toward base; movable finger with about 12 small, subequal teeth; galea a low elevation in ♀, barely discernible in ♂.

Palp as shown in Fig. 3; femur 3.55-3.8, tibia 1.6-1.8, and chela 4.25-

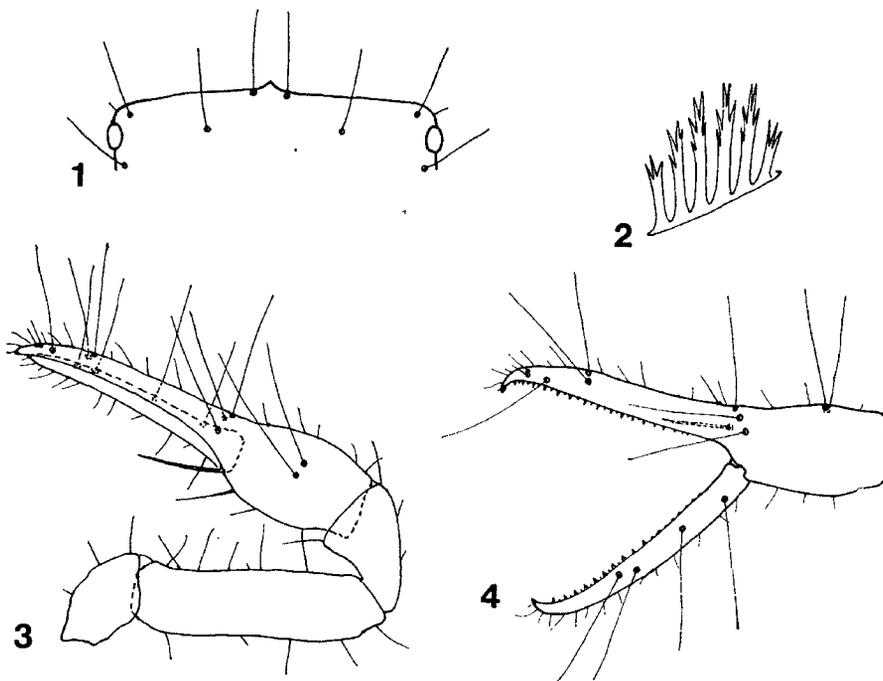


Fig. 1-4. *Tyrannochthonius bahamensis* Muchmore, new species. 1) anterior part of carapace; 2) coxal spines; 3) dorsal view of right palp; 4) lateral view of left chela.

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4.65 times as long as wide; hand 1.45-1.7 times as long as deep; movable finger 1.75-1.95 times as long as hand. Trichobothria as shown in Fig. 4; on movable finger *sb* midway between *st* and *b* or slightly nearer to *b*. Hand with 1 large spinelike seta on medial side near base of fingers and 1 or 2 other prominent setae proximad. Fixed finger with 15-17 widely spaced macrodenticles and 10-14 interspersed microdenticles (Fig. 4); movable finger with 10-12 widely spaced macrodenticles distally and 8-10 interspersed microdenticles, and 5-8 very low rounded teeth basally; sensillum on lateral side of movable finger close to dental margin near level of trichobothrium *st*.

Legs robust; leg IV with entire femur 2.2-2.3 times as long as deep. Long tactile setae on tibia, metatarsus, and telotarsus of leg IV.

MEASUREMENTS (MM): Figures given first for the holotype followed in parentheses by ranges for the 10 paratypes. Body length 0.98 (1.0-1.15). Carapace length 0.31 (0.31-0.35). Chelicera 0.27 (0.27-0.31) long. Palpal femur 0.30 (0.315-0.34) by 0.08 (0.085-0.095); tibia 0.16 (0.16-0.18) by 0.095 (0.095-0.105); chela 0.48 (0.47-0.52) by 0.11 (0.105-0.125); hand 0.17 (0.16-0.185) by 0.11 (0.105-0.125); movable finger 0.30 (0.31-0.345) long. Leg IV: entire femur 0.32 (0.31-0.34) by 0.14 (0.14-0.15); tibia 0.215 (0.215-0.235) by 0.06 (0.055-0.065); metatarsus 0.095 (0.10-0.115) by 0.05 (0.045-0.055); telotarsus 0.185 (0.19-0.21) by 0.03 (0.03-0.035).

REMARKS: With reference to Mahnert (1979: 742), *Tyrannochthonius bahamensis* belongs to that group of species within the genus wherein the movable chelal finger does not have a prominent basal apodeme. It seems likely to me that the species with the strongly modified finger base actually belong to the genus (or subgenus) *Lagynochthonius* Beier (1951: see also Chamberlin 1962).

Genus *Paraliochthonius* Beier, 1956

TYPE SPECIES: *Chthonius singularis* Menozzi, 1924: 1; from Italy (Beier 1956: 58).

In the general area of Florida and the Caribbean, 3 species of *Paraliochthonius* have been identified: *insulae* Hoff (1963) from Jamaica, *puertoricensis* Muchmore (1967) from Ramosito Key, Puerto Rico, and *weygoldti* Muchmore (1967) from Big Pine Key, Monroe County (not Dade County), Florida.

Representatives of *Paraliochthonius* are typically found on the sea shore, often in debris in the tidal zone of beaches (Muchmore 1972). A single specimen of *P. singularis* (Menozzi) has been recorded from a cave traversed by a warm spring near the coast in Anatolia (Beier 1963, 1965). *Paraliochthonius strinatii* Beier, reported from a cave in Guatemala, actually belongs in another genus (see below), and the cavernicolous forms from New Zealand assigned by Beier (1976b) to *Paraliochthonius* are in taxonomic limbo. Therefore, it is of interest to report here a genuine cavernicolous species of *Paraliochthonius*, collected by J. H. Carpenter on San Salvador Island, Bahamas.

*Paraliochthonius carpenteri* Muchmore, NEW SPECIES

MATERIAL: Holotype ♀ (WM 6079.01003) and 4 paratypes (1 ♂, 3 ♀) from Lighthouse Cave, San Salvador, BAHAMAS, 5-VI-1982; 2 ♀ paratypes

from same place, 19-VI-1980; all collected by J. H. Carpenter. The holotype and 4 paratypes (1 ♂, 3 ♀) have been mounted on microscope slides. Unfortunately, the single ♂ is fragmented and most of the appendages are missing. Types are in the Florida State Collection of Arthropods, Gainesville.

DIAGNOSIS: The new species is much larger than its nearest known neighbor, *P. weygoldti* Muchmore from Big Pine Key, Florida, and about the same size as *P. puertoricensis* Muchmore from Puerto Rico. From the latter it may be distinguished by the more slender palpal chela (total  $l/w = 4.75-4.9$  and hand  $l/d = 1.9$ ).

DESCRIPTION: With the characters of the genus (Muchmore 1972). Male smaller than ♀. Carapace and palps light brown, other parts much lighter. Carapace slightly narrowed posteriorly; epistome long, slightly dentate, the nearest setae some distance from the base (Fig. 5); chaetotaxy of holotype d4d-4-4-2-2, the setae long and heavy except for the dwarf setae (d) which are short and thin; one paratype ♀ lacking the dwarf setae; 4 corneate eyes present. Coxal area typical; a rounded process on anteriomedial corner of coxa I; coxal chaetotaxy 2-2-1:3-1 (or 0):2-1-CS:2-3:2-3; each coxa II with 5 or 6 irregularly dentate spines (CS) in an oblique row (Fig. 6).

Abdomen typical of the genus; tergal chaetotaxy of holotype 4:4:4:7:7:

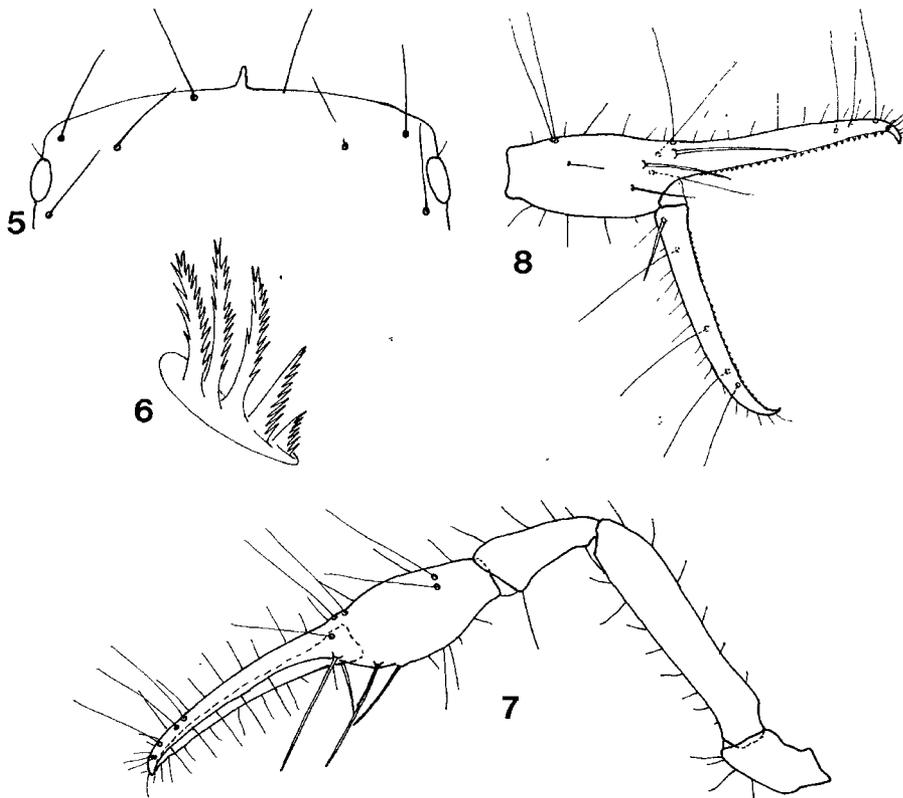


Fig. 5-8. *Paraliochthonius carpenteri* Muchmore, new species. 5) anterior part of carapace; 6) coxal spines; 7) dorsal view of right palp; 8) medial view of left chela.

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7:7:8:6:4:T2T:0; sternal chaetotaxy 11:(3)7(3):(3)8(3):10:9:8:9:9:9:0:2.

Chelicera about 7/8 as long as carapace; hand with 5 setae; flagellum of 7 or 8 pinnate setae, the distal one curved; fixed finger with 1 medium and 4-6 smaller, rounded teeth; movable finger with 5-6 small, irregular teeth; galea represented by a very low elevation of the finger margin.

Palp rather slender for the genus (Fig. 7); femur 4.75-4.9, tibia 2.2-2.35, and chela 4.65-4.8 times as long as wide; hand 1.9 times as long as deep; movable finger 1.51-1.57 times as long as hand. Trichobothria as shown in Fig. 8; on movable finger *sb* closer to *st* than to *b*. Chelal hand with 3 heavy spinelike setae on medial side near base of fixed finger and a more slender one near the middle; movable finger with a heavy seta on medial side near base. Fixed chelal finger with 28-30 spaced, acute teeth; movable finger with 36-38 teeth, retroconical distally, but becoming low, sharp denticles proximally. Movable finger with a small sensillum on lateral side about midway between trichobothria *st* and *sb*.

Legs rather slender: leg IV with entire femur 2.8-3.0 and tibia 4.5-4.6 times as long as deep. Leg IV with long tactile setae on tibia and both tarsi.

MEASUREMENTS (MM): Figures given first for the holotype followed in parentheses by ranges for the 3 mounted ♀ paratypes. Body length 2.0 (2.0-2.1). Carapace length 0.63 (0.63-0.66). Chelicera 0.55 (0.55-0.59) long. Palpal femur 0.785 (0.74-0.83) by 0.16 (0.155-0.175); tibia 0.40 (0.39-0.435) by 0.18 (0.17-0.19); chela 1.14 (1.125-1.21) by 0.245 (0.235-0.26); hand 0.46 (0.445-0.49) by 0.245 (0.235-0.26); movable finger 0.72 (0.69-0.74) long. Leg IV: entire femur 0.68 (0.66-0.73) by 0.23 (0.22-0.26); tibia 0.48 (0.475-0.51) by 0.105 (0.105-0.11); metatarsus 0.215 (0.20-0.215); telotarsus 0.465 (0.43-0.48) by 0.055 (0.05-0.06).

ETYMOLOGY: The new species is named for Jerry H. Carpenter who collected the specimens and brought them to my attention.

ECOLOGY: Lighthouse Cave is in the northeastern corner of San Salvador, about 1 km from the ocean. Though it is not obviously connected to the sea, its lower passages are flooded with saltwater, which is tidal. The pseudoscorpions were found under small sandstone chips on an island in the water passage of Hydrology Hall in the southern section of the cave in complete darkness; about 40 m from the entrance. In the same area of the cave were found 3 species of terrestrial isopods and a blind terrestrial snail (Carpenter 1981 and personal communication).

REMARKS: While *P. carpenteri* is not strikingly adapted for life in the cave, it is larger and has more slender palps than the other species reported from the West Indies.

COMPARISON OF *Tyrannochthonius* AND *Paraliichthonius*

In spite of the effort of Chamberlin (1962), the genera of the tribe Tyrannochthoniini have not been clearly defined, except for *Troglochthonius* Beier which is known from only 2 cavernicolous relicts in southern Europe. *Morikawia* Chamberlin (1962) has been shown to be synonymous with *Paraliichthonius* Beier (Muchmore 1972) and *Lagynochthonius* Beier has been both loosely used and neglected.

*Tyrannochthonius* and *Paraliichthonius* have been much confused in recent years, but I now find that they can be distinguished easily in spite

of basic similarities. As Chamberlin (1962) pointed out, they are both in the chthoniid tribe Tyrannochthoniini, having trichobothria *ib* and *isb* transversely paired in a median or subbasal position on dorsum of chelal hand, marginal teeth of chelal fingers acute and spaced, no intercoxal tubercle, and coxal spines present only on pedal coxae II. They may be separated by considering the following characters:

- 1) Epistome—In *Tyrannochthonius* this is usually small and triangular and is closely flanked by the 2 central anterior carapacial setae, as is illustrated by With for the type species, *Chthonius terribilis* (1906: Text Fig. 10).

In *Paraliochthonius* the epistome is usually long and pointed and the 2 central carapacial setae are placed at some distance from its base, as shown by Menozzi for the type species, *Chthonius singularis* (1924: Fig. 1) and by Beier (1965: Fig. 2).

- 2) Coxal spines—In *Tyrannochthonius* these are mainly long, clavate blades which are terminally incised, sometimes with additional sub-terminal incisions or spinules (see With 1906: Tab. I, Fig. 1h).

In *Paraliochthonius* the coxal spines are usually spinose on both sides nearly to the base (“beiderseits gefiederten”, according to Beier 1964: 77).

- 3) Chelal teeth—In *Tyrannochthonius* these are usually heterodentate on both fingers, at least in the distal halves; that is, the tooth row consists of alternating large, pointed macrodentacles and small, sometimes rudimentary, microdentacles. Microdentacles are not shown by With for *C. terribilis* (1906: Text Fig. 11); however, With might have overlooked tiny microdentacles, which are sometimes difficult to see except under high magnification of favorably oriented material.

In *Paraliochthonius* the chela is truly homodentate; that is, the dental row consists of a series of conical or retroconical teeth which do not alternate in size or shape, even though they may differ from one end of the row to the other. This feature is clearly shown for *P. singularis* by Beier (1965: Fig. 2).

- 4) Spinelike or guard setae on the chela—in *Tyrannochthonius* there is at most one large heavy seta on the medial side of the chelal hand near the base of the fixed finger; sometimes this seta is reduced or absent (none is shown or mentioned by With 1906); and sometimes, as in *T. bahamensis* above, there may be other setae which are larger than most vestitural setae but distinctly smaller than the major spinelike seta.

In *Paraliochthonius* there are usually 3 or 4 very heavy setae on the medial side of the chelal hand and usually a similar seta on the base of the movable finger. This is clearly shown for *P. singularis* by Menozzi (1924: Fig. 1) and Beier (1965: Fig. 2).

- 5) Trichobothria of movable chelal finger—In *Tyrannochthonius* trichobothrium *sb* is located midway between *st* and *b* or a little nearer to *b* (see With 1906: Text Fig. 11).

In *Paraliochthonius* *sb* is located nearer to *st* than to *b*, usually more distinctly so than is shown for *P. singularis* by Beier (1965: Fig. 2).

It is not within the purview of this paper to review the numerous species

## Muchmore: New *Tyrannochthonius* & *Paraliochthonius* 125

assigned to *Tyrannochthonius*, *Paraliochthonius* and *Morikawia*. However, the following species can be dealt with easily.

### *Tyrannochthonius strinatii* (Beier), NEW COMBINATION

*Paraliochthonius strinatii* Beier, 1974: 101.

The holotype and allotype from Cueva Chirrepeck, Alta Verapaz, GUATEMALA, have been examined. It is obvious that this species belongs in *Tyrannochthonius* as defined above. Features seen here, characteristic of *Tyrannochthonius*, are: the very small epistome with closely adjacent setae; the heterodentate chelal fingers; the occurrence of only 1 short, spinelike seta on the chelal hand; the placement of trichobothria on the movable chelal finger; and the inland location of the collection site. In all these and other general features it closely resembles *T. troglobius* and *T. pallidus* from caves in Mexico (Muchmore 1969, 1973), but it is much smaller and more robust than those species and has 4 eyes rather than 2.

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EFFECT OF SEXUAL EXPERIENCE ON MALE MATING  
SUCCESS IN A LĚK FORMING TEPHRITID  
*ANASTREPHA SUSPENS*A (LOEW)<sup>1</sup>

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ABSTRACT

Recently mated *Anastrepha suspensa* (Loew) males are less likely to copulate than virgin rivals when placed in competition. This effect is lost after 2 h. Mated males are as active as virgins in sexual advertising and the lack of mated male success appears to be due to female rejection. Females may be discriminating against males made relatively infertile through exhaustion of accessory gland fluids. Postcopula male unattractiveness

<sup>1</sup>Diptera: Tephritidae.

<sup>2</sup>Employed through a cooperative agreement between the Department of Entomology and Nematology, University of Florida and the Insect Attractants, Behavior, and Basic Biology Research Laboratory, Gainesville.

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Recently mated *Anastrepha suspensa* (Loew) males are less likely to copulate than virgin rivals when placed in competition. This effect is lost after 2 h. Mated males are as active as virgins in sexual advertising and the lack of mated male success appears to be due to female rejection. Females may be discriminating against males made relatively infertile through exhaustion of accessory gland fluids. Postcopula male unattractiveness

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might decrease the expected high variance in male sexual success associated with lekking species.

#### RESUMEN

Cuando están puestos en la competencia, los machos apareados de *Anastrepha suspensa* tienen menos probabilidad de copularse que rivales vírgenes. Se pierde este efecto después de 2 horas. Los machos apareados están tan activos en la ostentación sexual como los machos vírgenes y la falta de éxito de los machos apareados parece ser por causa del rechazo de ellos por las hembras. Puede ser que las hembras discriminan en contra de los machos los cuales vuelven relativamente infértiles por el agotamiento de los fluidos de la glándula accesoria. La falta de atractividad de los machos después de copularse podría rebajar la varianza alta esperada en los éxitos de los machos que está asociada con las especies las cuales utilizan los *leks*.

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Male investment in gametes and associated fluids is often considered negligible. However, sufficient energy and material can be expended in copulation to realistically limit a male's sexual success (Dewsbury 1982). Females recognize these periods of relative infertility and discriminate against recently mated males in a fish, the lemon tetra, *Hyphessobrycon pulchripinnis* Ahl (Nakatsuru and Kramer 1982), and an acalypterate fly, *Drosophila melanogaster* (L) (Markow et al. 1978). In the latter, males regain their attractiveness within 24 h, apparently upon the refilling of the accessory glands whose products are necessary for the transfer of sperm (see Lefevre and Jonsson 1962). Females recognize freshly mated males by scent (Markow 1984).

Caribbean fruit flies, *Anastrepha suspensa* (Loew), copulate within male aggregations (*leks*) (Dodson 1982, Burk 1983). This is a mating system believed to have evolved through selection exerted by choosing females and is generally considered to generate large variances in male reproductive success (Alexander 1975, Bradbury 1981). That is, if females can more accurately and cheaply compare males that are close to one another, they may prefer to choose mates from high male density "spots." If so, males will in turn be selected to aggregate. Assuming females have similar criteria for judging male quality, then the convenience of having many potential mates together should result in a small percentage of males acquiring the majority of copulations. Depending on female arrival rates in *leks*, a postcopula decline in male attractiveness could tend to reduce the expected differences in male sexual success.

Evidence is presented here that recently mated male caribflies are in fact less likely to mate than virgin rivals; that even males that would normally be preferred because of their large size are relatively unsuccessful if freshly mated, and that their failure may be due to female rejection rather than a loss of courting vigor.

#### METHODS

Flies were removed as 1- to 3-day-old virgins from laboratory colonies. After reaching sexual maturity (10 to 12 days of age) they were placed in 7.5 cm x 7.5 cm screen wire cylinders for observation.

To determine if virgin or experienced males are more likely to mate, one of each type was placed with a virgin female and sexual activity was recorded for an hour. As soon as copulation occurred the flies were taken aside for weighing. Male virgins were always the smaller of the 2 competitors. This minimized the possibility of confusing the attractiveness of virginity with the appeal of size. Normally, females overwhelmingly prefer bigger males as mates (Burk and Webb 1983). Experienced males had had their sexual encounters: 1) immediately prior to introduction ( $n = 33$ ), 2) 2 h earlier ( $n = 20$ ), and 3) 24 h earlier ( $n = 21$ ). These various passages of time allowed estimation of how long any postcopula effect on sexual success endures.

Since failure to mate may be due to female rejection or male disability, the sexual vigor of recently mated males was estimated through their acoustic behavior. Males sexually advertise by beating their wings to produce an attractive calling song that consists of repeated  $\sim 1/2$ -sec pulse trains (bursts) (Webb et al. 1983). The pulse trains produced by 3 caged males were counted for both virgin males and just previously mated males during alternating 5-min periods for 1 h. A total of 9 cages of each type were observed.

