THE ROLE OF THE NATURALIST IN ENTOMOLOGY AND A DEFENSE OF "CURIOSITIES"

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Entomology has always looked outward and attempted to apply its knowledge for the public good. In many ways we believe ourselves to belong to a "service science", standing in relationship to Zoology as Engineering does to Physics or Education to Psychology. A "pragmatic", medical or agricultural application is in the back or forefront of many of our minds as we pursue our interests in ion exchange across membranes or the relationship between light intensity and pheromone emissions.

I would like to mention a neglected set of consumers of insect information, a growing and urbanized population increasingly alienated from nature. One that only electronically experiences the once familiar, but now rapidly disappearing or impossibly remote "ice-age fauna" it evolved with. It is my belief that we are "innately" interested in the things that have been important to us through our evolutionary history. There is an appetite for watching animals, uncovering the patterns of their activity, the secrets of their lives. This appetite was critical to predicting the times and places deer could be hunted and where bear-wolves were likely to be hunting our ancestors (could our love of horror films be due to the pleasure of honing ancient anti-predator skills?—"You damn fool! Don't go in that door!"). Many of us, myself included, spend freely to fulfill an emotional design and catch (and then release) unneeded fish. However, I would suggest that our appetites are not specific for the great mammals and birds of the Pleistocene's prairies or any particular animals of any other place and time. And what animals are better suited for contemporary "hands on" natural history than insects? The pleasures of discovery are much more available to an insect *observer* than to a *tourist* watching a patch of elk hair disappear into a stand of pines.

Some of us already devote some of our energies to "public" education, and while I can't know other's motives, it is my impression that much of it is done to explain our "business". I would like to propose that we at least consider a change of heart; that we grant as much respect to the fulfillment of our culture's emotional-spiritual needs as we do to the patent of an attractant or the publication of scholarly work. The natural historian, a person with a net, a flower press and a curiosity about the colors of beetles and the poses of flies, should not strike us as eccentric but as profoundly purposeful.

The participants in this year's Behavioral Ecology Symposium would all admit to being naturalists. In general, their topics concern themselves with "adaptive coloration" defined in its broadest sense. I will address the often fantastic ornaments used by flies to intimidate sexual rivals and woo mates. There will be a number of peculiar curiosities discussed, obscure insects of no economic importance, some described by bemused 19th century travelers and then forgotten. In light of the contemporary concerns of entomology, I would like to briefly defend "curiosities" and offer you a reason to spend your time pondering insects that will never take a bite from a cabbage or inject a spirochete.

I perceive the sexual ornaments of flies to send a special message to human receivers. They bring to us news of intellectual liberation. By that I mean that their combination of the marvelous and the mundane reminds us that the world is a "very strange place." Rare curiosities are not trite, but points where that strangeness has come to the surface—as we see the surface. In my studies I sometimes find myself falling into a pitfall that Darwin warned against, that I base my hypotheses on what seems plau-

sible. Occasionally this model or that interpretation is dismissed, not on its merits, but because it is too challenging to the imagination. It is easy to become overly skeptical and stodgy. If I catch myself, I turn to a specimen of the truly bizarre *Achias* (Diptera) I keep on my desk. Here is an animal I couldn't even make up! *Achias* is discussed in the following, as are a number of other illuminating peculiarities. I hope that in addition to its other merits this symposium can serve, like a Zen parable, as an aspirin to treat a swollen and painful "common sense."

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ON RESEARCH AND ENTOMOLOGICAL EDUCATION, AND A DIFFERENT LIGHT IN THE LIVES OF FIREFLIES (COLEOPTERA: LAMPYRIDAE; *PYRACTOMENA*)

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ABSTRACT

Research at institutions of higher education could be restored to at least a shadow of its original role through publication in a manner appropriate for immediate classroom use, with questions that pique and direct the interests and activities of students. Studies on basic natural history may be good candidates for such publication and an example is drawn from fireflies: Two woodland species show directional orientation in their pupation sites on the trunks of trees; one uses southerly exposure and the other occurs on the north side of smaller trees, and much lower on the trunks. These contrasting positions have different thermal consequences, as demonstrated with a physical model, which possibly have a role in reducing interspecific sexual contact or prey competition.

Key Words: fireflies, behavior, life history, orientation, ecology

RESUMEN

La investigación en instituciones de educación avanzada podría ser restaurada parcialmente a su rol original a traves de publicaciones, de manera tal que las mismas puedan ser usadas para enseñar, con preguntas que atraigan el interés de estudiantes y que se relacionen con sus actividades. Los estudios de historia natural básica pueden ser buenos candidatos para ese tipo de publicaciones, y un ejemplo del mismo se puede obtener con luciérnagas: Dos especies de luciérnagas muestran diferencias en la ubicación de sus pupas en los troncos de los árboles; una especie las ubica expuestas hacia el sur y la otra usa el lado norte de árboles mas pequeños y en la zona mas baja del tronco. Estas posiciones contrastantes tienen diferentes consecuencias térmicas, como se demuestra con un modelo físico, las cuales podrían tener un papel en reducir el contacto sexual o la competencia por alimento entre las dos especies.

In times past it went without question that the connection between research and teaching was that professors who did basic research maintained their intellectual interest in scholarship and passed on to their students an inquisitive attitude and love of the pursuit of knowledge as the essence of life and a life-sustaining spirit. Students thus became living repositories of what was then acknowledged to be a civilizing Ideal of western culture. An academician of the time translated the expression "publish or perish" as meaning that if he did not publish he had mentally perished, and in doing so was failing in his professional responsibilities to his students and his civilization. Over the past 30 years this fundamental understanding and connection has been eroded and forgotten, and a great deal of what is now done as "scholarly publication" has little direct bearing on a "civilizing education."

The essence of scholarly research is discovery and originality. In my experience, good students find it more interesting to actively participate in doing something that relates to discovery than to see someone else do it on TV. It is worth exploring to determine whether some primary publications in science could be written directly for the classroom, rather than for the narrow and generally disinterested "readership" of a scientific journal, even leaving some obvious refinements for students to manage. Original research papers could be used as texts, and beginning students have direct contact with researchers themselves—who could speak directly to them in their papers, and then perhaps personally through the internet, thus achieving a quasi-oral tradition of wide dimensions! Students would use an original publication as a source of information and to stimulate their imaginations for initiating their own school-time and life-time pass-time research. What once might have been a scarcely read, esoteric and expensive "contribution to . . ." could be an informative introduction and background with suggestions and questions for personal projects and class discussion. Though it pains me to admit it, fans of electronic publication may be the first to see the desirability and simplicity of doing this.

There is another twist to this notion. Since I have chased fireflies for about a third of a century, I am often asked by citizens and reporters, by letter and phone, "what is happening to the fireflies, I don't see them anymore?" Only people who once knew and pursued fireflies can ask such a question, because those who have never known them cannot miss them. Similarly, might not students who learn by reading and doing original research and see it in connection with their personal education, understand and care more about what we have long considered to be the intellectual values and strengths of an enlightened civilization? The irony, the flip side of this is that here I address this notion to many who have never seen a firefly.

Obviously, some research subjects lend themselves to such instruction better than others, because of technical complexity and expense, but there are many available sources of inspiration. As John Sivinski has pointed out, one unfailing repository of observations and ideas worth developing are the anecdotes, sketches, and speculations that insect naturalists accumulate. From my search for new sources and angles, I would add that many taxonomists especially know what is lost to lab-bound and urban biologists, because of their solitary hours of collecting and observing their quarry in the field, which are as basic field investigations, typically followed by solo hours of contemplation as they curate their specimens. I have found that much of what can be done with firefly taxonomy and behavior can be used almost immediately in the classroom. It should be as a personal goal and measure of scholarly accomplishment and fulfillment to see the development of some significant area of insect research begun and developed by undergraduate students in a teaching/research connection. Think of the satisfaction that graduates would enjoy when they subsequently saw their own studies used in a general entomology text.

For several years I have taught a general biology course entitled *Biology and Natural History With Fireflies* in which every class meeting is a field trip or lab and involves some research-related activity. Instead of giving oral lectures, I write the students letters; instead of laboratory and field exercises with recipes and empty lines to write on, I give them a background text on a subject, the material and equipment they may want to use, and directions so they can do some things they will find interesting. English, religion, architecture, microbiology, German literature, journalism, pre med., and animal science majors, to mention a few of the represented fields, experience first hand the basics of biological research, including the design of empirical studies and the gathering of data, the use of statistical analysis, and the value of models and theoretical perspective. During class meetings students are only required to be focused and interested, and try to accomplish what they recognize with increasing skill as sound biology.

As an example, the "Letter" below provides the introduction and background for a number of field studies that students can make in winter in a flood plain forest in Gainesville, about two miles from the indoor classroom. The Letter is modified for use here. Scientifically, this Letter is the first publication of the outlines of a seemingly simple but perhaps very complex element of firefly biology. The Letter omits statistical descriptions and analyses, which are a field/lab experience themselves, but illustrates the observations and raises questions that students anywhere in the geographic range of the species can discuss and independently or jointly pursue in the lab and woods (Fig. 1). More than this, when students begin to address specific questions about this apparently simple behavior of mere beetle larvae, they discover that it is potentially so complex that it may never be completely understood, and for them this itself is encouragement to continue, to enjoy the study, and sometimes to see such biology as also of the arts and humanities.

LETTER XIII: A DIFFERENT LIGHT IN THE LIVES OF FIREFLIES

Dear Fireflyers, When fireflies and light are mentioned in the same breath, one reflexively thinks bioluminescence, and of the use that fireflies and taxonomists have made of pulses of living light for species recognition, that behavioral ecologists have made of firefly flashes for studying mate competition and mate choice, and finally, of the use that biochemists, cell biologists, and physicians now make of bioluminescence chemistry for enzyme analysis, cell physiology, exobiology (extraterrestrial life searches), and medical diagnoses. Our knowledge of firefly flash communication in nature began with the incidental observations of a chemist, Frank McDermott, who went to the field to observe fireflies out of an interest in the mechanism of their luminosity, but stayed to discover that some lightningbug species can be distinguished by their flashed mating signals. What I will tell here began with a taxonomist's interest in getting a photograph, and became an enigma in the realm of what some might call environmental physiology. It is about a connection that some fireflies have with light other than through their remarkable ability to generate it.

The larvae of one species may use sunlight to hasten or perhaps, maybe, even to manipulate their pupal duration and adult eclosion time ("date"). *Pyractomena* fireflies, and perhaps all of the fireflies in their tribe (Cratomorphini), unlike other lampyrids that do it in hidden chambers underground, climb up on vegetation to pupate. Aerial pupation was reported by Francis Williams near the beginning of the passing century and observed in some detail by Lawrent Buschman, who examined this behavior in the marsh-inhabiting species *Pyractomena lucifera* (Melsheimer). Aerial pupation would seem to be a reasonable adaptation for larvae that live on

emergent vegetation over water and hunt the aquatic snails below, or that could have their habitat submerged by the flood water of a creek or river spilled out of its banks onto adjacent flood plain. *Pyractomena borealis* (Randall) pupae hang on tree trunks, by means of laterally projecting points that extend into their cast larval skins they previously glued to the trunk by the tail-end. At eclosion, the pearly-white, teneral adults walk a few centimeters leaving behind the larval and pupal skins and dangling tracheal linings, and remain motionless until their cuticle has tanned. Sometimes adult males are found waiting next to or on top of pupae (female only?; Fig. 2).

In the winter of 1982-83 I visited the flood plain forest along Possum Creek in Gainesville to get photographs of pupating *Pyractomena borealis*, whose adults I had seen flying and flashing there in considerable numbers the previous March. I found one, then several, then numbers of them, and it soon became obvious that they did not occur randomly over the tree trunks. Sometimes pupae occurred together, sometimes alongside vines or in crevices, and occasionally below twig bases. They used trees of several species and bark textures, usually anchoring themselves between knee and basketball-rim height. I returned again and again for more photographs, notes, and measurements of pupation locations. Then, larvae and pupae of another woodland

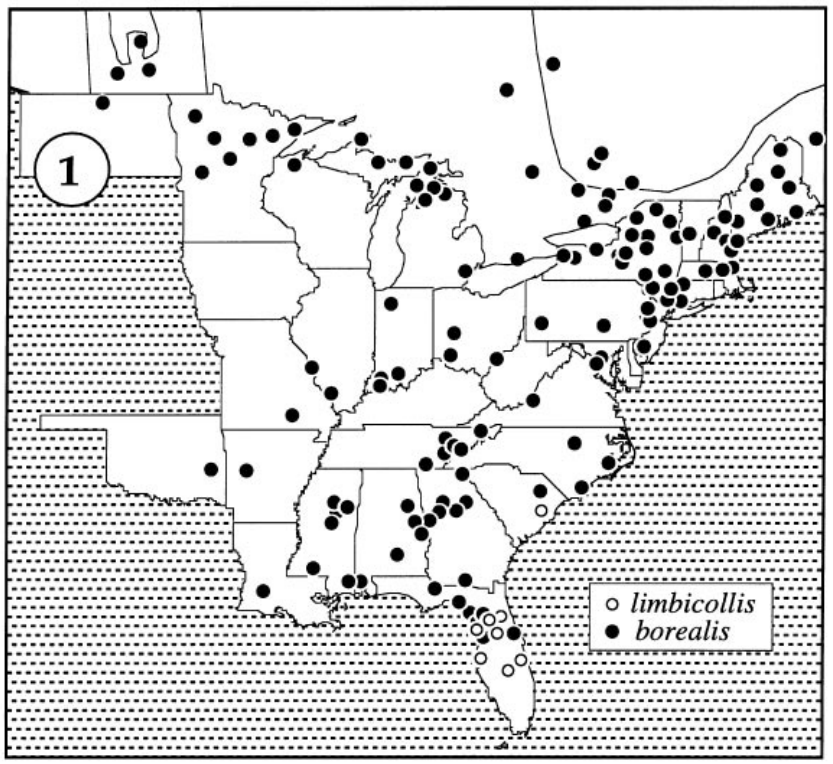


Fig. 1. Locations of specimen-label records for *P. borealis* and *P. limbicollis* from several North American collections. Woodland *Pyractomena* species in addition to these two probably also pupate up on the trunks of trees or shrubs.

Fig. 2. Male *P. borealis* with a *P. borealis* pupa, sex unknown.

species, *Pyractomena limbicollis* Green, began to appear up on trees and in many respects this species was as a foil for *P. borealis*, providing a useful and informative and certainly puzzling contrast.

P. borealis pupae show a surprising directional orientation in their choice of pupation sites on the trees. In a sample of 240 pupae during three winters, the mean direc-

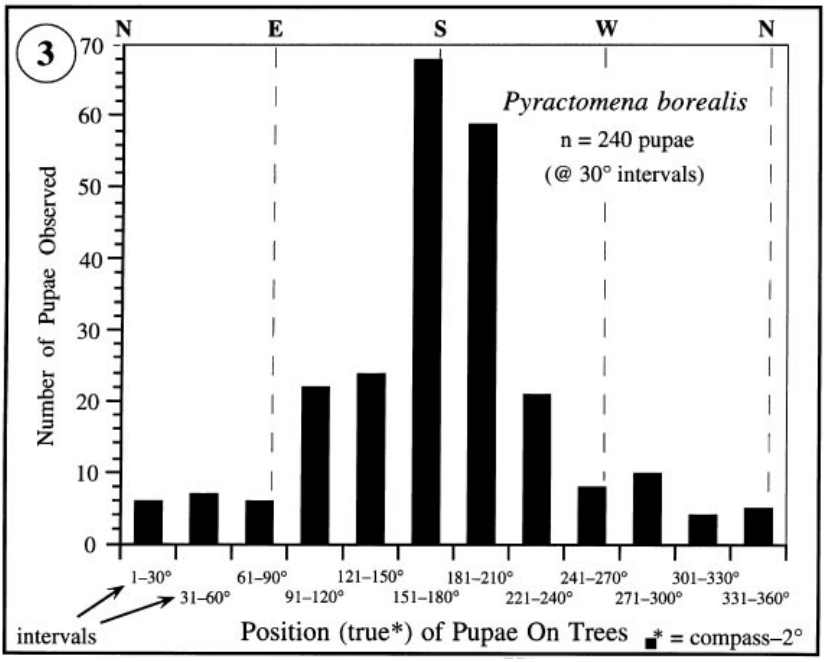


Fig. 3. Directional orientation on tree trunks of *P. borealis* pupae during three winters, at the Possum Creek-Hog Town Creek flood plain site.

tion was southerly, that is, about 180° true (= compass -2°; Fig. 3). But sunlight is more than illumination and a suitable directional cue for orientation—if indeed the larvae are using sunlight for orientation—because it warms what it shines upon. By choosing a pupation site at or near the south side of trees in January, when ambient temperature may be low for many days and even drop below freezing, *P. borealis* pupae raise their body temperature during pupal development by several degrees, presumably decreasing the duration of pupation. One potentially dangerous thermal consequence of the sun-exposing behavior of *P. borealis* is that they must be able to survive extreme temperature changes over a very short period of time; on a clear and sunny winter day the temperature of a dark-barked tree may reach over 90° F (32° C) at three in the afternoon, and by midnight drop well below freezing (32° F, 0° C). One wonders how they manage this!

Pupation up on trees has another conspicuous variable that has thermal consequences. Were the adaptive significance of aerial pupation merely the avoidance of rising flood water, we might expect their vertical distribution on the trees to be rather limited, with pupal distribution clumped around some height—perhaps just above a residual high-water mark left by previous flooding, possibly cueing upon chemical residues left by the water, or algal growth encouraged by flood borne nutrients. Not so; the vertical distribution has considerable spread (Fig. 4). Height may have thermal significance because (1) in winter the ground below may be a heat sink and have a tendency to hold lower-trunk temperatures down, and (2) with increasing altitude there is less shading from sunlight by the trunks, branches and leafless twigs of adjacent

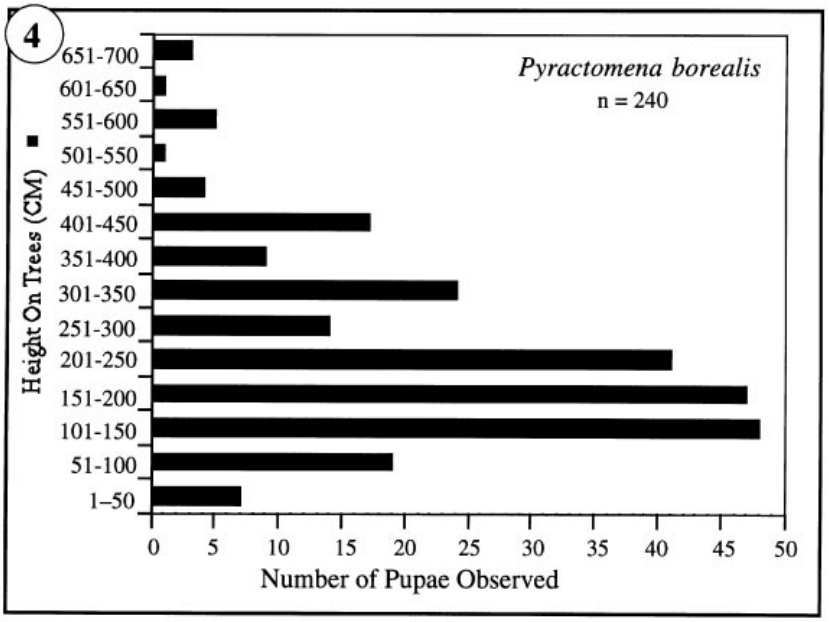
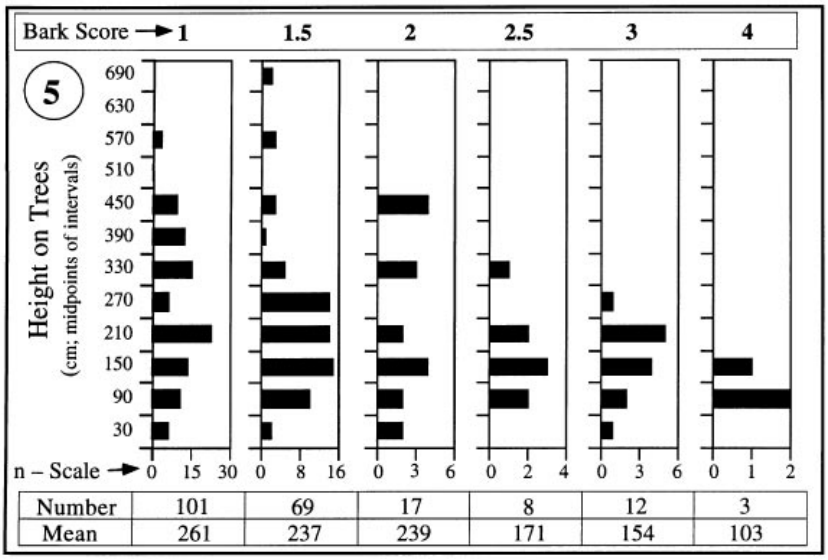


Fig. 4. The height of *P. borealis* pupae on tree trunks.

trees. Obviously then, vertical as well as circumferential positioning on a tree could potentially be used by larvae for manipulating the timing of their metamorphoses. And, there are other possible though more subtle influences on the thermal relations of these pupae. For example, larvae use different species of trees, species that vary in the smoothness of their bark and in the water content of their wood, and these are probably not independent in their effects.

The bark on beech trees is smooth and presents few cliffs and side-directing channels; the bark on oak is rough, with the crevices seemingly the equivalent of four story buildings and presenting an obstacle course for short-legged, prostrate larvae. I comparatively ranked the bark of each tree that larvae selected for the energy and time I expected would be required to climb over (up) them. Beech and sugarberry were typically toward the least expensive end of the ranking, and red maple and oak were at the most expensive end. In consideration of the difficulty of climbing, one would expect that pupae might be found higher on smooth than on rough trees, and perhaps there would be fewer of them. This is what I observed. Trees with smoother bark had more, and species with coarser bark had fewer pupae and they were not as high on the trees (Fig. 5).

Because trunks of different tree species vary in their water content, in sunshine a tree with more water will take longer to warm up, and remain warm longer into a cooling winter evening. Tree-water will also dampen temperature changes, preventing rapid extremes—only two pupae were found on dead (dried out?) trunks. Bark coarseness and thickness could have an influence through the insulation it places between a hanging pupa and the warm water held in the tissues of the trees. On the other hand, rough bark and its crevices provide protective and perhaps thermally amplified niches that provide dead air pockets and radiating walls.



Number	101	69	17	8	12	3
Mean	261	237	239	171	154	103

Fig. 5. The height of *P. borealis* pupae on trees with different bark roughness.

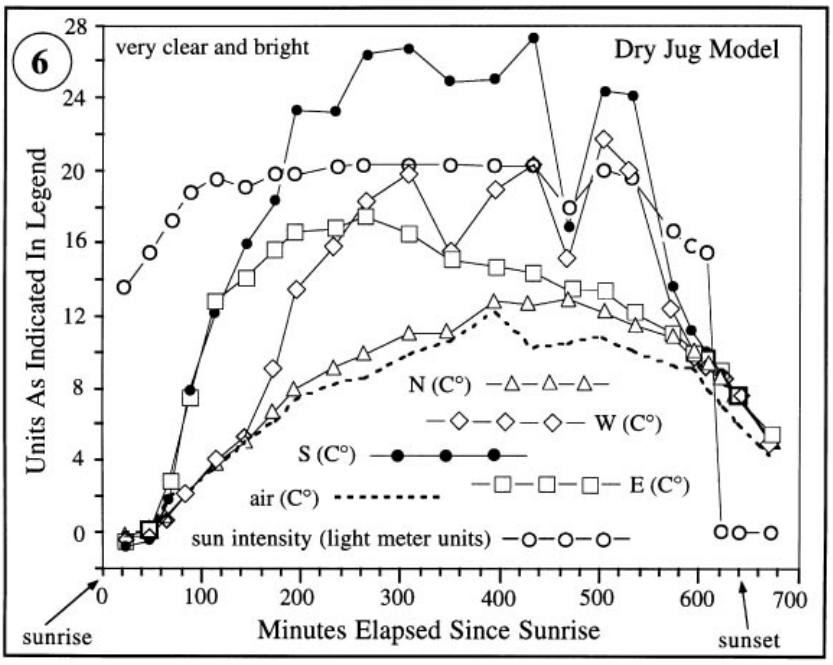


Fig. 6. The basic physical model of a tree with pupae. The tree was a photographic chemical jug filled with dry sand, painted flat black up to the sand level; the model fireflies were 1 cm clay spheres, painted black, each with a thermocouple inside.

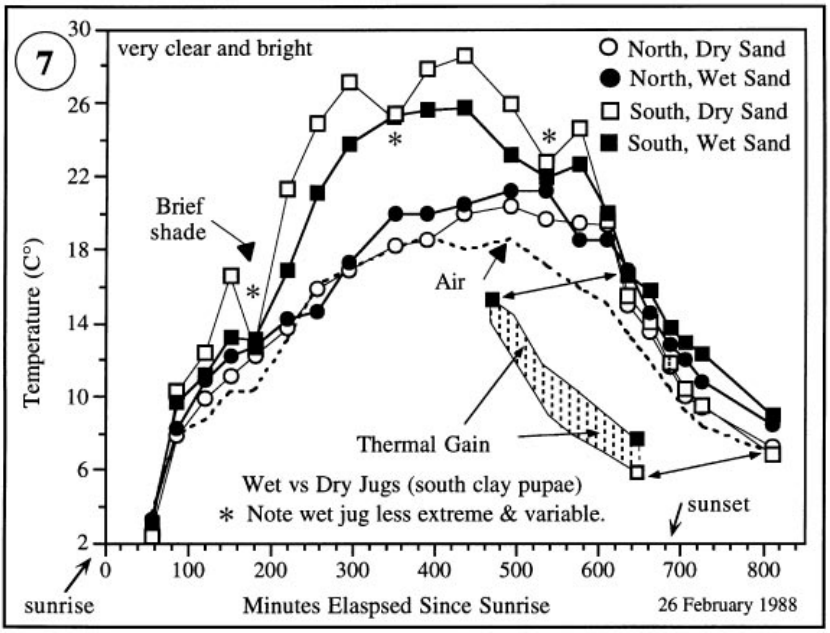


Fig. 7. The comparison of temperatures of model pupae at north and south positions on a dry-sand jug and a wet-sand jug; a physical model examining the influence of tree water content on pupal temperature.

Questions of water content and heat storage can be explored with a simple physical model. I made artificial tree trunks of plastic jugs used to store photographic darkroom chemicals, and hung them in the sun on cool winter days. Each bottle had a 1 cm clay sphere with a thermocouple inside, at each of four directions (N, S, E, W); spheres were painted flat (i.e., not enamel) black and held against the surface of their jug with an elastic band around the jugs and passing over the thermocouple wires. Jugs were of two "trunk" sizes, some contained dry sand and some water-saturated sand, some were hung near the ground and others more than a meter above the ground. Results were generally as expected. Figure 6 shows the temperatures recorded from the basic physical model, a large dry-sand jug, on a cold winter day, with air temperature for comparison, and also sunlight intensity as measured with a photographic exposure (visible light) meter.

Note that the temperature/time courses of clay spheres (model pupae) on different sides of a tree are not the same: the S (south) clay sphere (black dots) warmed more and climbed from freezing to nearly 28° C; the N sphere (open triangles) closely followed air temperature; and that a brief shading at 460 min. affected the S and W spheres but the E and N spheres scarcely if at all. Many comparisons among such spheres and jugs are possible; Figure 7 shows temperature/time plots for N and S clay pupae on wet and dry jugs, with the moderating effect and thermal gain from "tree water." However, one photographed pupa was discovered to be conspicuously arched out away from the tree, suggesting that it should not be presumed that pupae fastened to trees have no control over their body temperature; perhaps they press

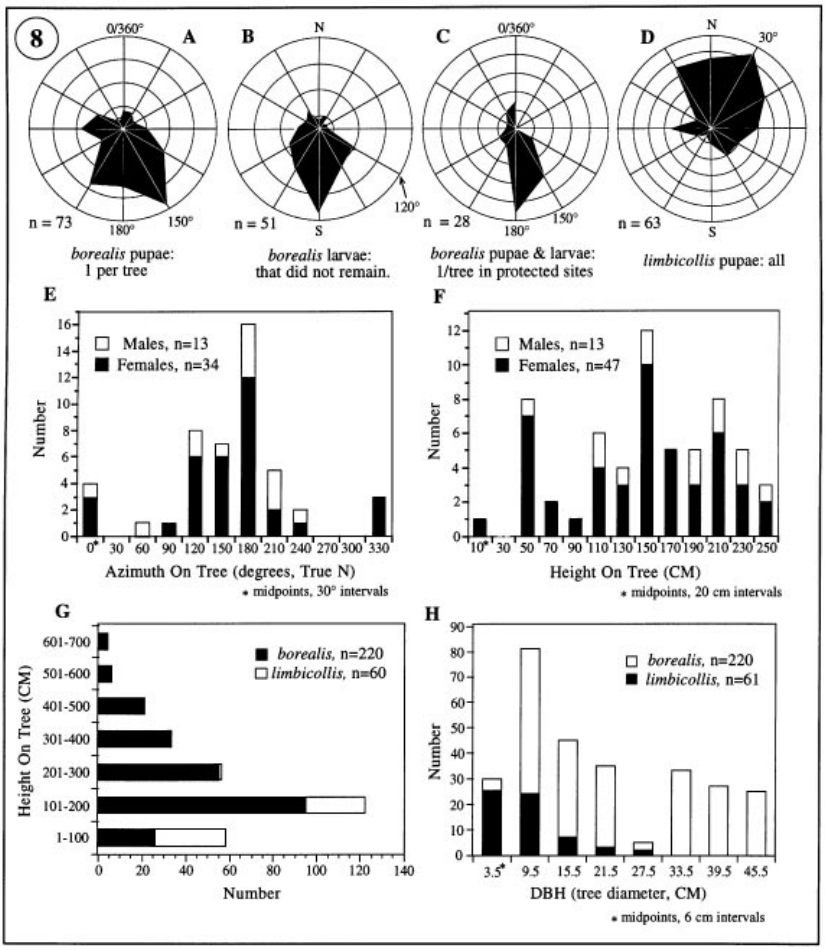


Fig. 8. Graphs illustrating data that are pertinent to some basic questions about *P. borealis* pupation biology, and the remarkably contrasting behavior of *P. limbicollis*. (A) Azimuth positions of solitary *P. borealis* pupae that presumably were not influenced by others; (B) Azimuths of *P. borealis* larvae that did not remain in position, showing that they abandoned what would seem to be a good angle—though they may have moved to fine-tune their positioning(?); (C) positions of *P. borealis* larvae and pupae situated in sheltered locations showing that the shelters did not have highly deviant azimuths; (D) The north-easterly azimuth orientation of *P. limbicollis* pupae; (E, F) Azimuth and height positions of male and female *P. borealis*. (G) Heights of pupal positions of both species; (H) Trunk diameters (DBH, diameter breast height) of pupation trees of both species.

against a warm tree to warm up, or arch out away to cool down by increasing air insulation and circulation between them and their too-warm tree.