#### RESULTS

Unmated males are more likely to copulate than experienced rivals that have just completed coupling ( $X^2 = 8.8$ ,  $p < 0.005$ ) (Fig. 1). This difference is especially noteworthy when the smaller size of the virgins is noted ( $\bar{X} = 8.1$  mg vs.  $\bar{X} = 10.2$  mg or 79% the weight of their competitors). Larger males are generally more sexually successful (Burk and Webb 1983). After 2 h, the advantage of inexperience is lost and after 24 h, clearly reversed ( $X^2 = 5.8$ ,  $p < 0.025$ ). The typical pattern of large male success is clearly established (male sizes were as follows: 2 h, 9.5 mg vs. 12.4 mg; 24 h, 6.8 vs. 9.6 mg).

Recently mated males are statistically as sexually vigorous as the unmated males. Their solicitation of sex *via* acoustic advertisement occurs at a similar rate (just mated males 0.20 pulse trains/fly per min vs. virgin males 0.15 pulse trains/fly per min). Mated males produced more pulse trains in 14 of 24 adjacent observation periods.

#### DISCUSSION

The cause of freshly mated male rejection is unknown. However, the  $\sim 2$ -h long recovery of attractiveness is similar to the time required to recharge accessory glands in another acalypterate fly (*D. melanogaster*, Markow et al 1978). Females are presumably avoiding less fertile mates.

It is interesting that females would trade mate size for time. Keeping in mind the artificiality of the conditions, the value of providing a big father for one's offspring would appear to be less than a 2-h wait. The mean duration of leks in the field is unknown, although in theory they could last throughout an afternoon. If durations are often only a few hours, perhaps the choice of a smaller male is better than a day's wait and a chance at a larger mate.

Postcopula unattractiveness could influence sterile male release techniques for control of *A. suspensa* and perhaps other tephritids. If operational

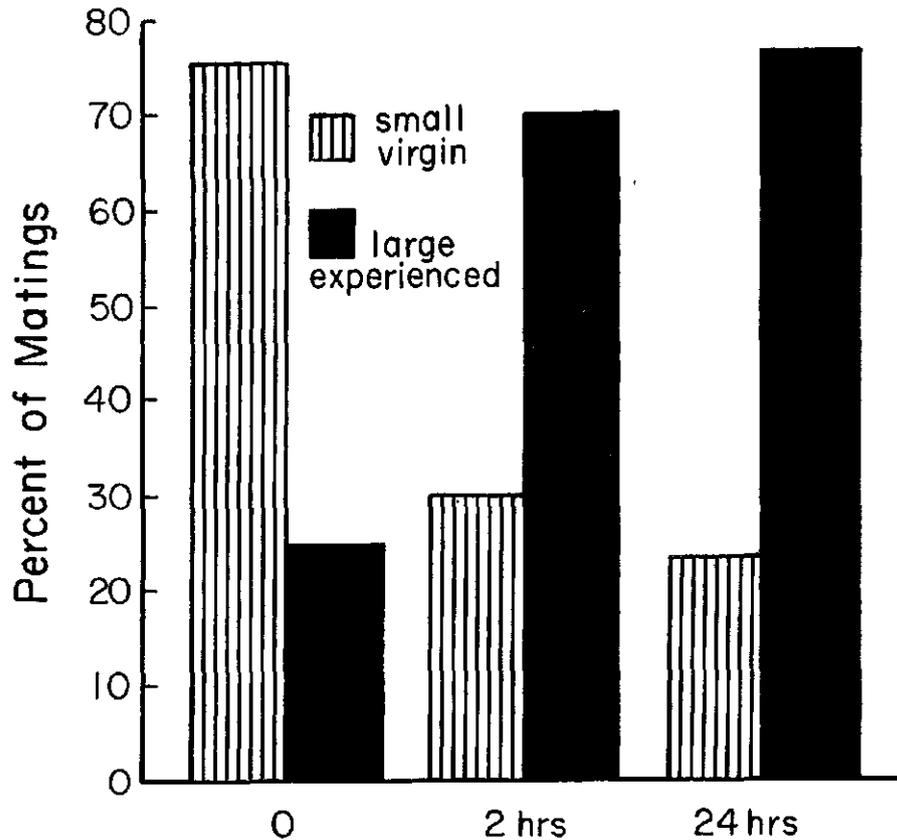


Fig. 1. The percentage of unmated males (white bars) and recently mated males (black bars) that copulate. Recently mated males (0) had their previous copulation immediately prior,  $n = 33$ ; 2 h previously,  $n = 20$  and 24 h previously  $n = 21$ .

sex ratios (available males: receptive females) are highly male biased and "wild" females arrive infrequently at leks, then variances in male reproductive success may be high. But as female arrival rates increase, for example, with a sterile release, the variance of male reproductive success should decline, i.e. what was a very attractive male to the first female becomes less so to those that follow.

In conditions where "wild" males are generally more successful, the release of sterile females along with sterile males might tend to blunt any edge the "wild" ones have in prolonged sexual competitions. When overflowing ratios still allow a reasonable chance of fertile individuals having sexual encounters, then plans to remove sterile female fruit flies from release groups might be ill-founded. How general such conditions might be remains to be determined.

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SURVEY OF *HELIOTHIS* SPP. LARVAE FOUND ON  
FLORIDA BEGGARWEED AND POSTHARVEST  
TOBACCO IN FLORIDA

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## ABSTRACT

*Heliothis* spp. larvae were collected from pre- and postharvest tobacco and Florida Beggarweed, *Desmodium tortuosum*. Five distinct adult *H. virescens* peaks were determined from pheromone-baited cone traps, but only 4 larval *Heliothis* spp. peaks followed them. The late July larval

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*Heliothis* spp. larvae were collected from pre- and postharvest tobacco and Florida Beggarweed, *Desmodium tortuosum*. Five distinct adult *H. virescens* peaks were determined from pheromone-baited cone traps, but only 4 larval *Heliothis* spp. peaks followed them. The late July larval

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<sup>2</sup>To whom reprint requests should be directed.

population was much lower than expected on tobacco and beggarweed, suggesting the existence of another alternate host. Maximum densities on beggarweed were 37 and 18 larvae/sweep sample (10 sweeps) in 1978 and 1979, respectively. The ratio of *H. virescens*: *H. zea* increased from 0.2:1.0 in July to over 20.0:1.0 by season's end. *Cardiochiles nigriceps* parasitized 44.5% of *H. virescens* larvae from postharvest tobacco, and 9.2% from beggarweed. *Archytas marmoratus* parasitized 2.9% of the *Heliothis* larvae collected from postharvest tobacco, but 20.0% of those from beggarweed.

#### RESUMEN

Se colectaron las larvas de *Heliothis* spp. de tabaco de pre-y post-cosecha y de pega-pega, *Desmodium tortuosum*. Se determinaron cinco picos de los adultos de *H. virescens* con trampas cónicas de feromona, pero los siguieron solo 4 picos de larvas de *Heliothis* spp. La población en los fines de julio fue mucho más bajo que lo que se esperaba sobre el tabaco y la pega-pega, lo cual hecho sugiere la existencia de otra planta hospedera alternativa. Las densidades maximas sobre la pega-pega fueron de 37 y 18 larvas/muestra de red (10 pasadas de la red) en 1978 y 1979, respectivamente. La razón de *H. virescens*: *H. zea* se aumentó desde 0.2:1.0 en julio hasta más de 20.0:1.0 hacia el fin de la temporada. *Cardiochiles nigriceps* infestó 44.5% de las larvas de *H. virescens* de tabaco de post-cosecha, y 9.2% de las de pega-pega. *Archytas marmoratus* infesto 2.9% de las larvas de *Heliothis* colectadas de post-cosecha, pero 20% de las de pega-pega.

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Larvae of the tobacco budworm (TBW), *Heliothis virescens* (F.) and the corn earworm (CEW), *H. zea* (Boddie) (Lepidoptera:Noctuidae), feed on a large number of cultivated crops and weed species (Barber 1937, Lincoln 1972, Roach 1975). Female moths of both species discriminate among plants and lay more eggs on some hosts, preference being influenced by morphological characteristics and chemical stimuli from the plants (Callahan 1957, Deutsch 1968, Widstrom et al. 1979). Within an agroecosystem, oviposition by a *Heliothis* species during a season shifts from host to host depending on the availability and phenological states of individual hosts (Snow and Brazzel 1965). These "adaptive host plant shifts" (Freeman et al. 1967) are distinctive for each geographical area with its particular cropping system and alternate host complex (Chamberlin and Tenhet 1926a, Barber 1937, Neunzig 1963, Graham et al. 1972, Roach 1975). Yearly differences in magnitudes of insect populations, weather conditions, cropping patterns, postharvest practices, and coincidental timing of plant phenologies may alter the observed importance of a particular plant species. The effects of associated predators and parasites of *Heliothis* spp. also vary geographically, seasonally, and among host plants (Ridgway and Lingren 1972, Roach et al. 1979).

While there have been many reports of *Heliothis* spp. larvae developing on wild hosts, there have been few attempts to quantify the importance of weed species on the population dynamics of TBW and CEW. This is not due to a lack of appreciation for the role of alternate hosts in these insects' life cycles, but due rather to difficulties in conducting quantitative research (Lincoln 1972). Weeds seldom occur in spatially or phenologically uniform stands, making estimations of the absolute quantity of plant material per unit area difficult. Weeds accepted as food by *Heliothis* spp. occur in

several families with considerable morphological variation, and these plants are typically mixed with other host and nonhost species. These factors coupled with inherent nonuniformities in CEW and TBW distributions further complicate sampling procedures (Roach 1975, Stinner et al. 1979).

The purpose of this study was to investigate the population dynamics of *Heliothis* spp. in tobacco fields and adjacent weedy areas in Alachua County, Florida. Because of the long frost-free period in North Florida, the total growing season extends well beyond the period of tobacco production. *Heliothis* spp. females emerging before tobacco transplanting or after harvest seek other hosts for oviposition. The primary early-season weed hosts for *Heliothis* spp. in the Florida-Georgia tobacco belt are toadflax, *Linaria canadensis* (F.) Dumont, and Carolina cranesbill, *Geranium carolinianum* L. (Barber 1937, Snow et al. 1966). Florida beggarweed, *Desmodium tortuosum* (Swartz) de Candolle, is the dominant late-season host plant (Chamberlin and Tenhet 1926a, Snow and Burton 1967), and smooth meadow-beauty, *Rhexia alifanus* Walter, is an important mid-season weed host of *Heliothis* spp. larvae (Barber 1937). Physical descriptions, distributions, and blooming periods of these plants may be found in Small (1933), Radford et al. (1968), and Duncan and Foote (1975). Tobacco, corn, and soybeans are the most common cultivated crops attacked by TBW and CEW in the study area.

#### MATERIALS AND METHODS

This study was conducted during 1978-1979 in 11 tobacco fields and 16 weedy locations on 6 farms in Alachua County, FL. This is an area of diverse agricultural, forest, and residential lands. We leased and managed one 12-ha farm, which was used for our control plots in 1979. No insecticides were used on 750 tobacco plants (ca. 0.07 ha), 350 transplanted *D. tortuosum* plants (ca. 0.03 ha) or around weedy field borders. Management of the 5 privately owned farms was left to the discretion of individual growers who employed a variety of insecticidal and cultural practices. These fields ranged in size from ca. 3 to over 12 ha.

During the tobacco growing period, 25 or 50 plants were checked for *Heliothis* spp. larvae at 5 locations within each field. Four fields each year were sampled twice weekly. In all but 2 postharvest fields, 5 plots of 25 tobacco plants were checked weekly, and all larvae were collected. When only completely harvested stalks remained, the plants were cut near ground level in the plots to allow regrowth. In 2 fields that were disked following harvest and had widely scattered regrowth, permanent plots could not be established. In these fields, 25 plants were chosen randomly from 5 areas each week. After sampling, these plants were destroyed.

Beggarweed was sampled with a 38-cm-diam. sweep net. Each sweep sample consisted of 10 sweeps of ca. 120-180° arc. All sweeping was done by the senior author. Depending on the size of the weed patch and the relative *Heliothis* population size, 10, 20, or more samples were taken twice weekly.

All *Heliothis* spp. larvae collected in the field were reared on pinto bean artificial diet (Burton 1969) in 30-ml cups at ca. 25°C. Because of the large number of larvae collected, species determinations were not made until individuals pupated. Parasitism rates were determined by rearing pupae or adults from *Heliothis* spp. larvae on diet. Dead larvae were not dissected

to determine parasitism or disease organisms. Pupae from late-season collections were examined for retention of larval eyespots (Phillips and Newsum 1966) to determine if they had entered diapause.

Cone traps (Hartstack et al. 1979) constructed of screen wire mesh and baited with Virelure [(*Z*)-11-hexadecenal:(*Z*)-9-tetradecenal16:1] were used to monitor male TBW activity in all fields. In postharvest tobacco fields and beggarweed patches, 4-8 traps were maintained and checked twice weekly. Pheromone dispensers (Hercon® laminates containing 10 mg pheromone) were changed monthly.

### RESULTS

During 1978 and 1979, 4184 *Heliothis* larvae were collected from *D. tortuosum* and postharvest tobacco (Table 1). Mortality was high after larvae were placed on artificial diet. Parasites reared from collected larvae accounted for 10.0% mortality, while disease, injury during handling, unsuccessful parasite development, and other unknown causes accounted for 66.6% mortality (Table 1). The remaining 23.4% of larvae collected became adult moths.

There were differences in crop and weed patch sizes and insect populations between farms. *Heliothis* spp. larvae were abundant in some fields, while collections were small in others. During the growing season, farmers often destroyed weeds after only a few sampling dates. Of particular importance to this study were the various postharvest practices. Each of the following was used on at least one of the study fields: 1) field abandoned until next season; 2) tobacco stalks mowed, but weeds along field edges and hedge rows left; 3) field completely mowed one or more times before winter; 4) field mowed and disked; and 5) cattle allowed to graze after one of the previous practices. A grower may employ one or more of these procedures over a postharvest season.

According to pheromone trap catches, there were 5 adult male TBW peaks during each year (Fig. 1). They were during late-April, early-June, mid-July, late-Aug. or early-Sept., and early-Oct. The small values early in the 1978 season are due to very high trap densities (22 traps/ha) in 2 of the fields. After harvest in 1978 and during all of 1979, trap densities were 0.7-1.5 trap/ha for all fields.

During 1978, 4 distinct peak collections of *Heliothis* spp. larvae were made from tobacco; 2 peaks (late-April, mid-June) were from preharvest and 2 (early-Sept., early-Oct.) from postharvest plants (Fig. 2). The data for 1979 were far less distinct, but were in general agreement with the previous year's collections. Maximum larval counts from individual preharvest tobacco fields were 0.57 larvae/plant (15 June 1979) and 0.32 larvae/plant (3 May 1979). The largest individual field collections from tobacco regrowth were 0.54 larvae/plant (6 September 1978) and 0.23 larvae/plant (21 September 1979).

Nearly an equal number of CEW and TBW adults were reared from postharvest tobacco (Table 1), but these data are not truly reflective of the CEW:TBW ratio because of selected parasitism by *Cardiochiles nigriceps* (Viereck) (Hymenoptera: Braconidae) on *H. virescens* (Lewis et al. 1967). Other parasite species reared from *Heliothis* larvae are not so specific. After adjusting for *C. nigriceps* parasitism, the ratio of *H. virescens* to *H. zea* became ca. 5:3.

TABLE 1. TOTAL NUMBER OF *Heliothis* SPP. ADULTS AND PARASITES REARED FROM LARVAL COLLECTIONS FROM FLORIDA BEGGAR-WEED AND POSTHARVEST TOBACCO OVER 2 SEASONS IN ALACHUA Co., FL.

Host plant	Total larvae collected	Dead larvae <sup>1</sup>	Pupae and adults		Parasites		Other <sup>2</sup>
			<i>H. zea</i>	<i>H. virescens</i>	<i>C. nigriceps</i>	<i>A. marmoratus</i>	
			<u>1978</u>				
Postharvest tobacco	247	150	31	36	23	4	3
<i>Desmodium tortuosum</i>	1740	1240	99	278	33	83	7
			<u>1979</u>				
Postharvest tobacco	430	251	65	50	46	4	14
<i>Desmodium tortuosum</i>	1767	1145	103	317	27	141	34
Total	4184	2786	298	681	129	232	58

<sup>1</sup>No species determinations.

<sup>2</sup>Primarily *Eucelatoria rubentis* (Coq.), *Netelia sayi* (Cushman), *Apanteles marginiventris* (Cresson).

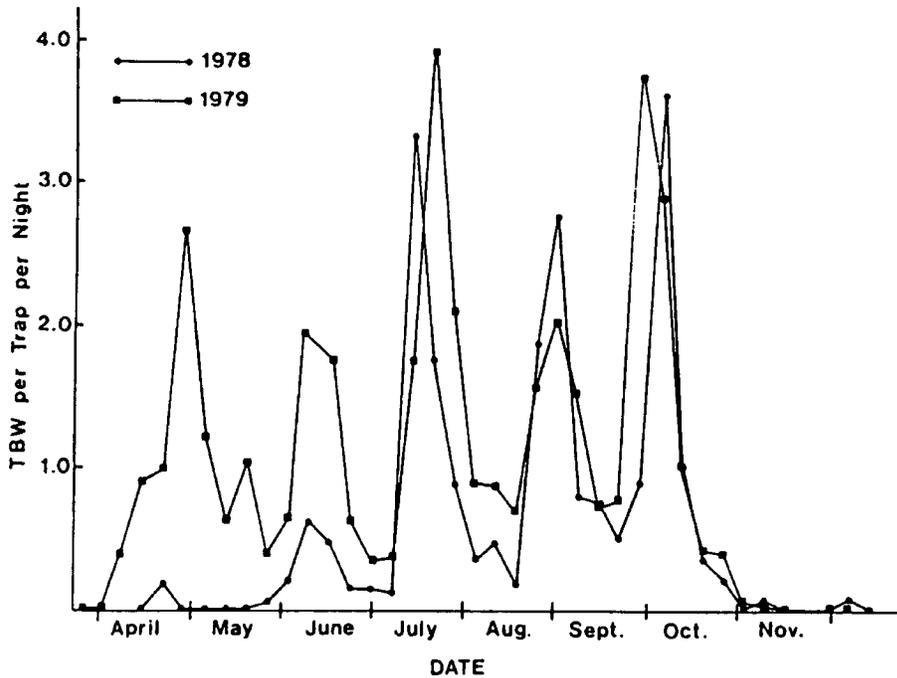


Fig. 1. Average weekly numbers of adult *Heliothis virescens* males (TBW) collected per cone-type trap baited with Virelure during 1978 (6 fields) and 1979 (7 fields) in Alachua Co., FL.

Larval *Heliothis* populations on beggarweed were more or less concurrent with those on postharvest tobacco. Sampling peaks were observed during Julian weeks 36 and 40 (early-Sept., early-Oct.) 1978, and weeks 35 and 43 (early-Sept., mid-Oct) 1979 (Fig. 3). The highest numbers of *Heliothis* larvae in any field were collected from *D. tortuosum* on 1 September 1978 (37.4 larvae/sweep sample) and 22 October 1979 (18.3 larvae/sweep sample). There was considerable variation between fields on the dates of maximum larval collections from beggarweed. The peaks for individual fields ranged over a 3-week span.

A field adjacent to the control field had a large stand of toadflax in 1979. During April a maximum of 5.4 *Heliothis* spp. larvae/sweep sample collected from this weed. Two-thirds of the larvae collected were TBW, and over 90% of these were parasitized by *C. nigriceps*.

*Archytas marmoratus* (Townsend) (Diptera: Trachinidae) and *C. nigriceps* were the most abundant parasites reared from *Heliothis* spp. larvae. *Netelia sayi* (Cushman) (Hymenoptera: Ichneumonidae), *Apanteles marginiventris* (Cresson) (Hymenoptera: Braconidae), and *Eucelatoria rubentis* (Coq.) (Diptera: Tachinidae) were found in lesser numbers. The ichneumonids *Hyposoter annulipes* (Cr.), *Pristomerus spinator* (F.), and *Mesochorus discitergus* (Say) and the tachinid *Lespesia aletiae* Riley were also collected.

*Cardiochiles nigriceps* were reared from *H. virescens* larvae from all host plants, and they were found from April-October. During the tobacco production season parasitism ranged 24-62%. Over both years 44.5% of all

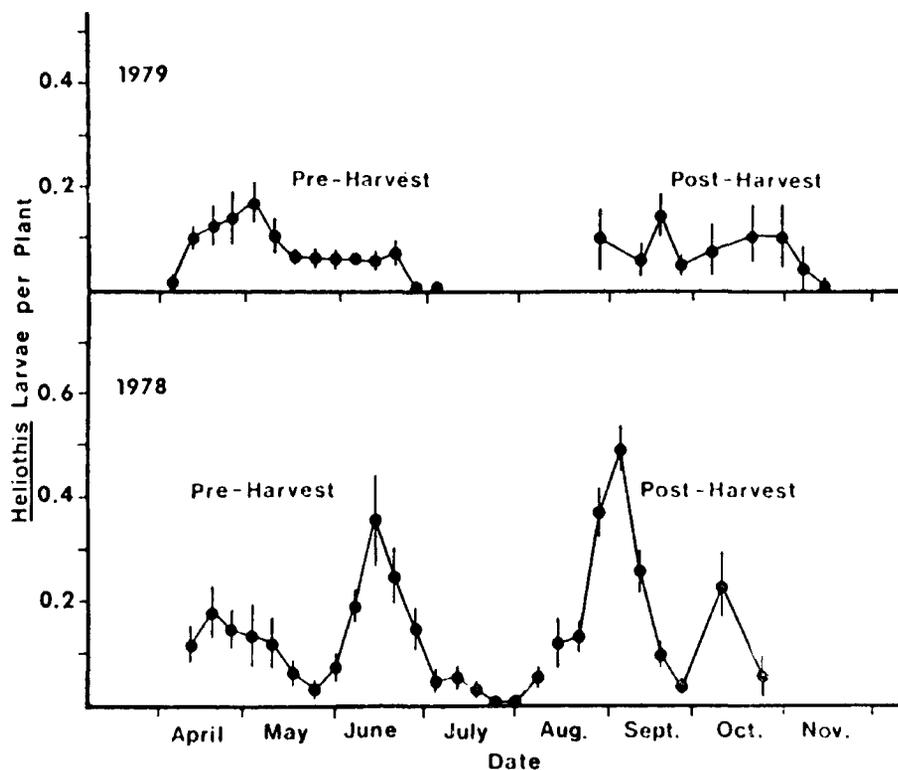


Fig. 2. Average weekly numbers of *Heliothis* spp. larvae collected from tobacco during 1978 and 1979 from 11 fields in Alachua Co., FL. Vertical lines indicate 95% confidence intervals around the means.