The behavior of these juvenile fireflies raises many questions that students can approach. Do larvae actually manipulate with some precision their thermal gains from

azimuth and height?—how about thermal conditions in pockets between the ridges of a muscle tree (Carolina beech)? Would a larva select a pupation site 15° from a "precise target position" or "ideal directional site," if other pupae or a sheltering vine were positioned there? Could a *P. borealis* juvenile be expected to integrate all or some of the variables noted or discussed, to control the moment when it, as an adult enters the competitive reproductive environment? Would a male-to-be larva that was late getting to a tree accelerate its development? Of course it would be absurd to ask whether a larva could control its gender by adjusting its developmental temperature.

Fundamental to comparing observations and sets of observations, and of interest to the mathematically-minded, note the problem of calculating statistical descriptions such as mean positions and amount of spread in circular data, that is, of angular positions around a tree—consider this: the average position of a pupa 5° west of north and another 5° east of north, is half of 355° + 005° and thus 180°, which is true south! Nor is it simple and straightforward to compare the means and deviations (spread) of samples to determine the likelihood that they are "identical" (drawn from the same population). Were my samples properly made?—my data show that more larvae climbed smooth-barked trees (Fig. 5), but were there more smooth trees in the woods; but, perhaps it is not relative abundance that should be considered, but rather the identity of nearest neighbors to trees actually climbed, because individual larvae may not move far in the days or weeks before pupation. If you are interested in physics or photo-journalism, can you suggest a better method of measuring insolation (solar radiation), or a way to see infrared patterns on and among the trunks of the trees that might be available to tree-seeking larvae?

Figure 8 illustrates data that bear on several questions: do azimuths of solitary *P. borealis* pupae show the same directionality? (Fig. 8A); did hanging larvae that subsequently moved, have the same near-southern azimuth? (Fig. 8B)—this question of course relates to the (proximate) mechanism of orientation; do solitary larvae and pupae that occur in protected sites deviate appreciably from an approximate southern azimuth? (Fig. 8C).

On several occasions I found adult *P. borealis* males attending pupae (Fig. 2). This raises questions related to mate finding and competition: are males able to recognize female pupae?; would guarding a sexually unidentified pupa have a better long run payoff than searching with a signal light at night, and would this probability and payoff change through the mating season?; might males accelerate their eclosion to appear earlier in the season to be ahead of and be waiting for unfertilized (high value) females? This last speculation presently finds no support in the azimuth and height data, assuming that accelerating males would show different pupation azimuths and heights than females (Fig. 8E and F). Perhaps *P. borealis* fireflies in north central Florida accelerate their seasonal appearance to avoid predaceous *Photuris* species, which pupate in the soil and thus are stuck in a cold cellar.

The pupation behavior of the smaller species *P. limbicollis* stands in such contrast to that of *P. borealis* that it reinforces the suspicion that there really is something significant occurring in *P. borealis*, providing both encouragement to proceed and another firefly subject for a comparative study. In my sample, *P. limbicollis* pupated toward the north (Fig. 8D) and much lower on smaller trees (Fig. 8G and H)—being low down on the north side of small trees would result in a cooler-than-air temperature regime.

The adult season of *P. limbicollis* is about three weeks later than that of *P. borealis*, and *limbicollis* adults appear with a versatile firefly predator belonging to the *Photuris versicolor* complex. The (sexual) flash pattern of *P. limbicollis* males is virtually identical with one flash pattern emitted by the males of this *Photuris*, an instance of the pattern-matching phenomenon seen in males of many *Photuris* species. What

would *P. limbicollis* gain by synchronizing with a pattern-mimicking predator, or is *limbicollis* manipulating its adult season to avoid a critical seasonal overlap with its congener *P. borealis*? If this is the case, is the avoided overlap that with mate-seeking adults or with first instar larvae that must find soft-bodied and perhaps only minute gastropod prey in the same forest litter?

These fireflies clearly present sufficient questions with respect to proximate mechanisms and ultimate consequences, to provide fireflyers many years of intriguing "off-season" field work. Find quiet and mysterious trails.

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IRIDESCENT DUNG BEETLES: A DIFFERENT ANGLE

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ABSTRACT

Iridescence, in both the visible and ultraviolet (UV) spectra, is produced by various means and may serve several functions in different animals. In insects, such colors are often considered as anti-predator adaptations, either crypsis or aposematism, or a means of thermoregulation. A less explored alternative is social signaling. Iridescent colors are particularly useful in this context because they are brightest from certain directions and body orientation could be employed to direct a visual signal to particular receivers. In phanaeine dung beetles the head and prothorasic shield reflect a visible-light and UV iridescence that is best seen from a position facing the insect. The less iridescent male horn is silhouetted against the prothorasic shield. Since horn size is indicative of male size, such a display may be directed to sexual competitors in agonistic interactions. Broad and reflective prothorasic surfaces on males might also be preferred by females choosing a mate, who will cooperate in future brood care, since they would make infestations of kleptoparasitic flies more obvious.

Key Words: Scarabaeidae, mate choice, intrasexual selection, ultraviolet reflectance, phanaeine

RESUMEN

La iridiscencia, en ambos espectros, visible y ultavioleta (UV), es producida de diversas maneras y puede ejercer diversas funciones en diferentes especies animales. En insectos, dichos colores generalmente son considerados como adaptaciones biológicas para protegerse de sus depredadores por mecanismos crípticos o de aposematismo, o como una forma de termoregulación. Otra alternativa, menos estudiada, es la iridiscencia como un medio de comunicación social. Los colores iridiscentes son particularmente útiles en este contexto porque son demasiado brillantes desde ciertas direcciones y la orientación corporal pudiera ser empleada para dirigir una señal visual a receptores particulares. En los escarabajos de estiércol (Phanaeine), la cabeza y la coraza protorácica reflejan una luz visible y una iridiscencia ultravioleta que se observa mejor desde una posición de frente al insecto. El cuerno de los machos, un poco menos iridiscente, forma una silueta contra la coraza protorácica. Si consideramos que el tamaño del cuerno del macho refleja el tamaño corporal, este mecanismo pudiera ser dirigido a competidores sexuales en interacciones agonistas. Las superficies protorácicas anchas y reflejantes presentes en los machos, pudieran también ser preferidas por hembras eligiendo su pareja sexual, quienes cooperarán en el cuidado futuro de su progenie, puesto que pudieran hacer más obvias las infestaciones de moscas cleptoparásitas.

Iridescence is found in many organisms, but among terrestrial animals it is most highly developed in two groups, birds and insects. Perhaps not coincidentally, these classes also exhibit well developed visual systems, and protean body coverings. The two groups frequently interact; birds are among the principal predators of insects, and iridescent species of both are largely diurnal, suggesting that these colors are used in interspecific and/or intraspecific communication. In this paper, the mechanics of iridescence are briefly described, as are some of the different structures that cause iridescence. Different

hypotheses are then proposed for the evolution of iridescent coloration, and each hypothesis is considered in relation to iridescence in dung beetles (Coleoptera: Scarabaeidae).

Animal coloration often correlates with a species visual capabilities. Mammals are typically colored with shades of brown and black, the hues of melanin. Most apparently do not see color, or do not respond to color stimuli. Primates are an exception, and not only respond to color but are often brightly colored themselves, e.g., the faces and rumps of mandrills, (*Mandrillus sphinx*). Humans generally see wavelengths between 400 and 790 nm (referred to from this point as the "visible" spectrum; Endler 1990). Birds perceive not only the colors visible to humans, but also detect ultraviolet colors with wavelengths shorter than 400 nm (Goldsmith 1980; Parrish et al. 1984). Bees perceive wavelengths from the UV range up to 650 nm, but do not distinguish orange (600-650 nm) from yellow (550-600 nm), or blue (400-480 nm) from violet (380-400). Other insects' visual systems vary. For example, the absorbance maxima of the photo pigments in some moth eyes are 345, 440 and 520, while the peaks in *Heliconius* butterflies are 350, 460 and 550 (Endler 1990). These differences may be due to differences in available light and other components of their respective environments (e. g., Lall et al. 1980).

Browns, reds, and yellows in animals are almost always formed by pigmentation, and can be washed out of the underlying structure with solvents. Blue and green colors are usually structural and cannot be permanently changed unless the structure itself is crushed.

Structural colors can be produced in two ways. One is through diffusion, i.e., the scattering of short wave colors, blue and violet, by submicroscopic particles, that results in Tyndall blue. The blues of the sky and human eyes are formed this way (Simon 1971), as are some blues on butterfly scales (Huxley 1976).

The other structural means of color production is through interference, which causes the brilliant changing hues common in iridescent insects. Thin films, such as oil on water, reflect some incoming light from their shiny top surfaces. The rest of the light enters the film and is refracted by the film's greater density compared to air. This light then slows as it passes through the film, and when it reaches the lower surface, is reflected back. When it rejoins the light reflected off the upper surface, it has been traveling slower, and is thus out of phase with the reflected beam of light. If the phase difference between the two beams equals one full wavelength, or a multiple thereof, the color of that particular wavelength will be reinforced. If the amplitudes (crests and troughs) of the two light beams are equal, reinforcement will be strongest, and the color purest. All other wavelengths are either weakened, if they are out of phase, or eliminated if the crest of one beam meets the trough of the other. If the angle of incident light is changed, a different color will appear. Changing the width of the film will also select for different wavelengths, and thus different colors (Simon 1971).

Thin films are not the only way to obtain interference colors. Thin slits arranged equidistant from each other, called diffraction gratings, also cause iridescence (Hinton 1973). Additionally, a structure called a space lattice, where minute particles suspended in a medium are arranged in layers stacked on top of each other, produces iridescent reflections. The microscopic structure of iridescent bird feathers are made up of stacks of melanin rods within layers of keratin, creating a space lattice (Simon 1971).

A Survey of Iridescence

Feathers

Of all soft body coverings bird feathers are the most strikingly iridescent. Many birds are largely iridescent, such as the Resplendent Quetzal (*Pharomachrus mocino*). Others are dull, but exhibit patches of iridescent feathers. These patches, in

otherwise dull-colored birds, also strongly reflect ultraviolet wavelengths (Radwan 1993). As will be seen in insects, iridescent patches are highly directional, appearing brightest from particular angles of view.

Butterfly scales

In butterflies, several types of iridescent scales have been described. The average lepidopteran wing has rows of alternate long and short scales. The longer are cover scales, which arch over and hide the short, ground scales. In iridescent patches, the cover scales are specialized, but the ground scales are usually undifferentiated. Iridescence may arise from "lamellar thin-film iridescent" scales, "microrib thin-film iridescent" scales, "laminar thin-film iridescent" scales, or "diffraction lattice" scales, whose interiors are filled with crystals of a cubic lattice that produces a diffraction color (Ghiradella 1985). These various ways of producing iridescence can be readily modified, as demonstrated by ultraviolet reflectance in *Colias*, where the lamellar thin-film color is inherited at a single locus (Silberglied & Taylor 1973). Because of this plasticity and that several scale types can be found in taxa without any particular correlation to phylogenetic associations, iridescence in butterflies probably evolves in response to selection (Ghiradella 1985).

Some butterflies have intense UV reflection caused by interference, and produced in the same manner as visible iridescence. This ultraviolet reflectance can overlay visible colors (Silberglied 1979). Additionally, most iridescent scales also contain melanin, which absorbs much of the light not reflected by the iridescence and enhances the brilliance of the color (Nijhout 1991). The intensity of most colored surfaces varies linearly with the angle between the light source, the reflecting surface, and the observer (Endler 1990). With interference colors, reflectance at a given wavelength "cuts on" and "cuts off" more abruptly, and the peak wavelength (that is, the color), shifts with changes in the angle (Silberglied 1979). Additionally, at certain angles the reflected light will be highly polarized. When flying *Colias eurytheme* and other species are observed through a UV-viewing device, they resemble flashing beacons (Silberglied 1979). Crane (1954) writes: "With every wingbeat, a flying *Morhpo* butterfly changes the angle of light incidence through the entire possible range. To the human eye, a *Morhpo* in flight is simply a flickering flash of varying tints of blue. However, to another *Morhpo*, in sunlight, there should be a brilliant shift from blue-green or blue to ultraviolet, then momentary extinction and back again through the spectral arc; conceivably this may be an exceptionally potent stimulus. The well known dipping of these butterflies to blue papers and other objects suggests strongly that the wing color may prove to be a sign stimulus in inter-male or courtship behavior."

Beetles

In some beetles that live under bark the microsculpture in the cuticle may produce a type of iridescence. This microsculpture has a characteristic orientation and asymmetrical sculpture, and is thought to be a by-product of the frictional properties of the cuticle (Crowson 1981). The more common bright iridescence seen in many Coleoptera is produced from light interference in thin films in the endocuticle. As with iridescence in feathers, and butterfly scales, these colors vary with the direction of incident light. The most frequent color is metallic green, but blue, red, gold, and purple are also common (Hinton 1973).

Colors are often a result of an animal's relation to activity and habitat. Green iridescence typically occurs in diurnal, leaf feeding beetles (Crowson 1981). Beetles that

are obligate cave dwellers are pale brown, not black, suggesting that this shade is the natural color when no selection for color occurs. Generally, nocturnal beetles are black (Crowson 1981).

One group of new world, scarab dung beetles, the phanaeine, is known for iridescent colors, diurnal habits, and conspicuous behavior (e.g., Edmonds 1994). A conventional interpretation for this suite of characters is that the beetles may be bad tasting, and advertise their unpalatability to bird predators who subsequently avoid them (Arrow 1951). However, evidence for this hypothesis is minimal, and several other arguments for the adaptive benefit of iridescence in these beetles can be invoked with equal conviction.

Adaptive Hypotheses

Not all examples of iridescence in animals may be adaptive. For example, some fly larvae infected with a particular virus become iridescent. Unless iridescence attracts new hosts or agents of dispersal, such coloration is probably an artifact and has no selective advantage. But given the striking apparancy of iridescence in diurnal dung beetles and other insects, it is reasonable to investigate adaptive hypotheses for their coloration.

Thermoregulation

Dung beetles of many species perch on leaves in tropical forests. While much of this behavior is related to foraging, one beetle species is thought to perch as a way of regulating body temperature (Young 1984). This beetle, however, is dull black. Bright, large scarabs probably possess internal mechanism that allow for large increases in body temperature prior to flight, and sun-basking in these beetles is not necessary (Young 1984). Further, iridescence reflects light, rather than absorbing it. Possibly, iridescence might serve to prevent overheating, allowing diurnal insects to forage in open habitats. Brilliantly colored species of phanaeines are found in both forests and more open habitats (Edmonds 1994).

Distracting glare

Hinton (1973) argues that diffraction gratings can produce warning colors, and because some of the light reflected is of the complete spectrum, will also produce intense glare. This glare might prevent a predator from judging the exact distance of the animal.

Crypsis

Endler (1990) stressed that the conspicuousness of an animal in its environment is a function of the receiver's visual system, and the intensity, hue, saturation, and degree of contrast between different patches on the animal and its environment. What may be described as bright when seen out of context by humans may actually be cryptic in its environment. Many bright green iridescent leaf beetles could be cryptic to avian predators; e.g., the iridescence might resemble dew on leaves (Crowson 1981).

Visual signals

Colors can be used to pass information visually from one organism to another. In the case of insect iridescence, signals are most likely directed at either conspecifics or

at diurnal predators. Bats do not use vision in hunting, and generally, defense against these predators involves interference with their sonar, or evasive action (Dunning & Roeder 1965). Nocturnal mammals usually hunt by smell, and most diurnal mammals are not thought to have color vision. The main predators that would encounter visual signals from prey are birds, some reptiles, and other insects (Crowson 1981).

The physiology of bird sight is well known, but behavioral responses to specific colors are not. For example, there have been a number of studies examining birds' reaction to signals in the ultraviolet spectra. Birds have been known to have receptors sensitive to UV wavelengths for over 20 years (Bennett et al. 1996), but controlled studies to determine if they respond behaviorally to these frequencies are rare. Birds can distinguish between visible light that differs only in the presence or absence of the UV component (Goldsmith 1980). Studies using filters that screen out particular wavelengths in choice experiments reveal that female zebra finches respond preferentially to males that are displayed behind filters that allow transmittance of both UV and visible light as opposed to those that only allowed in visible light (Bennett et al. 1996). Because birds make mate choices based on UV reflectance, it might not be surprising to find that they perceive and react to UV reflectance in insects (see Parrish et al. 1984).

A—*Aposematism*: Bright colored insects, including certain dung beetles, are often thought to be aposematic. Arrow (1951) recorded an instance where one of the African ball-rolling beetles *Gymnopleurus virens,* which is bright green, blue, or crimson, was shown to induce nausea in a captive baboon. Furthermore, this beetle is usually found in association with 2 other similarly colored species, which are presumed to be Batesian mimics.

On Barro Colorado Island (BCI), two diurnal ball-rolling species, *Canthon c. sallei* and *C. moniliatus* are also brightly colored and conspicuous, flying slowly at 15-30 cm above the ground (Gill 1991). *Canthon c. sallei* produces a secretion that repels blowflies from its food (Bellés & Favila 1984), and these beetles captured in flight have an unpleasant aroma. *Canthon angustatus* displays with pygidium raised when threatened. The secretion of the exposed gland has been shown to repel assassin bugs (Gill 1991). Staphylinids and assassin bugs are known to eat other dung beetles. Small, metallic colored dung beetles like *Ateuchus*, and some *Canthon*, made up 74% of the captures by a robber fly on BCI (Shelly, cited in Gill 1991). Bats are also known to occasionally eat dung beetles (Bellwood, pers. comm.). Burrowing owls are a persistent predator of north American Phanaiines (Woodruff 1971), and other birds have been seen to eat them (Sivinski, pers. comm.).

Aposematism in other iridescent beetles has been more convincingly demonstrated. Many cicindelids are iridescent, and a number of these have been shown to be distasteful (Acorn 1988). One tiger beetle species appears to mimic an iridescent sympatric blister beetle species. Others are thought to be Mullerian mimics of each other. There is also a purported Mullerian complex of tiger beetles and mutillid wasps in Africa (Acorn 1988). Whether the iridescent colors of dung beetles are aimed at aposematic deterrence of predation remains to be demonstrated.

B—Social signaling: If the brilliant colors of some dung beetles are used in signaling conspecifics, the conspecifics must be able to detect either the colors or some aspect of them. The eyes of most Scarabaeidae are of the eucone type believed to make possible the discrimination of colors, and of polarized light (Horridge 1975). Electrophysiological evidence for color sensitivity has been found in some Cetoniinae (Scarabeidae) (Mazokhin-Porshnyakov 1964).

Most insects appear capable of seeing ultraviolet reflectance. Their visual system often has one absorbance maximum around 350 nm (Silberglied 1979). Many species of butterflies use UV for communication (Silberglied 1979). In a number of butterflies,

ultraviolet patterns and iridescence are not related to the visible wing patterns (Silberglied & Taylor 1973), whereas UV reflectance patterns in birds often parallel the visible patterns (Bleiweiss 1994; Bennett et al. 1996).

To examine iridescent coloration in dung beetles, several species of *Phanaeus* and related genera were photographed at various angles and under different lighting conditions. Because insect perception is vastly different than ours, naturally, the inferences made about the photographs must be made with caution (Endler 1990). Photographs were taken from the front to simulate a beetle's eye view of another, interacting, beetle, with 100 ISO Fuji daylight slide film and a Cokin ring flash with color temperature 5600 K. Iridescent reflectance changed dramatically with the angle and intensity of the light, as is typical with interference coloration. The iridescence on the horn and clypeus disappears when not directly illuminated. The same light reflected onto the subject completely changes the pattern on the prothorax. A front view of *Sulcophanaeus imperator* reveals iridescent spots on either side of the head that resemble large red eyes. This is unlikely to be the region of the beetle typically encountered by attacking predators. Photographing an iridescent beetle, *Phanaeus mexicanus*, with daylight film under flash and UV lights yields even more psychedelic color patterns; i.e., the insect fluoresces by absorbing UV light and reemitting it in the visible spectrum. Finally, photographing phanaeine under UV light (Spectroline model MB100, peak wavelength 365 nm), with a Kodak UV 18A Wratten filter (passes only wavelengths between 310 and 400 nm), and a Panasonic AG-150 videocamera with a TV Zoom lens (6-54 mm; 1:1.4) (Eisner et al. 1988; Bleiweiss 1994; Van der Kerkovan, pers. comm.), demonstrated UV reflectance from various iridescent areas of the beetles, notably the front of the pronotum which forms an expansive shield (Fig. 1a and b). The UV reflectance could be seen only at specific light angles, and small changes of light source direction extinguished it. These dramatic and abrupt changes in light reflectance due to angle (in both the visible and ultraviolet spectra) could be a potentially efficacious method of communication, either between or within the sexes.

Beetle horns are thought to be used in combats between males for access to females or over resources that attract females. However, male-male encounters are rarely seen in the phanaeines (Halffter & Lopez 1977; Rassmussen pers, comm.; but see Otronen 1988). Fighting requires energy and may lead to injury or at least the loss of a mating opportunity (see Sivinski this symposium). As an alternative to fighting, I suggest that males assess other males, particularly their size, by the appearance of the horn, and that this presentation is enhanced by iridescence. While the horn itself is less reflective, it is highlighted against the backdrop of a bright pronotal shield (Fig 1b). The relationship between horn size and body size in *Phanaeus* spp. can be complex and polymodel, however the two characters are generally positively and allometrically correlated (J. Sivinski unpublished data; see also Otte & Stayman 1979). Allometry may be characteristic of structures designed to transmit visual signals concerning male body size (e.g., Green 1992; see Sivinski this symposium).

In some phanaeines, such as *Diabroctus mimas*, male horns are small but the prothorasic shield is massive (Edmonds 1972), and may provide a broad signaling surface. The various bosses, projections, horns, sculpturing and textures that occur on phanaeines might be due to adaptations for signaling in different environments or even result from selection for species isolation through different patterns of reflective points. There is some intriguing evidence that color patterns in phanaeines may have simple inheritance patterns similar to that in the butterfly *Colias*. The blue and green morphs of *Phanaeus difformis* were bred in the laboratory with results consistent with Mendelian ratios in the offspring (Blume & Aga 1976).

Horns and prothorasic shields could also be used in male - female signaling. Females may choose males on the basis of many criteria (Arnold 1983). Hamilton and

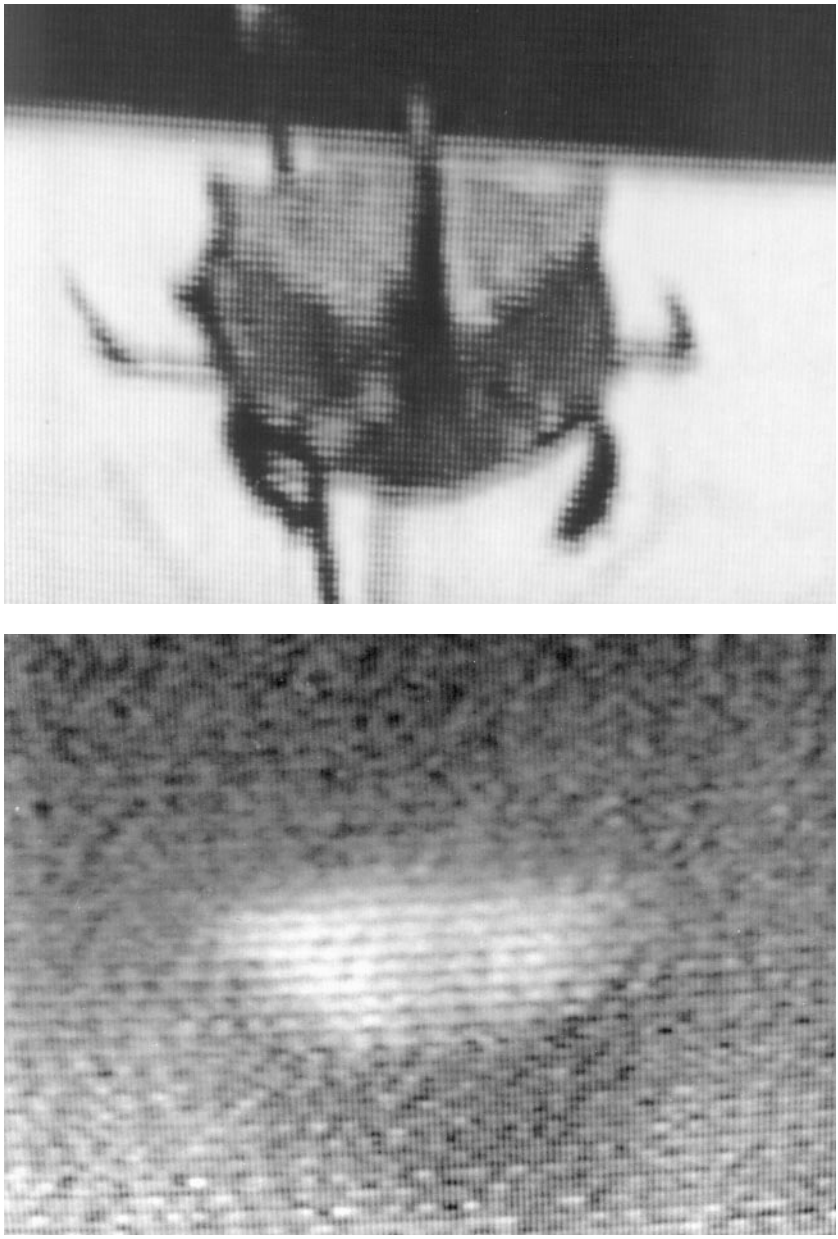

Fig. 1a—A photograph of a male *Phanaeus vindex* taken from a video screen displaying the specimen video-taped under light produced by a tungsten bulb.

b—The same specimen video-taped with a camera fronted by an ultraviolet filter and illuminated only by ultraviolet light. Note the strong UV reflectance of the prothorasic shield.

Zuk (1982) proposed that parasites can influence the evolution of sexually selected traits. Individuals increase their net fitness by choosing mates with high genetic resistance to parasites. This model assumes that heritable variation in fitness is maintained in host-parasite coevolution. Hosts will select mates based on condition-dependent traits that indicate parasite loads. For example, parasites in brightly colored birds may cause dulling in the plumage, or a change in courtship displays.

Many birds signal with patches of feathers that reflect UV and/or are iridescent in the visible spectrum (Radwan 1993). Male hummingbirds have iridescent patches on head and neck that can be seen only from certain angles (Tyrrell & Tyrrell 1990). In pigeons, iridescent feathers around the neck region have been hypothesized to inform potential mates of the health of the bird (Hamilton & Zuk 1982). Birds with little or no louse infestations are expected to show less iridescence. However, louse damage doesn't affect the distal end of the feather, which is the part visible on an intact bird. One study on mate choice in pigeons with artificially enhanced louse loads demonstrated that females are less likely to mate with males which have high louse loads (Clayton 1990). However, to human observers there is no difference between the birds. Unfortunately, these birds were not examined under ultraviolet light, and feather reflectance patterns may be affected in those wavelengths. Clayton hypothesizes that females see louse infestations during close encounters during courtship. Further, Clayton presents an alternative to the Hamilton-Zuk "good genes" hypothesis that mates are chosen for their genetic resistance to parasites. He argues that choosiness may be explained more parsimoniously by a female's aversion to contracting lice herself or passing them to offspring.

The bright triangular pronotum of *Phanaeus vindex* and related species can be occupied and partially obscured by phoretic kleptoparasitic flies (Sphaeroceridae), such as *Norbommia frigipennis*. The flies ride scarabs down into their subterranean chambers and deposit eggs in the fecal food-masses and brood balls, where the fly larvae develop (Sivinski 1983). The dung consumed by rapidly developing fly larvae may decrease the fitness of the slower developing beetle larvae. Because *Phanaeus* forms pair bonds and the pair cooperate in long periods of nest construction (Haftler & Edmonds 1982), it would be advantageous for a female to determine, prior to mating, that a male carries flies that might be deleterious to her offspring. Females may choose males that exhibit traits which clearly demonstrate their freedom from kleptoparasites.

The plausibility of the male-advertisement/female-mate choice hypothesis is effected by the absence of obvious behaviors that suggest female comparison of mating partners in phanaeine dung beetles (Arrow 1951; Otte & Stayman 1979). However, females of most species are turtle-shaped, and difficult for a male to mount. Furthermore, the female's genital opening is covered by a plate that would be difficult for a male to pry open. Such a structure suggests the possibility of covert female choice at the time of pair formation (Otronen 1988). Arrow (1951) suggests that female beetles have inadequate vision to assess male horn size. Iridescent and ultraviolet reflective surfaces, that change radically with small increments in angle of view, may serve as signal enhancement for the visually impaired.

Since males participate in securing provisions for their offspring they may also prefer mates without phoretic kleptoparasites. However, females appear to present fewer opportunities for males to discern an infestation. While females are typically the same color as males they are generally not horned and often have a less developed prothorasic shield. Exceptions are the nearly sexually monomorphic *Coprophanaeus lancifer* and *ensifer* (Edmonds 1972). These are extremely large insects that form brood masses from carrion. Perhaps in keeping with their nocturnal habits they are among the darkest colored of their tribe. Female horns are used in combats with other females and males in competitions over cadavers (Otronen 1988).

The hypotheses that iridescent surfaces are due to sexual selection through mate choice and intrasexual competition are not necessarily mutually exclusive. Neither does the use of iridescent characters in sexual contexts preclude the hypothesis that iridescent dung beetles may also be aposematic to diurnal predators or even cryptic in certain habitats. Iridescence in insects may be influenced by numerous selective pressures. The least explored is the hypothesis of social signaling, and male - male competition and perhaps intersexual assessment could be important in the evolution of iridescence in dung beetles. If so, the bright flashing patterns of still other iridescent insects may more often be territorial or sexual displays rather than aposematic or disruptive predator defenses (Crane 1954).

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ORNAMENTS IN THE DIPTERA

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ABSTRACT

Occasionally, flies bear sexually dimorphic structures (ornaments) that are used, or are presumed to be used, in courtships or in aggressive interactions with sexual rivals. These are reviewed, beginning with projections from the head, continuing through elaborations of the legs and finishing with gigantism of the genitalia. Several functions for ornaments are considered, including advertisement of genetic properties, subversion of female mate choice and "runaway" sexual selection. Neither the type of ornament nor the degree of elaboration necessarily indicates which of the above processes is responsible for a particular ornament. Resource distribution and the resulting possibilities for resource defense and mate choice explain the occurrence of ornaments in some species. The phyletic distribution of ornaments may reflect foraging behaviors and the type of substrates upon which courtships occur.

Key Words: sexual selection, territoriality, female mate choice, arms races

RESUMEN

Ocasionalmente, las moscas presentan estructuras sexuales dimórficas (ornamentos) que son utilizados o se cree sean utilizadas en el cortejo sexual o en interacciones agresivas con sus rivales sexuales. Dichas estructuras han sido evaluadas, comenzando con proyecciones de la cabeza, continuando con las estructuras elaboradas de las extremidades y terminando con el gigantismo de los genitales. Se han considerado distintas funciones para dichos ornamentos, incluyendo la promoción de sus propiedades genéticas, subversión de la elección de la hembra por aparearse, y el rehusare a la selección sexual. Tanto el tipo de ornamento como el grado de elaboración no necesariamente indicaron cual de los procesos mencionados es el responsable de un ornamento en particular. La distribución de los recursos y la posibilidad resultante de un recurso de defensa y de elección de apareamiento pudieran explicar la aparición de ornamentos en algunas especies. La distribución filial evolutiva de los ornamentos pueden reflejar comportamientos relacionados con la búsqueda del alimento y con el tipo de sustratos sobre los cuales el cortejo sexual se lleva cabo.

In general, the body shapes of flies fall into a few familiar categories, ranging from the willowy (e.g., Tipulidae) to the robust (e.g., Muscidae). Sporadically added onto these ordinary forms are extraordinary elaborations apparently fashioned by sexual selection. These have been called "ornaments," but it is useful to think of them as "organs of propaganda," designed to communicate with, and manipulate, potential mates and/or sexual rivals (c.f., Krebs & Dawkins 1978). In considering the ornaments of Diptera, first I survey their types and locations, starting with the head and working back to the genitalia. Then I will address whether the nature of ornaments provides clues to their "messages" and for whom the messages are intended. Finally, I attempt to correlate certain forms of decoration with different types of mating systems in various taxa of flies.

I. The Head

A. Eyes

Sexual dimorphism of the eyes is commonplace in the Diptera, but ornamented eyes are rare. In order to make this distinction clear, the term "ornament" needs to be clarified. Males flies, particularly those that swarm, often have larger eyes with portions modified to locate the motions of incoming females (e.g., Sivinski & Petersson 1996). However, this sexual difference does not constitute ornamentation. For one thing, these dimorphic eyes are not suspected of being signaling devices. Colors and patterns, common in eyes in families such as Tabanidae, Dolichopodidae and Tephritidae, and which could act as signals, will not be considered ornaments either. Rather, ornaments will be defined, perhaps somewhat arbitrarily, as elaborated or novel structures, sculptures rather than paintings. An example of ornate eyes are those of the male Brazilian drosophilid *Zygotricha dispar* Wiedemann (Fig. 1b). They are much enlarged, and prolonged into sharpened horns that resemble those of a water buffalo (Bristowe 1925). In certain congeners, the tip of the eye curls like a ram's horn (Grimaldi 1987; Grimaldi & Fenster 1989).

B. Extensions of the Head Capsule (Stalk-eyes and Antlers)

In eight acalypterate families, male's heads, and occasionally female's heads, are sometimes stretched laterally until the eyes are supported at the ends of remarkable "stalks" (Fig. 1a; Wilkinson & Dodson 1996). There is a considerable literature regarding the behavior of stalk-eyed Diopsidae that will be addressed when the significance of ornaments is discussed (e.g., Burkhardt & de la Motte 1983; de la Motte & Burkhardt 1983; Shillito 1960, 1976; Wilkinson 1993; Wilkinson & Dodson 1996).

Antlers, projections from the head capsule, occur, to one extent or another, in five families of flies (Wilkinson & Dodson 1996). Those of the tephritid genus *Phytalmia* originate under the eyes and are by far the most elaborate (Fig. 1c; see McAlpine & Schneider 1978; Schneider 1993). In his classic "The Malay Archipelago", Wallace (1869) describes his collection of four species from New Guinea: ". . . these horns (of *P. cervicornis* Gerstaecker) are nearly as long as the body, having two branches, with small snags near their bifurcation, so as to resemble the horns of a stag. They are black, with the tips pale . . . the eyes (when alive) are violet and green. . . . The horns (of *P. megalotis* Gerstaecker (= *wallacei*)) are about one third the length of the insect, broad, flat, and of an elongated triangular form. They are of a beautiful pink color, edged with black, and with a pale central stripe. The front of the head is also pink, and the eyes violet pink, with a green stripe across them, giving the insect a very elegant and singular appearance. . . . The horns (of *P. alcicornis* (Saunders)) are very remarkable, being suddenly dilated into a flat plate, strongly toothed round the outer margin, and resembling the horns of an elk (*moose*) . . . the head (of *P. brevicornis* (Saunders)) is compressed and dilated laterally, with very small, flat horns . . ."

C. Mouthparts and Face

Mouthparts are occasionally ornamented in the Dolichopodidae. Males of the tiny *Chrysotus pallipes* Loew have much enlarged labial palps (see Van Duzee 1924), which emit silver flashes as males signal from the surface of leaves (Sivinski 1988a). The expanded gold-silver palpi of the Hawaiian *C. pallidipalpus* Van Duzee reflect light as males pursue females (Parmenter 1952). The palpi of males in the closely re-

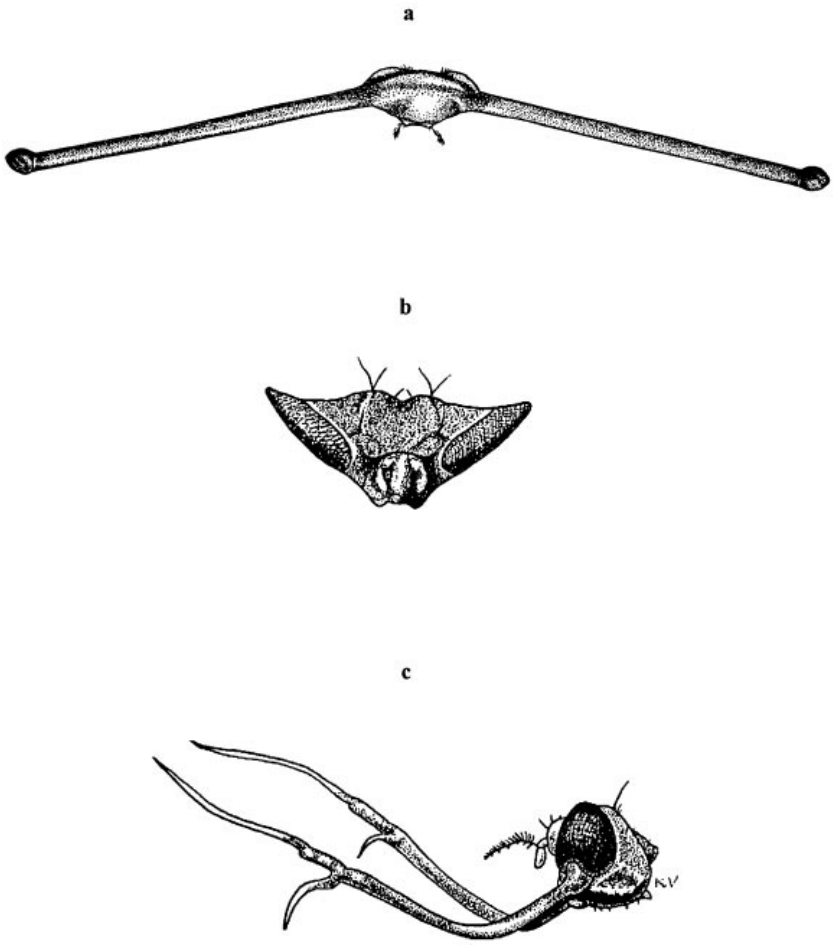

Fig. 1. Projections from the heads of acalypterate flies:

a) Stalk-eyes on a male *Achias* sp. (dorsal view), a large platystomatid fly from New Guinea. Similar projections in diopsid flies are perceived as signals by both males and females in the contexts of aggression and mate choice respectively.

b) The head (frontal view) of a male drosophilid, *Zygotricha dispar*, a tiny, but pugnacious, fly from Brazil that uses its horn-like eyes in intrasexual combats and perhaps as an advertisement of size directed to potential mates and rivals.

c) The antlered head (lateral view) of a male *Phytalmia cervicornis*, a large and aggressive tephritid fly from the rain forests of New Guinea where males defend oviposition sites from other males and mate with females that come to lay eggs.

lated genus *Asyndetus* are also sometimes ornate. Those of *A. flavipes* Van Duzee are bright yellow and covered with long yellow hairs (Van Duzee 1932). A male of *Aphrosylus raptor* Walker, searching for mates on seaweed covered rocks, flashes his large silver palpi "as he swings his shoulders and head in his stride" (Parmenter 1952). Silver reflections are found on the elongated faces of certain male dolichopodids. In *Poly-*

medon spp. the face extends to form a "plate or ribbon" that hangs down over the proboscis (Van Duzee 1927).

D. Setae

Male tephritids often have highly modified setae. Some species of *Ceratitis*, tephritids that include the infamous Mediterranean fruit fly, *C. capitata* (Wiedemann), bear orbital setae on the face above the antennae. These hairs can be strikingly long; those of *C. caetrata* Munro reach more than twice the width of the head in length (Munro 1949). The setae, tipped with either black or white expansions (Bezzi 1924), are "waved" about during courtships (e.g., Arita & Kaneshiro 1989).

E. Antennae

Many flies, such as mosquitoes and chironomid midges, bear sexually dimorphic antennae (see Sivinski & Petersson 1996). In most cases, these differences result from one sex, usually the male, being adapted to perceive pheromones or acoustic cues. However, some antennae appear to be modified to emit a signal of their own. Chloropids are rarely dimorphic, but males of the sole species of *Gampsocera* in Hawaii have various unique markings and thickened and black aristae (Kanmiya 1989). Males of *Camposella insignata* Cole, an acrocerid from Ecuador, have "an astonishing development" of the third antennal segment that renders it enlarged, flattened and patterned (Cole 1969). Dolichopodid males sometime have elongated antennae which are plumed at the tip (e.g., *Tachytrechus* spp. (Greene 1922)), or in the case of *T. binodatus* Loew, plumed at the tip and in the middle. Tachinids commonly have sexually dimorphic antennae. Some, such as those of male *Lispidae triangularis* Aldrich which contain a much broadened third segment, seem decoratively large (Aldrich 1929). Exaggerated and plumed antennae occur in some tephritids (White 1988).

II. The Thorax

A. Forelegs

Various dolichopodids wave and/or touch potential mates with ornamented forelegs (Gruhl 1924; Fig. 2a). Males of *Neurigonia quadrifasciata* Fab. and *Poecilobothrus nobilitatus* (L.) approach a female from the rear and reaching over her, curve their plumed tarsi over her head (Smith 1959). They then wave their tarsi alternately, one over each eye. Male *Dolichopus omnivorax* Van Duzee wait for foraging females on floating vegetation (Steyskal 1938). When a potential mate is found, he approaches with his forelegs extended laterally. The tibiae hang down and forward, displaying a large black pad on the terminal tarsi. If the female remains still, the male's advance will bring the pads almost into contact with her eyes. Sometimes the front femora of dolichopodids are decorated. Those of *Tachytrechus olympiae* Aldrich are swollen and marked with a dark spot (Greene 1922). The pinnacle of foreleg ornamentation in the Dolichopodidae is occupied by *Campsicnemus magius* (Loew), whose limbs are so swollen, pendanted, hairy and bizarre that the dipterist Gerstaecker accused his colleague Loew of describing a species from a specimen deformed by fungus (Verrall 1905; Lundbeck 1912; Fig. 2b). Some male asilids in the genera *Heteropogon* and *Cryptopogon* bear decorated front tarsi (Bromley 1933; Wilcox & Martin 1936). Curiously, only American species of the latter genus, and not those from Europe, have tarsal elaborations (Hull 1962). In addition to waving their ornaments, robber fly males

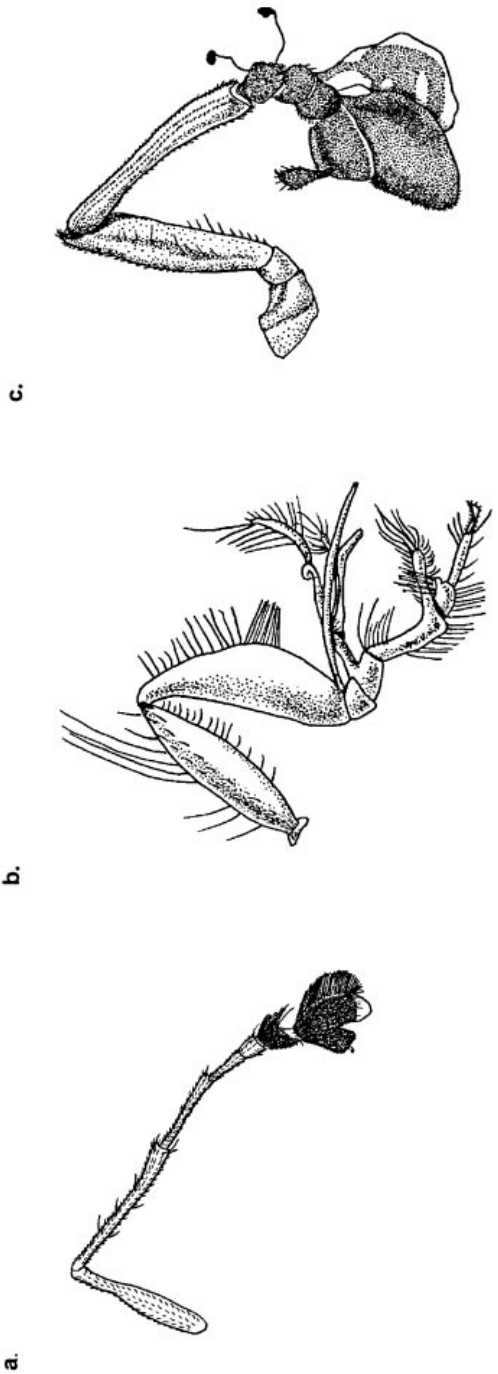

Fig. 2. Ornaments on the legs of flies:
a) The front legs of the dolichopodid *Dolichopus pulchrimanus* bear a dark plume of setae and what appears to be a reflector.
b) The front legs of the paleoarctic dolichopodid *Campsicnemus magius* are contorted into one of the more elaborate male ornaments to be found in the Diptera.
c) The hind legs of *Calotarsa insignis*, a platypezid from North America, are drooped below swarming males in flight. They have reflective patches and glitter in the sunlight.

may stroke the female's head and thorax. It is not uncommon for male syrphids to have dilated front legs, spotted with clumps of setae (e.g., Verrall 1901). This tendency achieves the fantastic in the complex decorations of the west African species *Tityusia regulas* Hull (Hull 1937). The fore tibia are "enormously thickened, grooved, twisted and distorted" with an "extremely long, extremely matted" dark pile of fringe. The fore tarsi are "extravagantly flattened . . . the lateral edges of the second, third and fourth segments prolonged into narrow, down curving lobes." Among acalypterates, the yellow front legs of the tephritid *Ectopomyia baculigera* bear a large down-pointing projection on the femur, while the front basitarsis of the male *Euphranta maculifemur* is broadened and concave (Hardy 1973).

B. Midlegs

A mosquito, *Sabethes cyaneus* (F.), bears elongated, iridescent blue and gold scales that transform the midlegs into "paddles" (Hancock et al. 1990; smaller setae occur on the other legs as well; *S. tarspus* Dyar & Knab and some other congeners also bears leg paddles; Fig. 3; smaller setal expansions occur on the legs of certain *Wyeomyia* spp.). Males fly toward resting females with their ornate legs held perpendicular to their bodies. After landing on twigs, they suspend themselves by their forelegs, then swing and wave their paddles. Undulating waving motions persist after the initial coupling, until the genitalia are fully clasped. "Waggling," during which the midlegs rise and fall, continues throughout the copulation (see Eberhard 1994 for a discussion of courtship during mating). Remarkable middle tarsi occur in males of the empidid *Rhamphomyia scaurissima* Wheeler (Wheeler 1896). The first joint consists of a globular base beset with prominent hairs and a scale-like appendage, the second is large and symmetrical and has a club-shaped extension clothed in a pencil of long hairs, and the third is enormously enlarged into a boat-shaped structure. A few tephritids of the genus *Ceratitis* have either mid and/or hindlegs expanded and feathered along the margins (Silvestri 1914). Male dolichopodids sometimes employ ornate midtarsi in courtship displays (e.g., Qvick 1984). Those of *Sympycnus cuprinus* are dilated and fringed with black bristles (Cole 1969; see also Harmston & Knowlton 1943). The midlegs of certain species of *Campsincnemus* are much more elaborate (e.g., Curran 1933; Harmston & Knowlton 1942). Robber flies of the genus *Cryptopogon* often bear tufts of black or silver hairs on the tarsi of both the front and middle legs (Wilcox & Martin 1936). In general, ornaments upon the midlegs of flies appear to be rare relative to forelegs (Wheeler 1896).

C. Hindlegs

Some of the most amazing ornaments in the Diptera adorn males of the platypezid genus *Calotarsa* (Fig. 2c). Three species are found in widely separated North American locations. Their enlarged hindlegs bear a variety of curious projections and glittering aluminum-colored flags (Kessel 1963). Snow (1884) noted how swarming males ". . . allow their hindfeet to hang heavily downward and look as if they were carrying some heavy burden." There is a degree of convergence between the design of the posterior tarsi in *Calotarsa* and the fore tarsi of the syrphid *T. regulus* (Hull 1937; see section on front legs), but the hover fly has a peculiarity upon its hind tarsi as well, "an enormous brush of dark, matted hair." Conspicuous hairs decorate the hind tarsi of certain asilids (Wilcox & Martin 1936). The entire hindleg of males in the genus *Lagodias* is fringed in long flattened setae (Hull 1962). Male anthomyids sometimes have patterned legs with elongated setae. The hind tibia of *Rhynchtrichops aculeipes*

Fig. 3. The middle leg of the male mosquito *Sabethes cyaneus* ends in an iridescent blue, purple and gold plume made up of flattened setae. These feather like objects are employed in the various displays that make up the only complex courtship described in the Culicidae.

Zett. has an odd projection that renders it reminiscent of a wishbone (Seguy 1923). Males of the dolichopodid genus *Scellus* are remarkable not only for their caudal ribbon-like projections (see below), but for the enlarged corkscrew-like spines and long hairs that project from the hindlegs (e.g., Greene 1924). If these are ornaments, and not a grooming apparatus for the abdominal projections (or something else), their being on the hindlegs is noteworthy. It is my impression that dolichopodid hindlegs bear fewer peculiar modifications than the midlegs, which in turn are less often ornamented than the front (e.g., Van Duzee & Curran 1934). Perhaps the presence of a caudal appendage creates a posterior focus of attention in females, into which the hindlegs can be profitably included. Female empidids of the genus *Rhamphomyia* have large scale-like setae on their legs. These are held away from the body while in flight and glitter in the light (Evans 1988).

D. Wings

Like the antennae, wings are commonly sexually dimorphic in size, although this is often because of adaptations to different flight requirements (e.g., Sivinski & Dodson 1992). Wings are sometimes dimorphically marked, or have sexually distinct venation (e.g., Alexander 1936; Kanmiya 1989), and serve important roles in courtships and aggressive interactions (e.g., Land 1993; Lunau 1992), but, for present purposes, these are not considered to be ornamented. Possible exceptions occur among the oddly shaped, rounded and patterned wings of certain female empidids who participate in sex-role reversed swarms (see Cumming 1994) and the combined peculiar wings and modified tarsi of the dolichopodid *Collinellula magistri* Aldrich (Aldrich 1932).

III. The Abdomen

A. Enlargement of the Abdomen

Females of the empidid *Rhamphomyia longicaudata* Loew inflate their abdomens with air until the pleural membranes are greatly stretched and collapse when punctured (Steyskal 1941; Newkirk 1970). Similarly, the membrane of the third abdominal segment in females of the New Zealand species *Hilara flavinceris* Miller forms an extensible bladder that stands out to the sides (Miller 1923). Cumming's (1994) examination of the extensive holdings of Empididae in the Canadian National Collection of Insects and Arachnids (Ottawa) revealed that 29% of the described species of *Rhamphymyia* and 26% of *Empis* (583 species total) had females with pinnate scales on the legs or abdomen and pleural sacs. Male abdomens may sometimes be modified as well; that of the swarming Ugandan stratiomyid *Platyna hastata* F. is expanded and flattened, and ". . . brilliantly reflects a white light. . . . The glistening appearance of the upper surface . . . is very striking" (Carpenter 1923). Unfortunately, no females were observed, or at the time had ever been collected, and a sexual dimorphism is only presumed.

B. Modified Glandular Projections

Females of the chironomid *Palpomyia brachalis* evert long glandular strings from their abdomens as they participate in sex-role reversed female swarms (Edwards 1920). These have been interpreted as pheromone organs, but their bright orange color contrasting with the black body suggests a visual role as well. Since similar tubes in other species of *Palpomyia* and the related genus *Bezia* are colorless, their great size may not be ornamental but a means of increasing surface area for pheromone dispersal.

C. Caudal Ribbons

Males of the dolichopodid genus *Scellus* have odd, twisted, ribbon-like structures projecting from the dorsum of the abdomen (Green 1924). Some are as long as the abdomen itself, fringed and tufted with hairs, or tipped with a spoon-like enlargement. Often white in color, with black bases and yellow ends, their function is mysterious. These strange appendages may have evolved solely for communication, or perhaps they are ornate elaborations of structures that serve an additional purpose (pheromone dispersion?). In addition to long, twisted, reddish or orange-yellow ribbons, male *S. virago* Aldrich have enlarged fore tibia furnished with a large blunt protuberance and tufts of curly hairs on the middle tibia. Despite these multiple male ornaments, the female appears to be more sexually aggressive (Doane 1907); ". . . she seemed suddenly to become very much excited, now squatting low, now rising high and waving the wings frantically. The cause of this extra excitement was a male fly. . . . He seemed to paying but little attention to her. . . . (After) facing each other, going through the curious performance. . . . The male then turned away and seemed about to leave, but the female quickly flew in front of him again and began her antics."

D. Modified setae

Males of the large ropalomerid *Scatophga gigantea* Aldrich have "very striking long, dense . . ." hair on their abdomens (Aldrich 1932). Tephritid fruit flies sometimes bear modified setae on the abdomen; e.g., males of *Trupanea brunnipennis* have a mass of strong yellowish bristles along the posterior margin of the 5th tergite (Hardy 1973). *Copiolepis quadrisquamosa* Enderlien is perhaps the most dramatically plumed tephritid (Enderlein 1920). It somewhat resembles the Birds of Paradise with which it shares habitats in New Britain and New Guinea.

E. Genitalia

It has been argued that the notorious complexity of some male insect genitalia, including those of certain Diptera, is in fact ornamentation, but ornamentation on a tactile level (Eberhard 1985). Giant male genital regions in dolichopodids are employed in courtships prior to physical contact. A number of species carry enlarged terminalia (hypopygium) slung under the abdomen. In *Dolichopus omnivagus* this is raised and lowered during the male's courtship advance (Steyskal 1938). I observed a more dramatic effort by an unidentified male on the upper surface of a leaf. It raised itself up on its long legs, beat its wings and then lowered the hypopygium until it hung perpendicular to the body. At this point the genitalia began to slowly twirl. As in some other structures discussed previously, it is not clear whether the terminal segments are enlarged to send a message or if the great size serves a mechanical function and is secondarily used in courtships.

WHAT DO ORNAMENTS "MEAN"?

A. Size and Aggression in Horn-eyed, Stalk-eyed and Antlered Flies

The evolution of horn-eyes, stalk-eyes and antlers illustrates how organs of communication and manipulation might arise through aggression among members of the same sex. McAlpine (1979) offers a diabolical hypothesis of how a blunt instrument (the head) could evolve through deceit into a sophisticated piece of propaganda. Male flies often fight head to head. The broad head and abundant cheek bristles of the Aus-

tralian platystomadid *Pogonortalis doclea* (Walker) are used in such combats (McAlpine 1975). The enlarged and hairy surface area better applies force and prevents slippage. Bristles may even become interlocked to grip an opponent, a technique that may have been further perfected by the clusiid *Clusoides gladiator* McAlpine, whose males' facial vibrissae are spiraled (McAlpine 1976), perhaps to twist into those of a rival's. These elaborations serve as practical weapons, but are they organs of communication; i.e., are they ornaments? Perhaps not, but proceed one step further. Suppose, as is often the case, a smaller fly retreats from a confrontation after determining that his opponent is too large to successfully engage. If the size of the rival is assessed by the breadth of his head, as gauged by the degree of overlap between the two sets of eyes, then males can appear large and conquer psychologically by simply widening the head. As deceitfully widened heads become common, even further exaggeration is required to sustain a bluff and the resulting "arms race" pulls eyes farther and farther out until they are held at the ends of extraordinary stalks, each of which may be longer than the body (e.g., an 8 mm long male of an undescribed diopsid from Borneo supported eyestalks with a combined span of 20 mm; Burkhardt et al. 1994).

In the end though, there are practical conclusions to arms races. Accumulating expenses and increasing vulnerability may dictate the final state of an ornament. Perhaps truly extraordinary ornaments, such as stalked-eyes in certain *Achias* spp. (McAlpine 1994), are cases where selection has exploited every opportunity and no further mechanical demands can be made on the overall "fly design." Wilkinson & Dodson (1996) found the relationship between antler size and body size within *Phytalmia* spp. reached a plateau. At this point signals are no longer deceptive, they are genuine burdens that reflect the qualities of their bearers. Wilkinson & Dodson (1996) suggest that since there is a strong positive allometric correlation between body size and projections from the head, "(*ornament*) size is an honest indicator of overall size, which itself is a predictor of fighting success . . . (*ornament*) size could be used by males to assess an opponents fighting ability, thereby avoiding unnecessary contests." One might ask why body size should be advertised by an ornament that does not increase in size at the same rate as the actual body; i.e., why do larger males have proportionately longer projections? Positive allometry might allow more accurate judgements of size; i.e., since a small increase in body size results in a larger and more obvious increase in the ornament, "the projection span scale will be finer than the body length scale." Allometry might also suggest that the cost of stretching the head, in terms of energy and maintenance, does not increase at the same rate as that of enlarging legs and guts and the other sophisticated and enervated body parts that make up "size." If so, larger flies might spend a similar proportion of their resources to advertise their bulk as smaller individuals but obtain a relatively greater return on their advertising budget. Still another hypothesis for the existence of allometry is that larger individuals may be more likely to use force in their interactions with other males. As a consequence they might invest more in weapons and propaganda (see Green 1992).

Females in some diopsid species are found in groups associated with individual males. However, these harems in *Cyrtodiopsis whitei* are not the result of males excluding rivals, but of a *female preference* for males with long stalks (Burkhardt & de la Motte 1988). Allozyme markers have revealed that males with longer stalks sire relatively more offspring (Burkhardt et al. 1994). In *C. dalmanni,* females likewise prefer longer stalked males (Wilkinson & Reillo 1994). What may have originally been propaganda to intimidate rival males has come under scrutiny from females and is now used as a factor in mate choice.

Like eye-stalks, antlers are both weapons and symbols of prowess. Males of *Phytalmia mouldsi* clash by rising up on their legs and pushing hard against each other's remarkable heads, although the antlers themselves do not play a major role in

the battle (Moulds 1978). However, those whose horns are experimentally lengthened or shortened are respectively more and less likely to win fights (Dodson 1989). In addition, males with their horns removed are treated by their rivals like females (Wilkinson & Dodson 1996). Hence antlers serve, at least in part, as signaling organs. The massive antlers of *P. alicornis* are more involved with actual pushing.

B. Material Resources and Deception in the Empididae

Horns and stalks have been depicted as evolving through interactions among males (intrasexual selection), although females might come to prefer a particular state of ornamentation and influence its form. The ornaments considered from this point forward are presumed to have originated in a different context, that of interactions between the sexes, i.e., intersexual selection. They are employed, or are believed to be employed, in courtships or in attracting the opposite sex.