TBW larvae collected from postharvest tobacco were parasitized by *C. nigriceps*. In contrast, only 9.2% of all TBW from beggarweed were parasitized by this species (Table 1).

Very few (2.9%) *Heliothis* spp. larvae from postharvest tobacco were parasitized by the late-season *A. marmoratus*. On the other hand, an average of 20% of the *Heliothis* spp. larvae from beggarweed over the 2 seasons were parasitized by these flies.

The percentage of TBW of both *Heliothis* spp. collected on beggarweed increased dramatically in late August, until only a few CEW were found by season's end. Over both years 76.4% of *Heliothis* larvae collected from beggarweed and 61.8% collected from postharvest tobacco were TBW. Most diapausing TBW larvae were produced from beggarweed late in the season (Fig. 4).

#### DISCUSSION

Alternate weed hosts play an important role in the population dynamics of *Heliothis* spp. in the southeastern United States. Tobacco transplanting commences in April, but they are a poor host until the seedlings become established. In general, *Heliothis* spp. larvae prefer plants in the flowering or fruiting stage (Johnson et al. 1975, Neunzig 1963, Parsons 1940). Toadflax blooms from March to May, and is the primary early-season host of

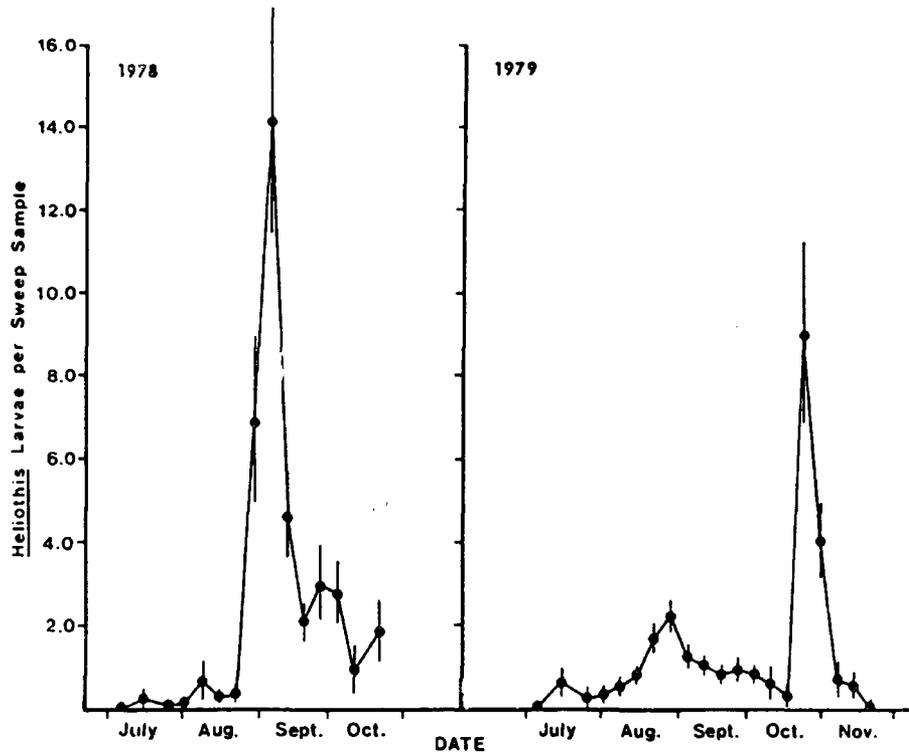


Fig. 3. Average weekly numbers of *Heliothis* spp. larvae collected per sweep sample of 10 sweeps from Florida beggarweed, *Desmodium tortuosum*, during 1978 and 1979 from 16 locations in Alachua Co., FL. Vertical lines indicate 95% confidence intervals around the means.

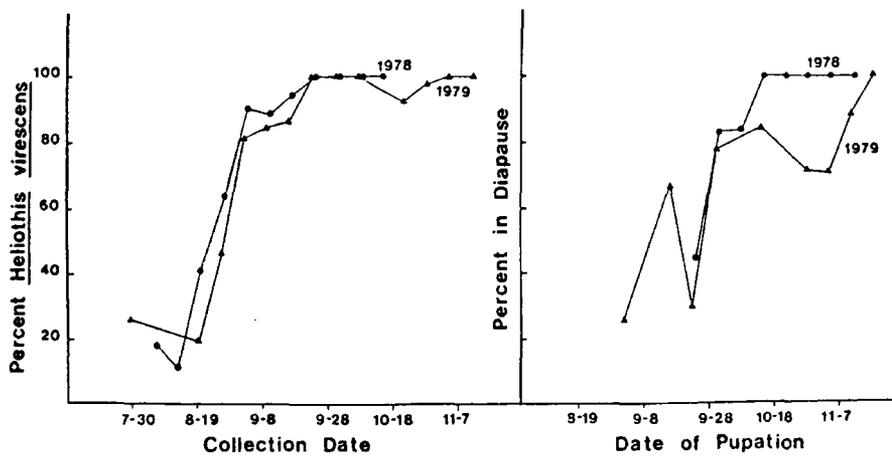


Fig. 4. Percentage *Heliothis virescens* of all *Heliothis* spp. larvae collected from *Desmodium tortuosum*, and the percentage of *H. virescens* pupae collected from *D. tortuosum* entering diapause in Alachua Co., FL.

both CEW and TBW in Florida, eastern Georgia, eastern South Carolina, and eastern North Carolina (Chamberlin and Tenhet 1926a, Barber 1937, Neunzig 1963, Roach 1975). Toadflax was the only weed found in the spring in Alachua County in sufficient quantities to be considered an important host plant. A few widespread *G. carolinianum* plants were found, but no *Heliothis* spp. larvae were collected from them.

Fall hosts are equally important to the survival of these species. A large diapausing population is needed to insure sufficient numbers surviving the winter season. Florida beggarweed is by far the most important late-season host in North Florida and southeastern Georgia (Chamberlin and Tenhet 1926a, Barber 1937, Snow and Burton 1967), but it is less important further north, and is only a minor host in eastern North Carolina (Neunzig 1963). Most diapausing TBW in this study were collected from *D. tortuosum*.

The practice of using *D. tortuosum* as a forage crop dates back many years. Barber (1937) described beggarweed as a crop sometimes cultivated for hay. Conversations with Alachua County farmers revealed that grazing in old tobacco or corn fields and along roadsides has been common for many years. Therefore, growers are often reluctant to destroy beggarweed stands. After cultivation, mowing, or heavy grazing, *D. tortuosum* may regrow and produce new flowers and seeds. Since these cultural practices are performed at different times, plants of all phenological stages may be found at any time from July to October. Often weeds in different stages of growth are found in the proximity of an old field. This provides a more continuous food source for *Heliothis* than would occur naturally. Old *D. tortuosum* plants put on some new leaves after dropping their seeds. *Heliothis* spp. larvae were also collected from these small, tender leaves.

Chamberlin and Tenhet (1926a) delineated 5 *H. virescens* larval peaks in North Florida. They felt that the first 2 (late-May, late-June) were produced primarily from tobacco, the middle peak (early-August) from tobacco and Florida beggarweed, and the final 2 peaks (mid-Sept. and early-Oct.) from beggarweed. They observed no appreciable discontinuity in the food supply as beggarweed matured about harvest time.

Data from this study support the conclusions of Chamberlin and Tenhet (1926a), except that only 4 distinct *Heliothis* spp. larval peaks were encountered. Few *Heliothis* spp. larvae were collected from tobacco or *D. tortuosum* in late-July to early-August (Fig. 2, 3). This is normally the height of the tobacco harvest and there is little food available on mature, topped, and suckered plants. Also, there is little mature beggarweed at this time. Snow and Burton (1967) did find one *H. virescens* peak on *D. tortuosum* near Tifton, GA on 11 August 1965.

The possibility of an additional weed host cannot be ruled out, but none was found. The meadow-beauties, *Rhexia alifanus* and *R. mariana* L., were reported as important mid-season hosts of *Heliothis* spp. in Georgia and South Carolina (Barber 1937, Roach 1975). These plants are found in moist pineland and bogs (Duncan and Foote 1975) which were not sampled in our study.

Parasitism rates by *C. nigriceps* were higher for larvae collected from tobacco than from *D. tortuosum*. Chamberlin and Tenhet (1926b) reported similar findings. *C. nigriceps* females are attracted to tobacco in the absence of host insects (Vinson 1975). However, we did not observe these

parasites in the vicinity of beggarweed in the absence of *Heliothis* spp. infestations.

The opposite situation exists with *A. marmoratus*. Here parasitism rates among larvae collected from *D. tortuosum* were much higher than those from tobacco. *A. marmoratus* parasitizes a number of host species from several host plants (Hughes 1975), and levels of parasitism are often different on various cultivated crops (Hughes and Rabb 1976). Female flies are stimulated to larviposit by *Heliothis* spp. frass and larvae (Nettles and Burks 1976). Differences in the rates of parasitism by flies on larvae from tobacco and beggarweed may have been due to increased larviposition on beggarweed where *Heliothis* spp. levels were higher. However, the possible attraction of gravid flies to beggarweed itself cannot be ruled out.

#### ACKNOWLEDGMENTS

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

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## MITES ATTACKING CASSAVA IN SOUTHERN FLORIDA: DAMAGE DESCRIPTIONS AND DENSITY ESTIMATE METHODS

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### ABSTRACT

*Mononychellus caribbeanae* (McGregor), *Tetranychus urticae* Koch, and *Panonychus citri* (McGregor), were collected from cassava leaves. *Mononychellus caribbeanae* was observed mainly on the upper leaves, with a virus-like pattern damage. *Tetranychus urticae* and *P. citri* were observed on the lower leaves. Stippling and leaf browning were the damage symptoms for these species. The number of mites attacking the plant was correlated with a visual damage rating. Three times more damage was obtained from *M. caribbeanae* than from *T. urticae* and *T. citri*. Distribution of the mite species on 3 areas of the leaf was assessed. The use of a relative sampling method estimated ca. 63% of the total population per leaf.

### RESUMEN

*Mononychellus caribbeanae* (McGregor), *Tetranychus urticae* Koch, y *Panonychus citri* (McGregor) se colectaron de hojas de yuca. *Mononychellus caribbeanae* se observó principalmente sobre las hojas superiores las cuales tenían daños parecidos como los causados por virus. *Tetranychus urticae* y *P. citri* se observaron sobre las hojas inferiores. El punteado y el tostarse de las hojas fueron los síntomas de los daños de estas especies. Se correlacionaron el número de ácaros que atacaban la planta con una clasificación visual de los daños. *Mononychellus caribbeanae* hizo 3 veces mas daños que *T. urticae* y *T. citri*. Se determinó la difusión de las especies de ácaros sobre 3 áreas de la hoja. Por el uso de un método de tomar muestras se estimó cerca de 63% de la población total por hoja.

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Three phytophagous mite species, the cassava mite, *Mononychellus caribbeanae* (McGregor), the two spotted spider mite, *Tetranychus urticae* Koch, and the citrus red mite, *Panonychus citri* (McGregor), damage cassava foliage in southern Florida (Pena and Waddill, 1982). Differences in the response of the host to these mites are marked. In addition, spatial differences in species distribution occur (Rodriguez, 1978). We report here the mites damage distribution and seasonal pattern on cassava plants during 1979-80, and determine a relationship between a relative sampling method with an absolute mite population on the leaves.

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## MITES ATTACKING CASSAVA IN SOUTHERN FLORIDA: DAMAGE DESCRIPTIONS AND DENSITY ESTIMATE METHODS

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### ABSTRACT

*Mononychellus caribbeanae* (McGregor), *Tetranychus urticae* Koch, and *Panonychus citri* (McGregor), were collected from cassava leaves. *Mononychellus caribbeanae* was observed mainly on the upper leaves, with a virus-like pattern damage. *Tetranychus urticae* and *P. citri* were observed on the lower leaves. Stippling and leaf browning were the damage symptoms for these species. The number of mites attacking the plant was correlated with a visual damage rating. Three times more damage was obtained from *M. caribbeanae* than from *T. urticae* and *T. citri*. Distribution of the mite species on 3 areas of the leaf was assessed. The use of a relative sampling method estimated ca. 63% of the total population per leaf.

### RESUMEN

*Mononychellus caribbeanae* (McGregor), *Tetranychus urticae* Koch, y *Panonychus citri* (McGregor) se colectaron de hojas de yuca. *Mononychellus caribbeanae* se observó principalmente sobre las hojas superiores las cuales tenían daños parecidos como los causados por virus. *Tetranychus urticae* y *P. citri* se observaron sobre las hojas inferiores. El punteado y el tostarse de las hojas fueron los síntomas de los daños de estas especies. Se correlacionaron el número de ácaros que atacaban la planta con una clasificación visual de los daños. *Mononychellus caribbeanae* hizo 3 veces mas daños que *T. urticae* y *T. citri*. Se determinó la difusión de las especies de ácaros sobre 3 áreas de la hoja. Por el uso de un método de tomar muestras se estimó cerca de 63% de la población total por hoja.

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Three phytophagous mite species, the cassava mite, *Mononychellus caribbeanae* (McGregor), the two spotted spider mite, *Tetranychus urticae* Koch, and the citrus red mite, *Panonychus citri* (McGregor), damage cassava foliage in southern Florida (Pena and Waddill, 1982). Differences in the response of the host to these mites are marked. In addition, spatial differences in species distribution occur (Rodriguez, 1978). We report here the mites damage distribution and seasonal pattern on cassava plants during 1979-80, and determine a relationship between a relative sampling method with an absolute mite population on the leaves.

## MATERIALS AND METHODS

Mites were collected weekly from an untreated cassava crop near Homestead, Florida during the last three months of 1979 and 1980. One leaf was collected both from the upper and the lower half of each plant. Leaves were bagged and transported to the laboratory where mobile stages were counted. To assess the distribution of mites on the leaves, leaf surfaces from a random sample of 20 leaves were sub-divided into 3 areas: the central part of the leaf where the petiole joins the leaf, the external lobes, and the middle lobes (Fig. 1). Mites were counted in each area and means

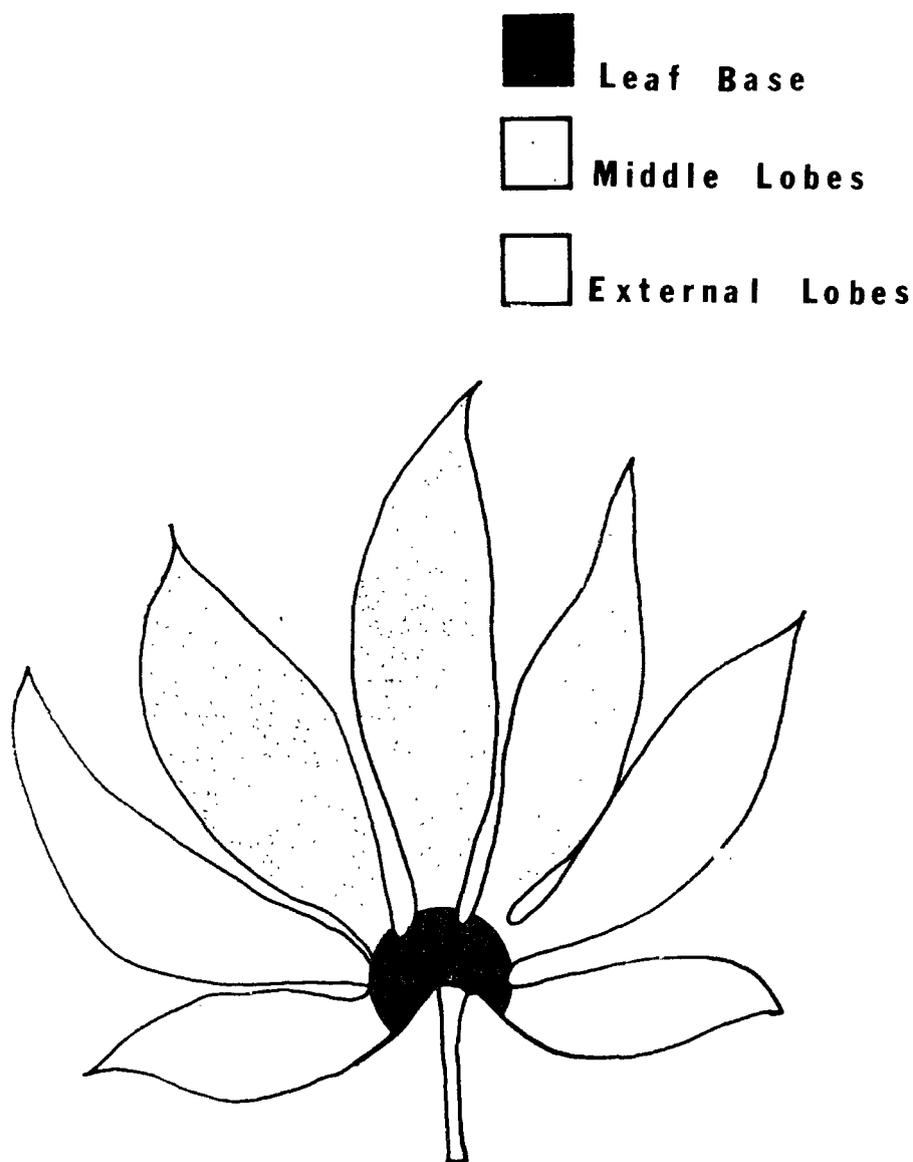


Fig. 1. Cassava leaf areas under study: central lobes, stippled; external lobes, white; central or basal area, black.

(mites/cm<sup>2</sup>) for each area were separated by Duncan's multiple range test. To correlate visual estimation with the actual number of mites/leaf, leaves were rated for mite damage according to damage scales adapted from Bellotti and Schoonhoven (1978). *Mononychellus caribbeanae*: 0 = no damage observed; 1 = few spots on the leaves with no deformation; 2 = fairly abundant yellow spots on the leaves, spots coalesce/abundant spots in the mid-veins; 3 = abundant coalescing spots, leaf deformation/brown spots. *Tetranychus urticae* and *P. citri*: 0 = no damage; 1 = initiation of silver spots on lower and/or intermediate leaves; 2 = fairly abundant silver or yellow spots on lower and/or intermediate leaves 3 = damage manifest; many spots, small necrotic dots, curling of basal leaves. Counts were taken on 5 different dates and the mean numbers of mites and standard errors were calculated.

A modification of the technique published by De and Konar (1956) was evaluated. An adhesive (Scotch® tape) was pressed to the underside of mite-infested leaves. The mites adhering to the tape were counted under a microscope. To facilitate counts, the tape was covered with a glass slide. The accuracy of this technique was evaluated by determining the

TABLE 1. RELATIVE DENSITY OF *Mononychellus caribbeanae* AND PREDATORS ON CASSAVA PLANTS AS AFFECTED BY ENVIRONMENT AND PLANT AGE.

Date	Mean of mites/leaf	Rainfall <sup>b</sup> (mm)	Mean T °C	Mean predators leaf <sup>c</sup>
1979, Oct 24 <sup>a</sup>	14.6	56	22.1	1.6
31	41.3	0	19.7	—
Nov 9	27.3	0	20.2	—
16	31.1	4.8	18.6	3.8
23	16.0	0.7	20.3	1.2
Dec 2	9.5	3.0	17.8	1.6
1980, Oct 4	10.8	32.5	25.6	—
24	3.3	9.1	25.6	—
Dec 15	0.5	0	22.2	—

<sup>a</sup>Represents 8 month old plants.

<sup>b</sup>Rainfall for 5 days prior to sampling.

<sup>c</sup>*Euseius hibisci* (Chant) (Acarina:Phytoseiidae), was one of the most common predators.

TABLE 2. DISTRIBUTION OF *M. caribbeanae*, *Tetryanychus urticae* AND *P. citri* IN 3 DIFFERENT CASSAVA LEAF AREAS.

Leaf region	Mean number of mites/cm <sup>2</sup> <sup>1</sup>	
	<i>Mononychellus</i>	<i>Tetryanychus/Panonychus</i>
Central	0.71 a	0.93 a
Middle lobes	0.55 a	0.06 b
Extreme lobes	0.28 a	0.07 b

<sup>1</sup>Number followed by different letters are statistically different at P = 0.05 by Duncan's multiple range test.

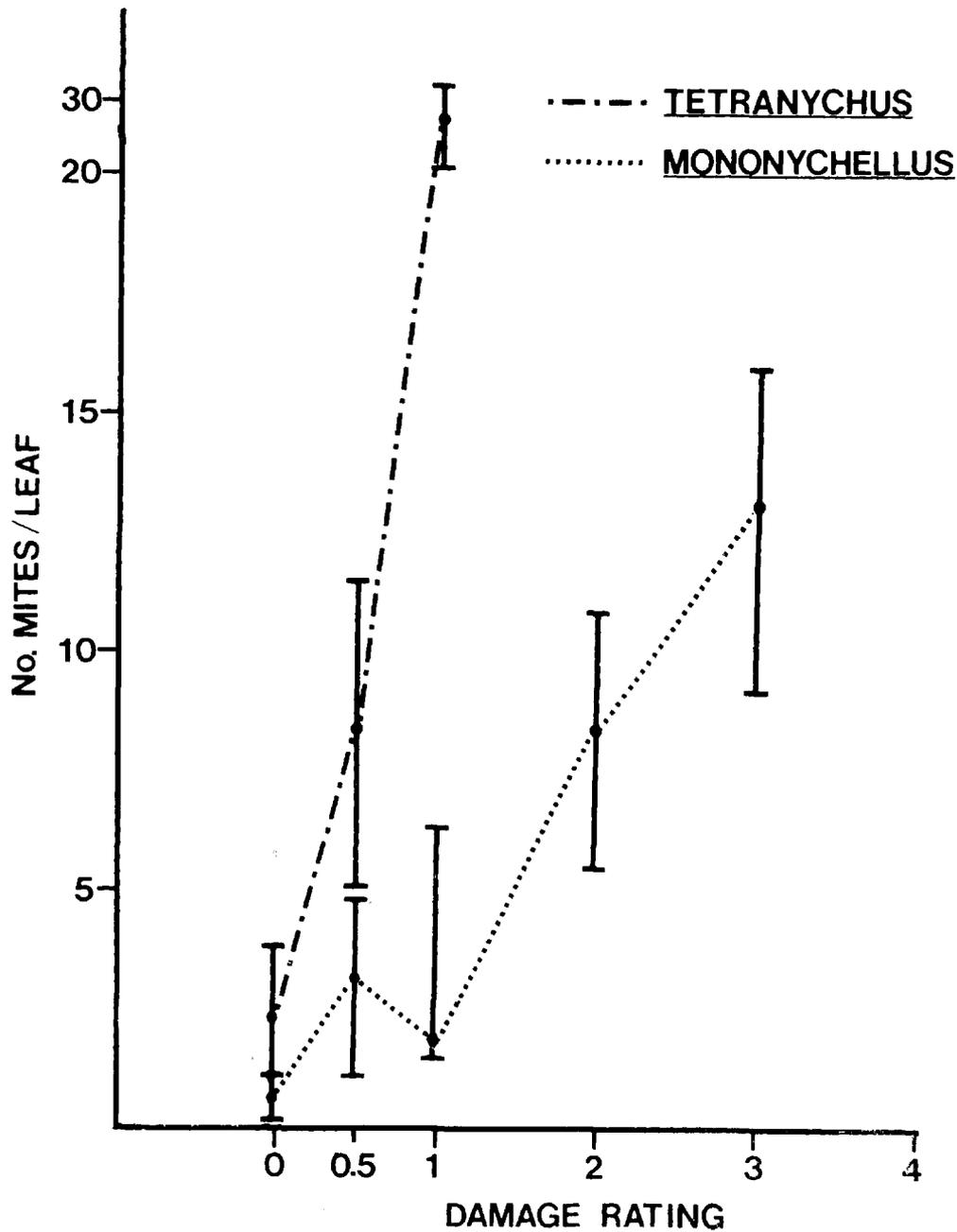


Fig. 2. Number of mites found on cassava leaves related to a damage rating (vertical lines denote standard error of the mean).

correlation between the number of mites on the tapes and the total number of mites present on the leaves.