A number of male empidids present mates with insects they have killed or stolen from spider webs (e.g., Chvala 1976). Often these are the only animal meals females will have as adults. Female mate choice is sometimes based on this nuptial gift and in certain cases the importance of the gift is so great that a sex-role reversal takes place. Females swarm and choosey males examine a series of potential mates before feeding and inseminating a particular individual (Svensson et al. 1989). The addition of a resource to courtship has consequences for ornamentation. Both sexes have "goods," the nuptial gift of the male and the eggs of the female, that can be advertised to a potential "customer."

Male *Rhamphomyia scaurissima* have peculiar growths protruding from the midlegs (Fig. 4a). I have found no behavioral records for *R. scaurissima*, but other species in the genus form swarms. Congeners provide females with a nuptial gift of a small dead insect which they hold in their legs (Downes 1970; Fig. 4b). Only males with a gift succeed in mating. Could this mass of swellings and projections deceitfully suggest a resource the insect doesn't have or exaggerate the size of one that it does?

On the other side of sexual bartering are females whose apparent fecundity might influence whether or not they obtain a valuable meal. Females of many *Rhamphomyia*, *Empis* and *Hilaria* species inflate their abdomens while participating in sex-role reversed swarms (Cumming 1994). It is tempting to think that such swellings may be exaggerated promises of fecundity directed toward males who provide a nuptial gift. Larger females are preferred by resource-providing males in other empidids (e.g., Svensson et al. 1989). Like stalk-eyes, abdominal enlargements may evolve into "honest advertisements" if only the largest females can fly with the most swollen abdomens. In *Rhamphomyia* species females bear glittering setae on their legs. When extended in flight these ornaments may call attention to the females' abdomens, as might the coloration of another empidid, an unidentified Alaskan species "garishly marked with an extensive silvery abdominal 'saddle' which flashes conspicuously as she crosses beams of sunlight."(Frohne 1959).

C. Good Genes, Manipulation and Runaway Selection

Some ornaments suggest original functions; the air-filled abdomens of female empidids may have been false advertisements of fecundity, just as stalk eyes exaggerated size and dangles from midlegs gave the impression that a male empidid has a nuptial gift. But putting these instances with perhaps more obvious histories aside, a number of very puzzling objects remain. Just why does stroking a female's head with tarsal plumes improve the reproductive success of a male robber fly? If simple species isola-

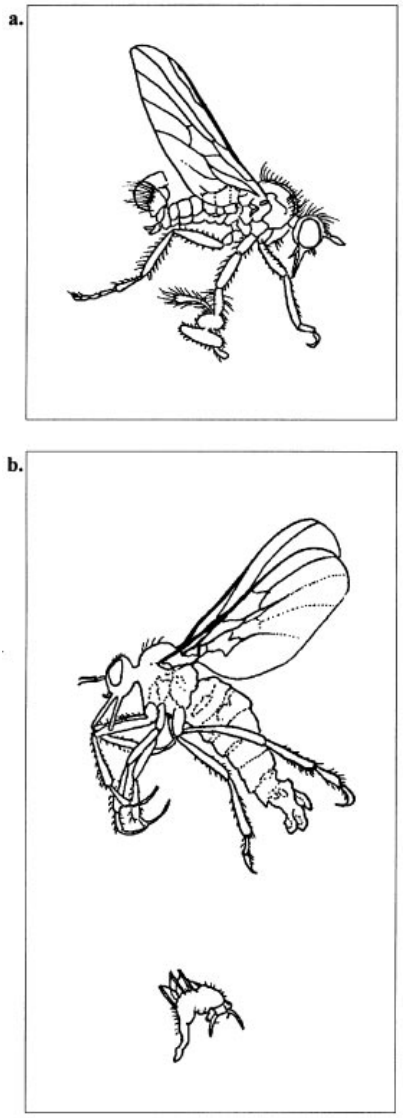

Fig. 4. A comparison of the appearance of two species of *Rhamphomyia*:

a) The middle legs of males of the empidid *R. scaurissima* end in a remarkable complex of swellings and projections (from Wheeler 1896).

b) These peculiarities are absent from the legs of *R. ursinella*. However, the ornaments of *R. scaurissima* might bear a resemblance to the more mundane species carrying a nuptial gift, such as the chironomid *Smittia* sp. (smaller insect figured below; from Downes 1970). Perhaps originally, ornamented males appeared to be holding a gift and so were allowed to copulate with females who would otherwise have mated only when provided with a prey item.

tion is involved in ornamentation, why are such decorations relatively uncommon? Are ornamented species in some particular danger of engaging in unprofitable hybridizations? The opposite is often the case (e.g., West-Eberhard 1984). The spectacular genus *Calotarsa*, for example, consists of three widely separated North American species, one so rare it appears to have never been recollected.

There are a number of other paths that might lead to ornamentation, any one of which could result in a world with only a single species being inhabited by ornamented animals.

1) The production and use of expensive and unwieldy growths may provide a potential mate (or sexual rival) with an estimate of genetic (or phenotypic) quality; i.e., the displayer has foraged well enough or avoided debilitating infections long enough or is big enough to put on his show (e.g., Sivinski 1988b). Body symmetry is a correlate of genetic quality and a trait preferred by choosing females in some animals (Moller 1992; Thornhill 1992; Watson & Thornhill 1994). The flags and feathers of some displays could test the genome's ability to produce symmetry.

2) The receiver may be manipulated by an ornament. Nervous systems are imperfect. A flaw in perception or information processing can be exploited by the behavior of others (cf. Dawkins 1982). For instance, a resting dragonfly can be "hypnotized" by tracing a narrowing spiral in the air. Such an event is presumably so rare that selection has not favored a brain resistant to the influence of a moving finger. Perhaps flaws in female nervous systems allow them to be approached and handled by rhythmically waving, plumed, or otherwise ornamented, males.

3) A female preference for extreme examples of a certain characteristic in a mate begins an episode of "runaway sexual selection." That is, when females prefer the most ornate male available, genes for both choosing the very elaborate (expressed in daughters, but present in both daughter and sons) and being very elaborate (expressed in sons, but present in both daughters and sons) can generate a sort of "chain reaction" self selection for the increasingly extreme. A lucid explanation of this complex procedure can be found in Dawkins (1986). This form of selection requires that females sample the range of male decoration and mate with the most ornate. It has been suggested that such mate comparisons are not typical of insects, who are presumed to have a limited time to acquire courtship experiences and little capacity to remember those that they had (Alexander et al. 1997). If so, perhaps only rare circumstances, where potential mates are compared simultaneously or where females have unusually good memories, give rise to the occasional "runaway monstrosity" (Sivinski & Petersson 1997).

Could these various kinds of "messages" be recognized by the nature of the ornament that carries them? This categorization may prove to be difficult. I can imagine many ornaments of the "puzzling" variety (those not originally exaggerating size or a resource) resulting from any of the above. The male robberfly rhythmically stroking the female's head with leg plumes could be displaying his coordination, seducing her "hypnotically," or satisfying her taste for an extreme in courtship.

Though similar *types of ornaments* could be derived from different types of selection, might the different types of selection generate different *degrees of ornamentation*? To the entomologist's eye not all ornaments are equally elaborate. Some dolichopodid legs seem to be practical semaphores, others appear contorted and absurd (Fig. 2a &b). Would advertisers of genetic quality tend to invest as much in their displays as participants in a "runaway" situation, or vice versa? Unfortunately, this to might be a difficult approach to finding meaning. Each type of selection could direct varying amounts of resources to ornaments, so that complexity and simplicity may not be indicative of particular sets of selection pressures. For example:

1) There are several explanations for variance in ornaments evolved to advertize "genetic quality." A simple ornament may sometimes be sufficient; i.e., there might be

types of messages that are just not improved by increased broadcasting. Genetic identity (species identification or lineage identification) is one possibility. Under some circumstances, mate choice based on symmetry might select for simplicity. If complexity can overwhelm perception and hide asymmetry, females may come to prefer simpler ornaments, clearly displayed.

However, there may be few such inherent limitations on how elaborate ornaments that reflect genetic quality can become. If an ornament is "improved" from the signaler's perspective by exaggeration, then potential mates or sexual rivals with new and higher criteria for what they find attractive or intimidating will be better adapted than "gullible" individuals with out-of-date tastes, and so on and so on (see discussion of stalk-eyes). An alternative to linked escalation of ornamentation and discrimination is selection for a new ornament that will, at least temporarily, be a more honest indicator of genetic quality (see also Iwasa & Pomiankowski 1994). Multiple male ornaments are commonly found in the Dolichopodidae (e.g., the genus *Scellus;* see above).

It is unlikely that all ornaments are equally burdensome or that all bearers of ornaments would have similar resources to spend on advertisement. Different limits would lead to variety in ornamentation. On the other hand, some signal systems may be relatively simple because they have not been in existence long enough for arms races to bring them to the brink of being maladaptive handicaps to their carriers.

2) Males may exploit weaknesses in female nervous systems, but females might evolve "immunity", and this could ultimately lead to interspecific differences in the elaborateness of male ornaments. If the subversion of females' ability to choose a mate has a sufficiently negative effect on their reproductive success, then flaws in their brains might be eventually corrected and the degeneration of their sexual control stopped. Males might then respond with more potent stimuli, escalating yet another arms race. Assuming different female susceptibilities and different costs to being manipulated, a range of ornamentation could develop in various males.

3) Where runaway sexual selection occurs (if it occurs) the ability of the receiver to discriminate differences in signals would influence the capacity to choose among mates, and eventually how far "taste" can dictate male ornamentation. The abilities of different males to bear the burdens of their "beauty" could also determine how elaborate any particular display may become. What is extreme in an aerial predator might appear simple in a fruit fly. Parenthetically, the male empidids who carry objects as diverse as flower petals (Hamm 1913) and silk balloons, (Kessel 1955; which sometimes, but not always, contain a prey item), into mating swarms may be using a disposable "ornament" that would not interfere with the other parts of their lives.

Another characteristic of an ornament that might help translate its meaning is the *variance* in the display among the individuals of a population. It has been suggested that when females choose a male trait in lekking species, "modifier genes" to generate variance in that trait might be selected as well (Pomiankowski & Moller 1995). The explanation is that the combination of the highest mean value of a character along with its greatest variance will produce the most extreme manifestations of that trait in the next generation. In both "runaway selections" and "arms races" extreme individuals can be the most successful (up to a point), perhaps enough so to make up for extremely unattractive sons that a large variance also produces. But again, an unusual degree of variance in an ornament could be due to either runaways and many of the hypothetical arms race causes we have considered. This unenlightening conclusion suggests that perhaps the best strategy is to consider the function of each ornament individually and not expect that the form of an ornament will immediately reveal its significance.

Ornamentation and Mating Systems

Let us assume that ornate signals are advertisements of male (or less frequently, female) qualities directed to potential mates and / or sexual rivals. Do these organs of propaganda occur in any sort of pattern? Are they associated with certain behaviors and are these behaviors typical of particular mating systems?

There are circumstances where an individual can profitably advertise and situations where it cannot (Burk 1981; Prokopy 1980). One place where there is little profit in investing in an ornament is where females are predictably located at resources, (e.g., oviposition sites), and these resources are discrete, scattered and rare. Males can then wait by the resource and attempt to copulate with an arriving female. Under these conditions it might be more beneficial for her to immediately mate rather than spending time and energy choosing a particular male, all the while being distracted from exploiting the resource. Where there is little opportunity for females to choose, there is no reason for males to advertise (e.g., Sivinski 1984). If the resource is small enough for a male to exclude its rivals, then signals directed to competitors can evolve. Where males cannot predictably locate females by waiting by a resource (e.g., the resource is common relative to females), then the costs of mate choice are lower, females may be able to afford to discriminate among males, and males may compete for attention by producing signals.

Can this scheme explain the occurrence of ornaments in flies? Some instances seem to be textbook examples of the "resource distribution model of sexual selection". For example, antlered males of *Phytalmia* spp guard rare, scattered oviposition sites, "pin holes" in the freshly fallen trunks of particular trees. They dispute with rivals for control of the resource, through displays of their horns and combat, and females that attempt to use it must mate with the resident male (Dodson 1987, 1989). The elaborate leg decorations of *Calotarsa* and the facial setae of *Ceratitis*, which are presumably used to communicate with females, adorn males that participate in swarms and leks, respectively. These male aggregations are formed solely for the purpose of mating and in the absence of any of the resources females require (e.g., Sivinski & Petersson 1996). The sex life of many ornamented flies is unknown, and how well resource distribution explains ornamentation in general remains to be seen.

The Phyletic Distribution of Ornaments

While resource distribution seems to be successful in explaining why ornaments have evolved in certain instances, there are puzzling phyletic patterns (Table 1). Eyestalks and antlers are concentrated among the acalypterate families. Resource guarding is commonly described in acalypterates, but is also found in a number of other Diptera, including the calypterates which are conspicuous by the scarcity of their ornaments. Also puzzling is the apparent scarcity of elaborate ornaments displayed in acalypterate courtships (outside of the Tephritidae and related families). Mating behaviors are often complex and include movements of head and legs, organs ornamented in other taxa (e.g., section "Conclusion: the locations of ornaments"). Rather there seems to be a concentration of intersexually selected ornaments in the more primitive Brachycera.

There is considerable variance in the range of ornamentation within a family. Why are the Dolichopodidae so rich in decorations? Or perhaps even more curious, why does ornamentation sporadically evolve in otherwise ordinary appearing taxa? The complicated waving of huge blue leg paddles in *Sabethes* spp. make up the *only* courtships described in the Culicidae! Can resource distributions alone account for either

the commonness or the rarity of ornaments within various taxa? Are there other factors involved?

Why do dolichopodids seem to bear so many and such various ornaments, on antennae, faces, mouthparts, legs and abdomens? As predators, females may not be concentrated onto a small resource that males can control and this might encourage male advertisement. But other orthorrhaphous Brachycera, such as the similarly predaceous asilids and the closely related empidids, are only occasionally ornamented. One possible explanation is that dolichopodids, unlike many asilids and empidids, generally feed on small prey that they glean from a surface; i.e., they spend a good deal of time standing and walking (e.g., Chvala 1976). It may be easier to present a complicated display involving the movement of patterned body parts while both parties have their feet upon the "ground" (or the water's surface in the case of some *Campsicnemus*). At least some of the ornamented robber flies both forage for food and display to mates on substrates, e.g., tree trunks (Wilcox & Martin 1936). Those insects that reveal their ornaments in flight (e.g., *Calotarsa*), fly in a slow dignified manner that allows their decorations to be seen (Sivinski & Petersson 1996).

Why *Sabethes* should differ so much from other mosquitoes is a mystery, although there are two factors that might contribute to their unique ornamentation. First, the tribe Sabethini is diurnal. Shannon (1931) in Brazil and Haddow & Corbet (1961) in Africa noted that diurnal mosquitoes were more brightly colored than the drab species active at twilight or during the night. They presumed that coloration was useless in the dark. Second, the mating system of *Sabathes* does not include male swarms or males waiting by emergence sites, both common behaviors in the Culicidae (see Hancock et al. 1990). Rather, males patrol areas searching for resting females on twigs, or occasionally pursue flying females until they land. As in the dolichopodids, there is more of a stage available for their showmanship than is typical for a mosquito.

Conclusion: The Locations of Ornaments

Wonders occur everywhere along the bodies of flies. Ornaments that appear to be used in aggressive interactions with members of the same sex seem to be concentrated on the head. Since the head is often used in the pushing style of confrontation and combat typical of Diptera, such elaborations are probably embellishments of weapons or advertisements of size and the ability to use weapons. They may then take on a presumably secondary function by advertising sexual competitiveness to potential mates (e.g., stalk-eyes). The rare instances of female ornamentation, swellings and glandular (?) projections are concentrated on the abdomen. The reproductive organs are likely to be a focus of male interest and where females would center their propaganda. Male ornaments that appear to be solely directed to females are more widespread, but still are concentrated in the anterior regions of the body, the head, and fore and mid legs.

The prominence of legs as platforms for signals may be because of their mobility. Movement might enhance perception of the ornament because objects in motion are more apparent to insect compound eyes. Alternatively, it could be the movement itself that is embellished by the ornament; i.e., displays of coordination, timing and flexibility made more impressive by the equivalent of a cheerleader's pom poms (or as W. B. Yeats might say . . . "how can we tell the dancer from the dance").

Evidence for it being the motions that are enhanced by the ornaments comes from the common employment of unornamented legs in communications between flies. Male forelegs, without decoration, are often used by flies to brush the female's face and eyes during courtship and copulation. For example, when mating, male *Platystoma*

TABLE 1. THE PHYLETIC DISTRIBUTION OF VARIOUS FORMS OF ORNAMENTS IN THE DIPTERA. THE TOP TO BOTTOM AXIS OF THE TABLE IS DIVIDED INTO SECTIONS REPRESENTING THE NEMATOCERA, THE ORTHORRHAPHOUS BRACHYCERA AND THE MUSCAMORPH BRACHYCERA. THE HORIZONTAL AXIS IS DIVIDED INTO SECTIONS REPRESENTING BODY LOCATIONS, THE HEAD, THORAX AND ABDOMEN. DATA ARE TAKEN FROM THE LITERATURE (SEE TEXT). WHILE THE LITERATURE REVIEWED WAS EXTENSIVE THERE IS NO ASSUMPTION THAT THE REPORTS INCLUDED IN THE TABLE CONSTITUTE A RANDOM SAMPLING OF THE FLIES.

	eyes-stalks and antlers	antennae	labial palps	facial modification	plumose setae	foreleg	midleg	hindleg	expanded abdomen	abdominal projections	enlarged genetalia
Culicidae						♂	♂	♂			
Chironomidae										/	
Stratiomyidae									?		
Asilidae						♂	♂	♂			
Acroceridae		♂									
Empididae						♀	♂♀	♀	♀		
Dolichopodidae		?	?	?		?	?	?		?	?
Platypezidae								?			
Syrphidae						♂					
Micropezidae	♂										
Diopsidae	♂♀										
Richardiidae	♂										
Otitidae	♂										
Platystomatidae	♂										
Tephritidae	♂	♂			♂		♂	♂		♂	
Periscelididae	♂										
Clussidae	?										

TABLE 1. (CONTINUED) THE PHYLETIC DISTRIBUTION OF VARIOUS FORMS OF ORNAMENTS IN THE DIPTERA. THE TOP TO BOTTOM AXIS OF THE TABLE IS DIVIDED INTO SECTIONS REPRESENTING THE NEMATOCERA, THE ORTHORRHAPHOUS BRACHYCERA AND THE MUSCAMORPH BRACHYCERA. THE HORIZONTAL AXIS IS DIVIDED INTO SECTIONS REPRESENTING BODY LOCATIONS, THE HEAD, THORAX AND ABDOMEN. DATA ARE TAKEN FROM THE LITERATURE (SEE TEXT). WHILE THE LITERATURE REVIEWED WAS EXTENSIVE THERE IS NO ASSUMPTION THAT THE REPORTS INCLUDED IN THE TABLE CONSTITUTE A RANDOM SAMPLING OF THE FLIES.

	eyes-stalks and antlers	antennae	labial palps	facial modification	plumose setae	foreleg	midleg	hindleg	expanded abdomen	abdominal projections	enlarged genetalia
Drosophilidae	♂										
Chloropidae		♂									
Anthomyidae								♂			
Tachinidae		♂?									

seminaionis F. signal the start of a bout of nuptial feeding with a regurgitant by moving their front legs from the base of the female's wings to the inner margins of her eye (Michelmore 1928). In a similar vein, copulating males of the micropezid *Cardiacephala myrmex* alternatively scratch and regurgitate onto their mate's eyes (Wheeler 1924). In Mexico, mounted males of the asilid *Efferia cressoni* (Hine) rest their foretarsi on the females eyes (Dennis et al. 1986). However, in Wyoming they do not. Perhaps the mechanics of copulation remain the same, while selection on signaling does not. In addition to the actual placing of tarsi on the females' eyes, male flies may wave relatively unmodified front legs from a distance (e.g., Alcock & Pyle 1979; Spieth 1982). Both forms of signaling, the placing of the foretarsi on (or very near) the female eye and motions from a distance, might provide more information (or misinformation) when a more conspicuous front leg is employed. Plain midlegs are also sometimes used to signal. For example, the particularly complex courtship of the ottiid *Physiphora demandata* (F.) includes sessions where the male raises the middle leg with its light colored tarsi on the side away from the female (Alcock & Pyle 1979). Mounted males of the dolichopodid *Scapius platypterus* rest their front legs over the female's head while the midlegs are held to the side near her eyes and waved back and forth (Grootaert & Mueffels 1988). The unornamented mosquito, *Sabethes chloropterus* (Humboldt), quivers its plain midtarsi against its mate's antennae during copulation (Hancock et al. 1990). Its relative, *S. cyaneus*, has apparently escalated the display by using spectacularly plumed midlegs in a complex visual and tactile sexual performance.

Though wings are mobile, ornamented examples are rare in true flies. Perhaps the single pair is too critical to survival to bear the additional costs of carrying elaborate signals. The same combination of mobility and relative expendability characteristic of fly legs may have concentrated many of the more spectacular displays of birds' onto their tails.

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MYRMECOMORPHY AND MYRMECOPHILY IN SPIDERS: A REVIEW

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ABSTRACT

Myrmecomorphs are arthropods that have evolved a morphological resemblance to ants. Myrmecophiles are arthropods that live in or near ant nests and are considered true symbionts. The literature and natural history information about spider myrmecomorphs and myrmecophiles are reviewed. Myrmecomorphy in spiders is generally considered a type of Batesian mimicry in which spiders are gaining protection from predators through their resemblance to aggressive or unpalatable ants. Selection pressure from spider predators and eggsac parasites may trigger greater integration into ant colonies among myrmecophilic spiders.

Key Words: Araneae, symbiont, ant-mimicry, ant-associates

RESUMEN

Los mirmecomorfos son artrópodos que han evolucionado desarrollando una semejanza morfológica a las hormigas. Los Myrmecófilos son artrópodos que viven dentro o cerca de nidos de hormigas y se consideran verdaderos simbiontes. Ha sido evaluado la literatura e información de historia natural acerca de las arañas mirmecomorfas y mirmecófilas . El myrmecomorfismo en las arañas es generalmente considerado un tipo de mimetismo Batesiano en el cual las arañas están protegiéndose de sus depredadores a través de su semejanza con hormigas agresivas o no apetecibles. La presión de selección de los depredadores de arañas y de parásitos de su saco ovopositor pueden inducir una mayor integración de las arañas mirmecófílas hacia las colonias de hormigas.

Myrmecomorphs and myrmecophiles are arthropods that have evolved some level of association with ants. Myrmecomorphs were originally referred to as myrmecoids by Donisthorpe (1927) and are defined as arthropods that mimic ants morphologically and/or behaviorally. The literature on myrmecomorphs is enormous and has recently been reviewed by McIver & Stonedahl (1993).

Myrmecophiles were defined by Donisthorpe (1927) as arthropods that live in or near ant nests. Wasmann (1894) developed a classification system for myrmecophiles consisting of distinct categories, each suggesting increasing specialization and integration into the host colony. However, as pointed out by Hölldobler & Wilson (1990), such categorization of myrmecophiles can be misleading as some guests take on multiple roles within a colony.

McIver & Stonedahl (1993) stated that myrmecomorphy and myrmecophily both fall under the general category of ant mimicry, since even myrmecophiles which lack morphological resemblance to ants may mimic chemical or textural characters of their hosts. However, myrmecophiles may not mimic their hosts in any way and may simply be tol-

erated by their otherwise aggressive hosts because they are either neutral in odor or are below some critical size to be recognized by the hosts as intruders (Cushing 1995a). Because of this and because the selective pressures involved in the evolution of myrmecomorphy and myrmecophily are quite different (discussed below), it is more useful to view these as separate phenomena and not as subcategories under ant mimicry.

The literature on myrmecomorphs and myrmecophiles in general has been summarized by McIver & Stonedahl (1993) and by Hölldobler & Wilson (1990). The purpose of the present paper is to expand coverage of myrmecomorphs and myrmecophiles in the Order Araneae.

Myrmecomorphy in Spiders

Table 1 presents information about known spider myrmecomorphs. The putative ant models are those to which the mimics bear a generic or specific resemblance and which are sympatric with the mimics. In fact, the majority of the models presented are found in the same microhabitat as the mimics and are often collected with them. Details about the natural history of the mimics or about the form of their mimicry are also presented. As far as possible, the taxonomy of the spider myrmecomorphs follows that presented by Brignoli (1983) or Platnick (1993). The taxonomy of the models follows that presented by Bolton (1995).

Morphological and Behavioral Adaptations

The morphological adaptations involved in achieving a resemblance to ants among spider myrmecomorphs were first discussed by Banks (1892). Reiskind (1972, 1977) lists and illustrates these morphological adaptations and they are described in McIver & Stonedahl (1993). They include a variety of color and body-form modifications that give the spider the appearance of having three body segments instead of two and of having long, narrow legs instead of shorter, more robust legs. Mandibles, compound eyes and even stings are sometimes mimicked by the spiders through modifications in the chelicerae, pigmentation in the cuticle, or special positioning of the spinnerets. In many cases, the extent to which the mimics resemble a particular model is extraordinary (see Fig. 1). Reiskind (1977) compares specific features of the mimic with similar features in the model which enhance the many cases of species-specific mimicry found among spider myrmecomorphs.

The overall body of spider myrmecomorphs is much narrower than non-mimics, and this appears to reduce their fecundity. Female myrmecomorphs lay fewer eggs per eggsac than non-mimetic spiders of similar size (Bristowe 1939, 1941, Collart 1941, Edmunds 1978, Wanless 1978, Bradoo 1980, Boevé 1992). However, myrmecomorphs may compensate for this limitation by laying more eggsacs so that their life-time fecundity may be about equal to that of non-mimetic spiders.

McIver & Stonedahl (1993) list myrmecomorphs which show morphological, behavioral, or pattern mimicry. All spider myrmecomorphs are morphological mimics, and the majority are also behavioral mimics. Spider myrmecomorphs move in a much more erratic, more ant-like fashion than non-mimics. This behavior is described throughout the literature for most of the species of myrmecomorphs (Pocock 1908, Donisthorpe 1927, Bristowe 1941, Marson 1946, 1947, Reiskind 1972, 1977, Wanless 1978, Wing 1983, Brignoli 1984, Fowler 1984, Oliveira 1988, Lighton & Gillespie 1989, Boevé 1992). Behavioral mimicry also involves raising either the first or second pair of legs and using them to mimic the movements of antennae (Reiskind 1977, Jackson 1986). This functionally reduces the number of legs in the mimic from four

Fig. 1 (drawn from photographs in Reiskind 1977). a) A female *Zuniga magna* Peckham (Salticidae). Note how the front pair of legs is used as pseudo-antennae and how the abdominal constriction mimics the third body segment of the model. b) A female *Mymarachne parallela* (Fabricius) (Salticidae). Note the constriction of the cephalothorax and the lighter band of setae around the mid-section of the abdomen—both of which add to the illusion of additional body segments. The legs of this mimic have been effectively "shortened" through the lighter pigmentation of the terminal segments. The darkening of the metatarsal segments of the first pair of legs adds to the antennal mimicry as it gives the illusion that the pseudo-antennae are being held off the ground when, in fact, the legs are in contact with the substrate. c) A male *Synemosyna americana* (Peckham) (Salticidae). Note the constrictions of the cephalothorax and the abdomen. The color pattern of the spider also closely mimics the coloration of the model.

pairs to three. Sometimes the terminal segments of these mimetic antennae are darker giving the impression that the mimic has clubbed antennae (Reiskind 1977). Pocock (1908) suggests that behavioral mimicry may have evolved before morphological mimicry among spider myrmecomorphs. Bristowe (1941) agrees with this view.

Transformational and Polymorphic Mimicry

Spiders undergo gradual metamorphosis. During the earlier developmental stages (instars) only smaller ant species found in the vicinity would serve as appropriate potential models for young myrmecomorphic spiders. Because of this, it might be predicted that the suite of models would change as the spiders passed through each successive instar. A mimetic complex in which the identity of the model species changes as the mimic develops is called transformational mimicry (Mathew 1935) and has been documented for several species of myrmecomorphic spiders (see Table 1). In fact, McIver (1989) predicts that transformational mimicry "probably occurs in most systems where the ant-mimic develops through gradual metamorphosis." Wanless (1978) believes that transformational mimicry may occur in the majority of *Myrmarachne* myrmecomorphic species (Salticidae). In a study of transformational mimicry complexes among *Myrmarachne* spp., Edmunds (1978) demonstrated that the model species involved in each example of transformational mimicry were either positively associated with one another or tolerated each other's presence in the area. In other words, the set of models mimicked by each instar of the spider were always present in the same habitat.

In several species of myrmecomorphic spiders, the adults are polymorphic. It is thought that each morph mimics a different model. Such polymorphic mimicry appears to be fairly common among myrmecomorphic species (see Table 1). In some cases, there is sexual dimorphism among the adult spiders and the sexes each mimic a different model (Reiskind 1970, Cutler 1980, Wanless 1978, Oliveira 1988).

In all these cases of polymorphic mimicry each morph either corresponds to one model ant species that is also polymorphic or to two or more different model species. For example, light yellow or brown morphs of *Synemosyna aurantiaca* mimic *Pseudomyrmex flavidulus* (F. Smith) and *P. oculatus* (F. Smith) while black morphs mimic *P. gracilis* (Fabricius) and *P. sericeus* (Mayr) (Table 1 and Oliveira 1986). In these polymorphic mimicry systems, it is not known to what extent the different color forms of the mimic are sympatric nor to what extent the polymorphism is a result of differential predation. Predators could be eliminating the "wrong" color morph from an area where its model is absent creating an apparent geographic separation of the different morphs or the different color morphs could be genetically distinct.