#### RESULTS AND DISCUSSION

The cassava mite appeared late in the growing season (8 month-old plants) and caused considerable leaf stippling even at low population densities. They were distributed mainly on the lower surface of the top leaves

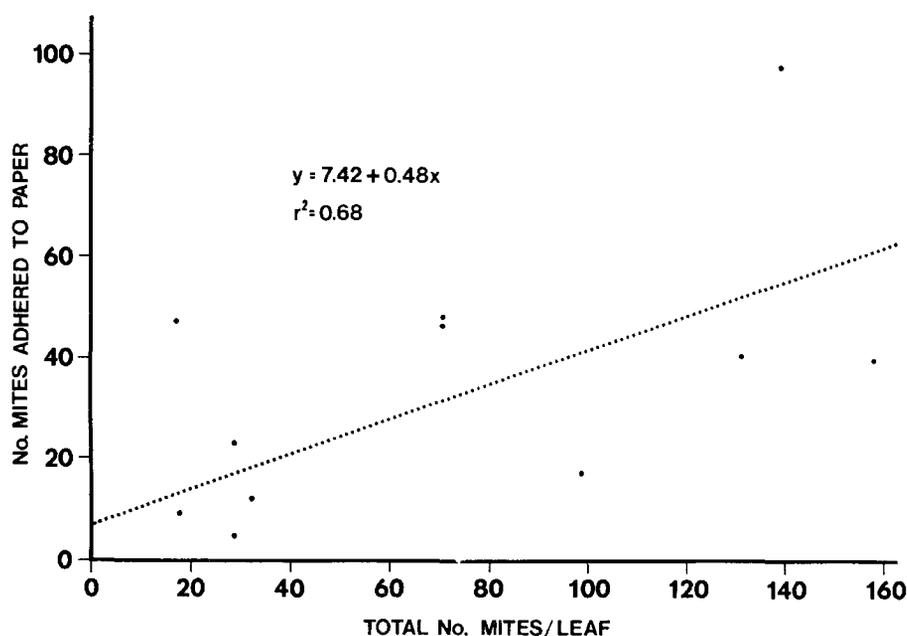


Fig. 3. Relationship between number of mites in the leaf and number impressed to adhesive paper.

and on the apical buds, and caused considerable damage expressed as light yellow leaf stippling with a virus-like pattern and leaf distortion. Both the twospotted spider mite and the citrus red mite were found on the bottom and middle leaves. Typical symptoms were stippling and leaf browning. The stippling caused by both species did not appear to differ. Plant damage in terms of yield loss appeared to be minimal, since the plants normally lose their leaves by mid December. This observation is in agreement with Anonymous (1979) who reported no differences in cassava yield during heavy mite attack in plants 7-9 months old.

In southern Florida, it has not been possible to detect a major factor (Table 1) influencing cassava mite populations. However, the effects of temperature, dry or rainy weather, presence or absence of suitable leaves for food and natural enemies do seem to act together affecting the mites population buildup. The distribution of the cassava mites (mites/cm<sup>2</sup>) did not differ significantly between the central area and the external and middle lobes (Table 2). This result indicate that for this species there is not a difference in suitability between leaf lobes. Significantly larger population of *T. urticae* and *P. citri* were localized on the central leaf area compared to the mite population in the leaf lobes. The central area may provide a better feeding and survival site than the leaf lobes. It is not known what differences in suitability on leaf areas cause these differences for both species.

Although *T. urticae* and *P. citri* were more abundant than *M. caribbeanae*, they produce less damage (Fig. 2). The low population densities for *M. caribbeanae* could be explained by the sensitivity to damage of meristematic tissue along with a cassava nutrient deficiency observed in

the top leaves of the plant. Increased number of *T. urticae* and *P. citri* mites per leaf resulted in a reduction in standard error. The opposite was observed for *M. caribbeanae*.

Regression analysis between total number of mites/leaf and the relative estimate by adhesive tape indicated a intermediate correlation ( $r^2 = 0.68$ ), which demonstrated that 79.3% of the variation in total mites/leaf can be explained by the use of the adhesive tape (Fig. 3). A combination of several techniques (visual damage rating, population counts, etc.) should be used not only where a single species is the key pest, but also when there are several. These techniques may assess the regular mite outbreaks in the large cassava growing regions of Brazil, Africa, and Asia.

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### OBSERVATIONS ON THE NESTING OF THREE SPECIES OF *CERCERIS* (HYMENOPTERA: SPHECIDAE)

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#### ABSTRACT

Quantitative data obtained from the nests and provisioning activities of 3 species of *Cerceris* are presented. Those for *C. flavofasciata floridensis* compare favorably with information on the nominate subspecies and reveal 4 new genera and 5 new species of prey Chrysomelidae. Data from 2 populations of *C. rufopicta* confirm previous nesting information on this species, bring to light 2 new genera and 6 new species of chrysomelid prey and introduce a new prey family, Eucnemidae. Biomass data in the form of total prey weight per cell for *C. fumipennis* substantiate previous information on male and female cells. Observations on the Florida population of *C. fumipennis* reveal the use of conspecific nests from previous generations and disclose a new cleptoparasite, *Senotainia rubriventris* (Macquart) (Sarcophagidae).

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## RESUMEN

Se presentan datos cuantitativos sobre los nidos y las actividades de aprovisionar de 3 especies de *Cerceris*. Los datos sobre *C. flavofasciata floridensis* comparan favorablemente con la información sobre la especie nominada y revelan 4 géneros nuevos y 5 especies nuevas de presas de Chrysomelidae. Datos de 2 poblaciones de *C. rufopicta* confirman información precedente sobre la nidificación de esta especie, revelan 2 géneros nuevos y 6 especies nuevas de presas crisomelidas, y introducen una nueva familia presa, Eucnemidae. Datos sobre biomasa en la forma del peso total de presas por celda de *C. fumipennis* verifican la información previa sobre las celdas de los machos y de las hembras. Las observaciones sobre la población floridano de *C. fumipennis* revelan el uso de nidos conespecíficos de las generaciones previas y revelan un nuevo cleptoparásito, *Senotainia rubiventris* (Macquart) (Sarcophagidae).

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*Cerceris*, the largest genus in the Sphecidae, is behaviorally one of the best studied genera in the family. Most of the Nearctic species nest in aggregations in bare firm soil, the nest dimensions often reflecting the friability of the soil. The entrances are left open during the provisioning and are surrounded by a prominent rim of soil which is removed by weathering. A female often constructs and remains with only one nest during her lifetime (Evans 1971). Thus some of the nests become extensively multicellular. In some tropical and subtropical species of *Cerceris* these nests may be enlarged further by the daughters and, possibly, granddaughters of the founding female (Salbert and Elliott 1979, Evans and Hook 1982, a. b). Burrow storage, aided by an inner plug of soil, is prevalent in the genus (Evans 1971). The North American species of *Cerceris* provision exclusively with adult Coleoptera (Scullen and Wold 1969), whereas some of the exotic species store Hymenoptera (Tsuneki 1965, Gess 1980).

Much of the information on nesting in this genus exists in the form of anecdotal descriptions such as those published by Krombein (1952, 1953, 1959, 1964, 1981). Evans (1971) found few differences between some Nearctic species in nest architecture and provisioning behavior but noted significant interspecific diversity in prey selection. Evans and Rubink (1978) reported remarkable intraspecific constancy in the prey preferences of several Nearctic species. Alcock (1975) found a "high level of burrow switching, burrow stealing, and communal provisioning" in *Cerceris simplex macrosticta* Viereck and Cockerell. Some other species of *Cerceris*, particularly those in the tropics and subtropics, have also been implicated in communal nesting, i.e., several females live together in the same nest and cooperate or share in the nesting activities (Grandi 1961, Tsuneki 1965, Evans and Matthews 1970, Evans et al. 1976, Salbert and Elliott 1979, Alcock 1980, Evans and Hook 1982 a, b). The factors related to communal nesting remain obscure. Evans and Hook (1982a) found no reproductive division of labor in some Australian species of *Cerceris* despite an apparent division of labor into provisioning and non-provisioning females.

Our studies on the nesting of members of this genus encompass 3 species: *C. flavofasciata floridensis* Banks, which has been studied briefly (Krombein 1964); *C. rufopicta* F. Smith (= *robertsonii* Fox) which has been studied in some detail (Krombein 1952, 1953, Evans 1959, 1971); and, *C. fumipennis* Say, which has been studied rather well (Evans 1971, Evans and Rubink

1978). Our observations were made in northwestern Pennsylvania (*C. rufopictus*), central New York (*C. rufopictus*, *C. fumipennis*) and southern Florida (*C. fumipennis*, *C. flavofasciata floridensis*) during 1970-83. They add much qualitative and quantitative behavioral information to the knowledge of species in the genus. Wasp and prey specimens bear corresponding ethology note numbers.

*Cerceris flavofasciata floridensis* Banks

This species nested in an almost vertical sand cliff, 2.7 m high, at the Archbold Biol. Sta., Lake Placid, FL during 5-11 April 1971. All nests were in the north-facing portion of the cliff, near the bottom. We excavated several nests but will present data only from the 2 largest, 8- and 7-celled.

The burrows, 6-8 mm in diameter, entered the cliff at slight upward angles for 3.5-8 cm, then progressed slightly downward for an additional 24-54 cm before undulating downward for another 12-26 cm (Fig. 1). Two such burrows were 72 and 88 cm in length. The cells were located off the semi-vertical or vertical portions of the burrows, 3-16 cm from the burrow walls. Cells successively made within a nest were unearthed 2-12 cm apart.

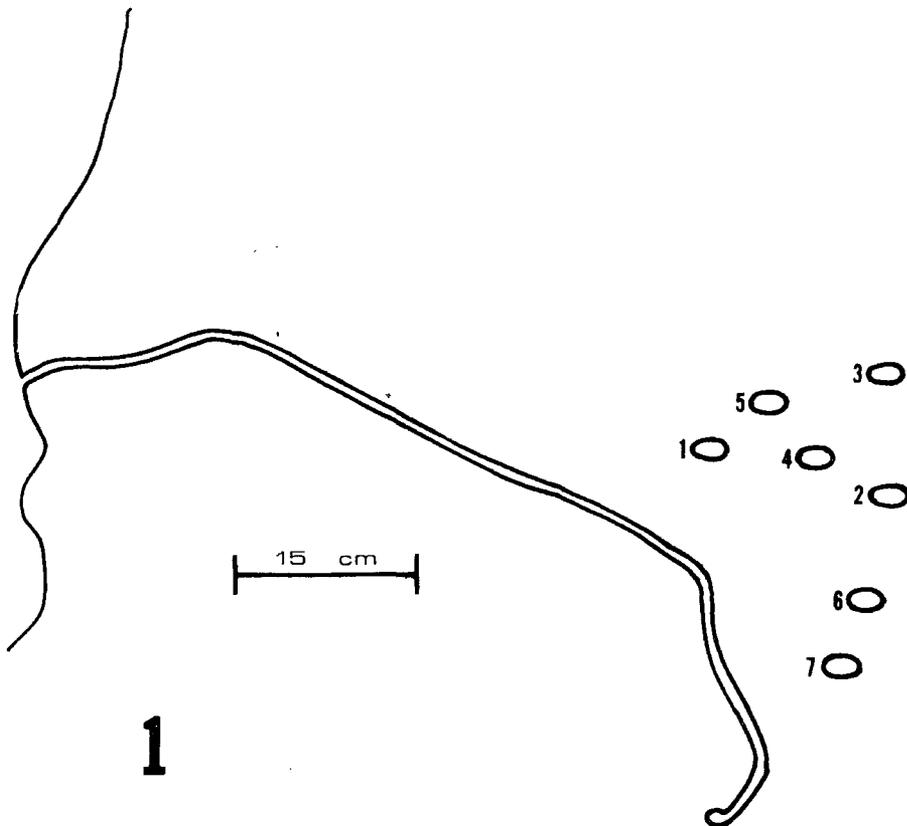


Fig. 1. Nest of *Cerceris flavofasciata floridensis*, as viewed from the side, showing burrow, terminal storage chamber and cells. Cells are numbered in the order in which they were built and provisioned, based upon their contents.

The oval cells (N = 15) averaged 7.7 (6-9) x 13.3 (11-17) mm in height and length. Those containing older larvae and cocoons were invariably larger (9x15-17 mm) than those with eggs or younger larvae. Nine completed cells, i.e., those containing an egg or larva, held from 12 to 30 ( $\bar{x}$  = 19.7) prey. Individual prey (N = 121) averaged 12.5 (5.5-57) mg in body (wet) weight, whereas the total prey weight of a single cell ranged from 168 to 322 ( $\bar{x}$  = 252.4) mg. Three associated wasps weighed (wet) 41.5, 36 and 61 mg.

Although many prey in the cells faced head inward, often ventral side upward, some were positioned head outward or sideways. In certain cells the prey seemed to be "fitted" around the centrally located, pedestal prey bearing the wasp's egg or larva. The stout, slightly curved, hyaline egg, 3.5 mm long, was loosely attached longitudinally to the ventral side of the thorax of the prey.

Prey (\*new host record) in the cells comprised adult Chrysomelidae, with their numbers in parentheses, as follows: \**Bassareus croceipennis* LeConte (82); *Cryptocephalus binomis rufibasis* Schaeffer (122); *C. bivius* Newman (37); *C. guttulatus* Olivier (4); *C. notatus fulvipennis* Haldeman (1); \**Griburius equestris* Olivier (4); \**Pachybrachis discoidea* Bowditch (3); \**Exema gibber* (Fabricius) (1); \**Anomoea nitidicollis crassicornis* Schaeffer (4); *Coscinoptera dominica franciscana* (LeConte) (1).

All 7 cells in one nest contained cocoons or wasp larvae in various stages of development; however, one cell in another nest contained red ants and prey fragments, 2 cells each held one maggot (Sarcophagidae) feeding on the prey, and 2 other cells had decomposed prey with neither a wasp's egg nor larva.

*Cerceris rufopicta* F. Smith  
(= *Cerceris r. robertsonii* Fox)

We excavated 10 nests of this species, 2 of them being 8- and 10-celled, in sand pits and blow-outs at Auburn, NY (24 July 1970, 21-27 July 1983) and Presque Isle St. Pk., PA (28-30 July 1970, 5-10 July 1971). Seven cells of 2 nests at Auburn averaged 21.7 (17-24) cm in depth below the surface, whereas 34 cells of 7 nests at Presque Isle St. Pk. averaged 22.9 (16.5-38) cm in depth. The cells themselves averaged 8.2 x 14.0 (7-10x10-18) mm at Auburn and, 8.3 x 12.7 (7-10x11-15) mm at Presque Isle in height and length.

From 4 to 9 ( $\bar{x}$  = 7.0; N = 8) prey were placed in individual cells at Auburn, whereas from 3 to 20 ( $\bar{x}$  = 8.9; N = 31) prey were put in cells at Presque Isle. The total weights of the prey in a cell averaged 134.8 (82-177; N = 5) mg at Auburn and 122.9 (60-217; N = 14) mg at Presque Isle. Individual prey from Auburn and Presque Isle averaged 16.8 (7-33; N = 47) and 13.9 (4.9-31; N = 187) mg, respectively, in body (wet) weight. Associated wasps from these localities weighed (wet) 33-39 ( $\bar{x}$  = 36; N = 2) and 34-44 ( $\bar{x}$  = 39.6; N = 5) mg.

One, 2 or 3 prey were stored either head inward or outward in the 15.5-37-cm long burrows, with some burrows having 2 or 3 such storage areas. Prey in the cells were placed mostly head inward but some were sideways and others head outward. Prey from the cells at both localities were lively, able to move around and even walk when taken from the cell.

The prey on which the wasp's egg was laid was usually slightly larger than an average-sized prey and weighed 19.0 (14-23; N = 11) mg. Such

prey were placed in the cell head inward and ventral side upward or on the side. Eggs were white and elastic, measured 3.3-3.7 x 0.8-0.9 mm, and were loosely attached.

The prey (\*new host record) comprised adult Chrysomelidae, with the number of specimens in parentheses, as follows: \**Cryptocephalus quadruplex* Newman (38); \**Fidia viticida* Walsh (65); \**Colaspis suilla* Fabricius (10); \**C. brunnea* (Fabricius) (82); *Tymnes tricolor* (Fabricius) (63); \**Pachybrachis relictus* Fall (87); \**Metachroma angustulum* Crotch (1). One record of *Deltometopes amoenicornis* (Say) (Eucnemidae) from a cell at Auburn represents a new family of prey for this species of wasp.

One 2-celled nest from Auburn contained a cell with 2 maggots (Sarcophagidae) and prey, whereas a 3-celled nest from Presque Isle St. Pk. had 1 maggot (Sarcophagidae) feeding on the prey in each of 2 cells. One cell in a 5-celled nest at Auburn contained prey fragments and small red ants.

#### *Cerceris fumipennis* Say

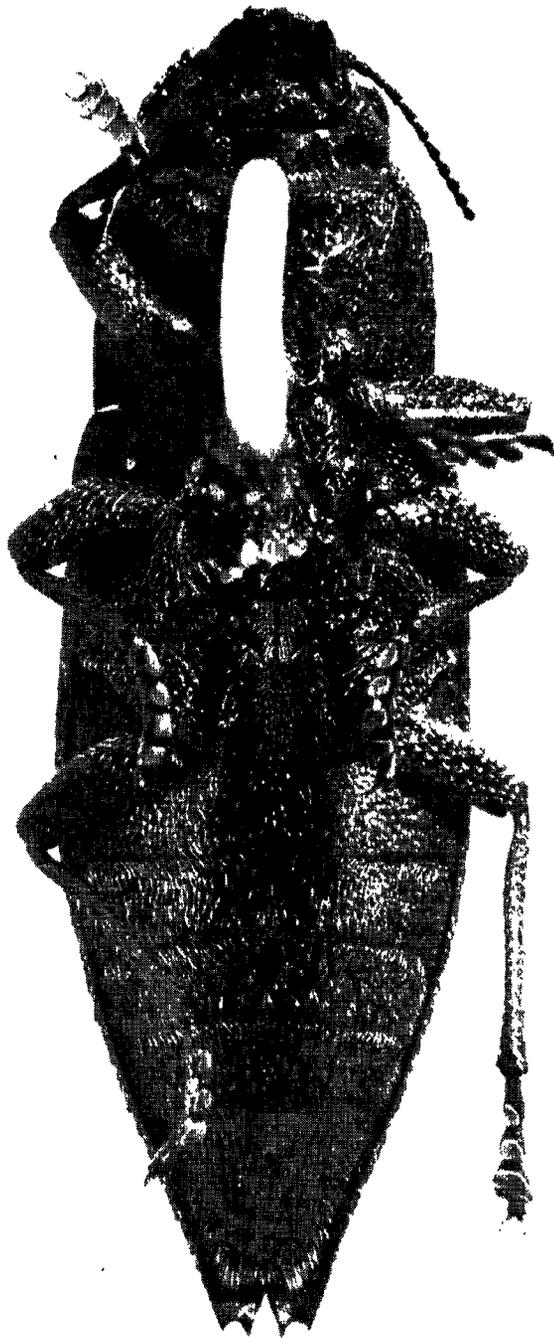
This species nested in hard-packed sand near Auburn, NY (17 July - 4 August 1970, 18 July - 3 October 1983) and in very hard-packed sand-clay of a firetrail at the Archbold Biol. Sta., Lake Placid, FL (16-30 April 1973). We excavated 7 nests at Auburn and 6 at the Archbold Biol. Sta. One nest at Auburn contained 17 cells. Cells at Auburn were unearthed 11-17 ( $\bar{x}$  = 15.0; N = 7) cm beneath the surface, and those at the Archbold Biol. Sta., 12-17 ( $\bar{x}$  = 14.9; N = 13) cm. The cells were 8-13 x 15-26 ( $\bar{x}$  = 10.9 x 20.5; N = 27) and 8-10 x 15-21 ( $\bar{x}$  = 9.2 x 17.7; N = 15) mm high and long at the 2 localities, respectively. Larger cells invariably contained older larvae and cocoons.