Adaptive Significance of Myrmecomorphy

McIver & Stonedahl (1993) discuss the adaptive significance of myrmecomorphy in depth. Four different hypotheses have been proposed to explain myrmecomorphy: 1) Wasmannian mimicry, 2) Müllerian mimicry, 3) Aggressive, or Peckhammian mimicry, and 4) Batesian mimicry. In Müllerian mimicry, both the model and the mimic are unpalatable. As McIver and Stonedahl point out, the hypothesis that myrmecomorphs are Müllerian mimics is not well supported, especially for spider myrmecomorphs. Although the ant models may be unpalatable to most predators, there is no evidence that the spider mimics are unpalatable. Therefore, this hypothesis will not be discussed.

Wasmannian mimicry involves the evolution of resemblances between a model and its mimic that facilitates a mimic living with its host (Rettenmeyer 1970). Retten-

TABLE 1. MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
APHANTOCHILIDAE			
Aphantochilus sp.	*Cephalotes* sp.(probably *atratus* (L.))	preys on ants	Pocock 1908; Bristowe 1941
Aphantochilus rogersi O. Pickard-Cambridge	*Cephalotes atratus* (L.), *Zacryptocerus pusillus* (Klug)	preys on ants & carries dead ants (aggressive mimicry); polymorphic mimicry	Bristowe 1941; Oliveira & Sazima 1984; Oliveira 1986; Parker & Cloudsley-Thompson 1986
Bucranium sp.	*Cephalotes* sp. (probably *atratus* (L.))	preys on ants and carries dead ants (aggressive mimicry)	Bristowe 1941
Cryptoceroides cryptocerophagum Piza	*Zacryptocerus pusillus* (Klug)		Piza 1937; Reiskind 1972
ARANEIDAE			
Melyciopharis cynips Simon			Pocock 1908
Micrathena sp.		only males and juveniles resemble ants; may be mimosis rather than mimicry	Reiskind 1977; Levi 1986
CORINNIDAE			
Castianeira cingulata (Koch)			Reiskind 1969
Castianeira cubana (Banks)	*Camponotus planatus* Roger		Myers & Salt 1926; Reiskind 1969
Castianeira dentata Chickering			Reiskind 1977
Castianeira dubia (O. Pickard-Cambridge)			Reiskind 1969; Reiskind 1977

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Castianeira longipalpus (Hentz)	myrmicine or ponerine ant		Reiskind 1969
Castianeira memnonia (Koch)	*Pachycondyla obscuricornis* Emery		Reiskind 1977
Castianeira rica Reiskind	*Atta* sp., *Odontomachus* sp., etc.	transformational mimicry & polymorphic mimicry	Reiskind 1969, 1970
Castianeira trilineata (Banks)	*Camponotus castaneus* (Latreille)		Reiskind 1969
Castianeira tenuiformis Simon	*Pachycondyla obscuricornis* Emery		Pocock 1908
Castianeira sp. (undesc.)	*Camponotus parius* Emery	preys on ants	Hingston 1928
Castianeira sp.	*Camponotus* sp., etc. (may mimic several different kinds of ants)	some prey on ants	Hingston 1928; Reiskind 1977
Corinna vertebrata Mello-Leitão	*Acromyrmex fracticornis* (Forel), *Labidus praedator* (F. Smith)	behavioral and morphological mimic; preys on ants (aggressive mimicry)	Fowler 1981, 1984
Mazax pax Reiskind	*Ectatomma ruidum* Roger		Reiskind 1977
Mazax spinosa (Simon)			Reiskind 1977
Myrmecium bifasciatum (Taczanowski)	*Camponotus femoratus* (Fabricius), *Megalomyrmex modestus* Emery	polymorphic mimicry	Oliveira 1986
Myrmecium cf. *gounelley* Simon	*Camponotus femoratus* (Fabricius), *Crematogaster limata* F. Smith	transformational mimicry	Oliveira 1986
Myrmecium cf. *velutinum* Simon	*Ectatomma lugens* Emery		Oliveira 1986

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Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Myrmecium sp.	*Pachycondyla unidentata* Mayr		Oliveira 1986
Myrmecium spp.	*Anochetus* sp., *Atta* sp., *Dendromyrmex fabricii* (Roger) or *Megalomyrmex* sp.		Pocock 1908
Myrmecotypus cubanus Banks	*Camponotus planatus* Roger		Myers & Salt 1926
Myrmecotypus fuliginosus O. Pickard-Cambridge	*Camponotus planatus* Roger		Jackson & Drummond 1974
Myrmecotypus pilosus (O. Pickard-Cambridge)			Reiskind 1977
Myrmecotypus rettenmeyeri Unzicker	*Camponotus sericeiventris* (Guérin-Méneville)		Reiskind 1965,1969; Lighton & Gillespie 1989
Sphecotypus (=*Myrmecium*) *niger* (Perty)	*Pachycondyla villosa* (Fabricius)		Pocock 1908; Oliveira 1986
DYSDERIDAE			
Harpactea hombergi (Scopoli)	*Formica cunicularia* (=*fusca* var. *glebaria)* Latreille, *F. fusca* L., *F. sanguinea* Latreille, *Lasius brunneus* (Latreille), *L. fuliginosus* (Latreille)	preys on ants; behavioral, not morphological, mimic	Donisthorpe 1927
ERESIDAE			
Seothyra schreineri Purcell	*Camponotus fulvopilosus* (De Geer)	male spiders mimic smaller castes	Pocock 1908

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
GNAPHOSIDAE			
Callilepis nocturna (L.)	*Lasius niger* (L.)	preys on ants	Boevé 1992
Micaria alpina Koch			Donisthorpe 1927; Bristowe 1941
Micaria longipes Emerton		running near unident. models	Banks 1892
Micaria pulicaria (Sundevall)	*Formica* spp., *Lasius niger* (L.), *Lasius* spp., and *Tetramorium caespitum* (L.)	mimic found running with various models	Pocock 1908; Donisthorpe 1927; Bristowe 1941
Micaria romana Koch	*Formica fusca* L., *Formica rufibarbis* Fabricius		Pocock 1908; Donisthorpe 1927
Micaria scintillans O. Pickard-Cambridge	*Formica cunicularia* (=fusca var. glebaria), *F. rufibarbis* Fabricius	mimic running with model	Donisthorpe 1927; Bristowe 1941
Micaria sp.	*Aphenogaster beccarii* Emery		Hingston 1928
Micaria sp.	*Pheidole indica* Mayr	only mimics smaller caste	Hingston 1928
LINYPHIIDAE			
Linyphia furtiva O. Pickard-Cambridge	*Formica sanguinea* Latreille	also mimics larvae of Hemipteran, *Alydus calcaratus;* both found running w/ *F. sanguinea* workers	Donisthorpe 1927
Meioneta beata (=*Micryphantes beatus*) (O. Pickard-Cambridge)	*Tapinoma erraticum* (Latreille)		Donisthorpe 1927
LIOCRANIDAE			
Phrurolithus claripes (Dönitz and Strand)	*Lasius niger* (L.)	may prey on ants	Komatsu 1961

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Phrurolithus festivus (Koch)	*Formica fusca* L., *F. rufa* L., *F. sanguinea* Latreille, *Lasius flavus* (Fabricius), *L. fuliginosus* (Latreille), *L. niger* (L.).	running with ants, preys on ants; may be myrmecophile*	Donisthorpe 1927, Bristowe 1941
Phrurolithus komurai Yaginuma		may also be a myrmecophile*	Komatsu 1961
Phrurolithus minimus Koch	*Formica fusca* L., *Myrmica scabrinodis* Nylander, and *Tapinoma erraticum* (=nigerrima) (Latreille)	running w/ants; preys on ants; may be myrmecophile*	Donisthorpe 1927; Bristowe 1941
Phruronellus sp.			Chamberlin 1925
OONOPIDAE			
Opopaea (=*Diblemma*) *donisthorpi* (O. Pickard-Cambridge)	*Wasmannia auropunctata* (Roger)		Donisthorpe 1927
SALTICIDAE			
Belippo calcarata (Roewer)	*Pheidole* sp.		Roewer 1942; Wanless 1978
Belippo ibadan Wanless	*Anochetus bequaerti* Forel, *Crematogaster depressa* (Latreille), *Pachycondyla* (=Mesoponera) *ambigua* (Weber)		Wanless 1978
Bocus sp.	*Polyrhachis* sp.		Parker & Cloudsley-Thompson 1986
Consingis dakota Cutler	*Leptothorax* sp. & *Myrmica americana* Weber	transformational mimicry	Cutler 1970

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Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Consingis spp.		general mimic	Cutler 1970
Corcovetella aemulatrix Galiano	*Camponotus* sp.		Galiano 1975
Martella furva (Chickering)	*Camponotus* spp.		Reiskind 1977
Martella spp.	*Camponotus* spp.		Galiano 1965
Myrmarachne chapmani Banks			Banks 1930
Myrmarachne collarti Roewer	*Odontomachus troglodytes* Santschi		Wanless 1978
Myrmarachne dundoensis Wanless	*Camponotus* sp.		Wanless 1978
Myrmarachne elongata Szombathy	*Pheidole megacephala* (Fabricius), *Tetraponera anthracina* (Santschi)	transformational mimicry	Edmunds 1978; Wanless 1978
Myrmarachne foenisex Simon	*Crematogaster castanea* F. Smith, *Oecophylla longinoda* (Latreille)	transformational & polymorphic mimic; tends coccids and imbibes their exudate (also feeds on coccids); may be myrmecophile*	Collart 1929a, 1929b, 1941; Edmunds 1978; Wanless 1978,
Myrmarachne foreli Lessert	*Tetraponera natalensis* (F. Smith)		Wanless 1978
Myrmarachne formicaria (De Geer)	*Formica cunicularia* (=*fusca* var. *rubescens*) Latreille, m *F. rufa* L., *F. rufibarbis* Fabricius, *Myrmica rubra* (=laevinodis) (L.), *M. scabrinodis* Nylander	transformational mimic	Pocock 1908; Donisthorpe 1927; Bristowe 1941; Galiano 1969a
Myrmarachne inermichelis Bösenberg & Strand			Komatsu 1961

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Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Myrmarachne inflatipalpis Wanless	*Crematogaster* sp.		Wanless 1978
Myrmarachne insulana Roewer	*Tetramorium* sp.		Wanless 1978
Myrmarachne kiboschensis Lessert	may mimic *Camponotus vestitus* (F. Smith), *Odontomachus troglodytes* Santschi		Wanless 1978
Myrmarachne legon Wanless	*Acantholepis* sp, *Camponotus acvapimensis* Mayr & *Crematogaster* sp.	transformational mimicry	Edmunds 1978; Wanless 1978
Myrmarachne marshalli Peckham & Peckham	*Camponotus* spp.		Wanless 1978
Myrmarachne nigeriensis Wanless	*Camponotus* sp.		Wanless 1978
Myrmarachne parallela (Fabricius)	*Pachycondyla* spp.		Reiskind 1977
Myrmarachne plataleoides (O. Pickard-Cambridge)	*Anoplolepis gracilipes* (=*Plagiolepis longipes*) (F. Smith), *Oecophylla longinoda* (Latreille), *O. smaragdina* (Fabricius), *Plagiolepis* sp., *Prenolepis* sp., *Solenopsis geminata* (Fabricius), *Solenopsis* sp.	transformational mimicry	Bhattacharya 1939; Marson 1946, 1947, Mathew 1934, 1954; Edmunds 1978; Wanless 1978
Myrmarachne platypalpus Bradoo	*Camponotus* sp.		Bradoo 1980
Myrmarachne providens (Peckham)	*Tetraponera* (=*Sima*) *rufonigra* (Jerdon)		Pocock 1908

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Myrmarachne richardsi Wanless			Wanless 1978
Myrmarachne transversa (Mukerjee)	*Diacamma vagans* (Smith), *Camponotus sericeous* (Fabricius)		Mukerjee 1930
Myrmarachne uvira Wanless	*Camponotus flavomarginatus* Mayr, *C. sericeus* (Fabricius)		Edmunds 1978; Wanless 1978
Myrmarachne spp.	*Camponotus compressus* (Fabricius), *Oecophylla* sp., *Paratrechina* (=*Prenolepis*) *longicornis* (Latreille), *Pheidole indica* Mayr, *Polyrachis lacteipennis* (=*simplex*) Smith	some may prey on ants	Hingston 1928
Paradamoetas cara (Peckham & Peckham)	*Zacryptocerus* sp.	found on *Acacia* trees w/ *Pseudomyrmex ferrugineus* (F. Smith)	Cutler 1981
Peckhamia picata (Hentz)			Pocock 1908
Sarinda camba Galiano	*Camponotus* sp.		Galiano 1969b
Sarinda imitans Galiano	*Camponotus* sp.		Galiano 1967
Sarinda linda Reiskind	*Camponotus planatus* Roger		Jackson & Drummond 1974
Sarinda marcosi Toledo-Piza	*Camponotus* sp.		Galiano 1965
Synageles occidentalis Cutler			Cutler 1991
Synageles venator (Lucas)	*Lasius niger* (L.), *Myrmica scabrinodis* Nylander		Donisthorpe 1927; Bristowe 1941; Engelhardt 1970

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Synemosyna americana (Peckham & Peckham)	*Pseudomyrmex boopis* (Roger), *Pseudomyrmex* spp.	polymorphic mimicry	Reiskind 1977; Cutler 1985
Synemosyna aurantiaca (Mello-Leitão)	*Pseudomyrmex flavidius* (F. Smith), *P. gracilis* (Fabricius), *P. oculatus* (Fr. Smith), *P. phyllophilus* (F. Smith), & *P. sericeus* (Mayr)	polymorphic mimicry	Galiano 1965; Oliveira 1986
Synemosyna decipiens (O. Pickard-Cambridge)	*Pseudomyrmex* sp.	polymorphic mimicry	Cutler 1985
Synemosyna edwardsi Cutler	*Crematogaster* sp.		Cutler 1985
Synemosyna formica Hentz	*Camponotus* sp., *Formica* sp., & *Myrmica* sp.		Cutler 1985
Synemosyna smithi Peckham	*Pseudomyrmex cubaensis* (Forel), *P. pazosi* (Santschi)	polymorphic mimicry	Myers & Salt 1926; Galiano 1965
Synemosyna sp. (undesc.)	*Pseudomyrmex gracilis* (=*mexicanus*) (Fabricius)		Reiskind 1977
Synemosyna spp.	*Pseudomyrmex* spp.		Pocock 1908; Cutler 1985; Oliveira 1986
Tutilina cf. *similis* (Banks)	*Camponotus* sp.	preys on ants; one mimic found w/ two dead workers of *Pogonomyrmex occidentalis* (Cresson)	Wing 1983
Uluella formosa Chickering			Reiskind 1977
Zuniga laeta (Peckham)	*Camponotus femoratus* (Fabricius)		Oliveira 1986

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Zuniga magna Peckham	*Camponotus crassus* Mayr, *Camponotus* spp., *Pachycondyla villosa* (Fabricius), *Pseudomyrmex gracilis* (Fabricius), *Pseudomyrmex* spp.	transformational mimicry	Reiskind 1977; Oliveira 1986
THERIDIIDAE			
Anatea formicaria Berland	*Lordomyrma* sp., *Monomorium* (=*Chelaner*) *croceiventre* Emery, *Monomorium* sp., *Pheidole* sp., or *Tetramorium* (=*Xiphomyrmex*) *tenuicrine* (Emery)	males only; females are not known	Berland 1927; Reiskind & Levi 1967; Reiskind 1972; Levi 1986
Cerocida strigosa Simon			Reiskind & Levi 1967
Coleosoma floridanum Banks		males only; females stay on web and are not ant-like	Reiskind & Levi 1967; Levi 1986
Helvibis brasiliana (Keyserling)			Reiskind & Levi 1967
Helvibis chilensis (Keyserling)			Reiskind & Levi 1967
Heleosoma floridanum Banks		males only	Reiskind & Levi 1967
THOMISIDAE			
Amyciaea forticeps O. Pickard-Cambridge	*Oecophylla smaragdina* (Fabricius)	preys on ants; uses behavioral mimicry to attract and kill ants (aggressive mimicry)	Shelford 1902; Hingston 1928
Amyciaea lineatipes O. Pickard-Cambridge	*Oecophylla smaragdina* (Fabricius)		Pocock 1908

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Amyciaea spp.	*Oecophylla* spp.	only found in company w/ models	Brignoli 1984
Strophius nigricans Keyserling	*Camponotus crassus* Mayr	preys on ants & carries dead ants (aggressive mimicry)	Oliveira & Sazima 1985
ZODARIIDAE			
Storena spp.	*Iridiomyrmex purpureus* (F. Smith)	three different spp. mimic three morphs of model *I. purpureus* sensu strict., *I. purpureus* var *viridioeneus* Viehmeyer, and undesc. var.)	Greenslade & Halliday 1983
Zodarion gallicum (Canestrini)		preys on ants	Boevé 1992
Zodarion sp.	*Messor barbarus* (L.)	preys on ants	Hingston 1928

* see Table 2

meyer considers the relationship between the model and mimic to be either exploitative on the part of the mimic or beneficial to both the model and the mimic. As Wasmannian mimics are, by definition, myrmecophiles, they will be discussed in the section on spider myrmecophiles.

At least some spider myrmecomorphs are clearly aggressive, or Peckhamian mimics (Table 1 and McIver & Stonedahl 1993). Aggressive mimicry complexes involve a predator mimicking its prey (Wickler 1968). In such a system, the prey species acts as both model and operator (in the terminology of Vane-Wright 1980), or as both model and selective agent. The aggressive mimics often use both morphological resemblance as well as behavioral tactics to attract and prey on the models. For example, the thomisid, *Amyciaea forticeps* O.P.-Cambridge, assumes the alarm attitude of its model (abdomen and "antennae" raised). This apparently attracts workers of the model, *Oecophylla* sp. (which have good eyesight). When an ant approaches, the spider attacks it (Table 1, Hingston 1927, Bristowe 1941). The aphantochilid, *Bucranium* sp. carries dead ants of the genus *Cephalotes* aloft, perhaps as a mimetic device (chemical mimicry?) to attract other ants (Table 1, Bristowe 1941). This same strategy is used by *Aphantochilus rogersi* O.P.-Cambridge (Table 1, Oliveira & Sazima 1984). Oliveira & Sazima (1984) suggest that "close similarity of integument texture (granular) and pilosity of body and legs (sparse hairs) apparently facilitates the obligatory intimate contact *A. rogersi* must make with cephalotines in order to capture an ant among other ants." The models may, therefore, exert selective pressure for more perfect mimicry in their own predators.

However, not all myrmecomorphs that prey on their models are aggressive mimics. In order for the spider to be considered an aggressive mimic, the model must be the operator, or selective agent. This is unlikely for models which have poor eyesight (the majority of ants) or which do not approach or investigate the spider. Table 1 lists as aggressive mimics only those spiders that lure their prey to them using a behavioral strategy and/or a behavioral strategy combined with morphological similarity.

Most myrmecomorphic spiders are probably Batesian mimics (Pocock 1908, Bristowe 1941, Marson 1947, Reiskind 1977, Edmunds 1978, Wanless 1978, Parker 1984, Oliveira & Sazima 1984, Oliveira 1986, Parker & Cloudsley-Thompson 1986, Cutler 1991, McIver & Stonedahl 1993). Ants are generally considered to be distasteful, noxious, or unpalatable to vertebrate and invertebrate predators. Many species are particularly aggressive and will mob predators that attack individual ants (Hölldobler & Wilson 1990). Others have particularly potent bites or stings or a hard cuticle with spines making them less appealing prey for most vertebrate and invertebrate predators. Myrmecomorphic spiders would, therefore, gain protection against generalist arthropod predators.

However, it has been suggested that myrmecomorphy in spiders is not an example of Batesian mimicry since there are so many predators that do specialize on ants (Brignoli 1984). The myrmecomorph would be trading one set of predators for another. Instead, Brignoli (1986) proposed that myrmecomorphy allows the spider "to live in many different habitats from which most other species, which ants perceive as different from themselves, are excluded." Certainly, specialized ant predators exist. Certain species of Crabronid wasps stock their nests with ants (Pocock 1908, Bristowe 1941). Species of wasps in the genus *Tracheliodes* are also ant specialists (Krombein 1967). Some spiders are specialist ant predators (Hölldobler 1971, MacKay 1982, Porter & Eastmond 1982). McIver & Stonedahl (1993) cite additional examples of vertebrate and invertebrate ant predators.

Nevertheless, Edmunds (1978) points out that myrmecomorphy in spiders probably provides protection, despite the existence of specialized ant predators, since spiders respond much differently to disturbance (including attack by an ant predator)

than the models. Ants, when disturbed, tend to respond aggressively to the threat, whereas spiders tend to dodge the threat, hiding beneath a leaf or in a crevice, or dropping on a drag line. It has been noted that spider myrmecomorphs, which are also behavioral mimics, abandon their ant-like gait when disturbed (Emerton 1911, Marson 1947, Fowler 1984, Brignoli 1984). This sudden, unexpected change in the behavior of the spider would most likely facilitate its escape from an ant predator. Marson (1947) points out that living in close proximity to their models (often in the midst of foraging ants), as do many spider myrmecomorphs, also reduces the risk of predation, even by ant predators, simply because the likelihood of an ant predator preying on a less common mimic than one of the more common models is slim.

Important agents selecting for myrmecomorphy in spiders are probably spider predators such as sphecid or pompilid wasps (Pocock 1908, Bristowe 1941, Edmunds 1978, Wanless 1978, Parker & Cloudsley-Thompson 1986). These predators might not recognize myrmecomorphic spiders as potential prey. However, it has been reported that some wasps, such as *Trypoxylon placidum* Cameron, *Pison* sp., and an unidentified sphecid wasp, had myrmecomorphic spiders of the genus *Myrmarachne* in their nest cells (Richards 1947, Edmunds 1978). However, these may be isolated instances of individual wasps that have learned to differentiate *Myrmarachne* mimics from their models. It is generally uncommon to find myrmecomorphic spiders in the nest cells of spider hunting wasps (Bristowe 1941).

Indirect support for the hypothesis that myrmecomorphs are Batesian mimics lies in the fact that, in general, myrmecomorphic spiders mimic either the dominant ants in a habitat or aggressive, well protected ants (Edmunds 1978). Edmunds (1978) further points out that transformational and polymorphic mimicry provide indirect support for the hypothesis that myrmecomorphy in spiders evolved as an anti-predator strategy. "Evidence for the strength of predator selection in perfecting the resemblance between mimic and model is the infrequency of finding a *Myrmarachne* with the 'wrong' species of ant, and the occurrence of different color morphs of mimic wherever the model has a different colour" (Edmunds 1978).

Direct experimental studies in which arthropod predators have been presented with choices between myrmecomorphic and non-mimetic prey also support the hypothesis that myrmecomorphs are Batesian mimics (Oliveira 1985, McIver 1987, McIver 1989, and Cutler 1991). The results of these experimental studies are summarized in McIver & Stonedahl (1993). In general, the predators avoid the myrmecomorphs and the models while preying readily on the non-mimetic species, and they treat the mimic as if it were an ant.

Myrmecophily in Spiders

Table 2 presents information about known spider myrmecophiles. Included in this table are those spiders that have either occasionally or exclusively been found in or just outside ant nests. Hölldobler & Wilson (1990), in their review of myrmecophiles, included as myrmecophiles spiders that were specialized ant predators such as *Steatoda fulva* (Keyserling) (Theridiidae) (Hölldobler 1971), *Euryopis coki* Levi (Theridiidae) (Porter & Eastmond 1982), and *Latrodectus hesperus* Chamberlin & Ivie (MacKay 1982). Although these spiders have evolved specialized hunting strategies for capturing ants, they probably do not feed exclusively on ants and are only occasionally or never found inside ant nests. Therefore, they are omitted from Table 2. A few other spider genera listed as myrmecophiles in Hölldobler & Wilson (1990) are more accurately described as myrmecomorphs and are included, instead, in Table 1.

The ants with which the myrmecophilic spiders are associated are also listed in Table 2, as is information about the natural history of the spiders. Very little informa-

tion is known about spider myrmecophiles. Only a very few studies have investigated aspects of the spider-ant associations in any depth (Shepard & Gibson 1972, Noonan 1982, Porter 1985, Cushing 1995a, 1995b). Much more work must be done to determine how the spiders become integrated into the host colonies, how the ants react to these guests, what adaptations enable the spiders to live inside the nests, and to what extent the spider affects the life of the host colony.

General Information about Myrmecophily

Many arthropods have evolved symbiotic relationships with ants. Some are found at the periphery of the nest, either near the entrances or on refuse piles; others are found within the chambers of the nest, either in the peripheral chambers or deeper in the nest in the brood and storage chambers (Hölldobler 1977, Hölldobler & Wilson 1990). They range from tiny collembolans to beetles and caterpillars many times the size of their hosts. These myrmecophiles have evolved various adaptations enabling them to exist in this hostile environment. Many of the myrmecophiles acquire cuticular hydrocarbons similar or identical to those of their hosts (Vander Meer & Wojcik 1982, Vander Meer et al. 1989). This allows them to become integrated with hosts that are otherwise hostile to intruders with foreign, non-colony odors. Others, such as some staphylinid beetles and lycaenid caterpillars, have evolved specialized glands that produce appeasement substances (reviewed in Hölldobler & Wilson 1990).

In many myrmecophiles, the evolution of a symbiotic association can be intimated through an examination of extant species that show varying degrees of behavioral integration (Hölldobler & Wilson 1990). For example, Akre & Rettenmeyer (1966) described species of staphylinid beetles that show varying degrees of association with army ants. Some species live only around the edges of the bivouacs or in the refuse piles but are not otherwise integrated into the colonies, others are found running along the edges and sometimes within the emigration columns of ants, and yet others are found directly in the midst of ants in the center of the emigration colonies. Some species even hitch rides on the booty or the brood carried by ants. Certain staphylinid species can only live within a narrow range of conditions found within colonies and die shortly after removal from the colonies.

If each stage in this process of gradual integration into colonies is correlated with the evolutionary history of the lineages, then the various adaptations of the myrmecophiles leading to greater integration could be viewed as characters on the phylogenetic tree (Brooks & McLennan 1991). Kistner (1979) takes this idea a step further by superimposing the phylogenies of termites in the family Rhinotermitidae with their associated termitophiles in the family Staphylinidae to illustrate the evolution of host specificity.

Adaptations of Myrmecophilic Spiders

Myrmecophilic spiders are unique because their close relatives apparently have no preadaptations to a symbiotic lifestyle. Most spiders are solitary predators and symbiosis with other arthropod groups should be rare; yet myremcophilic spiders are found in at least 12 different families (Table 2). Some of these species may be only occasional visitors into ant colonies, using the entrance and upper chambers as temporary refuges (see Table 2). However, some appear to be commensals that have become more dependent on the conditions present within the nest and spend their entire lives within this complex ecosystem.

Masoncus pogonophilus Cushing (Linyphiidae) is the best known example of the latter group of spider myrmecophiles (Porter 1985, Cushing 1995a, 1995b). This spi-

TABLE 2. MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
CORINNIDAE			
Corinna bacalcarata (Simon)	*Pogonomyrmex* sp.	collected from inside the nests and from the surface of mounds in California & New Mexico	Fowler 1984
**Corinna vertebrata* Mello-Leitão	*Acromyrmex fracticornis* (Forel)	associated with nest turrets; seen in foraging columns; preys on ants	Fowler 1984
CTENIZIDAE			
Bothriocyrtum sp.	*Atta texana* (Buckley)	collected inside fungus garden	Walter *et al.* 1938; Waller and Moser 1990
DICTYNIDAE			
Circurina robusta Simon	Atta texana (Buckley)	collected inside detritus chambers	Walter *et al.* 1938; Waller and Moser 1990
Mastigusa (=*Tetrilus*) *arietina* (Thorell)	*Formica rufa* L.,*Lasius brunneus* (Latreille), *L. fuliginosus* (Latreille), *L. umbratus* (Nylander)	females fasten egg-sacs to walls of nest cells and galleries; collected both outside and inside nests	Donisthorpe 1908, 1927
DYSDERIDAE			
Harpactea hombergi (Scopoli)	*Formica cunicularia* (=*fusca* var. *glebaria*) Latreille, *F. fusca* L., *Lasius brunneus* (Latreille), *L. fuliginosus* (Latreille)	collected near and in nests; feeds on ants; behavioral mimic; only occasional guest	Donisthorpe 1927

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
GNAPHOSIDAE			
Cesonia bilineata (Hentz)	*Atta texana* (Buckley)	collected from fungus garden inside nests	Walter *et al.* 1938; Waller and Moser 1990
Eilica puno Platnick & Shadab	*Camponotus inca* Emery	adults found only inside nests; when rocks covering nests were removed, hosts transported spider eggsacs inside nests; spiderlings seen to enter nests	Noonan 1982
**Micaria pulicaria* Sundevall		found inside nests	Bristowe 1941
LINYPHIIDAE			
Acartauchenius scurrilis (O. Pickard-Cambridge)	*Formica rufa* L., *Lasius flavus* (Fabricius), *Tetramorium caespitum* (L.)	found in nest galleries moving around with ants	Donisthorpe 1908, 1927
Cochlembolus formicarius Dondale & Redner	*Formica obscuripes* Forel	collected inside nests	Dondale & Redner 1972
Evansia merens O. Pickard-Cambridge	*Formica cunicularia* (=*fusca* var. *glebaria*) Latreille, *F. fusca* L., *F. sanguinea* Latreille, *Lasius niger* (L.)	most spiders collected inside nests of *F. fusca*; lives in galleries of nests where hosts ignore spiders; adults found throughout year but males found mainly in Sept. & Oct.	Donisthorpe 1908, 1927
Grammonota pictilis (O. Pickard-Cambridge)	*Atta texana* (Buckley)	collected inside detritus chambers	Walter *et al.* 1938; Waller and Moser 1990

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
Masoncus pogonophilus Cushing	*Pogonomyrmex badius* (Latreille)	obligate guest; all instars found throughout the year inside chambers of nest; spiders emigrate with ants; females attach eggsacs to chamber ceilings; spiders feed on collembolans inside the nest	Porter 1985; Cushing 1995a,b
Masoncus sp.	*Atta texana* (Buckley)	collected inside galleries and empty chambers	Waller and Moser 1990
Thyreosthenius biovatus O. Pickard-Cambridge	*Formica fusca* L., *F. pratensis* Retzius, *F. rufa* L., *F. rufa* var. *rufopratensoides* Forel	found inside nest galleries; females lay eggs inside the nests	Donisthorpe 1908, 1927
LIOCRANNIDAE			
Attacobius leuderwaldti (Mello-Leitão) (= *Myrmeques attarum* Roewer)	*Atta sexdens* L.	found inside fungus gardens where it is transported on the backs of the ants; appears to be phoretic, although the adaptive significance of the phoresy is unknown; carried to new nests on back of female alates	Roewer 1935; Eidmann 1937
**Phrurolithus festivus* (Koch)	*Formica rufa* L., *F. sanguinea* Latreille, *Lasius brunneus* (Latreille), *L. fuliginosus* (Latreille), *L. niger* (L.)	common inside nests as well as outside; sometimes preys on ants; only occasional guest	Donisthorpe 1927; Bristowe 1941; Boevé 1992
**Phrurolithus komurai* Yaginuma		always found beneath stone covering ant nest of undesc. species	Komatsu 1961

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
**Phrurolithus minimus* Koch	*Formica fusca* L., *Myrmica scabrinodis* Nylander, *Tapinoma erraticum* (=*nigerrima*) (Latreille)	found inside nests and outside; sometimes preys on ants; only occasional guest	Donisthorpe 1927; Bristowe 1941
Phruronellus formica (Banks) (described as *Phrurolithus formica* Banks)	*Crematogaster lineolata* (Say)	probably obligate guest; when ants emerge from nests in Spring, spiders found amongst them; disappear into nest when disturbed	Banks 1895; Emerton 1911
LYCOSIDAE			
Aulonia albimana (Walckenaer)	*Tapinoma erraticum* (Latreille)	may be occasional associate	Boevé 1992
Pirata spiniger (Simon)	*Atta texana* (Buckley)	collected inside galleries and empty chambers	Waller and Moser 1990
MYSMENIDAE			
Brucharachne ecitophila Mello-Leitão	*Neivamyrmex raptor* (=Eciton raptans) (Forel)	found in nests; appears to have trichome-like structures on femurs of second legs	Mello Leitão 1925; Fage 1938
OONOPIDAE			
Gamasomorpha sp.	*Myrmecia dispar* (Clark)	found in general utility & main brood chambers	Gray 1971
Myrmecoscaphiella borgmeyeri Mello Leitão	*Eciton* sp.	found in nests; appears to have trichome-like structure on its palps	Mello-Leitão 1926; Fage 1938

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
SALTICIDAE			
Continusa sp.	*Tapinoma melanocephalum* (Fabricius)	spider built silken retreats at periphery of nest; seem to emigrate with host	Shepard & Gibson 1972
**Myrmarachne foenisex* Simon	*Oecophylla longinoda* (Latreille)	sometimes found inside nests where it may feed on ant larvae (only occasional guest)	Wanless 1978
THERIDIIDAE			
Dipoena sp.	*Pheidole indica* Mayr	found on pile of debris outside nest &, when alarmed, curls up to mimic the decapitated heads of its hosts scattered in the debris	Hingston 1928
Theridion riparium Blackwall	*Formica sanguinea* Latreille, *Lasius niger* (L.), *Myrmica rubra* (=*laevinodis*) (L.)	collected in nest of *F. sanguinea*; sometimes preys on ants; only occasional guest	Donisthorpe 1927
ZODARIIDAE			
Zodarium frenatum (Simon)	*Cataglyphis bicolor* (Fabricius)	preys on ants; digs open nests in order to force the hosts outside; spends most of its hunting time near nests of host	Harkness 1977

* These taxa are also myrmecomorphs (see Table 1)

der lives within the colony chambers of the Florida harvester ant, *Pogonomyrmex badius* (Latreille). All life stages of *M. pogonophilus* are found inside the nests throughout the year. The spiders feed on collembolans (springtails) found in the nest chambers. When the host ants emigrate to a new nest site, the spiders (and collembolans) move with the ants along the emigration trails (Cushing 1995a, 1995b). There is also evidence that spiders disperse between ant nests (Cushing 1995a, and in prep.). The mechanism by which spiders locate new host colonies or become integrated into new colonies is not yet known.

Adaptive Significance of Myrmecophily

Some myrmecophilic spiders may be considered Wasmannian mimics since they are also myrmecomorphs (see Table 2). However, in Wasmannian mimicry, the model itself (in this case, the host ant) is the selective agent (Rettenmeyer 1970). In other words, the resemblance of the spider to the host ant must have been selected for by the host itself and must facilitate the integration of the spider into the host colony. However, very little is known about any of the myrmecomorphic myrmecophiles. Most of them apparently spend at least some of their time outside the ant nests (see Table 2) where they would be subject to predation by visually hunting predators in which case their morphological resemblance to the host ants may simply be another example of Batesian mimicry. The host ants may have little, if anything to do with their myrmecomorphy.

As Hölldobler & Wilson (1990) propose, an ant colony can be considered an isolated ecosystem. Arthropods that have evolved mechanisms for integrating themselves into this specialized community are greeted with a stable microclimate, abundant food, and protection from predators and parasites. Predation pressures, in particular, may trigger greater integration into the ant societies in these myrmecophilic spiders since association with the aggressive hosts may afford a high degree of protection to the guests. Several of the myrmecophiles, such as *Mastigusa arietina* (Thorell) (Dictynidae), *Eilica puno* Platnick and Shadab (Gnaphosidae), *Masoncus pogonophilus* (Linyphiidae), and *Thyreosthenius biovatus* O.P.-Cambridge (Linyphiidae) lay their eggsacs inside the chambers of the host's nest (Donisthorpe 1908, 1927, Noonan 1982, Porter 1985, Cushing 1995a, 1995b). Spiders are particularly vulnerable to eggsac parasitism (Bristowe 1941). Eggsac parasitism or predation may also be a particularly important factor selecting for greater integration into ant colonies.

Conclusions

Detailed studies of myrmecomorphic spiders and their associated models can provide insight into the ecological and evolutionary implications of mimicry. The hypothesis that myrmecomorphic spiders are Batesian mimics must be further tested experimentally (Cutler 1991). It is important to use not only generalist predators in such experiments, but also, if possible, spider predators as these may also be important selective agents for the evolution of more exact mimicry.

The distribution of mimics and models, especially in transformational or polymorphic mimetic complexes must be documented as Edmunds (1978) has done for *Myrmarachne* spp. in order to determine what effect community structure among the model species has on the distribution and survival of color morphs in the mimic. It is not known to what extent the geographic distribution of intraspecific polymorphic mimics is dictated by genetic patterns or by differential predation of morphs in areas with and without the appropriate model.

A great deal more research must be done to uncover (literally) the basic natural history of myrmecophilic spiders. For most spider myrmecophiles, it is unknown to what extent they are obligate versus occasional guests in ant nests. For the obligate guests, it must be determined how the spiders become integrated into the nests, how they maintain the association, what part they play in the life of the colony, and what part the colony plays in the survival of the guest. Noonan (1982) indicates that, for the myrmecophile *Eilica puno* Platnick and Shadab (Gnaphosidae), the host ants protect and tend the spider's eggsacs (see Table 2).

Certain families of spiders, such as the Linyphiidae and Liocrannidae, seem to have more myrmecophilic representatives than others. It would be interesting to determine the phylogenetic relationship between myrmecophilic taxa and their free-living relatives. Are there certain preadaptations that make myrmecophily more likely for certain lineages and less likely for others? It is important to document those myrmecophilic spiders that may be encountered in the field. Studies of myrmecophilic spiders can provide insight into the evolution of interspecific associations between social hymenopterans and their guests.

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INSECT COLORATION AND IMPLICATIONS FOR CONSERVATION

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ABSTRACT

Large, conspicuously colored insect taxa, due to associated logistical and anthropocentric biases in knowledge, public support and legislative consideration, are favored as targets of species protection, environmental monitors and education tools. They are also vulnerable to collection and perhaps, due to ecological specializations associated with apparency, to extinction. I discuss the implications for conservation.

Key Words: insect conservation, insect coloration, insect apparency, insect conservation policy

RESUMEN

La taxa de insectos grandes y visiblemente coloreados, por estar asociados a prejuicios en el conocimiento antropocéntrico y logístico, apoyo público y consideración legal, son favorecidos como blanco por grupos dedicados a la protección de especies, a monitorear el medio ambiente y a utilizarlos como herramienta educativa. Estos insectos también son vulnerables a la colección y quizás, debido a especializaciones eco-

lógicas asociadas con la apariencia, también son vulnerables a la extinción. Se discuten las implicaciones en términos de conservación.

Insects dominate terrestrial ecosystems in terms of species, biomass, number of individuals, and importance of ecological roles (Ricklefs et al. 1984, Wilson 1987, 1988). Approximately 80% of all described metazoan species are insects (Samways 1992). Insect global distribution is highly biased, with over 50% living on less than 7% of the earth's surface in tropical rain forests (Samways 1994). It has been estimated that only about 5% of insect species have been described, and significant information is thought to exist on less than 1% of these (Raven 1990). Almost all of that information has been garnered from either pest or charismatic species in temperate areas; neither are representative samples of insect biological diversity.

Insects are susceptible to the same anthropogenic threats as vertebrates. Wilson (1988) estimates that species extinctions are occurring at a rate of at least 1000 times faster than before human-induced extinction pressures. However, most insect population declines and extinctions go unnoticed or unappreciated. This is largely a result of apparency-related obstacles. Small size and inconspicuous habits, together with tremendous diversity and a mostly tropical distribution, make insects largely invisible to human attention and concern.

Humans most readily learn about, care about, and make sacrifices for animals that are apparent, familiar, aesthetically appealing, and demonstrate positive benefits to mankind. Such glamorous species often enjoy special privileges in species-oriented conservation efforts, due to research, funding, and political and public support. On the other hand, they may be particularly susceptible to anthropogenic impacts, directly through their status as commodities and indirectly through special ecological needs associated with their apparency. Familiar and appealing insects also offer special advantages for larger-than-species-scale conservation efforts. Existing historical and ecological knowledge, sampling methodologies, expert interest, and financial support enhance the use of glamorous species as indicators of biological diversity and as monitors of environmental change.

Animal apparency and aesthetic appeal are related to their coloration, morphology, behavior, and size. Strikingly colored, shaped, or behaviorally interesting creatures benefit from heightened conservation attention. However, with regard to insects, size is a limiting factor. Glamor status occurs only when a species is large enough 1) to be well-studied and sampled, and 2) to overcome anthropocentric biases that favor larger animals. Such threshold sizes are atypical of insects; by far, most insects are minute or small. In North America, described insect species vary from less than 1 mm to approximately 15 cm, with more than half being less than 6 mm long (Borror & White 1970). Of approximately 430 species of adult beetles collected by fogging in four tropical forests in Brazil, 97% were less than 8 mm in length (Erwin 1983). Although speciose groups, including Coleoptera, Lepidoptera and Diptera, contain some of the largest, most well-studied and charismatic species, flamboyance is not typical even within these taxa.

I will briefly discuss the roles of the environment, life history strategies, sexual selection and predator defense in shaping adaptations associated with apparency and beauty in insects. I will then consider how these adaptations influence 1) the way we value species, 2) anthropogenic threats to their populations, and 3) how we treat species in conservation policy and management.

Sources of Variation in Apparency and Aesthetic Appeal, and Implications for Conservation

Sources of variation in apparency and aesthetic appeal in insects include adaptations associated with the environment, particular life history strategies, predator defense, sexual selection, and the interplay of these. Population and species differences in size, shape, and coloration can reflect variation in temperature, humidity, and day-length. Differing ecotypes contain species with characteristic arrays of adaptations that influence diversity at all levels of biological organization. For example, tundra ecosystem thermal and daylight constraints and structural simplicity limit within and among species variation. Few species are naturally rare. Such environments and their relatively uneventful insect species are seldom the focus of conservation efforts. Only under larger-scale efforts that focus on preservation of representative ecotypes are such landscapes and species given significant conservation attention. On the other hand, tropical areas are generally characterized by seasonally stable, structurally complex environments, and strong biotic selective pressures. Intra- and interspecific diversity is extreme in size, coloration, and associated behaviors, habitat specialization, and distribution patterns. Such environments receive high conservation priority. Ironically, these areas represent our greatest conservation challenges specifically because such extreme variation eludes current conservation strategies.

Phenotypic variation can occur through the season or through a species' range and can be genetic and/or environmentally controlled. The nature of this control is important in conservation theory and practice. Color polymorphisms can be sources of biological diversity (Samways 1994), sources of confusion in monitoring populations (Crother 1992), and focuses of interest for researchers and collectors. Differing color forms can be associated with differing macro- or micro-habitat preferences affecting within-species vulnerabilities to anthropogenic changes to the environment. For example, the peppered moth (*Biston betularia*) demonstrates how genetic polymorphisms in color, form and associated resting surface preferences can lead to color form-specific responses to human-induced changes to the environment.

Where biological variation over space is relatively gradual, conservation efforts are often directed at range extremes. These areas are often marked by apparency-related characters. Variation in insect color, morphology, behavior and size are also used to map areas of abrupt environmental change, increased variability within and among species, and speciation hot spots.

Complex life cycles are common in insects, especially speciose taxa with large, readily apparent species such as Coleoptera, Lepidoptera, and Diptera. Variation in appearance and ecological specialization associated with different life stages can be extreme and influence both our concern and our ability to conserve species. Extreme differences in life stage forms can lead to conflicts of interest, taxonomic confusion and a need for increased research efforts.

Insect size and coloration are integral parts of life history strategies that are associated with factors such as mobility, longevity, degree of habitat specialization, activity periods, flight patterns, predator avoidance, and feeding strategies. For example, reproductive rate is related to insect size. Some of the largest and most dramatically colored insects, such as the birdwings (*Ornithoptera*, Papilionidae), are considered K-selected species. Because such long-lived species produce relatively few eggs at a low rate, they can be especially vulnerable to extinction. Furthermore, large, conspicuous species often live in closed or sedentary populations that are thought to be especially threatened by habitat fragmentation (Thomas 1984, Thomas & Mallorie 1985).

Large, conspicuous species, due to their associated ecological specializations, may exist as groups of local sub-populations. Such metapopulations are potentially buff-

ered from extinction within an area by re-colonization from surrounding sub-populations. Such populations may by particularly vulnerable to habitat destruction and require regional approaches to their conservation (Murphy et al. 1990). Metapopulations are thought to be common in insects in general and differ from those used to develop vertebrate models used in population viability assessments and recovery plans (Murphy et al. 1990).

Insect apparency is increased when aggregations are formed in association with roosting, feeding, mating, predator defense, moderation of the environment, or overwintering. Such aggregations increase the apparency of the group to potential predators and to collectors. Insect behavior and aggregation site characteristics may further increase exposure. For example, swarming or hilltopping mating aggregations often occur in exposed locales and individuals remain in flight almost constantly. Although long-term aggregations associated with warning coloration may function to deter predation (Vulinec 1990), they may be especially vulnerable to collection due to the increased accessibility and the economic value associated with aposematism. When aggregations involve a large portion of the population for an extended time, their members become especially vulnerable to very specific habitat threats.

At least in tropical butterflies, aggregations are associated with other life-history strategies, such as restricted home ranges, low reproductive rates, and increased longevity (Turner 1975), that magnify their vulnerability to human-induced threats to their habitat. Congregated organisms also bias our perception and measurement of rarity, thereby favoring aggregated species and populations in conservation priority rankings.

Predation pressures not only impact conservation efforts through the evolution of aggregation behavior, but as selection agents in the evolution of warning coloration, concealment, crypsis, and mimicry. Depending on the adaptation and the particular threat faced, these adaptations may benefit or harm the conservation of a species. For example, insects that rely on concealment or blend into their background are often small and drab. While such adaptations may lessen potential anthropogenic threats such as insect collection, inconspicuous species are not likely to be well-studied and their conservation is unlikely to gain public support. Because their inconspicuousness is dependent on specific associations with a component of the insect's environment, these insects can be especially vulnerable to changes in their habitat. Cryptic species that mimic a particular object such as a leaf, due to their often exposed resting and feeding habits and their associated low population densities, may be particularly vulnerable to climate change, pollution, and pesticides. Furthermore, once discovered by collectors, cryptic species may become economically valued due to their aesthetic intrigue. For the same reason, they may also gain research favor and public support.

Chemically protected aposematic insects are thought to have evolved bright, bold coloration, often involving black, yellow, orange or red, as an advertisement of their unpalatability to visual predators such as birds and lizards. Aposematic insects are among the most-valued aesthetically, the most-studied, and the most-exploited in trade largely because human visual systems are also attuned to such colors and patterns.

Such species often attain their chemical protection by sequestering secondary substances produced by plants as adaptations against phytophagous insects. Plant and insect counter-adaptations lead to very specific and dependent relationships. Such co-adaptations increase insect vulnerability due to the indirect impacts of disruptions to their associated plant ecology. Insect-plant associations can restrict geographical and ecological tolerance increasing susceptibility to climate change (Samways 1994). Batesian and Mullerian mimicry complexes are commonly associated with warningly colored insects. These complexes can be confusing taxonomically. Because of scientific interest in using mimicry complexes as tools to understand ecology and evolution, the

associated species are often some of the best understood ecologically and genetically. Their apparency also enhances the practicality of their study.

Sexual selection pressures account for many adaptations that we associate with beauty in insects, and why we often prize males as commodities. Secondary sexual characters that function in intrasexual interactions and/or mate choice include size, bright coloration, ornamentation, weaponry and behaviors. In terms of intraspecific visual signaling coloration, size, and shape can be viewed as a compromise between the needs to attain mates and avoid being eaten. For example, the bright and bold upper wings of many male butterflies are exposed in flight and used in intraspecific signaling while the under wings, exposed when resting and feeding, are cryptically colored to avoid predation. Such visual compromises are common in some of our most glamorous butterfly species. They are sources of intraspecific genetic diversity and are of great interest to researchers and collectors.

Sexual dimorphisms in coloration in butterflies are a common result from the interplay of sexual selection and predation pressures. Females are relatively inconspicuous while the brightly colored males risk increased predation for increased reproductive success. Because males generally show the most dramatic coloration, and the taking of males is generally thought to have no effect on future population numbers, potential threats by collectors or predators can be lessened or negated by such adaptations. However, in female-limited mimicry complexes in which females, but not males, mimic other brightly colored, chemically protected species, it may be that females stand out and are particularly sought after.

The Influence of Apparency and Beauty in Valuation of Insects in Conservation

Economic, ethical, ecological, educational, and practical values attributed to particular species are used to prioritize conservation efforts (for reviews see IUCN 1983, Morris et al. 1991, New 1995, Pyle et al. 1981, Samways 1994). Insect apparency and beauty impact how we value insects in all of these areas.

Insects are generally little valued economically (IUCN 1983). Small size and the associated lack of information contribute to this situation (Samways 1994). While some species are used as sources of products, medicines, and biological control, only a very few taxa are commercially valuable because of their apparency. These are typically traded as dead stock. Worldwide, dead stock trade of insects is valued at tens of millions of dollars annually (Morris et al. 1991). Single specimens of birdwings have been advertised for up to US $7000 (Morris et al. 1991). An unexplored way that aposematic insects might be commercially valuable is through their co-evolved chemical systems with plants. Because insect conspicuousness can serve as a flag for novel plant chemistry, such insects might be used as probes to survey for medicines or other useful bio-chemicals (Kremen et al. 1993).

Ethical arguments for insect conservation that are based on intrinsic values of individuals are philosophical extrapolations of human-based morality (Lockwood 1987). Such an ethical framework cannot favor individuals of undescribed species nor individuals of endangered versus common species (Samways 1994). Individual-based moral consideration is effectively apparency-biased because only insects that are obvious to humans gain support on such grounds (New 1995). Furthermore, aesthetically-valued taxa are more likely to gain support, especially when economic, cultural, ecological or practical values conflict with moral consideration (Samways 1990). Ethical considerations are practically without application in undeveloped countries and are often incongruent with community or landscape level conservation strategies. However, by focusing on the interdependence of the genome and the individual, con-

flicts between ethical and biological justifications of insect conservation are often reconciled (Samways 1994). The above arguments do not negate the importance of moral consideration of individuals of all species. Such consideration is commendably the basis of insect collection ethical codes.

Insects are by far most valued in conservation for their ecological roles. They are key components in the composition, structure and function of ecosystems (Hafernik 1992, Ricklefs et al. 1984, Wilson 1987). Insects are abundant herbivores and detritivores influencing directly and indirectly elemental cycling and net primary productivity (Seastedt & Crossley 1984). Ecological importance and beauty only rarely coincide. The human bias in favor of the apparent and beautiful may be particularly shortsighted in this regard.

Charismatic species can be successfully used in the communication of issues, needs, knowledge, and the benefits of insect conservation (Salwasser 1991). Environmental educational objectives in which glamorous insect species are particularly useful include the study of diversity, abundance and biomass, complexity, species radiation, history, biological and economic importance, and interaction with plants (Robinson 1991, in New 1995). Conservation studies that demonstrate population declines of glamorous species, especially butterflies, have increased the general public's awareness of the need to protect insects and their habitats (Hafernik 1992, Samways 1989, Thomas 1984).

Amateur involvement in conservation efforts, such as the Fourth of July Butterfly Count (Swengel 1990) and the Entomological Society of Victoria Butterfly Mapping Scheme (New 1990(92)) are generally limited to well-appreciated, large, easily assessed taxa. Zoo and museum displays use almost exclusively large, apparent, and attractive species. Butterfly gardening has become a popular hobby and is promoted as a means to effectively demonstrate important ecological principles using mostly large, attractive species. It is common for naive butterfly gardeners to want to discourage unattractive larval stages that devastate their store-bought plants. However, the association of the less conspicuous, and usually less attractive, larvae with the appreciated, sought after adults teaches the need for the less-than-beautiful and the need to provide habitat. Experienced gardeners usually come to appreciate larval forms and behaviors.

Large, conspicuous insects offer unparalleled opportunities for conservation-related research. Unlike their vertebrate counterparts, they are accessible, easily reared, short lived, diverse, and inexpensive to study. Theoretical studies of apparent species provide important models for developing conservation methodology and setting conservation priorities that are unique to invertebrates (e.g. Hanski & Thomas 1994, Ehrlich & Murphy 1987, Murphy et al. 1990, Murphy & Weiss 1988).

Anthropogenic Threats to Insects, and Vulnerabilities of Large, Apparent Insects

Public support for conservation continues to rest on emotional rather than intellectual motives, and has been garnered primarily by the cute and cuddly vertebrates. Most adults dislike or are afraid of arthropods. This reflects our biased awareness of almost exclusively injurious insects (Byrne et al. 1984, Kellert 1993). Modern agriculture, and the usual resulting information bias toward small, unattractive, harmful pests, is largely responsible for such negative public perceptions (Barnes 1985). Innate fears may also contribute to human biases against insect conservation, especially when species are inconspicuous, unattractive, and economically unimportant (Kellert 1993). Such fears may be especially well-ingrained by certain aposematic insects. On the other hand, it is also the bright, big and bold insects, especially beneficial

ones, that can be used most effectively to overcome ignorance, prejudice, innate fears, and anthropocentric biases against the small and often ugly world of insects (Morris 1987, Samways 1992).

Insects face the same anthropogenic threats as vertebrates, including changes to their habitat, impacts by exotics, pollution, climate change, pesticides, and, potentially, their collection for profit. The most important threat is habitat loss, fragmentation, and/or degradation. Unlike that seen in vertebrates, there is no general positive relation between insect size and their vulnerability to extinction (Samways 1994). This suggests that, although large, conspicuous species may sometimes face increased vulnerabilities due to their associated ecological needs, the conservation focus on large, conspicuous species is not biologically sound in general.

Climate change potentially affects insects both directly and indirectly through plant associations (Dennis 1993, New 1995). Apparency-related aspects of butterfly biology have led to their use as models for understanding the direct impacts of atmospheric pollutants and for predicting the indirect effects of climate change. For the same reasons, butterflies are promoted as monitors of climate change (Dennis 1993).

Pesticides have been blamed for insect species extinctions, but there have been no documented cases of such extinctions (IUCN 1983, Pyle et al. 1981, Thomas 1984). This is not to say that pesticides have not or can not lead to insect extinctions under certain circumstances. Furthermore, pesticides may influence insect community structure by changing the distribution and relative abundance of species (Samways 1994).

After habitat destruction, the negative impacts of non-indigenous species is considered the greatest threat to insect conservation. Including all known animal taxa, by far, most documented non-indigenous species in the US are accidentally introduced insects. Their impact is assumed to come primarily through interspecific competition and increased predation pressures (US Congress, Office of Technology Assessment 1993). However, the impacts of these non-indigenous species are rarely documented, except for economically important or charismatic species, because insects are generally unapparent, unappreciated, and, therefore, neglected in conservation.

Size also influences our knowledge of the environmental risks posed by biological control organisms. For example, microorganisms are thought to offer the greatest potential in biological control. However, due to their great diversity, minute size, and inaccessibility, we know almost nothing about their biology and ecology (Pimentel 1980). Classical biological control agents, such as nematodes, fungi, protozoa, bacteria, and viruses may have host ranges beyond their targeted species (Pimentel 1980, Samways 1988). However, their potential impact is rarely studied. When impacts are assessed, they are judged by aesthetically pleasing or economically valued species. For example, *Bacillus thuringiensis* has been shown to negatively affect more than 135 non-target species (Laird 1978, in Pimentel 1980), but it has generally received positive reviews because it has not been documented to be harmful to the natural enemies of economically important pest species. *Bacillus thuringiensis israelensis*, used in mosquito control, has received conservation attention because it has been shown to cause mortality in mayfly and dragonfly larvae (Zgomba, Petrovic & Srdic 1986, in Samways 1994). The general lack of conflict of interest between insect conservation and classical biological control lies partly in the fact that biological control is most often aimed at small, inconspicuous, unpopular, exotic species, while conservation efforts are aimed at large, conspicuous, popular, rare, and, often, specialized species (Samways 1988). The general absence of public demand for more strict pre- and post-release assessments of imported exotic biological control agents is related to the fact that obvious, charismatic species have rarely been noticeably impacted. *Bacillus thuringiensis*, released for gypsy moth control, may raise public concern if butterflies,

even non-indigenous species, are found to be negatively impacted as suspected (Harbrecht 1991).

Insect collection for trade, commodity production and research is biased toward large, apparent species due to their aesthetic value and practical advantages. Taxa that are valued by collectors may benefit through the associated increased knowledge that is necessary for most species-oriented conservation efforts. Live trade of insects is highly biased toward large, aesthetically pleasing species but these are often bred from very few wild-caught animals. Butterfly farming and ranching are considered viable sustainable use strategies in which very high demand species are reared or encouraged to breed by providing them with host plants in their natural environment. A subset of these are then collected and used for economic gain, while the remaining are left to maintain or even boost natural populations.

The potential impact of collectors on insect populations remains a hotly debated topic, especially among lepidopterists. For recent controversial opinions, see *The News of the Lepidopterists' Society* (38 (1-2) 1996). The consensus appears to be that collectors rarely, if ever, are the primary cause of insect population or species extinctions (IUCN 1983, Morris 1987, New 1995, Orsak 1978(81), Pyle et al. 1981, Samways 1994, Thomas 1984). However, the scientific study of the impact of collection on vulnerable species is lacking. Insect collection is considered an ethical issue, but only specialist trade of wild-caught specimens, where value is heightened by rarity, is considered potentially threatening to populations. These rare species are often K-selected. Low reproductive rates, limited ranges and very specific host plant associations can increase vulnerability to collection and the habitat destruction that can be associated with economic gain. *Parnassius apollo* and New Guinea birdwings are examples of K-selected insects that are apparently threatened by collecting (Pyle 1978(81)).

Insect Apparency and Conservation Policy

Insect conservation policy primarily addresses the protection of rare species, with provisions for those species' habitats, and/or general restrictions on insect collection. Such policies are extensions of vertebrate-based conservation philosophies and are generally not objective nor consistent (New 1995). This is partly due to logistical constraints related to the small size and inconspicuousness of most insect taxa. It is easier to assess population status, develop management plans, and monitor large, conspicuous species. Their conservation need is more likely to be demonstrated by pre-existing data necessary to document population decline. Their study is more likely to secure funding and public support.

Just as with vertebrates, charismatic insect species are sometimes intentionally given conservation priority for political reasons. In Britain, the Swallowtail, *Papilio machaon*, was included in the Wildlife and Countryside Act (1981) as a political ploy. Its inclusion was based on glamour status and historical focus and was contrary to scientific data that indicated a low priority in conservation need (Morris 1987). Furthermore, charismatic species that are not considered a high conservation priority may be listed because their preservation is expected to serve as an umbrella for other species. Such an umbrella can be quite effective. Habitat protection for the El Segundo blue, *Euphilotes bernardino allyni*, has helped to protect 15 other less-glamorous invertebrate species that co-inhabit the preserved California sand dune ecosystem (Mattoni 1992).

The US Endangered Species Act (ESA) of 1973 is considered the most powerful conservation policy in the world. Although the ESA theoretically gives equal status to all species, in practice charismatic species are strongly favored. Fewer than 10% of

listed species received more than 90% of the funding in 1990, and none of these is an insect (New 1994)! ALL insects receive little attention relative to their representativeness in species diversity or their ecological importance. Small size, lack of aesthetic appeal, and associated lack of knowledge, support, and funding further bias listing efforts within the Insecta (Boecklen 1987, Hafernik 1992, Murphy 1991, Van Hook 1994). As of 1989, 95% of the 427 insect species assessed for listing were not listed due to insufficient information (Opler 1991). There have been 28 insects put on the list of endangered and threatened wildlife, 19 of which are butterflies. Recovery plans exist for only four species, all of which are butterflies (Opler 1995).