Cells at Auburn held 2-15 ( $\bar{x}$  = 5.4; N = 39) prey, whereas those at the Archbold Biol. Sta. held 2-5 ( $\bar{x}$  = 3.3; N = 13) prey. Cells exhibited distinct bimodality in prey weight per cell as follows: 128-233 ( $\bar{x}$  = 189.3; N = 7) and 308-430 ( $\bar{x}$  = 345.3; N = 6) mg at Auburn; and, 98-259 ( $\bar{x}$  = 205.5; N = 4) and 409-441 ( $\bar{x}$  = 423.5; N = 4) mg at the Archbold Biol. Sta. At Auburn male and female wasps, respectively, were reared from these cells. Individual prey at these localities weighed (wet), on the average, 61.9 (18-109; N = 36) and 93.2 (20-188; N = 27) mg, respectively. Wasps associated with these prey weighed (wet) 74-95 ( $\bar{x}$  = 84.5; N = 2) and 85-149 ( $\bar{x}$  = 121.7; N = 6) mg, respectively.

The prey on which the egg was laid was about average-sized: 68.0 (30-97; N = 6) mg at Auburn; and, 81.2 (61-98; N = 5) mg at the Archbold Biol. Sta. The egg, 3.5-4.5 x 0.8-0.9 mm, elastic and hyaline, weighed 2 mg and was attached tightly and longitudinally to the venter of the prey's thorax (Fig. 2).

Females at Auburn brought consecutive prey to their nests at intervals of 14-117 ( $\bar{x}$  = 45.1; N = 12) min. and spent 2-12 ( $\bar{x}$  = 7.5; N = 12) min. inside between entering with prey and exiting.

Prey (no new records) recovered from the cells comprised adult Buprestidae, with their numbers in parentheses, as follows: *Agrilus anxius* Gory (171); *Agrilus* sp. (1); *Buprestis maculipennis* Gory (23); *Cinyra gracilipes* Melsheimer (59); *Dicerca lurida* (Fabricius) (85); *Poecilnota cyanipes* Say (3).



2

Fig. 2. Prey of *Cerceris fumipennis* with egg attached in position typical of the genus (Photo by D. J. Peckham).

One 5-celled nest at Auburn contained 1 maggot feeding on the prey in each of 2 cells. Of 16 cells in Florida, only 5 had the potential of giving rise to adult wasps in the next generation. Five cells contained small red ants and prey fragments, 5, prey fragments only and 1, prey being fed upon by a maggot which was reared to *Senotainia rubriventris* (Macquart) (Sarcophagidae).

In Florida 3 wasps were seen to enter nests with other females inside. In each case the entering wasp remained inside the nest for many minutes, then exited, returned with prey, and entered with the other wasp still inside. The female that remained in the nest would often station herself with the head inside the entrance for many minutes, back down and remain inside, or fly out, circle, and reenter. No contact was observed between females occupying the same nest. In 2 of the nests only 1 brood cell each was being provisioned at one time. In 2 of the 3 nests some of the side burrows led to cells that contained prey fragments and cocoon remnants from a previous generation.

#### DISCUSSION

*Cerceris flavofasciata floridensis*, *C. rufopicta* and *C. fumipennis* are, more or less, ecologically isolated from one another. Although pairs of these species were studied at the same localities, they were spatially separated from one another. At Auburn, NY *C. fumipennis* nested in the hard-packed sand of a roadway leading into a sand pit, whereas *C. rufopicta* nested off to the side near the edge of a field. In Florida *C. fumipennis*, likewise, occupied a firm, sand-clay car path while *C. flavofasciata floridensis* nested in a sand bank some distance away.

Based upon collecting records *Cerceris flavofasciata* and *C. robertsonii* appear to be multivoltine in the warmer parts of their ranges, whereas *C. fumipennis* probably has a partial second brood in the south (Ferguson 1984, pers. comm.). In the Northeast *C. r. robertsonii* may be univoltine because the majority of collection and observational records are from July-August.

The nests of *C. flavofasciata floridensis* were similar in architecture to those described for the nominate subspecies by Krombein (1959). Those of *C. rufopicta* were similar in design to those described by Krombein (1952) and illustrated by Evans (1971). The burrow configuration and nest architecture of *C. fumipennis* were not only similar to those illustrated by Evans (1971) and described by Evans and Rubink (1978), but the depths of the cells from many widely separated geographic localities were remarkably close. Burrow storage, as noted by Evans (1971), was commonplace in all 3 species.

Evans (1971) noted that, in *Cerceris*, cells are of 2 sizes, small ones with less prey giving rise to male wasps and large ones with more prey giving rise to female wasps. We were able to substantiate this, using biomass in the form of total prey weight per cell, only for *C. fumipennis*. In all 3 species the number of prey per cell was inversely related to the sizes of the prey. Evans and Rubink (1978), likewise, noted an inverse relationship between size of prey and number of prey per cell in *C. californica* Cresson.

Prey of all 3 species were placed in the cells usually in a head inward and ventral side upward position, a position typical of species in the genus (Evans 1971). In at least *C. flavofasciata floridensis* some prey were

"fitted" around the centrally located prey bearing the wasp's egg or larva. Many prey of *C. rufopicta* were lively and able to walk when taken from the cells, and we attribute the variety of positions in which some prey were found (not always head inward, venter upward) to this light paralysis. Prey of *C. flavofasciata floridensis* and *C. fumipennis*, on the other hand, appeared to be rather thoroughly paralyzed as indicated by their acquiescent states. Evans and Matthews (1970) noted that the prey of some Australian species of *Cerceris* were "deeply paralyzed."

The position of the wasp's egg on the prey in at least those species of *Cerceris* that store adult Coleoptera appears rather constant (see Tsuneki 1965, Evans 1971, Alcock 1974, our Fig. 2). We noted that eggs of *C. flavofasciata floridensis* and *C. rufopicta* were attached more loosely than those of *C. fumipennis*. Eggs of *C. binodis* Spinola and *C. simplex macrosticta* were laid "diagonally" across the thorax and anterior abdomen of the prey (Evans 1971, Alcock 1974), whereas that of *C. fumipennis*, as observed by Evans (1971), was placed "longitudinally" on the prey. Interestingly, *C. flavofasciata floridensis*, *C. rufopicta* and *C. binodis* use prey belonging to the same family, Chrysomelidae, while *C. fumipennis* captures Buprestidae.

Much has been written about the prey preferences of species of *Cerceris* (Tsuneki 1965, Scullen and Wold 1969, Evans 1971, Gess 1980). All of the Nearctic species capture and store adult Coleoptera. There is much agreement between Scullen's (1965) species groups of *Cerceris* and type of beetle used as prey. Thus, *C. rufopicta* and other members of Scullen's Group III use Chrysomelidae while *C. fumipennis* and other species belonging to Group II store Buprestidae. Evans (1971) reported much diversity in prey selection between 10 Nearctic species of *Cerceris* and *Eucerceris*, a related genus. Evans and Rubink (1978) noted much intraspecific constancy among the prey of 6 of 7 Nearctic species of *Cerceris*. The number of new prey records we present for *C. flavofasciata floridensis* and *C. rufopicta* reflects a previous inadequate amount of such knowledge for these species, whereas our lack of new prey records for *C. fumipennis* reflects the vast amount of work that has been done on this species.

The amount of mortality we report from the cells of *C. flavofasciata floridensis* (33%, 5/15 cells), *C. rufopicta* (40%, 4/10), and *C. fumipennis* (62%, 13/21) is high. We noted maggots of Miltogrammini (Sarcophagidae) and worker ants in the cells of all 3 species. Surprisingly, the highest amount of mortality was for *C. fumipennis* which had 2 or more females each occupying at least 3 nests in Florida and had females guarding these nests with their heads stationed in the entrances! Evans and Hook (1982b) have theorized that females of *Cerceris* stationed in nest entrances are effective in deterring the entry of ants and nest parasites, yet our data do not bear this out.

In Florida it appeared that some females of *C. fumipennis* were renovating and using older conspecific nests, and we attributed this to the difficulty of excavating in extremely hard-packed soil. Individual nests of species of *Cerceris* may be maintained by 2 or more successive generations of wasps (Tsuneki 1965, Evans et al. 1976, Salbert and Elliott 1979, Evans and Hook 1982a, b). In such cases one or more females overwinters in the nest and expands and provisions the nest in the spring. Such nests usually contain one or a few, older females with badly worn wings and mandibles and

perhaps one or more freshly emerged females with complete wings and mandibles (Salbert and Elliott 1979, Evans and Hook 1982a). Evans and Hook (1982b) observed that such nests of some Australian *Cerceris* contained well over 100 cells and believed that the success of such species was based upon communal nesting, including overlapping generations.

#### END NOTES

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The correct address of the junior author is not known.

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CUTICULAR LIPIDS FOR SPECIES RECOGNITION OF  
MOLE CRICKETS (ORTHOPTERA:GRYLLotalpidae)  
I. *SCAPTERISCUS DIDACTYLUS*, *SCAPTERISCUS*  
*IMITATUS*, AND *SCAPTERISCUS VICINUS*

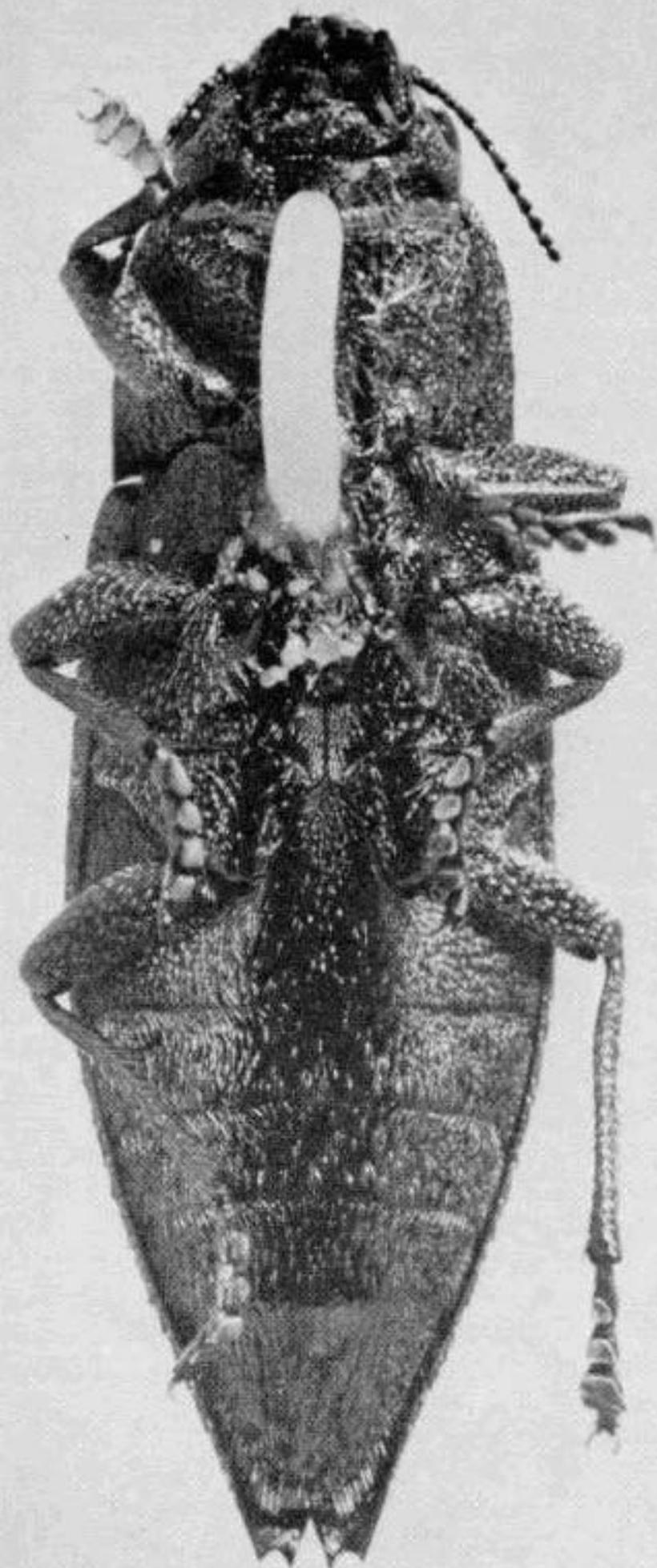
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ABSTRACT

Whole-body cuticular extracts of *Scapteriscus didactylus* and *Scapteriscus imitatus* collected from Puerto Rico, and of *Scapteriscus vicinus* collected in Florida, were analyzed by isothermal and temperature programmed gas chromatography. Calculated Kovats Indices indicated an homologous series of straight-chain and branched-chain alkanes in the cuticular lipids of each mole cricket. No differences were found between the sexes of species, but small variations in qualitative and quantitative patterns were present among individuals. The profiles of GC peaks were easily distinguishable, providing data for species and region of origin recognition, and supporting morphological and acoustical evidence that the crickets represent 3 species.

RESUMEN

Se analizaron por cromatografía isotermal y cromatografía de gas



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MOLE CRICKETS (ORTHOPTERA:GRYLLotalpidae)  
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ABSTRACT

Whole-body cuticular extracts of *Scapteriscus didactylus* and *Scapteriscus imitatus* collected from Puerto Rico, and of *Scapteriscus vicinus* collected in Florida, were analyzed by isothermal and temperature programmed gas chromatography. Calculated Kovats Indices indicated an homologous series of straight-chain and branched-chain alkanes in the cuticular lipids of each mole cricket. No differences were found between the sexes of species, but small variations in qualitative and quantitative patterns were present among individuals. The profiles of GC peaks were easily distinguishable, providing data for species and region of origin recognition, and supporting morphological and acoustical evidence that the crickets represent 3 species.

RESUMEN

Se analizaron por cromatografía isoterma y cromatografía de gas

programada por temperatura unos extractos de la cutícula del cuerpo entero de *Scapteriscus didactylus* y *S. imitatus* colectados en Puerto Rico y *S. vicinus* colectado en Florida. Indices de Kovat calculados indicaron una seria homóloga de alcanos de cadena derecha y cadena ramificada en el lípido cuticular de los cortones. No se encontró ninguna diferencia entre los sexos de las especies, pero variaciones pequeñas entre los individuos existían en los patrones cualitativos y cuantitativos. Las perfiles de los picos de cromatografía de gas resultaron bien distinguible, proveyendo datos para la reconocimiento de las especies y sus regiones de origen, y conformandose a la evidencia morfológica y acústica de que los cortones representan 3 especies.

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Mole crickets (Orthoptera: Gryllotalpidae) are fossorial insects capable of causing extensive damage to turf and agriculture. An estimate of the total losses and costs of control for 1980, due to mole crickets in Florida, was \$35.0 million (Southern 1982). Until recently, mole crickets found in Puerto Rico (called "changas" in Puerto Rican Spanish) were believed conspecific with *Scapteriscus vicinus* Scudder (Walker and Nickle 1981), an introduced pest now widespread throughout the southeastern United States. Current knowledge suggests that at least 3 species of mole crickets exist in Puerto Rico, none of which is *S. vicinus* (unpublished). One species, *Scapteriscus abbreviatus* Scudder, has only been reported rarely while another has been identified as *Scapteriscus didactylus* (Latreille). The third is a new species that has been named *Scapteriscus imitatus* Nickle and Castner. One way to recognize and to collect these mole crickets is to broadcast their distinctive calling songs (Walker 1982, Forrest 1983). The present work was undertaken to determine if gas chromatographic (GC) volatile analyses of the cuticular lipids of these mole crickets might have taxonomic value and be of use in the search for the homeland of the introduced *S. vicinus*.

#### MATERIALS AND METHODS

Puerto Rican mole crickets were collected as live adults in the field. *S. imitatus* were collected in Isabela (Aguadilla Province) by broadcasting the male calling song, using an electronic caller of the type described by Walker (1982). *S. didactylus* were collected in Dorado (Arecibo Province) from soil samples taken at the Cerromar Beach Hotel golf course. Live specimens of each species were shipped to Gainesville, Florida, and unpackaged at the Florida Division of Plant Industry. Specimens for hydrocarbon analysis were frozen for lipid extraction later. *S. vicinus* were collected from Gainesville, Florida, and Jacksonville, Florida, by broadcasting the male calling song.

Hydrocarbons and other lipids were extracted by immersing a frozen adult mole cricket in 5 ml of pentane and gently agitating it for 1 minute. The solvent was evaporated with a stream of nitrogen to a final volume of 1 ml. From 1-2 ul of the concentrated extract was injected into a Varian 3700 gas chromatograph equipped with a flame ionization detector. Data were collected and processed directly from the chromatograph by a Hewlett-Packard 3390A integrator. Hydrocarbons were separated on a 2 mm by 1.83 m coiled glass column packed with 3% OV-1 coated on 100/120 mesh Gas

Chrom Q. The carrier gas was nitrogen at a flow of 27.3 ml per minute. Injector port and detector were held at 220°C.

Kovats Indices (Fig. 1) were calculated from isothermal chromatography at 190°C with docosane (C 22 alkane) and tetracosane (C 24 alkane) hydrocarbon standards for *S. vicinus* and *S. imitatus*, and at 220°C with octacosane (C 28 alkane) and triacontane (C 30 alkane) standards for *S. didactylus*. Temperature programmed analyses following the procedure of Vander Meer and Wojcik (1982) were made by increasing the column temperature from 150°C to 270° at 2°C/min and holding at 270°C for 10 minutes. The injector port and detector were kept constant at 270°C.

### RESULTS

Individual cuticular extracts of more than 25 *S. vicinus* (mixed adult sexes and nymphs), 4 (1 ♂, 3 ♀) adult *S. imitatus*, and 5 (2 ♂, 3 ♀) *S. didactylus* were analyzed. The GC traces from temperature programming are presented in Fig. 1. Although all 3 species have some cuticular components in common, chromatogram profiles and relative quantities of constituents are characteristic to individual species.

Prior to gas chromatography, cuticular lipid extracts of *S. vicinus* were purified by chromatography on a column of Florisil (30g deactivated by addition of water to a final concentration of 7% by weight) (Carroll 1961). Hydrocarbons were eluted from the column by 75 ml hexane. Gas chromatographic patterns produced by the hydrocarbons eluted from the Florisil column were not appreciably different from patterns obtained from crude cuticular lipid extracts. Consequently the Florisil column purification step was eliminated from *S. vicinus* analyses, and was not used with *S. imitatus* or *S. didactylus*.

The major components in the cuticle of *S. vicinus* have calculated KI values of 2201, 2247, 2304, and 2324. There were minor peaks at 2100, 2406, 2453, 2471, and 2800, with traces (less than 1% of total) of other components. Co-injection of extracts with authentic alkane standards showed that the peaks with KI values of 2100, 2201, 2304, 2406, and 2800 in *S. vicinus* were chromatographically identical to C21, C22, C23, C24, and C28 alkanes, respectively. The peaks with KI values of 2247, 2324, 2453, and 2471 are probably branched chain alkanes. The primary cuticular constituents of *S. imitatus* had KI values of 2497, 2545, 2567, and 2625. Minor peaks were calculated at 2303, 2399, 2434, and 2599, with traces of additional compounds. The KI values of major components in the *S. didactylus* cuticle were 2870, 2900, 2938, 2980, 3008, 3041, 3092, and 3183, with minor peaks at 2699 and 2802, plus traces of a few shorter chain molecules. Minor variations occurred between individuals of each species, but there were no characteristic sexual differences, and the overall profile for each species remained easily recognizable.

### DISCUSSION

In contrast to analyses of insect fatty acids, which are not very useful as taxonomic tools below the level of orders, analysis of cuticular hydrocarbons has been shown to be useful at the species level in several insect groups (Jackson 1970, 1972; Carlson and Service 1979, 1980; Carlson and Walsh 1981 and Lockey 1982). Hydrocarbons in the cuticle serve specific

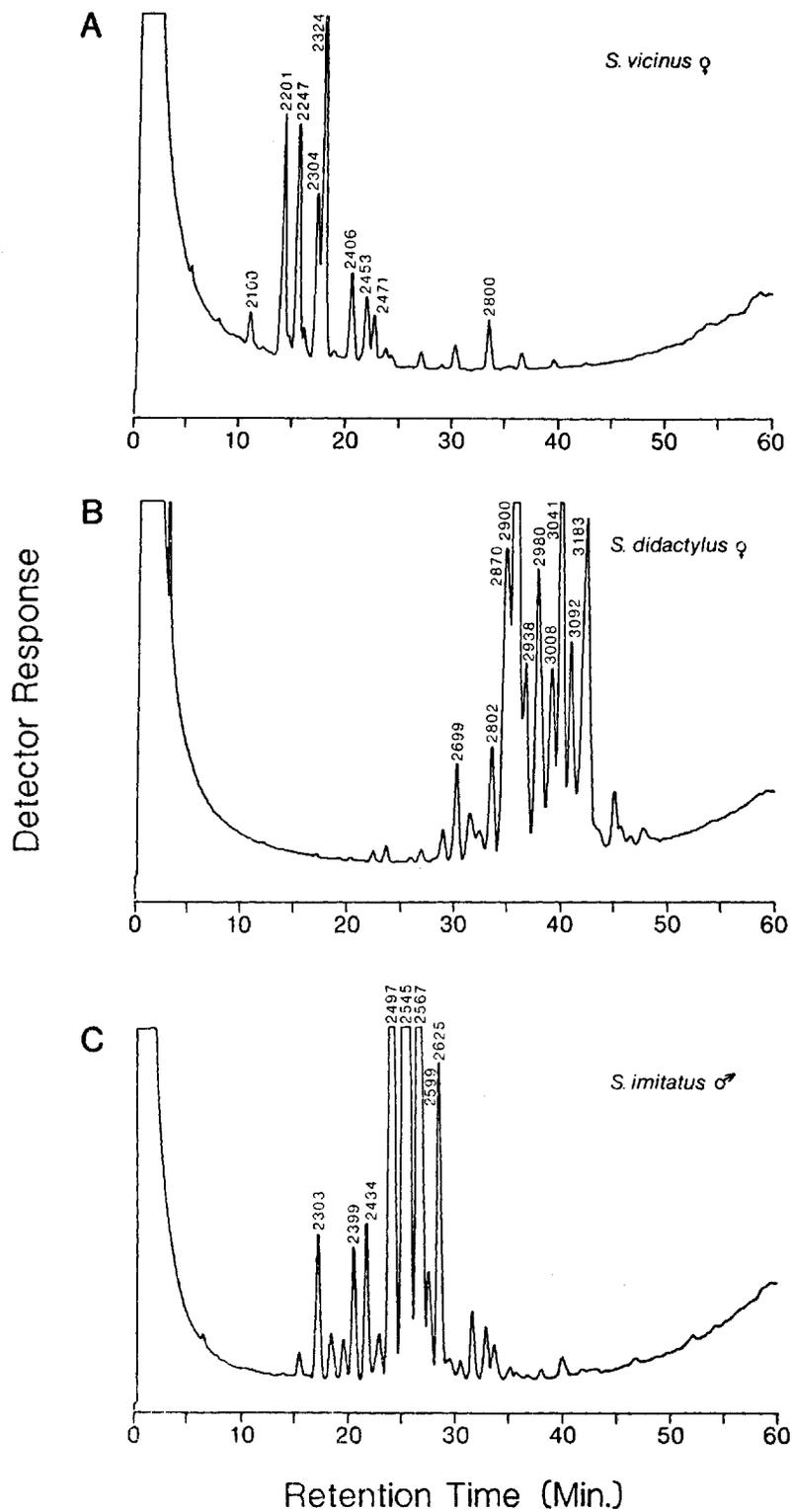


Fig. 1. Gas chromatographic traces of the cuticular hydrocarbons of individual mole crickets (A) *S. vicinus*, (B) *S. didactylus*, (C) *S. imitatus*. Numbers above peaks refer to calculated Kovats Index (KI).

functional roles integrated with the ecology of the insect (see review by Howard and Blomquist 1982), and thus it is not so surprising that they are often species specific. Fatty acids, on the other hand, serve a more universal metabolic role. Tartivita and Jackson (1970) found that hydrocarbons comprised over 90% of the cuticular lipids in 7 species of cockroaches. These lipids may also serve as a barrier to micro-organisms and toxic chemicals, and as a source of pheromones and kairomones (Baker et al. 1979). In higher Diptera, cuticular hydrocarbons were found to be responsible for male sexual stimulation and sex recognition (Carlson et al. 1978). Howard et al. (1980) showed that the biosynthesis of cuticular hydrocarbons probably served as the primary mechanism by which a termitophile *Trichopsepius frosti* Seevers, integrated itself into a termite colony. Similarly, Vander Meer and Wojcik (1982) have shown that the myrmecophilous beetle *Myrmecaphodius excavaticollis* (Blanchard), was able to integrate itself into ant colonies through the acquisition of host-specific hydrocarbons.

The hydrocarbons of mole crickets have not been investigated previously, and the major reason for the inception of this work was to determine if a gas chromatographic separation of the cuticular hydrocarbons was useful in species recognition. The results provide an affirmative answer, and hydrocarbon analyses should prove helpful in locating and/or confirming the original homeland of *S. vicinus*. In addition GC data may be useful in a general taxonomic revision of mole crickets. Gas chromatographic analysis of hydrocarbons is relatively simple and routine, and has the advantage that extracts can be prepared quickly in the field or lab, while the insect can be saved as a dry specimen for conventional morphological study.

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- . 1982. Sound traps for sampling mole cricket flights (Orthoptera: Gryllotalpidae: *Scapteriscus*). *Florida Ent.* 65(1): 105-10.

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## A NEW SPECIES OF *MEGAPODIELLA* (MALLOPHAGA: PHILOPTERIDAE) FROM THE MALLEE FOWL OF AUSTRALIA

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### ABSTRACT

A new species, *Megapodiella parkeri*, is described and illustrated from specimens taken off the Mallee Fowl, *Leipoa ocellata*, from Australia. Genitalic structures, details of chaetotaxy, and dimensions are used to separate this species from *M. nakatae*, the only other known species in the genus.

### RESUMEN

Se describe y se ilustra una especie nueva, *Megapodiella parkeri*, colec-

- plex by analysis of cuticular paraffins. *Acta Tropica* 38: 235-9.
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### ABSTRACT

A new species, *Megapodiella parkeri*, is described and illustrated from specimens taken off the Mallee Fowl, *Leipoa ocellata*, from Australia. Genitalic structures, details of chaetotaxy, and dimensions are used to separate this species from *M. nakatae*, the only other known species in the genus.

### RESUMEN

Se describe y se ilustra una especie nueva, *Megapodiella parkeri*, colec-

tado de un ave australiano, *Leipoa ocellata*. Se utilizan las estructuras genitales, los detalles de quetataxía, y las dimensiones para separar esta especie de *M. nakatae*, la única otra especie conocida en este género.

The new philopterid genus *Megapodiella* was described by Emerson and Price (1972) to include the single new species *M. nakatae*, whose type-host is *Aepyptodius arfakianus* (Salvadori) (Galliformes: Megapodiidae). At that time, we stated the likelihood that future collections from other host species in this family would yield additional species of *Megapodiella*. It is our purpose here to describe and illustrate a second species of this genus from specimens taken off the Mallee Fowl, *Leipoa ocellata* Gould, from Australia.

*Megapodiella parkeri* Price and Emerson, NEW SPECIES  
(Fig. 1-3)

**FEMALE:** As in Fig. 2. Each side of head with 2 long setae associated with "V"-shaped dorsoanterior suture and 3 long marginal temple setae. Pteronotum divided medially, each side of posterior margin with 3 very long lateral and 5-6 medial setae. Abdominal tergites II (first apparent segment)-VIII divided; II-IX with porous-appearing structure aligned mediad to spiracles; IV-VIII with single lateroposterior seta; IV-V with long postspiracular seta; and with following number of uniformly long marginal tergo-central setae: II, 8-10; III, 13-15; IV, 12-14; V, 11-12; VI, 6-7; VII, 2-3; VIII, 2. Tergite IX not divided, each side with very long and short lateral setae and 2 widely-spaced very long posterior marginal setae. With small terminal tergal plate. Abdominal sternal setae similar in size to tergo-central setae, with following number: II, 8-9; III, 11-13; IV-V, 9-11; VI, 5-8; VII, 1-2. Subgenital plate with flattened posterior margin bearing 11-13 very short setae, anteriorly with small transverse plate and scattering of short setae and 1 very long lateroanterior seta. Ventro-posterior margin with 9-10 short to very long setae on each side. Dimensions (in mm): temple width, 0.79-0.80; head length, 0.91-0.92; prothorax width, 0.47-0.48; pterothorax width, 0.65-0.68; abdominal width, 1.06-1.15; total length, 2.69-2.72.

**MALE:** As in Fig. 3. Except for terminalia, general morphology and lengths and distribution of setae much as for ♀. Pteronotum with 5-7 medial very long marginal setae on each side. Number of abdominal tergo-central setae: II, 8-10; III, 12-14; IV, 11-14; V, 7-9; VI, 4-7; VII-VIII, 2. Tergite IX very short, undivided, without apparent porous-appearing structure, with each side having 4-5 long setae medioposterior to plate. Very short tergal plate along posterior abdominal margin. Number of abdominal sternal setae: II, 7-8; III, 7-12, IV-V, 6-8; VI, 2-4; VII-VIII, 2. Subgenital plate of irregular shape. Genitalia as in Fig. 1; with broad evenly-tapered basal plate, essentially rectangular protruding medio-posterior sclerite, and parameres curved mediad, each with minute terminal seta. Dimensions (in mm): temple width, 0.73-0.75; head length, 0.85-0.86; prothorax width, 0.44-0.45; pterothorax width, 0.61-0.62; abdominal width, 1.04-1.07; total length, 2.18-2.26; genitalia width, 0.14-0.15; genitalia length, 0.47-0.53.

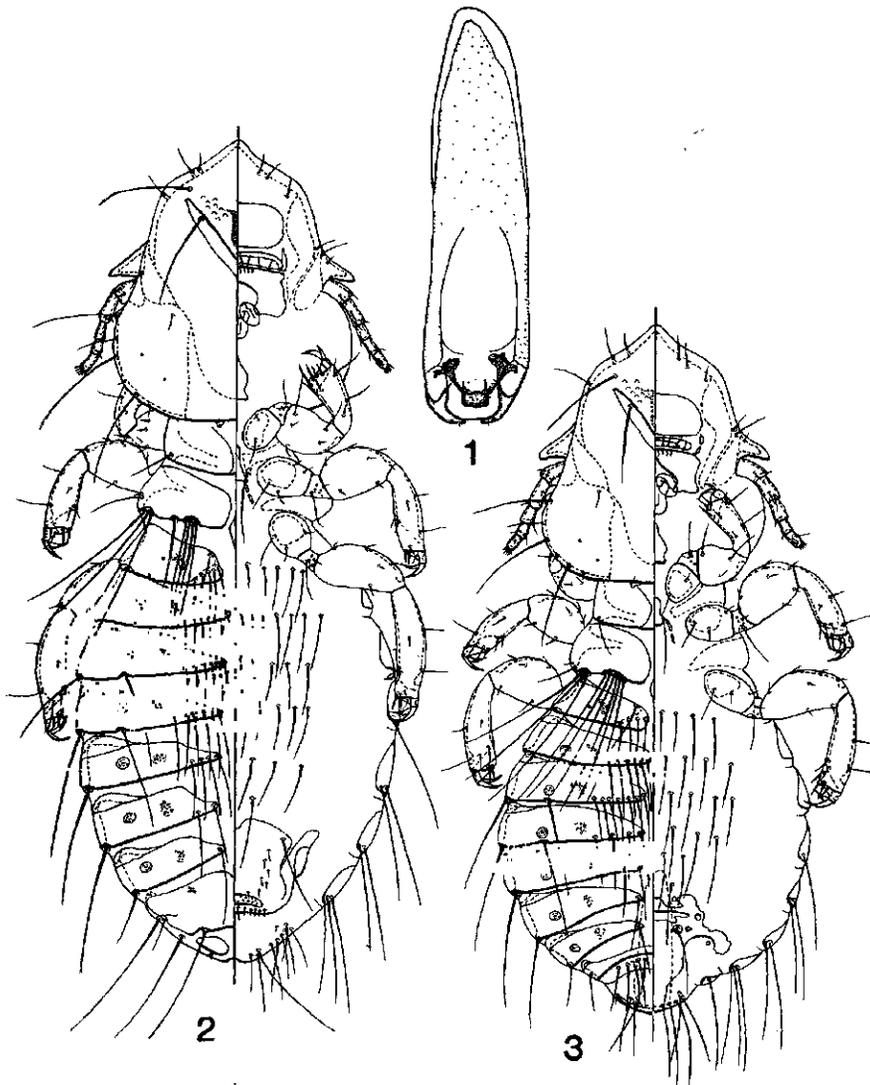


Fig. 1-3. *Megapodiella parkeri*. 1) ♂ genitalia; 2) dorsal-ventral view of ♀; 3) dorsal-ventral view of ♂.

Holotype ♀, ex *Leipoa ocellata* (South Australian Museum skin #B-36624), Zoo, Adelaide, South Australia, 1983; in collection of South Australian Museum. Paratypes, ex *L. ocellata*: 5 ♀, 2 ♂, same data as holotype; 8 ♀, 3 ♂, South Australian Museum skin #B-8347, Tintinasa, South Australia, 27.X.1906; 2 ♀, 2 ♂, South Australian Museum skin #B-8348, Murray Scrubs, South Australia, "early 1900's"; 1 ♀, Western Australia, no date. Paratypes will be deposited in the South Australian Museum, U.S. National Museum of Natural History, University of Minnesota, Florida State Collection of Arthropods, and K.C. Emerson Entomology Museum at Oklahoma State University.

While there are numerous characters possessed by *M. parkeri* that will separate it from *M. nakatae*, the only other known species of the genus, the following represent the most useful ones: (1) ♀ with flattened posterior margin of subgenital plate bearing only up to 13 very short inconspicuous setae; (2) ♀ ventroposterior abdominal margin with total of only 19-20 irregularly-placed short to very long setae; (3) tergite IX of ♀ with 2 widely-spaced very long setae on each side, ♂ with total of 9-10 medioposterior setae; (4) smaller specimens, temple width only up to 0.80 for ♀, up to 0.75 for ♂; (5) both sexes with abdominal tergites III-IV each with only up to 15 tergo-central setae; (6) ♂ tergo-central setae on II-VIII long, extending beyond bases of those of following tergite; and (7) ♂ genitalia with basal plate having evenly-tapered sides. Contrasted to these, the corresponding character states for *M. nakatae* are: (1) ♀ with evenly-rounded posterior margin of subgenital plate bearing row of about 40 short to medium setae; (2) ♀ ventroposterior abdominal margin with row of about 60 long setae; (3) tergite IX of ♀ with 2 close-set very long setae on each side, ♂ with total of only 5 medioposterior setae; (4) larger specimens, temple width over 0.88 for ♀, 0.81 for ♂; (5) both sexes with abdominal tergites III-IV each with at least 16 tergo-central setae; (6) ♂ tergo-central setae on II-VIII short, not extending to bases of those of following tergite; and (7) ♂ genitalia with basal plate constricted approximately 1/3 distance from anterior end.

#### ACKNOWLEDGMENTS

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**PELITROPIS ROTULATA (HOMOPTERA:  
TROPIDUCHIDAE) : HOST PLANTS AND DESCRIPTIONS  
OF NYMPHS**

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ABSTRACT

The 3rd, 4th, and 5th instars of *Pelitropis rotulata* Van Duzee are described and illustrated. Features useful in separating the nymphal instars include differences in body and wingpad sizes, spination of metatibiae and tarsomeres, and numbers of metatarsomeres and body pits. A list of 19 host plants observed in Florida and North Carolina is given.

RESUMEN

Se describen y se ilustran el tercero, el cuarto y el quinto instar de *Pelitropis rotulata* Van Duzee. Las características útiles en distinguir los instares ninfales incluyen diferencias en el tamaño del cuerpo y de los rudimentos de alas, las espinas de las metatibias y las piezas tarsales, y los números de las piezas de los metatarsos y de los fosos del cuerpo. Se presenta una lista de 19 plantas hospederas de Florida y Carolina del Norte.

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*Pelitropis rotulata* Van Duzee is a little-studied tropiduchid known from Florida, Mississippi, North Carolina, and Cuba (Metcalf 1954). Van Duzee (1909) noted that specimens were "beaten from bushes" in Florida. In Cuba, Bruner et al. (1945) reported collections from soursop or guanabana (*Annona muricata* L., Annonaceae), sugar apple (*A. squamosa* L.), and Australian pine (*Casuarina equisetifolia* J. R. & G. Forst., Casuarinaceae). This species also has been taken in blacklight traps (Frost 1964).

Little information is available on the morphology or ecology of the immatures of any tropiduchid. Metcalf and Bruner (1930) provided a brief, partial description of a *P. rotulata* nymph and illustrated but did not describe the 5th instar of *Neurotmeta sponsa* (Guerin-Meneville). Fletcher (1979, 1981) provided information on biology and described and illustrated the eggs and 5 nymphal instars of *Kallitambinia australis* Muir. Harris (1970) and Carnegie (1967) studied *Numicia viridis* Muir under laboratory and field conditions, respectively.

This paper presents descriptions of the 3rd, 4th, and 5th instar nymphs (by SWW), and lists host plants observed at the Archbold Biological Station, Florida and in North Carolina during 1982-1983 (by AGW).

MATERIALS AND METHODS

Specimens were preserved in 70% ethyl alcohol. The 5th instar is described in detail, but only major differences are described for 4th and 3rd

instars. Comparative statements refer to later instars (e.g., less numerous). Measurements are given in mm as mean  $\pm$  SE. Length was measured from apex of vertex to apex of abdomen, width across the widest part of the body, and thoracic length along the midline from the anterior margin of the pronotum to the posterior margin of the metanotum.

The collecting data for specimens used in the descriptions are: NORTH CAROLINA: Mecklenburg Co., Charlotte, 4-VII-1982, on amur privet (*Ligustrum amurense* Carr.) (3 third, 8 fourth, 1 fifth instar); FLORIDA: Highlands Co., Archbold Biological Station, 27-IV-1982, on Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) (3 fourth, 10 fifth instars), on wax-myrtle (*Myrica cerifera* L.) (1 fourth, 1 fifth instar).

#### DESCRIPTIONS OF NYMPHS

**FIFTH INSTAR** (Fig. 3, 4). Length  $4.82 \pm 0.072$ ; thoracic length  $1.91 \pm 0.026$ ; width  $2.07 \pm 0.049$ . Twelve specimens examined.

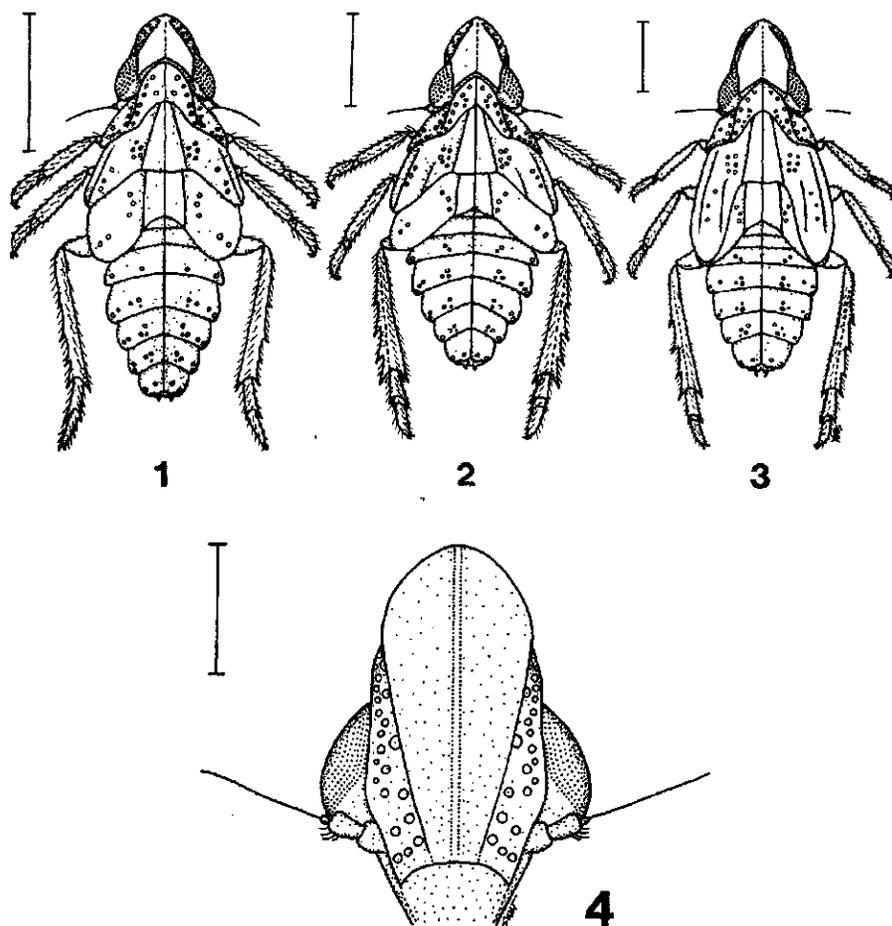


Fig. 1-3. Nymphs of *P. rotulata*. 1. Third instar. 2. Fourth instar. 3. Fifth instar. Vertical bars = 1.0 mm.

Fig. 4. Ventral view of frons of fifth instar *P. rotulata*. Vertical bar = 0.5 mm.

Form elongate, greatly flattened dorsoventrally, widest across mesothoracic wingpads. Body green in life with "tails" of wax; stramineous in alcohol.

Vertex produced anteriorly, narrowing and rounded at apex; lateral carinae extending anteromedially, fading just before apex; divided by longitudinal mid-dorsal intermembranous line into right and left halves. Frons (Fig. 4) ca.  $1\frac{1}{2}X$  longer than wide, rounded apically, broadening gradually to level of antennae then narrowing, concave at frontoclypeal juncture; outer lateral carinae originating anterior to eye and extending to frontoclypeal juncture, inner lateral carinae extending from border of frons and vertex almost to frontoclypeal juncture and paralleling outer lateral carinae in posterior  $\frac{3}{4}$ ; with weak longitudinal median carina fading before apex and base; with numerous pits in 2 irregular rows between each inner and outer lateral carina. Clypeus narrowing distally, consisting of subconical, basal postclypeus and elongate, subconical, distal anteclypeus. Beak 3-segmented, extending to mesocoxae; segment 1 covered by anteclypeus, segment 2 ca.  $1\frac{1}{2}X$  length of 3. Eyes red. Antennae 3-segmented; scape ringlike; pedicel ca.  $2X$  length of scape, lacking pitlike sensoria but covered with small setae on dorsal aspect; flagellum whiplike distally with bulbous base ca.  $\frac{1}{4}$  length of pedicel.

Thoracic nota divided by longitudinal mid-dorsal line into 3 pairs of plates. Pronotum with anterior margin rounded, posterior margin sinuate; each plate with outwardly curved carina originating anteromedially, forming part of anterior margin, and extending posterolaterally almost to posterior margin of plate; with ca. 22 pits on plate (lateralmost pits often not visible in dorsal view). Mesonotum with median length ca.  $2\frac{1}{2}X$  that of pronotum; each plate with longitudinal oblique (inner) carina in medial  $\frac{1}{4}$ , partial longitudinal (intermediate) carina originating near middle of plate and extending almost to medial edge of wingpad in lateral  $\frac{1}{2}$ - $\frac{2}{3}$ , and outwardly curved partial (outer) carina paralleling lateral margin in lateral  $\frac{1}{4}$ ; group of 6 pits just lateral to inner carina and row of 3 pits just medial to outer carina; wingpad extending to tip of metanotal wingpad. Metanotum with median length ca.  $\frac{2}{3}X$  that of mesonotum; each plate with longitudinal carina in median  $\frac{1}{4}$ , group of 3 pits lateral to carina; wingpad extending to abdominal tergite 4. Pro- and mesocoxae elongate, posteromedially directed; metacoxae globose, fused to metasternum; remaining segments of legs with rows of setae. Metatibiae with 3 black-tipped spines on lateral aspect of shaft and transverse row of 5 black-tipped spines at apex on ventral aspect. Pro- and mesotarsi each with 2 tarsomeres; tarsomere 1 wedge-shaped, tarsomere 2 subconical and curved near apex, with pair of brown claws and pulvillus apically. Metatarsi with 3 tarsomeres; tarsomere 1 elongate, subcylindrical with transverse row of 5 black-tipped spines at apex on ventral aspect; tarsomere 2 somewhat wedge-shaped, with 2 small black-tipped teeth on ventral aspect, 1 at apex and 1 laterally; tarsomere 3 similar to tarsomere 2 of other legs.