The ESA is an example of the wrong approach at the wrong scale (*sensu* Murphy 1989). The policy is criticized for lack of scientific bases, ineffectiveness and inconsistent use (Mann & Plummer 1992, Murphy 1991, Noss 1991, Rohlf 1990, Salwasser 1991, Scott et al. 1987, Tangley 1984, Wilcove 1992). All of these err in disfavor of insect conservation, and especially the less charismatic taxa. For example, vague terms like endangered and threatened have no consistent biological meaning. What constitutes a species is debatable, especially in plants and invertebrates. The use of such vague terminology creates both intended and unintended biases in conservation efforts and apparent species are often favored (Rohlf 1991). Below-species-level knowledge and conservation consideration are very rare in insects and restricted to glamorous taxa (Wilcove et al. 1992).

ESA biases in species listing that are related to apparency and appeal include 1) information is related to charisma, 2) species that are less charismatic are slower to be listed, even when data is available, 3) once listed, more attention and funding are directed toward charismatic species, and 4) small, inconspicuous species are difficult to survey (Tangley 1984). Once filtered through these biases, listed species are those thought to be especially threatened by anthropogenic impacts. Ecological specializations associated with, but not limited to, large, apparent species can increase these vulnerabilities (Murphy 1991).

Apparency-related biases in listing are also characteristic of state agency insect conservation policies. For example, the Technical Advisory Committee on Endangered Species for the Florida Committee on Rare and Endangered Plants and Animals is constrained in its efforts to identify rare species and develop recovery plans by apparency-related problems. These include small size, diversity of types, seasonality of form, lack of information and taxonomic problems (Weems 1977). Listed species are not necessarily the most worthy. They reflect the interests of taxonomic specialists and amateurs who provide the historical knowledge base needed to demonstrate population declines.

International conservation policies also generally favor charismatic species. For example, the criteria for nomination for the listing on the Berne convention (the Conservation of European Wildlife and Natural Habitats, 1979) includes a provision that the species must be easy to identify. Minute, inconspicuous insects, have undeveloped taxonomies, even in relatively well-studied areas like Europe, preventing listing of the major chunk of insect biological diversity. The International Union for the Conservation of Nature and Natural Resources (IUCN) Red Data Book is intentionally biased toward some glamorous groups, like butterflies and dragonflies, due to their high profile related to size, coloration, ease of identifying, and taxonomist specialization (Samways 1994). The aim is for these taxa to serve are umbrella species for the lesser endowed, less conspicuous species (Pyle 1978(81)). This bias is exemplified in the Sweden Red Data Preliminary List (1987) which includes 786 species, of which over 300 are Coleoptera and over 250 are Lepidoptera. This predominance reflects the high diversity of these groups, but also reflects their relatively greater number of large, conspicuous species compared to other groups. The Convention of International Trade in

Endangered Species of Wild Fauna and Flora (CITES) of 1973, an international agreement aimed at protecting rare species from economic abuses through trade, lists 10 insect species. All of these are lepidopterans (New 1995). The Bonn Convention on the conservation of migratory species of wild animals (1979) lists only the charismatic monarch butterfly.

As noted above, overcollection is rarely considered to threaten insect populations. Furthermore, there is no evidence that restrictions on collection benefit insect population numbers (Hama et al. 1989, in Sibatani 1990(92)). Inconsistent with this knowledge, most insect conservation policy consists only of restrictions on collectors or insect trade (Pyle et al. 1981). When broader-based policies exist, collection and trade restrictions are usually retained (e.g. ESA). This is a carry over of vertebrate-based evidence that population declines result from overexploitation. We need scientific consensus on if, when, where, and how collection impacts insect populations if we are to develop more appropriate insect conservation policy.

Biases in our perception and appreciation of insects contribute to the problems of policy restrictions on insect collection. These include 1) broad restrictions are often without biological rationale and may unduly restrict amateur interest, 2) restrictions are often biased in enforcement, 3) policy often does not reflect species need, but aesthetic appeal and the associated higher levels of knowledge, 4) bureaucratic, and enforcement costs may compete with habitat protection, 5) insect surveys necessary to document population declines are severely restricted, and 6) restrictions can increase exploitation when the perceived rarity is related to value (New 1995).

All insect collection is prohibited without a permit in most protected areas in many, especially developed, countries. These restrictions are meant to serve as umbrella protection measures, but such policies lack scientific bases and unduly inhibit the gathering of information and the development of amateur interest (Morris 1987, New 1990(92), Samways 1994, Sibatani 1990(92), and Thomas 1984). For example, in an effort to protect one species, the satyrid (*Erebia christi*), in some areas of Switzerland it is illegal to carry a butterfly net (New 1995). At the other extreme, The Indian Wildlife Protection Act lists approximately 450 butterfly taxa as protected and prohibits specifically the collection of these species (New 1995). The identification problems associated with small size and inter- and intraspecific phenotypic variation make such policies practically self-defeating.

All-inclusive collection restrictions are rarely enforced due to the necessary costs and bureaucracy. However, recently, the US Fish and Wildlife Service has brought several collectors to court over the taking of insect specimens without a permit on protected lands. Sporadic, inconsistent enforcement is biased in time and in space, is restricted primarily to charismatic taxa such as butterflies, and has estranged amateur collectors (for recent accounts of this controversy see *News of the Lepidopterists' Society* 38 (1-2) 1996).

When collection restrictions are less than all-inclusive, they are focused toward charismatic taxa. Such restrictions assume collection can negatively impact insect populations in general and then use collector interest to direct restrictions. This is a conservative approach that results from a lack of information. Under the British Wildlife countryside act of 1981, it is illegal to kill, take, or sell 14 insects (Drewett 1988), all of which are relatively conspicuous species. The Federal Republic of Germany prohibits collection of large lepidopterans (Morris 1987). In some European countries all butterflies are protected from collection. Interestingly, the pestiferous white pierids are exempted from such restrictions (Collins 1987, in New 1995).

In Germany, all Odonata are protected from collection, while the impact of acid rain in their conservation is largely ignored (Samways 1994). In Japan, protection legislation is limited almost exclusively to collection prohibitions for butterflies, thought

to be of little or no benefit, while preservation of insect habitats is ignored (Sibatani 1990(92)).

Many conservation, amateur, and scientific organizations have published voluntary insect collection codes. These often cover all species, but are aimed at glamorous, not necessarily rare, species. These restrictions are based on ethical rather than biological grounds. They rightly discourage collection of very rare species, over-collection of any species, and wasteful collection methods.

Insect Apparency and Practical Implications for Conservation

Practical problems with both species and larger-scale approaches to conservation that are related to apparency and appreciation of insects include 1) the paucity and complexity of taxonomic and ecological knowledge, 2) monitoring problems, and 3) biases in research, funding, amateur interest, and public support (New 1995).

There is approximately one taxonomist for every 425 described insect species (Samways 1994). This ratio creates a taxonomic impediment that becomes even more daunting when we consider that fewer than 5% of existing insect species are thought to be described (Raven 1990). The taxonomic limitations arising from the practical difficulties of observing and studying very small organisms is so great that microorganisms must be classified functionally rather than morphologically (Chapin et al. 1992). Funding and expertise interest are biased toward aesthetically appealing and economically important species, and both are most lacking in undeveloped, tropical areas where insect species diversity is highest.

Apparency differences associated with life stage, microhabitat, sex, and season are not appreciated by traditional taxonomic methods but are critical to ecologically-oriented conservation efforts (Samways 1994). Phenotypic variation, such as color polymorphisms, cryptic species, and sibling species, also confuse species-status determination. It is difficult to accurately assess the population status, develop management plans, or monitor such ambiguous groups. The use of dead specimens further compounds the problem of taxonomic designation. For example, the satyrid butterfly, *Oeneis bore*, has two color forms that behave as separate species in the field but is treated as one species using phenotypic techniques that rely on dead specimens (Ferris 1986). Naturalists studying live animals in their natural habitats and molecular systematic methods are necessary to overcome some of the shortcomings of traditional taxonomic methods. Both practical and theoretical problems with species status designation have not been adequately confronted in species-level conservation approaches. Community- and landscape-level conservation strategies overcome some of these taxonomic-related problems but these approaches also rely heavily on species classification.

The extreme diversity, small size, inconspicuous habits, and the taxonomic and ecological ignorance associated with these aspects of insect biology prevent species-by-species inventorying. New (1995) suggests three strategies aimed at getting around this problem: 1) the use of indicator groups, 2) taxonomic reduction, and 3) the use of ecologically functional groups. Taxonomic reduction includes grouping by higher than species level taxa and grouping by morphological characters or recognizable taxonomic units. Both taxonomic reduction and the use of functional groups rely on apparency-related adaptations to alleviate other apparency-related obstacles in insect conservation. For example, size, coloration, and morphological structures related to feeding strategies are used to group species with similar ecological function.

The assessment of potential impacts of climate change, pesticides, non-indigenous species, and collection on insect populations is primarily restricted to aesthetically pleasing and economically important species. This reflects interest, knowledge and

monitoring methodologies that are beauty- or necessity-biased. The potential impacts of pesticides are little-studied for any non-target species. To date, monitoring the impacts of non-indigenous species, including biological control agents, is almost exclusively restricted to economically important or glamorous species (Ehler 1991). It is expected that further studies will confirm the environmental safety of most classical biological control agents (Samways 1988). However, the potential environmental dangers of releasing irretrievable, mobile, evolving organisms and our paucity of data on the impacts of these non-indigenous species on their new environment are forming a barricade to the development of this important pest-control strategy (Samways 1994). Most attempts to document potential negative impacts of collecting on insect populations come from studies on attractive taxa, almost exclusively butterflies. This is appropriate since they are particularly sought after, but the documented impacts or lack thereof may not be representative of such a diverse group as the Insecta.

Problems Associated with Single Species Approaches to Insect Conservation

Species listing and the development of recovery plans are very demanding in terms of both historical and ecological information and financial and public support. We can afford these costs only for relatively glamorous species and only in relatively wealthy nations. For example, in the IUCN Invertebrate Red Data Book (1983), all examples of anthropogenic impacts on insects resulting from changes in land, water, pollution, loss of associated species, and importation of exotics were documented for large, apparent species in developed countries. Only water-pollution impacts were noted for inconspicuous species, probably reflecting a long history of using invertebrates as environmental indicators of water quality (Kremen et al. 1993).

Under the ESA, conservation priorities are based on biological uniqueness, degree of threat, and opportunity for success (Mann & Plummer 1992). Each of these is highly biased in favor of apparent and appreciated species for practical and emotional reasons. Most conservation efforts have been aimed at butterflies because they are obvious, enjoy high amateur interest, are easy to see and study, and are both harmless to humans and beneficial as pollinators. These aspects of butterfly biology make determination of uniqueness and threat easier to identify and also incite public support necessary to monitor and manage insect populations. In contrast, inconspicuous and unattractive parasites are generally ignored in conservation, even though they are considered extremely diverse and of conservation concern due to their generally extreme, obligatory specializations (Windsor 1995). Parasites are often only discovered when their hosts become extremely rare or extinct, and then they are often dismissed or even attacked in an effort to boost their host's survival (Windsor 1995). The demise of the Passenger Pigeon stands as one of the most exemplary, best-appreciated species losses. The simultaneous loss of its lice parasite has gone unnoticed and without concern (Stork & Lyal 1993, in Windsor 1995).

Species-oriented management plans are restricted almost exclusively to butterflies. The European Large Copper butterfly, *Lycaena dispar batava*, has been augmented since the 1930s, and this effort is expected to remain necessary for its continued survival in the wild (New 1995). Such costly efforts are not feasible for even the most well-studied and well-appreciated species in developed countries. They are likely to be counter-productive in understudied, speciose areas such as the tropics.

As with vertebrates, intensive management efforts, such as captive breeding, translocation and reintroduction programs, are initiated when species are at the brink of extinction with little chance of recovery. These risky and unpredictable tactics are costly in terms of funding, time, expertise, and research. They are restricted to charismatic or economically important species in developed countries. In Europe, 323

insect reintroductions or reinforcements have been attempted, with less than 60% established. All of these efforts were directed at butterflies (Oates & Warren 1990, in Samways 1994).

Recent releases of captive-bred Schaus Swallowtails (*Papilio aristodemus ponceanus*), an endangered subspecies under the ESA, demonstrate the sort of practical considerations that insect apparency forces on intensive management efforts. Researchers had to change from releasing cryptic pupae to adults because 65-99% of the pupae were lost to predation when placed in their natural habitat. Even in this relatively well-studied species, it is unknown how these rates compare to natural levels of predation, but it is thought that unnatural densities, positioning, and artificial pupation bases used in the releases may have voided the larvae's crypsis (Jaret Daniels, pers. comm.).

Variation in insect form and function related to seasonality, polymorphic types, sexual differences, and life stage specializations is an obstacle in species-oriented conservation strategies (Samways 1994). Such variation adds both confusion and time to the listing process and complexity to management plans, with apparent forms being favored. For example, critical habitat protection under the ESA includes areas outside the geographic area typically occupied, including hilltopping, hibernation, and aestivation areas. These are more likely to be known, and their preservation supported, for charismatic species.

Insect Apparency Biases and Implications for Large-Scale Conservation Strategies

It is not feasible or biologically rational to appraise insects species-by-species for conservation needs, due to their extreme diversity in species and ecological roles, and habitat requirements. More and more, single-species approaches are combined with ecosystem approaches to conservation. Larger-scale (than species) approaches rely on reducing the volume and complexity of information necessary to preserve and manage species and natural areas through innovative methods of assessment, management, and monitoring (Hunter 1991). These approaches rest on empirical knowledge, ecological theories, and model development that are in their infancy (Salwasser 1991). Large, brightly colored insects are most likely to contribute to each of these. They are also more likely to enjoy funding priority and expert attention.

Large-scale approaches in conservation relieve the need to prioritize conservation efforts by values associated with charisma. However, biases toward large, conspicuous species are retained for monitoring and assessing conservation sites. Five types of species are of paramount importance in ecosystem approaches to conservation. These include 1) species used as indicators of diversity or monitors of environmental change, 2) keystone species: those that play a critical role in the structure and function of an ecosystem, 3) umbrella species: those whose conservation serves to protect other species, 4) flagship species used as a focus for funding and generating support, and 5) species that are particularly vulnerable to extinction due to their biology and/or ecology (Noss 1991). The discovery and use of each of these types of species are apparency-biased due to disproportional levels of information and the prevailing anthropocentric conservation perspective.

Insects are increasingly used as indicators of biogeographic zones, areas of endemism, community richness, diversity, naturalness, typicalness, and centers of evolutionary radiation in conservation planning (see Kremen 1992, Kremen et al. 1993, and references therein). Favored groups are readily observed and collected, are well known taxonomically and ecologically, and are valued aesthetically and/or economically (Kremen et al. 1993). These biases are intended and often necessary. They may or may not be biologically legitimate. For example, dipteran and hymenopteran para-

sitoids are potentially good indicator species, due to their association with diverse ecological niches and microhabitats, widespread occurrence and correlated trends with other groups. However, Disney (1986b, in New 1995) showed that mapping the distributions of Diptera is limited due to practical shortcomings associated with their apparency. We must use the distribution and abundance of obvious, easily sampled species.

To better assess representativeness, uniqueness, and typicalness of areas in order to set conservation priorities, we need to develop more efficient sampling methods (New 1995). The use of parataxonomists or amateurs to help with the tremendous amount of sorting and identification necessary for conservation-related work is becoming increasing popular (but see Rosenberg et al. 1986). Such innovative approaches are necessary and effective, but accuracy is generally sacrificed for efficiency. Furthermore, the loss of accuracy is not consistent across taxa, but is apparency biased. For example, in a study of the performance of non-specialists in assessing samples of aquatic insects, Cranston and Hillman (1992) showed that increased variability was correlated with small body, increased number of closely related taxa, and morphological variability within species.

In management, insects are used to monitor human disturbance and ecological change, including changes in habitat, ecological disruption, climate change, and pollution. Insects are sometimes favored as monitors over vertebrates because they are particularly sensitive, respond rapidly, and offer a smaller-scale probe (e. g. Kremen et al. 1993, New 1995, Sparrow et al. 1994, Thomas & Mallorie 1985). They are also increasingly used to supplement vertebrate monitoring because of their unique habitat needs and responses to anthropogenic threats. Useful groups must be ecologically specialized and, due to the need for reproducible sampling methods and historical information, they are generally large, and apparent. Butterflies are preferred as indicator species and monitors of environmental change specifically because of their apparency and charisma (Samways 1994). They are specialized, well known taxonomically and ecologically, have established monitoring methods, and strong amateur interest and public support (Kremen 1992, Kremen et al. 1993, Thomas 1991).

Umbrella species are notable taxa that are characteristic of a particular habitat that, when preserved, benefit many unstudied, unappreciated species in the community. The value of a particular species to serve as a protective umbrella is based on ecological requirements, such as the need for large diverse habitats. However, the need for historical and ecological information, as well as public support, favors the designation of apparent and appealing species for this role (New 1994). The monarch butterfly is an example of an umbrella species. The focus of research, conservation attention, and public support for monarch conservation enhances the potential to preserve the remaining flora and fauna of the highly fragmented, isolated fir forest relics that constitute their threatened overwintering grounds in the highlands of Mexico.

DISCUSSION

Large, conspicuously colored insect taxa are given special attention in species-oriented conservation. This focus is both legitimate and intended. It is based on special threats and ecological needs associated with a species' apparency and on conservation values, public support and policy aims. However, the apparency bias is also a sometimes unintended, and sometimes unnoticed, bias, resulting from practical aspects of insect ecology and conservation methodology.

Empirical and theoretical contributions by entomologists are needed to improve existing species-focused conservation efforts, to better develop larger scale approaches, and to help build conservation policies that better reflect the unique conser-

vation needs of insects. Particularly important is the need to develop generally applicable population models using representative insects, to develop better sampling methods, and to better integrate conservation and agriculture programs.

In species-oriented conservation efforts, ALL insects are relatively small and inconspicuous, and are highly disfavored in conservation efforts relative to their vertebrate co-inhabitants. This reflects the lack of ecological and taxonomic knowledge, research, funding, public and policy support, and sampling problems. These impediments point to the value of increasing large-scale conservation research, education, and policy directives. The use of insects as tools for assessing, managing and monitoring landscapes promotes ecosystem and regional approaches that are critical to all future conservation efforts. Large-scale conservation strategies also rely on both intended and unintended biases toward large, conspicuous insects. Entomologists can help to identify and lessen detrimental biases and document strengths through theoretical and empirical contributions.

The relatively recent focus on insects as targets and tools in conservation points to the need to broaden the discipline of entomology and to better bridge our work with amateurs, ecologists and conservation biologists. The study of pest and glamour species has much to offer conservationists. However, to achieve the broader goals of sustainability in agriculture and conservation, entomologists need to discard our own biases. We need to better address the 99% of species not generally considered in pest-oriented research (Wilson 1987). We cannot afford to cut our funding or attention to the development of innovative, ecologically sensible solutions to pest problems. However, we can no longer ignore the fact that sustainable agriculture rests on functioning natural ecosystems both near and far from the agricultural fields. These natural systems are insect-dominated, but by neither characteristically beautiful or pestiferous species. Their study is critical both to the future sustainability of agriculture and to agriculture's contribution to the conservation of biological diversity.

Effective and efficient conservation strategies cannot depend solely on public support for charismatic species that are emotionally valued. Although we can, and must, learn affinities for species that are unfamiliar to and different from ourselves, we most readily learn about, care about, and make sacrifices for species that are apparent, aesthetically appealing and demonstrate positive human benefits. Exposure to glamorous insects will help bridge the gap between our natural human affinity for the cute and cuddly and the needed appreciation of often non-intuitive ecological principles. Until we cross that bridge, we will continue to make irresponsible personal and social decisions. Increasing the ecological awareness of policy makers and the general public is the most important and timely conservation challenge. Entomologists study the most diverse, ubiquitous and, arguably, most important taxa in conservation. We are the best equipped to rid negative biases against insects and to instill an appreciation of the importance of insects to our sustainable future.

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DISTRIBUTION OF *NEOSEIULUS CUCUMERIS* (ACARINA: PHYTOSEIIDAE) AND ITS PREY, *THRIPS PALMI* (THYSANOPTERA: THRIPIDAE) WITHIN EGGPLANTS IN SOUTH FLORIDA

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ABSTRACT

The distribution of the predacious mite *Neoseiulus cucumeris* (Oudemans) and its prey, *Thrips palmi* Karny, was studied in eggplant plots in Homestead, Florida. *Neoseiulus cucumeris* was more abundant on fruits ($\overline{X}$ = 3.39 ± 0.20) than on leaves ($\overline{X}$ = 0.95 ± 0.16) and it was not found in the flowers. *Thrips palmi* was more abundant on the leaves ($\overline{X}$ = 17.97 ± 5.07) than on the fruits ($\overline{X}$ = 3.22 ± 0.70) and flowers ($\overline{X}$ = 0.93 ± 0.03). Predacious mite populations on the fruits and leaves increased with *T. palmi* populations increase. Both predator and prey populations were low on the youngest leaf ($\overline{X}_{predator}$ = 0.00 ± 0.00; $\overline{X}_{prey}$ = 1.75 ± 0.28) and high on the oldest leaf ($\overline{X}_{predator}$ = 1.92 ± 0.79; $\overline{X}_{prey}$ = 50.83 ± 11.64). *Neoseiulus cucumeris* and *T. palmi* were more abundant on the adaxial surface of the leaf ($\overline{X}_{N. cucumeris}$ = 1.58 ± 0.56; $\overline{X}_{T. palmi}$ = 42.77 ± 8.29). Predators aggregated mostly on the adaxial base of the midrib vein. The fourth leaf is recommended for population sampling studies because the predators aggregate at the base of the adaxial midrib and *T. palmi* population levels are not extreme on that leaf.

Key Words: thrips, predacious mites, distribution, biological control

RESUMEN

Fue estudiada la distribución del ácaro depredador *Neoseiulus cucumeris* (Oudemans) y de su presa, *Thrips palmi* Karny, en Homestead, Florida. *Neoseiulus cucumeris* fue más abundante en los frutos ($\overline{X}$ = 3.39 ± 0.20) que en las hojas ($\overline{X}$ = 0.95 ± 0.16) y no fue encontrado en las flores. *Thrips palmi* fue más abundante en las hojas ($\overline{X}$ = 17.97 ± 5.07) que en los frutos ($\overline{X}$ = 3.22 ± 0.70) y flores ($\overline{X}$ = 0.93 ± 0.03). En los frutos y las hojas, la población del ácaro depredador aumentó con la población de *T. palmi*. Ambas poblaciones fueron bajas en la hoja más joven ($\overline{X}_{depredador}$ = 0.00 ± 0.00; $\overline{X}_{presa}$ = 1.75 ± 0.28) y altas en la hoja más vieja ($\overline{X}_{depredador}$ = 1.92 ± 0.79; $\overline{X}_{presa}$ = 50.83 ± 11.64). *Neoseiulus cucumeris* y *T. palmi* fueron más abundantes en el envés de la hoja ($\overline{X}_{N. cucumeris}$ = 1.58 ± 0.56; $\overline{X}_{T. palmi}$ = 42.77 ± 8.29). Los depredadores se agregaron mayoritariamente en la base de la vena central, en el envés de la hoja. Se recomienda la cuarta hoja para estudios de muestreo porque los depredadores se concentran en la base del envés de la vena central y porque los niveles polacionales de *T. palmi* no son extremadamente altos o bajos en esa hoja.

The melon thrips, *Thrips palmi* Karny, is an important vegetable pest in South Florida, attacking beans, cucurbits, eggplants, peppers, and potatoes (Seal & Baranowski 1992). *Thrips palmi* was described from Sumatra in 1925. It was considered an insect without economic importance for more than 50 years, but since 1978 it became a major threat to vegetable growers in Asia (Sakimura et al. 1986). In 1985 *T.*

palmi was detected in the Caribbean (Denoyes et al. 1986), and in 1991 it was found in Homestead, Florida (South 1991). Losses of more than 10 million dollars caused by *T. palmi* were reported on peppers in Palm Beach County, Florida, in 1993 (Nuessly & Nagata 1995).

The predacious mite *Neoseiulus cucumeris* (Oudemans) has been tested in the field as a potential biological control agent for suppression of *T. palmi* on eggplants (Castineiras et al. 1997). *Neosiulus cucumeris* is mass reared on fungus mites in wheat bran and sold for release in commercial greenhouses (Hoy & Glenister 1991). In eggplants, *N. cucumeris* is released by sprinkling the bran on top of the leaves (Castineiras et al. 1997).

To evaluate the efficacy of a biological control agent, both the predator and the prey must be monitored from the moment of release through harvest; thus, knowledge of their distribution within the plant is essential.

There is no information on the distribution of *N. cucumeris* in eggplant. *Thrips palmi* is known to be more abundant on eggplant leaves than on flowers and fruits (Kawai 1988). We examine here the distribution pattern of *N. cucumeris* and *T. palmi* within eggplants where controlled releases of the predator were made.

Materials and Methods

The study was conducted from Oct. 1995 through Apr. 1996 at the University of Florida Tropical Research and Education Center in Homestead. Three 11 × 12.5 m plots spaced 2.5 m apart were set in beds 0.2 m high and 0.9 wide, covered with black polyethylene mulch to retard weed growth. Five-week old eggplant (*Solanum melongena* var. Classic) seedlings were transplanted 0.6 m apart in double rows on 12 October 1995. A mix of maneb [1.38 kg (AI)/ha] and copper hydroxide [2.88 kg (AI)/ha] was sprayed weekly to prevent diseases. Weeds in the interbed spaces were controlled with a mixture of paraquat [0.87 kg (AI)/ha] and diquat [0.83 kg (AI)/ha].

Neoseiulus cucumeris (IPM Laboratories, Inc., Locke, NY) was released in wheat bran on the top of the leaves at a ratio of one predator per prey which is the recommended ratio for biological control of *T. palmi* by *N. cucumeris* (Castineiras et al. 1997). Number of *T. palmi* per plant was estimated before predator releases by averaging the number of larval and adult thrips on the second, fourth, and sixth leaves of 10 shoots on 10 randomly selected plants per plot and multiplying the mean by the average number of leaves per plant. The first leaf longer than 2.5 cm from the base to the apex on a shoot was considered the terminal leaf. One hundred predators per plant were released on week 7 after transplanting, when thrips population averaged 99.0 per plant, and 200 predators per plant were released on week 10 after transplanting, when thrips population averaged 198.5 per plant.

A sample of ten flowers, 30 fruits, and 30 leaves per plot was taken at random on the first and second week after each release. The fruit sample consisted of 10 small (2-4 cm long), 10 medium (5-10 cm long) and 10 large (15-20 cm long) fruit taken at random within each plot. The leaf sample consisted of the first, fourth, and seventh leaves of a shoot taken at random on each of 10 plants per plot. All samples were collected separately and taken to the laboratory in plastic bags.

The number of *T. palmi* larvae and adults and all stages of *N. cucumeris* inside the flowers, under the fruit calyx, and on the leaves was counted under the microscope. The leaf surface was divided in two halves, from the center to the tip and from the center to the base. Each half was also divided into 4 areas: Abaxial and adaxial leaf surfaces and abaxial and adaxial midribs.

The data from the four samplings were averaged for each replicate. Data were square root transformed and analyzed using general linear models (SAS Institute,

Inc. Cary, NC). A one-way ANOVA was used for fruit data, and three-way ANOVAS were used for leaf data. Leaf position (first, fourth, and seventh), leaf side (abaxial and adaxial) and leaf area (tip, base, midrib tip and midrib base) were considered the main effects in the three-way ANOVAS. Curves for *N. cucumeris* against *T. palmi* populations on leaves and fruits were fit by nonlinear regression analysis using TableCurve 2-D (Jandel Scientific, Inc., San Rafael, CA).

Results and Discussion

Neoseiulus cucumeris was observed on the fruits ($\overline{X}$ =3.39 ± 0.20) and leaves ($\overline{X}$ = 0.95 ± 0.16) but not inside the flowers. The number of *T. palmi* was lower in the flowers ($\overline{X}$ = 0.93 ± 0.03) than on the fruits ($\overline{X}$ = 3.22 ± 0.70) and leaves ($\overline{X}$ = 17.97 ± 5.07), as previously documented (Kawai 1988).

Predators tend to aggregate where prey densities are high (Varley et al. 1974). Regressions of *N. cucumeris* density on *T. palmi* density yielded significant relationships for the leaves [No. *N. cucumeris* = 1.18 + 0.01(No. *T. palmi*)$^{1.23}$; r^2 = 0.99, F = 867.17] and fruits [No. *N. cucumeris* = -24.72 + 4.04(No. *T. palmi*)$^{0.77}$; r^2 = 0.95, F = 63.63]. The regression equations show that increases in prey population were followed by increases in predator population on both leaves and fruits. *Neoseiulus cucumeris* also congregates on cucumber and cabbage leaves with high thrips population densities after release (Gillespie 1989, Hoy & Glenister 1991).

Neoseiulus cucumeris and *T. palmi* populations increased with fruit size (Table 1). *Thrips palmi* was on the fruit from the developing ovary phase through fruit maturity. After petal abscission, when the fruits were 2-4 cm long and the calyx began to open, *T. palmi* and *N. cucumeris* aggregated under the sepals.

Neoseiulus cucumeris preferred the ridges of the underside of the fruit sepals over the leaves for oviposition. Eighty-nine percent of *N. cucumeris* eggs were found under the sepals and 11% on the leaves. On the leaves, predator eggs were always found at the base of the adaxial midrib, hidden under the trichomes.