Abdomen 9-segmented; segments 1-7 visible dorsally, segments 8-9 telescoped anteriorly. Tergites 2-7 with weak median longitudinal carina; tergites 3-7 curving around lateral margin to ventral aspect; tergites 3-6 each with black mark on either side near posterior margins near lateral  $\frac{1}{2}$ ; tergite 7 with reddish marks on caudal margin. Each tergite with the following number of pits on either side of midline (lateralmost and ventral

pits often not visible in dorsal view) : tergite 3 with 2-3, tergites 4-6 with 6, tergite 7 with 4. Segments 7-8 each with pair of obscure, white caudal wax-pads. Segment 9 elongate vertically, surrounding anus.

FOURTH INSTAR (Fig. 2). Length  $3.82 \pm 0.112$ ; thoracic length  $1.48 \pm 0.021$ ; width  $1.54 \pm 0.019$ . Twelve specimens examined.

Antennae with bulbous portion of flagellum ca. 1/3 length of pedicel.

Pronotal plates each with ca. 19 pits. Each mesonotal wingpad strongly lobate, covering ca. 1/2 of metanotum laterally. Each metanotal plate with 2 pits in posterolateral corner, wingpad extending to abdominal tergite 2 or 3. Metatarsomere 2 obscure, with 1 very small black-tipped tooth on ventral aspect.

THIRD INSTAR (Fig. 1). Length  $3.07 \pm 0.067$ ; thoracic length  $1.17 \pm 0.183$ ; width  $1.17 \pm 0.183$ . Three specimens examined.

TABLE 1. HOST PLANTS OF *Pelitropis rotulata* OBSERVED IN FLORIDA AND NORTH CAROLINA DURING 1982-83. EACH COLLECTION RANGED FROM 1-10 + INDIVIDUALS.

Species	No. of collections	Locality
Aquifoliaceae		
<i>Ilex</i> sp.	1	FL
Compositae		
<i>Baccharis halimifolia</i> L.	5	FL, NC
Elaeagnaceae		
<i>Elaeagnus multiflora</i> Thunb.	3	NC
Ericaceae		
<i>Lyonia</i> sp.	1	FL
<i>Rhododendron</i> sp.	1	FL
<i>Vaccinium corymbosum</i> L.	1	FL
<i>Vaccinium</i> sp.	1	FL
Fagaceae		
<i>Quercus phellos</i> L.	1	FL
Hamamelidaceae		
<i>Liquidambar styraciflua</i> L.	1	NC
Hypericaceae		
<i>Ascyrum edisonianum</i> Small	1	FL
Lauraceae		
<i>Persea borbonia</i> (L.) K. Spreng.	1	FL
Myricaceae		
<i>Myrica cerifera</i> L.	4	FL
Oleaceae		
<i>Ligustrum amurense</i> Carr.	2	NC
Polygonaceae		
<i>Coccoloba uvifera</i> (L.) L.	1	FL
Rosaceae		
<i>Prunus serotina</i> J. F. Ehrh.	2	NC
<i>Pyrus communis</i> L.	1	NC
Ulmaceae		
<i>Ulmus alata</i> Michx.	2	NC
Vitaceae		
<i>Parthenocissus quinquefolia</i> (L.) Planch.	5+	FL, NC
<i>Vitis rotundifolia</i> Michx.	1	FL

Pronotal plates each with ca. 15 pits. Mesonotal plates each lacking intermediate carina, with group of 5-6 pits just lateral to inner carina; wingpad slightly lobate, covering ca. 1/3 of metanotum laterally. Metatarsi with 2 tarsomeres; tarsomere 2 similar to 3 of later instars.

Abdominal tergites 3-6 with black marks reduced. Each tergite with the following number of pits on either side of midline: tergite 3 with 2, tergites 4-6 with 5, tergite 7 with 3.

#### HOST PLANTS

Nymphs of *Pelitropis rotulata* were collected on 19 plant species (Table 1). Based on observations and collections made in Florida during mid-April, the largest populations (4th and 5th instars) of this apparent general feeder developed on Virginia creeper (*P. quinquefolia*), and wax-myrtle (*M. cerifera*). The various hosts were growing in bayheads, sand pine scrub, scrubby flatwoods, and palmetto flatwoods at the Archbold Biological Station, 13 km south of Lake Placid in Highlands County.

At Charlotte, North Carolina, the largest numbers were observed on groundsel bush (*Baccharis halimifolia* L.) and amur privet (*Ligustrum amurense* Carr.) growing along railroad tracks and in vacant lots. Third to fifth instars were collected during the 1st week of July; 5th instars and adults, during the 1st week of August. Based on 2 years of intermittent collecting from April through August, we believe that the North Carolina populations are univoltine.

#### ACKNOWLEDGMENT

We thank Dr. L. L. Deitz, Department of Entomology, North Carolina State University, Raleigh, for providing a copy of the paper by Bruner et al. (1945). We also thank Dr. J. N. Layne, Executive Director, and his staff at the Archbold Biological Station, Lake Placid, Florida, for use of research facilities.

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A NEW SPECIES OF *MACROTHEMIS* FROM CENTRAL  
AMERICA WITH NOTES ON THE DISTINCTION  
BETWEEN *BRECHMORHOGA* AND *MACROTHEMIS*  
(ODONATA: LIBELLULIDAE)

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ABSTRACT

*Macrothemis aurimaculata*, a new species from Guatemala and Costa Rica, is closely related to *M. inequiunguis* (Calvert), but differs in abdominal color pattern, shape of superior appendage and posterior hamule of the male, and color of the frons. The two species differ from other *Macrothemis* in the shorter tooth of the tarsal claw. The most constant distinction between *Macrothemis* and *Brechmorhoga* is the narrowed discoidal field in the front wing in *Macrothemis*.

RESUMEN

*Macrothemis aurimaculata*, una nueva especie de Guatemala y Costa Rica, está relacionada con *M. inequiunguis* (Calvert), pero difiere en el dibujo abdominal la forma del apéndice superior abdominal y el hámulo posterior del macho y el color de la frente. Las dos especies difieren de otras especies de *Macrothemis* en el diente más corta de la uña. La distinción más constante entre *Macrothemis* y *Brechmorhoga* es el campo dicoideo angosto de la ala anterior de *Macrothemis*.

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A new species of *Macrothemis* from Guatemala and Costa Rica differs, along with *M. inequiunguis* (Calvert), from all other *Macrothemis* in possessing short tarsal claws, and differs from the latter species in the following characters: 1) pale orange spot on 7 occupies more than 3/4 of dorsum (paired rounded yellow green spots in *inequiunguis* occupying less than half of tergum), 2) frons is iridescent purple, with small yellow spots at ventral-lateral corners (frons centrally iridescent purple but broadly bordered laterally and ventrally with yellow), 3) posterior hamule is stout, recumbent, with a straight distal portion, and has a small terminal projection (hamule thin, erect, arcuate in profile, with curved terminal hook), 4) superior appendage gradually thickens in profile with maximum thickness at 70% of length, the distal portion tapers, and has a very small tooth (superior appendage with parallel sided proximal portion, abruptly thickened at 40-50% of length, with large, many pointed tooth, and with distal portion parallel sided).

The new species has been taken at several localities in Guatemala and at one locality in Costa Rica. It flies along streams in the forested mountains, patrolling in the manner of *Brechmorhoga rapax* (Calvert).

*Macrothemis aurimaculata* Donnelly, NEW SPECIES

Fig. 1-5

HOLOTYPE ♂. *Head*: labium, mandibles, genae dark brown, shining;

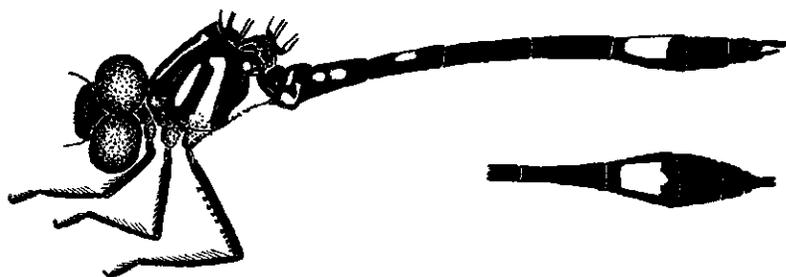


Fig. 1. Lateral aspect of *Macrothemis aurimaculata*, male (inset shows dorsal aspect of terminus of abdomen).

labrum glossy black; anteclypeus yellow brown, postclypeus yellow, centrally brown; frons iridescent purple with lateral-ventral corners yellow, rounded, with shallow median sulcus; vesicle iridescent purple, inflated; face and rear of head covered with short, dark hairs. *Prothorax*: brown, lacking pale markings. *Pterothorax*: dark brown, pale greenish yellow as follows: prominent tapering longitudinal stripes on mesepisternum pointed anteriorly and widened abruptly posteriorly into rounded "T"; rounded stripe on dorsal half of mesepimeron, narrowed posteriorly; rounded stripe occupying most of metepisternum, bent dorsally in posterior portion and expanded dorsally to occupy most of sclerite; small spot occupying postero-ventral corner of metepisternum; most of metepimeron, except dark band on dorsal margin, pale color expanded posteriorly to cover apical portion

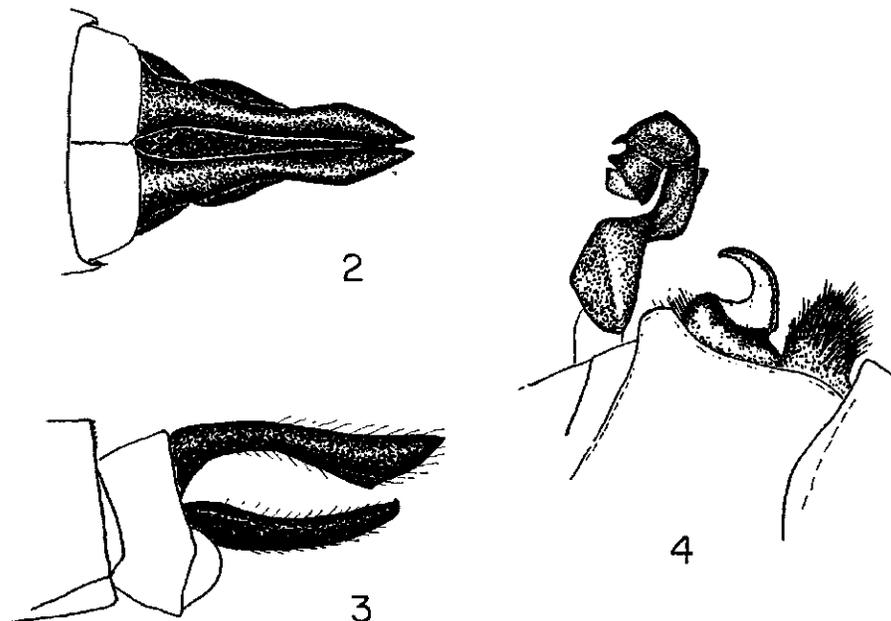


Fig. 2-4. Structural details of *Macrothemis aurimaculata*: 2 and 3) dorsal and lateral views of male appendages. 4) lateral view of second segment of male, showing penis extruded.

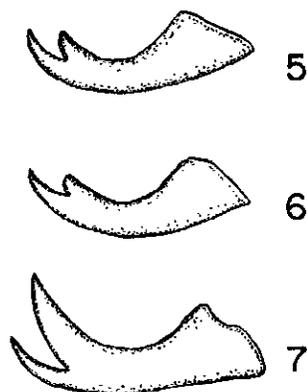


Fig. 5-7. Hind tarsal claws: 5) *M. aurimaculata*; 6) *M. inequiunguis*; 7) *M. pseudimitans*.

of sclerite. Pectus obscurely pale. Wings: venation black, stigma very dark red-brown; fore wing with 14/14 (left/right appendage) antenodals, 8/8 postnodals; hind wing with 11/11 antenodals, 8/8 postnodals. *Legs*: coxae brownish on outer side grading to yellow interiorly; remainder of legs black, with interior yellow color of coxae extending 2/3 the length of the inside of the fore femur and just beyond the base of the mid femur. Hind femora with 12/14 squarish spines terminating in proximally directed, pointed short spines. Tarsal claws with inner spine shorter than outer. *Abdomen*: dark, greenish yellow as follows: lateral rounded spot on 1; on 2, dorsal-proximal, ventral-proximal, and ventral-apical spots, all elongated vertically, the apical spots smaller than the 2 pairs of proximal spots. On 3, two pairs of large, rounded dorsal-proximal and dorsal-medial spots, separated by the dark transverse carina and the dark mid-dorsal stripe. On 4, a pair of small dorsal-medial rounded orange spots. Segments 8-10 expanded laterally, on 8 a large shield-shaped orange spot occupying most of the tergum, with dark border on proximal deflected posteriorly along mid-dorsal line, and pale color similarly deflected towards anterior margin of 9. Segments 9 and 10 dark. *Appendages*: black, superior appendage subcylindrical, swollen, produced ventrally with maximum thickness at 70% of length and having appearance in profile of an inverted triangle; tips slightly deflected dorsally, and with a very small ventral tooth; inferior appendage triangular, tips upturned, nearly length of superior appendage.

**ALLOTYPE** ♀: similar to male, with broader pale stripes on thorax. Abdomen cylindrical, abdominal pale spots wider on 1-4, with prominent pale stripes along ventral margin of tergum, similar but thinner stripe on 4. On segment 4, proximal-dorsal spots; on 5 and 6, dorsal-merial paired spots. On segment 7 the large pale spot occupies 90% of the tergum. Very small pale proximal-lateral spots on 8. Vulvar lamina extends 1/8 the length of 9 and is centrally incised by a rounded V-shaped notch. Femora with short spines (8/10) on hind femur. Fore wings with 14/15 antenodals, 8/9 postnodals; hind wings with 10/10 antenodals, 9/9 postnodals. Wings lightly infumated, with darker patch at wing base.

**DIMENSIONS** (in mm.): *Holotype* ♀: abdomen 27.5, hind wing 29. *Paratype* ♂♂: abdomen 27-29.5 (28.3, 0.8 = mean, standard derivation),

hind wing 28-31 (29.3, 1.1). *Allotype* ♀: abdomen 29.5, hind wing 33.5. *Paratype* ♀♀: abdomen 27.5-29, hind wing 28.5-31.

VARIATIONS AMONG THE PARATYPE SERIES: The 17 males and 4 females of the type series show limited variation. Teneral and sub-teneral males have larger pale markings on the abdomen; 7 males have tiny proximal pale spots on 4 and 4 males have small dorsal-medial paired spots on 5 and 6. One female has the spots on 5 and 6 reduced, and in another female these spots are absent. The discoidal index, defined here as the width of the discoidal field of the fore wing at its distal end (measured normal to the curved veins) divided by the width of the field at its proximal portion, is 0.94 in the holotype male and 1.10 in the allotype female. The index varies from 0.70 to 1.23 in the paratype males (0.94, 0.14) and from 0.85 to 1.13 in the paratype females.

Four male specimens from Costa Rica were not included in the type series, largely because of their poor preservation. These are smaller than the Guatemalan male (abdomen 25-26.5; hind wing 26-28) and all have small paired medial spots on 5. Their discoidal indices vary from 0.82 to 0.94.

MATERIAL EXAMINED: *Holotype* ♂ and *allotype* ♀: GUATEMALA; El Progreso Dept., Finca La Cajeta near Estancia La Virgen, 700 m., 20-VIII-1965, Coll. T. Donnelly. *Paratypes*: same locality and date, 6 ♂♂, Coll. T. Donnelly; 7 ♂♂ and 3 ♀♀, Coll. O. S. Flint, Jr.; same locality; 28-VIII-1965, 1 ♂, Coll. T. Donnelly. GUATEMALA: El Progreso Dept., Finca El Ciprés, near San Agustín Ac., 1200-2000 m., 14-VIII-1968, 1 ♂, Coll. T. Donnelly. GUATEMALA; El Progreso Dept., trib. Quebrada El Chorro, old road between Morazá and San Jerónimo, 1300 m., 17-VIII-1968, 1 ♂, Coll. T. Donnelly. GUATEMALA; Suchitepequez Dept., Finca Moca Grande, stream at reservoir, 17-VII-1977, ♂ larva coll. M. Westfall, emerged in Gainesville. Additional material: COSTA RICA; Puntarenas Prov., 4 mi. S. of San Vito de Java, 1200 m., 2 ♂♂, 21-III-1967, 1 ♂, 14-III-1968, 1 ♂, 15-III-1968, all Coll. H. A. Hespenheide.

DISPOSITION OF TYPE MATERIAL: The holotype, allotype, and some paratypes are deposited in the Florida State Collection of Arthropods, Gainesville. Paratypes are additionally deposited in the National Museum of Natural History and in private collections.

ETYMOLOGY: *aurimaculata* (Latin), meaning "golden spotted."

#### Distinction Between *Macrothemis* and *Brechmorhoga*

The discovery of a second species of *Macrothemis* aberrant for the shortness of its tarsal claw reopens a problem that has never been satisfactorily settled: the distinction between *Macrothemis* and *Brechmorhoga*. Kirby (1894) erected the genus *Brechmorhoga* for the species *grenadensis* (now placed as a subspecies of *praecox* (Hagen)), giving the following diagnostic characters: bifid frontal tubercle, the MSPL in the fore wing present, and a widened discoidal field in the fore wing. Kirby appeared to be relatively unacquainted with the *Dythemis*-group of genera; he suggested *Dythemis* was closely related to *Brechmorhoga*, and he failed to recognize that at least one species of *Macrothemis* (*M. pumila*) known at that time also had a distinctly bifid frontal tubercle. Calvert (1898, 1906) correctly noted that *Brechmorhoga* and *Macrothemis* were their own closest relatives, having

in common distinctively squarish armature on the hind femora. Calvert also noted the unusually elongated inner tarsal claws of *Macrothemis* and made this character his generic criterion. As a result, his new species *M. inequiunguis* was placed by him in *Brechmorhoga*. Calvert also said that venational characters were less reliable, and he suggested that the frontal tubercle was unworthy of generic distinction. Ris (1913) separated the 2 genera mainly by the double curve of R3 (M2 of Ris) and secondarily by the presence of MSPL in the fore wing. However, he admitted that his criteria created a problem for the species *B. nubecula* (Rambur) and *flavo-punctata* (Martin) (with which I am not familiar), but he suggested that the widening of the discoidal field distally would place these species in *Brechmorhoga*.

The dilemma faced by Calvert and Ris has never been satisfactorily resolved, and a single clear generic criterion has never been proposed, although no worker, to my knowledge, has suggesting reducing *Brechmorhoga* to synonymy with *Macrothemis*. The species generally placed in *Brechmorhoga* are large, and most are elongate, with a corduline aspect. *Macrothemis* species are variable in facies but generally smaller, and all but 2 have a highly distinctive long inner tarsal claw. I believe that the widening of the discoidal field is the most consistent criterion for generic diagnosis. The average discoidal index (defined above) for *Brechmorhoga* species is as follows: *nubecula* 1.59, *mendax* 1.77, *pertinax* 1.74, *praecox* 1.66, *tepeaca* 1.77, *vivax* 1.59, and *rapax* 1.38. Smaller *Macrothemis* species (*inequiunguis*, *flavescens*, *musiva*, *pumila*, and *tenuis*) have this ratio less than 1.0. Other species of *Macrothemis*, including several larger species, have higher values of the index: *pseudimitans* 1.13, *celeno* 1.19, *hemichlora* 1.25, *imitans* 1.27, *inacuta* 1.16, and *rupicola* 1.19. I have seen only single specimens of *mortoni*, *lauriana*, and *delia*, but they have values of the index close to 1.0. The problem with this criterion is that there is relatively large variation within populations, and on an individual specimen basis the criterion would fail at times.

I propose the following distinction between *Macrothemis* and *Brechmorhoga*:

*Macrothemis*: Discoidal field parallel sided, narrowed, or slightly widened distally; discoidal index less than 1.35; MSPL absent in fore wing; inner tooth of tarsal claw elongated (except for *inequiunguis* and *aurimaculata*).

*Brechmorhoga*: discoidal field widened distally, discoidal index greater than 1.35; MSPL present in fore wing; tarsal claws of "normal" aspect.

This distinction will fail in several individual cases: Several *Brechmorhoga rapax* and a few *vivax* and *praecox* may have smaller values of the discoidal index. In *Macrothemis* values of the discoidal index may exceed 1.35 for several *hemichlora* and a few *celeno* and *imitans*. Specimens of *Brechmorhoga* (including *nubecula*) in my collection all have a distinct fore wing MSPL, but Ris cautions that this vein is "nur angedeutet" for *nubecula*. The character of the tarsal claw is very clear, if one notes the 2 exceptional species.

#### ACKNOWLEDGMENTS

I am very grateful to M. J. Westfall, Jr., D. Paulson, and O. S. Flint, Jr., for the loan of specimens.

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## SCIENTIFIC NOTES

PASSALID BEETLE (COLEOPTERA: PASSALIDAE) INHABITANTS OF LEAF-CUTTER ANT (HYMENOPTERA: FORMICIDAE) DETRITUS—This is a summary of what is known concerning the relations between passalid beetles and leaf-cutter ants, including new information I have obtained recently in Guatemala.

The microhabitat characteristic of Passalidae is rotting wood (Schuster. 1978. *Coleopt. Bull.* 32: 21-8). Only 1 species of passalid, *Ptichopus angulatus* (Percheron),<sup>1</sup> is commonly found associated with leaf-cutter ants. All life stages have been found, in various parts of Mexico, in the detritus chambers or piles of *Atta mexicana* Fr. Smith (Hendrichs and Reyes-Castillo. 1963. *Ciencia Mex.* 22: 101-4; Reyes-Castillo. 1970. *Folia Ent. Mex.* 20-22: 1-240). This is apparently the primary microhabitat of this species. Though Reyes-Castillo (1970) mentions that adults are occasionally found in rotting wood, larvae and pupae haven't been found in wood. Laboratory preference tests showed preference for leaf-cutter detritus over rotting wood (Reyes-Castillo. 1970). In 7 years of collecting passalids in Guatemala, I have never found *Ptichopus* in rotting wood. They have been found under cattle droppings (Reyes-Castillo. 1970) and there is 1 record from under stones covering the entrance of a *Pogonomyrmex* nest (Hendrichs and Reyes-Castillo. 1963), but this record needs confirmation (Reyes-Castillo. 1970).

On 10 April 1982, I found 10 dead and 1 live specimens of *P. angulatus* in the detritus pile of a nest of *Atta cephalotes* L. near Ojo de Agua on a dirt road to San Lorenzo, Zacapa Department, Guatemala. This is the first record of *Ptichopus* associated with leaf-cutters other than *A. mexicana*. The pile was ca. 1 m wide and ca. 1 m below the exit of the ant nest from a roadside precipice where detritus was dropped. The live adult was found 30-40 cm deep in the pile. Though I excavated most of the mound, I found no immature stages; nor did Reyes-Castillo (1970) find immature stages in the dry season in Mexico. The nest was located in a dry, scrub habitat near the source of a spring at 350 m elevation in the Motagua Valley (see Stuart. 1954. *Contrib. Lab. Vert. Biol., Univ. Mich.* 65: 1-26, Plate VI, for photos of this region's habitat).

Later, on 15 June, I found the remains of 1 *P. angulatus* in a detritus chamber of *Atta* in a grassy area at 1525 m on Volcan Jumay near Jalapa. At 1800 m the cultivated area ends and a wet oak, perhaps cloud, forest begins. On the same day, my students encountered 6 dead individuals in a detritus pile of *A. cephalotes* at 1260 m and 4 live adults (1 teneral) with eggs in another pile at 1125 m near Laguna del Hoyo in Jalapa Dept. No larvae or pupae were found. This area, now extensively cultivated, was probably originally covered with pine-oak forest. These findings in Jalapa and Zacapa departments suggest a wide range of habitats for *P. angulatus* in Guatemala.

The variety of habitats occupied by *P. angulatus* and *Atta mexicana* in Mexico is also quite broad. Hendrichs and Reyes-Castillo (1963) and Reyes-Castillo (1970) report them from dry areas of the altiplano (e.g., Durango) to wet lowland forest (e.g., Catemaco, Veracruz). In the latter area, they

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<sup>1</sup>Reyes-Castillo (pers. comm. 1982) thinks *P. angulatus* may be a species complex, or perhaps a single polymorphic species.

were taken from detritus chambers 1 to 1.2 m deep (Reyes-Castillo, 1970). This author also mentions the occurrence of *P. angulatus* from 0 to 2000 or 2100 m elevation in habitats including semidesert, pine, pine-oak, tropical deciduous, and tropical rain forests. He mentions the occurrence of *A. mexicana* to 2300 m. *A. cephalotes* apparently doesn't occur above 1560 m in Guatemala (pers. comm. Margaret Dix, 1982).

Migration of *P. angulatus* apparently occurs during the wet season which begins in late April or early May in Guatemala. My 11 Guatemalan records of this species at lights are from April 22 to June 24. This coincides fairly well with the period May to August when they are attracted to lights in Mexico (Hendrichs and Reyes-Castillo, 1963).

*P. angulatus* ranges from the U.S.-Mexican frontier at Matamoros (Schuster, In press, Coleopt. Bull.) to Colombia (pers. comm. P. Reyes-Castillo, 1982). *A. mexicana* does not extend as far south as *P. angulatus*. Other *Atta* species are present, however, and their detritus probably is host to *P. angulatus*, as in the case of *A. cephalotes* in Guatemala. The only other species in the genus, *P. melzeri* Leuderwaldt, occurs in Brazil, but nothing is known concerning its ecology (Reyes-Castillo, 1970).

Concerning other passalids associated with ants, the remains of 1 individual of *Heliscus yucatanus* Bates were found in a nest of *A. cephalotes* in the Yucatan Peninsula (Reyes-Castillo, 1970). Occasionally, *Passalus punctiger* Lepelletier & Serville and *Passalus inops* Truqui have been found associated with *Atta* (Reyes-Castillo, 1970), but they apparently have not developed as close a relationship with their host as has *Ptichopus*. These species are usually found in rotting wood. *P. punctiger*, the commonest of these 2 species of *Passalus*, ranges from northern Mexico (Arizona?) to Argentina (Schuster, In press). *P. inops* is found in Mexico and Guatemala (pers. comm. P. Reyes-Castillo, 1982), though I have never collected it in Guatemala. The *P. inops* larva is extremely distinct from those of all other passalids, except *Ptichopus angulatus* (Schuster and Reyes-Castillo, 1981. An. Esc. nac. Cienc. biol., Mex. 25: 79-116). In both species, the larvae possess long, stout hairs scattered over most surfaces of the body. Could these be adaptations for living in *Atta* detritus? If so, *Passalus inops* may represent an early stage in the evolution of obligate colonization of *Atta* detritus chambers.

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EGG PREDATORS OF THE COCOONS OF THE SPIDER *MECYNOGEEA LEMNISCATA* (ARANEAE: ARANEIDAE): REARING AND POPULATION DATA—*Mecynogea lemniscata* (Walckenaer) is a common spider inhabiting the shrub layer of deciduous forests in the southeastern United States (Levi 1980, Bull. Mus. Comp. Zool. 149: 1-75). In Florida, this spider is commonly found in mesic oak hammocks where it places its dome-

were taken from detritus chambers 1 to 1.2 m deep (Reyes-Castillo, 1970). This author also mentions the occurrence of *P. angulatus* from 0 to 2000 or 2100 m elevation in habitats including semidesert, pine, pine-oak, tropical deciduous, and tropical rain forests. He mentions the occurrence of *A. mexicana* to 2300 m. *A. cephalotes* apparently doesn't occur above 1560 m in Guatemala (pers. comm. Margaret Dix, 1982).

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shaped web and associated egg cocoons in shrubs and dead tree branches approximately 1 to 3 m above the ground. The string of 1 to 10 silk cocoons, which hangs from a single horizontal support line, is deposited from late June to mid August.

From *M. lemniscata* cocoons collected in flood-plain woods surrounding Lake Alice, Gainesville, Alachua Co., FL, 2 species of egg predators, *Mantispa viridis* Walker, (Neuroptera: Mantispidae) and a *Tetrastichus* sp. (Hymenoptera: Eulophidae) [near the species *T. banksii* Howard, but the group needs revision and species are not identifiable, M. E. Schauff, pers. comm.] were recorded. Parasitism of the egg cocoons of *M. lemniscata* has not been previously reported (see Eason et al. 1967, J. Kansas Ent. Soc. 40: 422-34 for the most recent review of spider egg parasites).

In 1981, 7.2% of 290 cocoons were parasitized by the eulophid wasp. In 1982 the overall rate of parasitism rose to 8.7% of 252 cocoons; 6.7% by the eulophid wasp, and the remaining 2.0% by *M. viridis*. The attack of more than one cocoon in any single string by either of these predators was very rare: 0% of 83 strings in 1981, and 1.9% of 105 strings in 1982. In all cases, the cocoons in the multiply attacked strings were attacked by the eulophid.

The wasp averages 16 days to develop (1 day in the egg stage; 5 days as a larva; 10 days as a pupa) in 2 dram glass vials stoppered with cotton and maintained at 28° C and 70-80% RH (ambient conditions at the study site). Under the same conditions, unparasitized *M. lemniscata* eggs average 20 days to develop to the spiderling stage (16 days in the egg stage; 4 days in the deutova stage).

A spider cocoon may contain up to 30 eggs ( $\bar{x}$  = 13.5 eggs, sd = 6.32, N = 35 cocoons). Both the larvae of the eulophid and *M. viridis* are ectophagous on the host eggs and devour all the eggs within a single cocoon. The eulophid is superparasitic, with up to 23 adults ( $\bar{x}$  = 15.1, sd = 4.9, N = 14 cocoons) emerging from eggs oviposited into the spider cocoon. The triungulin-type larvae of *M. viridis* are obligate cocoon attackers; actively locating and burrowing into previously constructed cocoons (Redborg & Macleod 1982, Ecol. Ent. 7:87-196). While only one mantispid was produced per attacked cocoon in this study, the occurrence of more than one *M. viridis* from a single spider cocoon has been previously recorded (Parfin 1958, Ent. News 19: 203-7).

Observations of the contents of collected cocoons indicated that attacks by the wasp occur throughout the egg laying period of the spider. However, the presence of developing eulophid larvae in collected cocoons and wasp emergence from cocoons in the field appeared greater in early August (although no data were collected). These observations combined with the laboratory data on wasp development rates suggest that there may be a peak in wasp attack on the cocoons in mid to late July. Although no such pattern could be determined for the mantispid from the collected material, inspection of collecting data from *M. viridis* specimens in the Florida State Collections of Arthropods indicates that they are present year round. This suggests that they are capable of attacking cocoons throughout the egg laying period of the spider.

The low incidence of attack by *M. viridis* is most likely related to the low probability of a larva successfully locating the cocoon in the maze of silk lines surrounding it. In addition, the cocoon wall is extremely hard, which could make larval entrance into the cocoon difficult. For the wasp,

locating and attacking the cocoons presents less of a problem, and the wasp should utilize all available cocoons. However, the observed rate of attack is relatively low, and probably related to the timing of cocoon production and the developmental rates of the wasp and host eggs. *Mecynogea lemniscata* lays eggs approximately every 6 days (see also Eberhard 1979, *Biotropica* 11: 292-300), and this rate of production makes it unlikely that 2 cocoons in the same string will both be in the precise stage required by the wasp for attack (Vinson 1976, *Annu. Rev. Ent.* 21: 109-33), or that a new cocoon on a string will be available for emerging wasps from a previous attack. This results in emerging wasps having to move to other strings to locate suitable cocoons, and even at the relatively high density of cocoons in the environment (1981: 1.4 cocoons/m<sup>2</sup>, and 1982: 1.3 cocoons/m<sup>2</sup>), locating such a cocoon is probably difficult.

Mantispids have been recorded from the cocoons of a number of spider families including the Lycosidae (Withycombe 1924, *Trans. Royal Ent. Soc. London* 72: 303-411), Agelenidae and Gnaphosidae (Kaston 1938, *J. New York Ent. Soc.* 46: 147-53), Clubionidae (Milliron 1940, *Ann. Ent. Soc. America* 33: 357-60), Salticidae (Smith 1934, *J. Kansas Ent. Soc.* 7: 120-145), Oxyopidae (Killebrew 1982, *J. Arachnol.* 10: 281-2), and Araneidae (Biriben 1960, *Neotropica* 6: 61-4). Presumably *M. viridis* attacks a number of spider families here in Florida as well. It is unknown how common the *Tetrastichus* sp. is in the cocoons of other spiders in Florida. Howard (1892, *Proc. Ent. Soc. Washington* 2: 291-303) suggests that the closely related species, *T. banksii* Howard, is a hyperparasite of ichneuemonid egg predators of araneid egg sacs, rather than an egg predator itself. However, members of this genus attack a wide range of hosts in all stages of development, and many species are both parasites and hyperparasites depending on the host(s) utilized (Burks 1979, Pages 990-1002 in Krombein, Hurd, Smith & Burks, eds. *Catalog of the Hymenoptera in America North of Mexico*).

I thank Dr. M. E. Schauff (Eulophid), Systematic Entomology Laboratory, IIBIII, USDA, Beltsville, MD, and Dr. L. Stange (*M. viridis*), Division of Plant Industries, FDACS, Gainesville, FL for species identification. Voucher specimens have been deposited in the U.S. National Collection, Washington, D.C. and in the Florida State Collection of Arthropods, Gainesville, FL.—CRAIG S. HIEBER, Dept. of Zoology, University of Florida, Gainesville, FL 32611 USA.

## BOOK NOTICE

ANNUAL REVIEW OF ENTOMOLOGY, 1984, Vol. 29, 521 pp. (\$27.00 USA, \$30.00 elsewhere).

Contents: Frederick Simon Bodenheimer (1897-1959): Idealist, scholar, scientist, ISAAC HARPAZ; The role of microarthropods in decomposition and mineralization processes, T. R. SEASTEDT; Allergic and toxic reactions to non-stinging arthropods, R. A. WIRTZ; Induction of detoxication enzymes in insects, LEON C. TERRIERE; Host-parasitoid population interactions, M. P. HASSELL AND J. K. WAAGE; The Japanese pine sawyer beetle as the vector of pine wilt disease, FUJIO KOBAYASHI, AKIOMI YAMANE AND TOSHIYA IKEDA; Interaction between blood-sucking arthropods and their hosts, and its influence on vector potential, YU. S. BALASHOV; Economics of decision making in pest management, J. D. MUMFORD AND G. A. NORTON; The ecology and sociobiology of bumble bees, R. C. FLOWRIGHT AND T. M. LAVERTY; Defense mechanisms of termites, GLENN D. PRESTWICH; The functional morphology and biochemistry of insect male accessory glands and their secretions, P. S. CHEN; Bionomics of the Aphelinidae, GENNARO VIGGIANI; Astronavigation in insects, RUDIGER WEHNER; Spiders as biological control agents, SUSAN E. RIECHERT AND TIM LOCKLEY; Assessing and interpreting the spatial distributions of insect populations, L. R. TAYLOR; Developments in computer-based IPM extension delivery systems, S. M. WELCH; Modification of small farmer practices for better pest management, PATRICIA C. MATTESON, MIGUEL A. ALTIERI, AND WAYNE C. GAGNE; Insect molecular systematics, STEWART H. BERLOCHER; Apple IPM implementation in North America, M. E. WHALON AND B. A. CROFT; An evolutionary and applied perspective of insect biotypes, S. R. DIEHL AND G. L. BUSH; subject, cumulative author (vol. 20-29), and cumulative title (vol. 20-29) indexes.

## BOOK REVIEW

THE EVOLUTION OF INSECT MATING SYSTEMS. Randy Thornhill and John Alcock. 547 p. Harvard University Press, 1983. \$35.00.

This book is an interesting and comprehensive review of the natural history of insect mating systems. It is directed toward 2 audiences: the professional entomologist who would like to become acquainted with rapidly developing ideas on the evolution of mating behavior and beginning students of behavioral ecology, whether they be professionals from other fields or undergraduates. The book is not particularly appropriate for persons already acquainted with the field of insect mating systems, since no attempt is made to develop new theory or to critically examine existing ideas. The book is written in the wonderfully relaxed and easy to read style we have come to expect from John Alcock (in three editions of his *Animal Behaviour: An Evolutionary Approach*, Sinauer Associates) and Randy Thornhill. It is filled with fascinating details on insect reproduction and mating systems. Remarkably, the book does not contain a single equation (except for a few arithmetic operations). To some this might be considered a definite asset, but I think the authors might have taken the opportunity to explain ideas in their easy style and then to *teach* how these ideas can be readily translated into simple equations. For example, although the authors continually use the optimization approach, they make no attempt to formalize the arguments. I would prefer that my students were exposed to less detail about the fascinating things insects do and to more about the formalized theory which would give them easier access to the literature.

The first three chapters are good general introductions to the modern view of evolution, the diversity of insect reproductive mechanisms and current views on sexual selection. They explain the evolutionary process very thoroughly and show clearly how arguments can be thought out logically under the paradigm of individual selection. The question of how sex and sexual reproduction evolve is explained thoroughly. They also mention a number of other controversial topics in evolution, such as the debates over inter-demic selection, adaptationism and the unit of selection, but these are so inadequately explained that the uninitiated will not understand the nature of the debates. Surely it is the controversies of a field, as well as its fascinating facts, which encourage and excite further investigations.

The next 8 chapters cover the evolution of male behavior, including female-locating behavior, the eagerness and frequency of mating, competition among males, territoriality, mate guarding, mating patterns, courtship and sperm competition. The final 3 chapters discuss female reproductive behavior, including mate choice and selection for frequency of mating and numbers of mates. Most explanations are developed through extended examples of specific species, such as the love bug, dung fly and digger bee. Although there are many opportunities to draw out generalities, repeatedly the authors prefer to tell a series of stories. There is also a tendency throughout to state as fact what are at best conjectures or true in only some cases. For example, "The threat displays of insects generally convey information about a male's size and vigor" (p. 218). This complaint is part of a larger problem: in their effort to make their ideas straightforward, the authors come out sounding a little too glib, as though we have all the answers, which is simply not true.

The book provides many useful compilations of the species that show some trait, such as different mechanisms for locating mates, the prevalence of mate guarding or copulation durations. Although these tables are useful for organizing the diversity of traits along taxonomic grounds, the authors do not use the tables to extend our understanding i.e. they do not make full use of the comparative method (see J. P. Hailman 1976 and Harvey and Mace 1982).

One intriguing controversy which is not explicitly addressed is the contention that females can increase their fitness by choosing superior males. There is no question that this is correct if the female is choosing a male on the basis of his ability to invest in her or her offspring. However, there is a problem if the male is contributing nothing more than his genes: strong directional selection will quickly result in the elimination of genetic variation in those male characters that the females are using (see Halliday 1978). In a recent paper, Hamilton and Zuk (1982) have argued that if the selective pressures on males were constantly changing, then genetic variation could be maintained. They suggest that parasites might provide such a selective pressure and that females choosing the most socially dominant, healthiest-looking males might, in fact, be choosing those males with the greatest resistance to parasites.

Throughout the book, economics is used to explain the evolution of behavioral traits. Repeatedly the argument is made that a trait evolves because it alters the benefit-to-cost ratio. For example, in a discussion of selection for aggression, a simple list of costs and benefits to fighting is provided. Obviously, a trait such as fighting will not evolve if it results in a net loss to the individual (measured in long-term reproductive success), but the argument for its evolution is distinctly more complicated. What matters is that the long-term success of individuals that follow one strategy is greater than that accruing to individuals who follow other available options. It is not simply that insects are small and hence guard small territories (p. 129), but rather that there is selection for defending a territory of a particular size, i.e. individuals defending territories that are smaller or larger leave fewer surviving offspring than those with the optimal territory size. This problem is particularly evident in discussions on the evolution of paternal care. Comparisons are made between the long-term reproductive gains for female care as compared with male care. Although such comparisons are interesting in a broad sense, they do not explain the evolution of male behavior. This must be explained by examining the long-term reproductive gains for the various options available to males. The crucial question is, "How many surviving offspring does the male produce when he helps as compared with when he does not help?" One factor that figures prominently in explanations of paternal care is paternity assurance but this is only one of a number of factors and is in itself not essential. At one extreme, if the female is incapable of rearing any offspring on her own, then the male *must* help her if he is to have any surviving young, whether or not most of the offspring he helps to rear are related to him. Naturally, as the book argues, there will always be strong selection on males to increase their paternity, but this applies to all mating systems and not especially to cases of paternal care. What is usually different about paternal care is that when the male is providing care or some resource, he has more power over the female (he can withhold the resource) and more contact

with her and thus more opportunities to assure paternity without much additional investment. In summary, what is never made explicit in the book is that paternal care evolves regardless of paternity assurance if alternative routes to reproductive success result in fewer surviving offspring. In general, paternal care will evolve when the number of surviving offspring when the male helps ( $B_c$ ) times the male's relatedness ( $r$ ) to these offspring is greater than the number of surviving offspring when the male does not help ( $B_n$ ) times the male's relatedness ( $r'$ ) to these offspring or paternal care evolves if:

$$B_c \times r > B_n \times r'$$

I suspect that in many insects paternal care begins as a mate-guarding tactic. If the male is already around the nest guarding the female, he can further improve his long-term success by chasing away intruding parasites and predators and engaging in other nest-related activities that improve the number of surviving young.

There is no question that this book achieves its stated goal of telling professionals and students not acquainted with behavioral ecology about the field. It is also a thorough and clearly written review for those who know their reproductive ecology from a solely vertebrate perspective. My preference would be to use more precise, explicit and formalized explanations of general theory (including simple equations), to include more detail on controversial issues and to critically evaluate existing ideas. The failure to consider alternatives, probable phylogenetic history and constraints on the evolution of characters is, in my opinion, a weakness. However, I think my quibbles with this book amount to little more than pedagogical preference.—H. JANE BROCKMANN, Department of Zoology, University of Florida, Gainesville, FL 32611 USA.

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**STUDENT RESEARCH GRANTS**

The Florida Entomological Society has again established a \$500 fund to support entomological research by students. Students are expected to use the money for supplies, computer time, transport to field sites, publication costs, or other items connected with research (as opposed to course-work). Requests should not exceed \$50.

Applicants must be members of the Florida Entomological Society. Deadline for receipt of applications is 18 May 1984. Requests will be evaluated by the five members of the Student Activities Committee, and awards will be made by 21 May. Request for support should be on *one* sheet and include the following information:

1. Student's name and address
2. School and status (year, degree sought, expected date of graduation)
3. Proposed use of requested funds (items and costs)
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Please send requests to:

DR. THOMAS J. WALKER  
Department of Entomology and Nematology  
University of Florida  
Gainesville, Florida 32611

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**NEW TREASURER AND BUSINESS MANAGER FOR THE  
FLORIDA ENTOMOLOGICAL SOCIETY**

ANN C. KNAPP is the new treasurer and business manager for the society. She assumed these duties in December 1983. In this new role she will: bill, receive and acknowledge receipt of all membership dues, keep computerized membership lists, manage society business matters, prepare financial reports and handle society correspondence as appropriate. This is a huge job with many responsibilities but the Society is confident in her considerable talents for organization and thoroughness.

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### COMPETITION FOR STUDENT DISPLAY PRESENTATIONS AT 1984 FES MEETING

Earlier announcements concerning the 1984 FES meeting have given the rules and due dates for presentation of regular papers and student papers. For several years the Student Papers contest has provided monetary awards to winners of the competition.

Display presentations or poster sessions are a recent innovation for the annual meetings. Due to increased interest in these activities, FES is sponsoring student competition in the poster sessions. All student display presentations will be judged on content and preparation. The top 3 competitors will receive awards of \$125.00, 75.00 and 50.00. To present a student display presentation, the tear sheet must be postmarked and sent no later than 15 May 1984 to:

JAMES A. REINERT, Program Chairman  
Ft. Lauderdale Research and Education Center  
University of Florida  
3205 SW College Avenue  
Ft. Lauderdale, FL 33314 USA

Student authors *must* be members of the Florida Entomological Society and *must* be registered for the meeting.

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### NEW FORMAT FOR SCIENTIFIC NOTES

Associate Editor M. D. HUBBARD suggested a few minor changes in the format of Scientific Notes. They can be seen in this and following issues. Basically, complete literature citations now will be placed in a "References Cited" section at the end of the paper. This eliminates sentences broken by parenthetical information and gives readers more information to look up references. The transition will take a bit of extra work but hopefully authors and readers will approve of the results.

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### LOST MEMBER

Here is the name and address of a FES member who has paid her 1984 dues but her address is incorrect.

MARY JANE ANGELO....  
3103 McCarty Hall  
University of Florida  
Gainesville, FL 32611

If anyone can correct this information, please contact the Business Manager

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