In the shoots, numbers of *N. cucumeris* and *T. palmi* increased from the first through the seventh leaf (Table 2). Both predator and prey were more abundant on the adaxial surface of the leaves (Table 3). *Neoseiulus cucumeris* populations concentrated mostly on the midrib base. However, *T. palmi* populations distributed all over the leaf surface and seemed to avoid the midrib tip (Table 4).

Analyses of variance showed significant interactions of leaf position, leaf surface, and leaf area for both the predator and the prey (Tables 5 and 6). *Neoseiulus cucumeris* population density was highest on the adaxial midrib base of the seventh leaf. On

Table 1. Numbers of *N. cucumeris* and *T. palmi* on eggplant fruits of different sizes.

Fruit length	*N. cucumeris* (Mean ± SE)[1]	*T. palmi* (Mean ± SE)[2]
2-4 cm	1.23 ± 0.12	1.76 ± 0.08
5-10 cm	3.56 ± 0.12	3.40 ± 0.23
15-20 cm	5.36 ± 0.14	4.50 ± 0.15

[1]ANOVA on square root transformed data, untransformed means are presented. F = 257.69, p > 0.0001, df = 2, 6.

[2]ANOVA on square root transformed data, untransformed means are presented. F = 67.20, p > 0.0001, df = 2, 6.

TABLE 2. NUMBERS OF *N. CUCUMERIS* AND *T. PALMI* ON THE FIRST, SECOND AND THIRD LEAVES OF EGGPLANT SHOOTS.

Leaf position	*N. cucumeris* (Mean ± SE)[1]	*T. palmi* (Mean ± SE)[2]
First	0.00 ± 0.00	1.75 ± 0.28
Fourth	0.54 ± 0.30	20.04 ± 3.92
Seventh	1.92 ± 0.79	50.83 ± 11.64

[1]ANOVA on square root transformed data, untransformed data means are presented. F = 282.04, p > 0.0001, df = 2, 48.
[2]ANOVA on square root transformed data, untransformed data means are presented. F = 2702.70, p > 0.0001, df = 2, 48.

TABLE 3. NUMBERS OF *N. CUCUMERIS* AND *T. PALMI* ON THE ABAXIAL AND ADAXIAL SURFACES OF EGGPLANT LEAVES.

Leaf side	*N. cucumeris* (Mean ± SE)[1]	*T. palmi* (Mean ± SE)[2]
Abaxial	0.05 ± 0.03	5.63 ± 0.99
Adaxial	1.58 ± 0.56	42.77 ± 8.29

[1]ANOVA on square root transformed data, untransformed means are presented. F = 501.89, p > 0.0001, df = 1, 48.
[2]ANOVA on square root transformed data, untransformed means are presented. F = 3883.74, p > 0.0001, df = 1, 48.

the fourth leaf, predators were found only at the base of the adaxial midrib (Table 5). Highest *T. palmi* density was found on the adaxial tip of the seventh leaf (Table 6).

Considering that predator and prey only coincided on leaves and fruits, both leaves and fruits can be used for sampling proposes. It is more convenient to sample the leaves because they are easier to handle than the fruits. The fourth leaf is best for monitoring *N. cucumeris* and *T. palmi* because the predators aggregate at the base of

TABLE 4. NUMBERS OF *N. CUCUMERIS* AND *T. PALMI* ON DIFFERENT EGGPLANT LEAF AREAS.

Leaf areas	*N. cucumeris* (Mean ± SE)[1]	*T. palmi* (Mean ± SE)[2]
tip	0.00 ± 0.00	31.88 ± 11.52
base	0.38 ± 0.21	31.00 ± 10.61
midrib tip	0.08 ± 0.04	5.22 ± 1.10
midrib base	2.80 ± 1.05	28.72 ± 1.05

[1]ANOVA on square root transformed data, untransformed means are presented. F = 344.98, p > 0.0001, df = 3, 48.
[2]ANOVA on square root transformed data, untransformed means are presented. F = 443.89, p > 0.0001, df = 3, 48.

TABLE 5. NUMBERS OF *N. CUCUMERIS* ON EGGPLANT LEAVES. INTERACTION LEAF SURFACE × LEAF AREA × LEAF POSITION[1].

Leaf surface × leaf area	First leaf (Mean ± SE)	Fourth leaf (Mean ± SE)	Seventh leaf (Mean ± SE)
Abaxial tip	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Abaxial base	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Abaxial midrib tip	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Abaxial midrib base	0.00 ± 0.00	0.00 ± 0.00	0.68 ± 0.32
Adaxial tip	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Adaxial base	0.00 ± 0.00	0.00 ± 0.00	2.33 ± 0.44
Adaxial midrib tip	0.00 ± 0.00	0.00 ± 0.00	0.50 ± 0.00
Adaxial midrib base	0.00 ± 0.00	4.33 ± 0.33	11.83 ± 0.44

1ANOVA on square root transformed data, untransformed means are presented. F = 73.51, p > 0.0001, df = 6, 48.

TABLE 6. NUMBERS OF *T. PALMI* ON DIFFERENT AREAS ON EGGPLANT LEAVES. INTERACTION LEAF SURFACE × LEAF AREA × LEAF POSITION.[1]

Leaf surface × leaf area	First leaf (Mean ± SE)	Fourth leaf (Mean ± SE)	Seventh leaf (Mean ± SE)
Abaxial tip	2.66 ± 0.33	19.33 ± 2.33	4.66 ± 0.57
Abaxial base	1.33 ± 0.33	4.00 ± 0.57	3.00 ± 0.00
Abaxial midrib tip	1.00 ± 0.01	3.00 ± 0.57	14.00 ± 1.52
Abaxial midrib base	0.00 ± 0.00	3.00 ± 0.57	11.66 ± 0.88
Adaxial tip	1.00 ± 0.01	28.00 ± 0.57	135.66 ± 3.92
Adaxial base	4.66 ± 0.33	53.00 ± 1.52	120.00 ± 1.15
Adaxial midrib tip	1.33 ± 0.33	5.33 ± 0.88	6.66 ± 0.33
Adaxial midrib base	2.00 ± 0.01	44.66 ± 0.66	111.83 ± 3.78

1ANOVA on square root transformed data, untransformed means are presented. F = 253.66, p > 0.0001, df = 6, 48.

the adaxial midrib and *T. palmi* population levels are not extremely high or low on that leaf.

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APHIDS ASSOCIATED WITH CHRYSANTHEMUMS IN THE UNITED STATES

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ABSTRACT

A key to 15 aphid species known to colonize cultivated and native chrysanthemums in the United States is provided; each species is described and characteristic structures are illustrated. A brief summary of taxonomic characters, cultivated and wild hosts, and distribution within the United States and throughout the world are also given for each species.

Key Words: aphididae, aphids, chrysanthemum, taxonomic keys

RESUMEN

Se ofrece una clave para identificar quince especies de áfidos que se sabe colonizan crisantemos, cultivados y indígenas, en los Estados Unidos; se describen e ilustran las estructuras características de cada especie. Se incluye para cada especie un resumen breve de las características taxonómicas, los hospedantes cultivados y indígenos, y la distribución en los Estados Unidos y por todo el mundo.

Chrysanthemums are a long-time favorite of both professional growers and hobbyists. The genus *Chrysanthemum* (Asteraceae = Compositae) includes such well-known flowers as shasta-daisies, pyrethrums, marguerites or Paris-daisies, and annual chrysanthemums (Everett 1981). The great diversity of the plant's form, growing habits, and color has contributed to the popularity of the cultivated varieties of this flower, namely *Chrysanthemum morifolium* Ram. Although the share of the chrysanthemum market has declined since 1981 (Voigt 1989), potted chrysanthemums were the second leading potted flowering plant produced in the United States in 1987 (Anonymous 1991). The wholesale value of potted and florist chrysanthemums for 1993 was more than $95 million and nearly $9 million for standard chrysanthemums for 36 reporting states (Anonymous 1994).

Several species of aphids can become established on greenhouse and outdoor plantings. Large colonies of aphids can greatly reduce plant vigor and kill the plant through mechanical injury. However, even a few feeding aphids can damage plants because they produce a sticky substance called honeydew. As the aphids feed, honeydew is excreted and accumulates on the leaves and flowers. In the higher humidity of a greenhouse, honeydew provides an excellent substrate for the growth of black sooty mold. Large areas of mold covering the leaves can reduce photosynthesis and also result in an unattractive plant with a much lower market value. Additionally, aphids can transmit several viral diseases that injure chrysanthemums.

A diverse aphid fauna—at least 15 species—is known to colonize cultivated and wild chrysanthemums in the United States. A brief summary of taxonomic characters, hosts, worldwide distribution, and U.S. distribution is given for each of the 15 species. Aphids treated here are: *Aphis fabae* Scopoli, *Aphis gossypii* Glover, *Aulacorthum cir-*

cumflexum (Buckton), *Aulacorthum solani* (Kaltenbach), *Brachycaudus cardui* (L.), *Brachycaudus helichrysi* (Kaltenbach), *Coloradoa rufomaculata* (Wilson), *Macrosiphoniella sanborni* (Gillette), *Macrosiphoniella subterranea* (Koch), *Macrosiphoniella tanacetaria* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), *Myzus ascalonicus* Doncaster, *Myzus ornatus* Laing, *Myzus persicae* (Sulzer), and *Pleotrichophorus chrysanthemi* (Theobald). Descriptions, figures, and keys are included as an aid for those responsible for detection, identification, and control of aphids associated with chrysanthemums in the United States.

Materials and Methods

In the synonymy section, one asterisk (*) represents the name used by Palmer (1952) and two asterisks (**) represent the name appearing in Blackman & Eastop (1984). Common names are those approved by the Entomological Society of America (Stoetzel 1989).

Information on distribution and hosts is taken from labels on slides in the National Collection of Insects, Beltsville, Maryland, and from records in Palmer (1952), Smith & Parron (1978), and Blackman & Eastop (1984).

Identifications can be made of live aphids, alcohol preserved specimens, or cleared and slide mounted specimens. In the illustrated keys, the species are grouped by morphological differences in antennae, antennal tubercles, cornicles, and caudal setae. Characters used in the keys are apparent with a dissecting microscope with a power of at least 16X. Relative body size of aphid species is after Blackman & Eastop (1984): body length < 2.0 mm are "small," 2.0 - 3.0 mm are "medium," and > 3.0 mm = "large." Body length is measured dorsally from the center of the frons to the end of the abdomen, excluding the cauda (see generalized aphid, Fig. 1). Length of the antennal "terminal process" is measured as the distance from the large primary sensorium to the tip. Length of the "base" of the antenna is measured from the basal portion of the last antennal segment to the apex of the primary sensorium. The keys are not intended for identification of single, errant aphids but should be used for individuals fully colonizing chrysanthemums.

Aphids on Chrysanthemums in the United States

Aphis fabae Scopoli 1763

Figs. 1, 2, 3

Synonymy:

* & ***Aphis fabae* Scopoli

ESA approved common name: bean aphid

Other common name: black bean aphid

Taxonomic characters: Wingless adult female.- In life, body dull black. Small to medium sized, body length 1.8-2.6 mm, rounded. Antenna 6 segmented; tubercles not developed; terminal process approximately 2⅔-3 times length of base of antennal segment VI; no secondary sensoria on antennal segment III; setae on antennal segment III longer than diameter of segment. Cornicle dark, cylindrical, 3-3½ times as long as wide. Cauda dark, elongate with 8-12 lateral setae and 2-5 dorsolateral setae.

Winged adult female.—In life, body dull black, usually with dark lateral areas and bands on dorsum of abdomen; immatures often covered with wax; alatoid nymphs with tessellated abdomen. Small to medium sized, body length 1.9-2.4 mm, rounded. Antenna 6 segmented; tubercles not developed; terminal process approximately 2½-

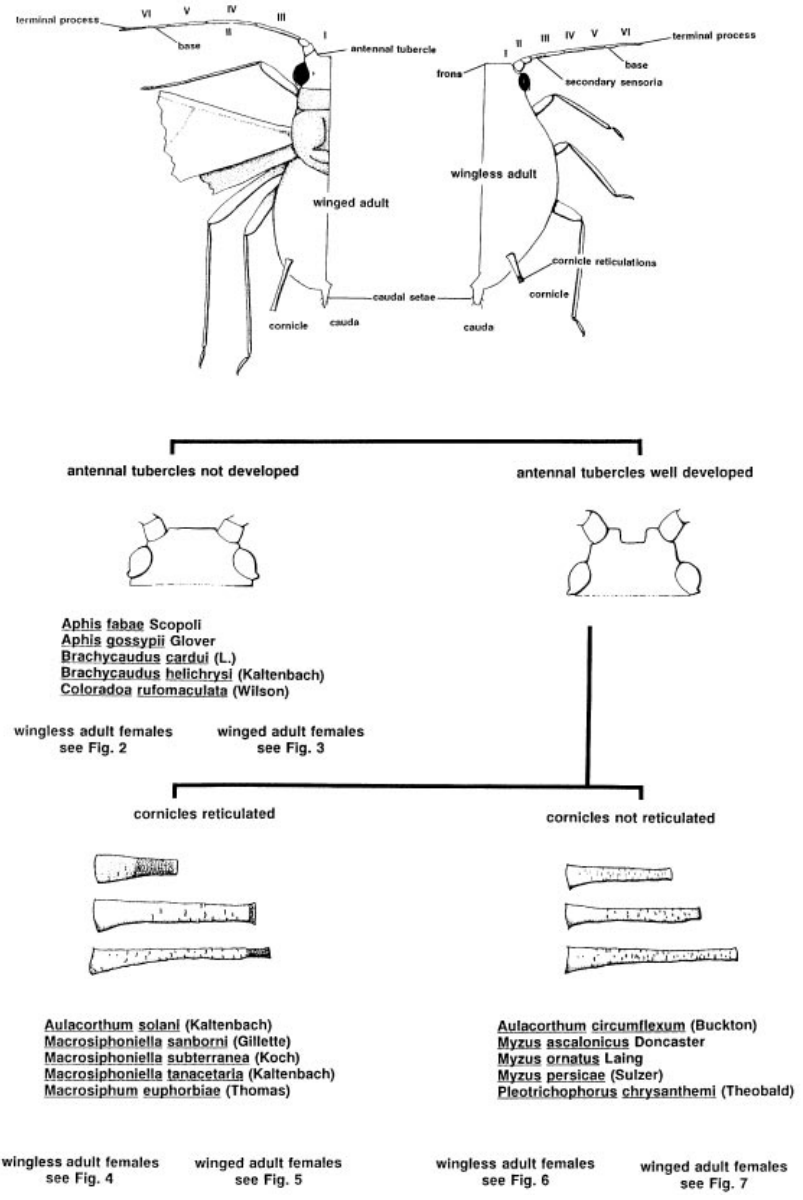

Fig. 1. Pictorial key to fifteen aphid species that colonize chrysanthemums in the United States.

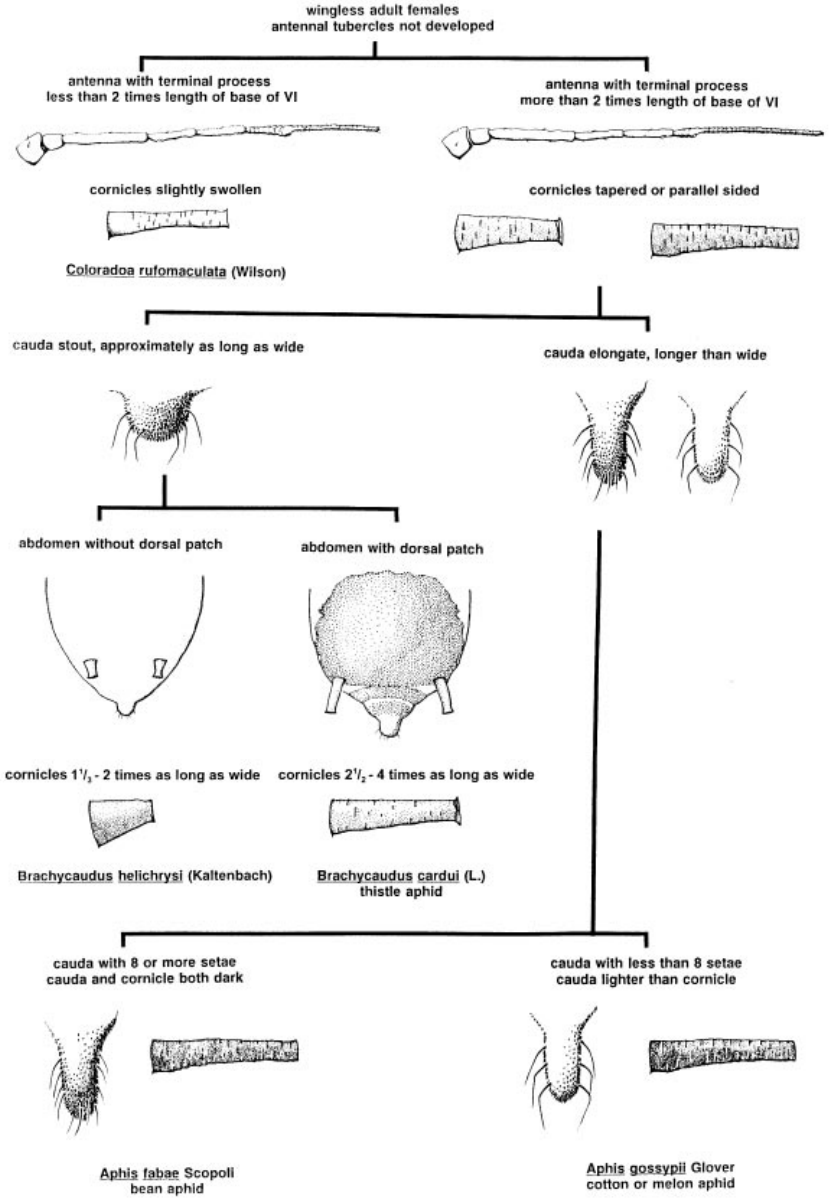

Fig. 2. Pictorial key to wingless adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles not developed.

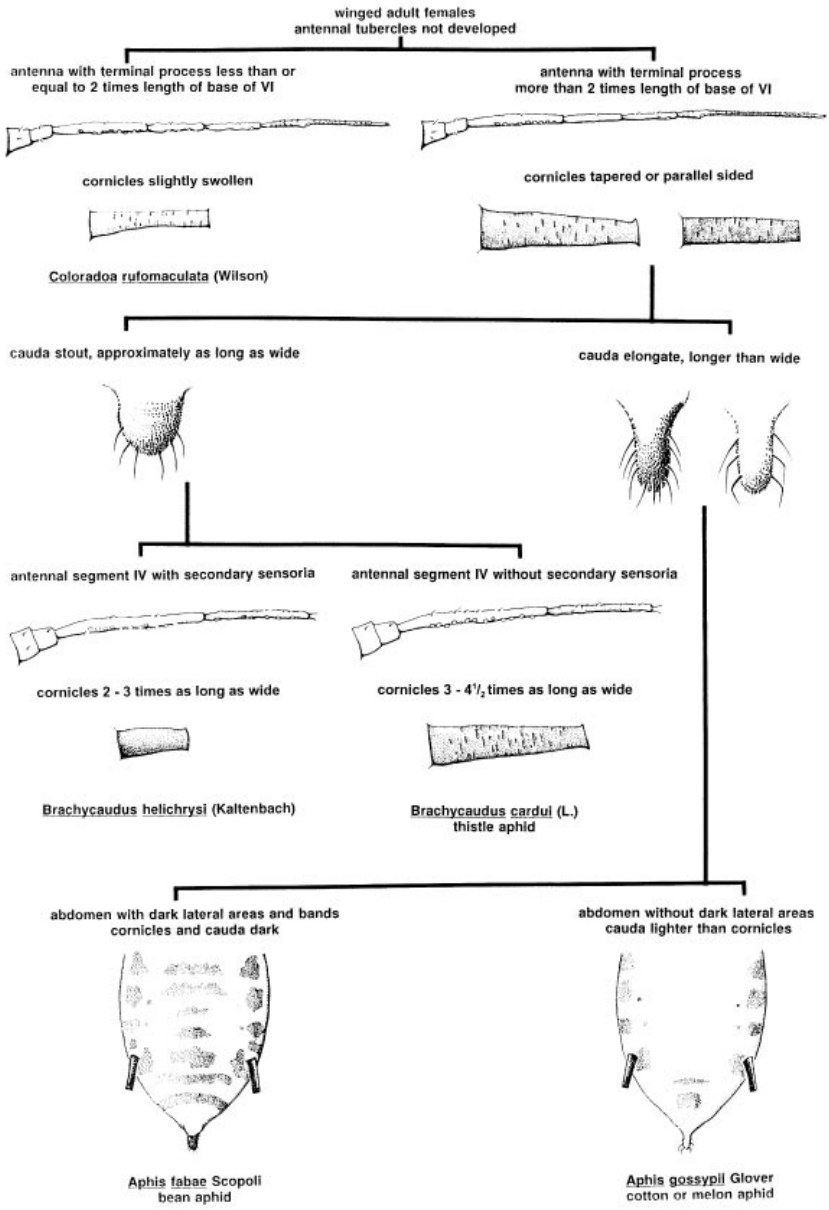

Fig. 3. Pictorial key to winged adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles not developed.

3¼ times length of base of antennal segment VI; 6-16 secondary sensoria of variable size on antennal segment III; 0-7secondary sensoria on antennal segment IV; setae on antennal segment III longer than diameter of segment. Cornicle dark, cylindrical, 3¼-4½ times as long as wide. Cauda dark, elongate with 8-12 lateral setae and 0-4 dorsolateral setae.

Hosts: Principal hosts are species of *Euonymus* and *Viburnum*, however, *A. fabae* is polyphagous on many additional plants.

U.S. distribution: Throughout.

World distribution: Widely distributed throughout the world.

Comments: *Aphis fabae* transmits 42 plant viruses but is not a known vector of the chrysanthemum viruses (Chan et al. 1991).

Aphis gossypii Glover 1877
Figs. 1, 2, 3

Synonymy:

* & ***Aphis gossypii* Glover

ESA approved common name: cotton or melon aphid

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body color varying from dark green to pale yellow or nearly white. Small sized, body length 1.4-1.7 mm, rounded. Antenna 6 segmented; tubercles not developed; length variable, terminal process approximately 2-3¼ times length of base of antennal segment VI; antennal segment III without secondary sensoria; setae on antennal segment III shorter than diameter of segment. Cornicle dark, cylindrical, slightly tapering to apical flange, approximately 3-4 times as long as wide. Cauda pale to dusky, elongate with 4-6 (usually 6) lateral setae.

Winged adult female.—In life, body shape and coloration similar to wingless adult female. Small sized, body length 1.4-2.0 mm, rounded. Antenna 6 segmented; tubercles not developed; terminal process approximately 2-3 times length of base of antennal segment VI; antennal segment III with 4-9 secondary sensoria; antennal segment IV with 0-1 secondary sensorium; setae on antennal segment III shorter than diameter of segment. Cornicle dark, cylindrical with apical flange, approximately 3-5 times as long as wide. Cauda pale to dusky, elongate with 4-6 (usually 6) lateral setae.

Hosts: Polyphagous and very damaging to many plants of economic importance, including species of *Chrysanthemum*.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Aphis gossypii* transmits 76 plant viruses but is not a known vector of the chrysanthemum viruses (Chan et al. 1991).

Aulacorthum circumflexum (Buckton 1876)
Figs. 1, 6, 7

Synonymy:

**Myzus circumflexum* (Buckton)

***Aulacorthum* (Neomyzus) *circumflexum* (Buckton)

ESA approved common name: crescent marked lily aphid

Other common names: mottled arum aphid

Taxonomic characters: Wingless adult female.- In life, body color varying from nearly white to yellow or green, abdomen with dark U-shaped dorsal patch, thorax with a pair of dorsolateral patches or transverse bars. Small to medium sized, body length 1.7-2.2 mm, spindle shaped. Antennae 6 segmented; tubercles well developed with inner faces parallel; terminal process approximately 4-5 times length of base of antennal segment VI; antennal segment III with 0-3 (usually 1) secondary sensoria, antennal segment IV without secondary sensoria. Cornicle pale, cylindrical, flaring slightly apically, approximately 3¾-6 times as long as wide. Cauda pale, elongate with 4-6 (usually 4) lateral setae and occasionally a single dorsal preapical seta.

Winged adult female.—In life, head and thorax black, abdomen yellow to green with dark bands often coalescing to form a single patch; body shape similar to wingless adult female. Small to medium sized, body length 1.4-2.2 mm. Antennae 6 segmented; tubercles well developed with inner faces parallel; terminal process approximately 4⅓-7⅓ times length of base of antennal segment VI; antennal segment III with 10-17 secondary sensoria; antennal segment IV with 0-1 secondary sensoria. Cornicle pale cylindrical, approximately 4-7 times as long as wide. Cauda pale, elongate with 4 lateral setae and 1-2 dorsal preapical setae.

Hosts: Extremely polyphagous, occurring on many greenhouse and house plants, including *Chrysanthemum*.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Aulacorthum circumflexum* transmits 31 plant viruses but is not a known vector of the chrysanthemum viruses (Chan et al. 1991).

Aulacorthum solani (Kaltenbach 1843)
Figs. 1, 4, 5

Synonymy:

**Myzus solani* (Kaltenbach)

***Aulacorthum solani* (Kaltenbach)

ESA approved common name: foxglove aphid

Other common names: glasshouse-potato aphid

Taxonomic characters: Wingless adult female.- In life, body color varying from pale green to yellow. Small to large sized, body length 1.8-3.0 mm, ovoid. Antennae 6 segmented, apices dark; tubercles well developed with inner faces parallel; terminal process approximately 5-6 times length of base of antennal segment VI; antennal segment III with 1-6 secondary sensoria, antennal segment IV without secondary sensoria. Cornicle pale with dark tips, cylindrical, gradually tapering with distinct large apical flange and 2 rows of reticulations, reticulations less than ⅓ length; approximately 4¼-5¼ times as long as wide. Cauda pale, elongate with 4-6 (usually 6) lateral setae and a single dorsal preapical seta.

Winged adult female.—In life, yellow green with brown head, dark thorax and abdomen with pale to dark transverse bands; body shape similar to wingless adult female; medium to large sized, body length 2.0-3.0 mm. Antennae 6 segmented; tubercles well developed with inner faces parallel; terminal process approximately 5-6 times length of base of antennal segment VI; antennal segment III with 8-13 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle pale with dark tips, cylindrical, gradually tapering with distinct large apical flange and 2 rows of reticulations, reticulations less than ⅓ length; approximately 4⅔-7⅔ times as long

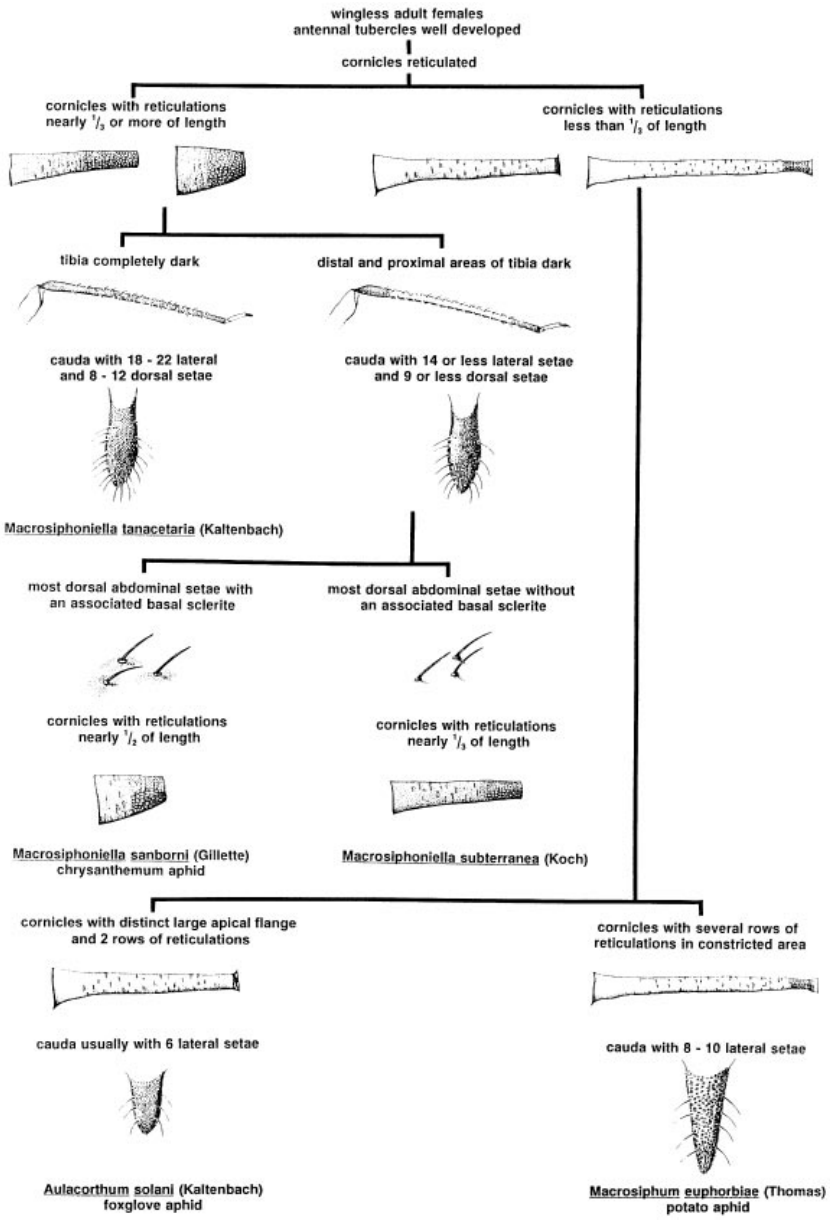

Fig. 4. Pictorial key to wingless adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles well developed and cornicles reticulated.

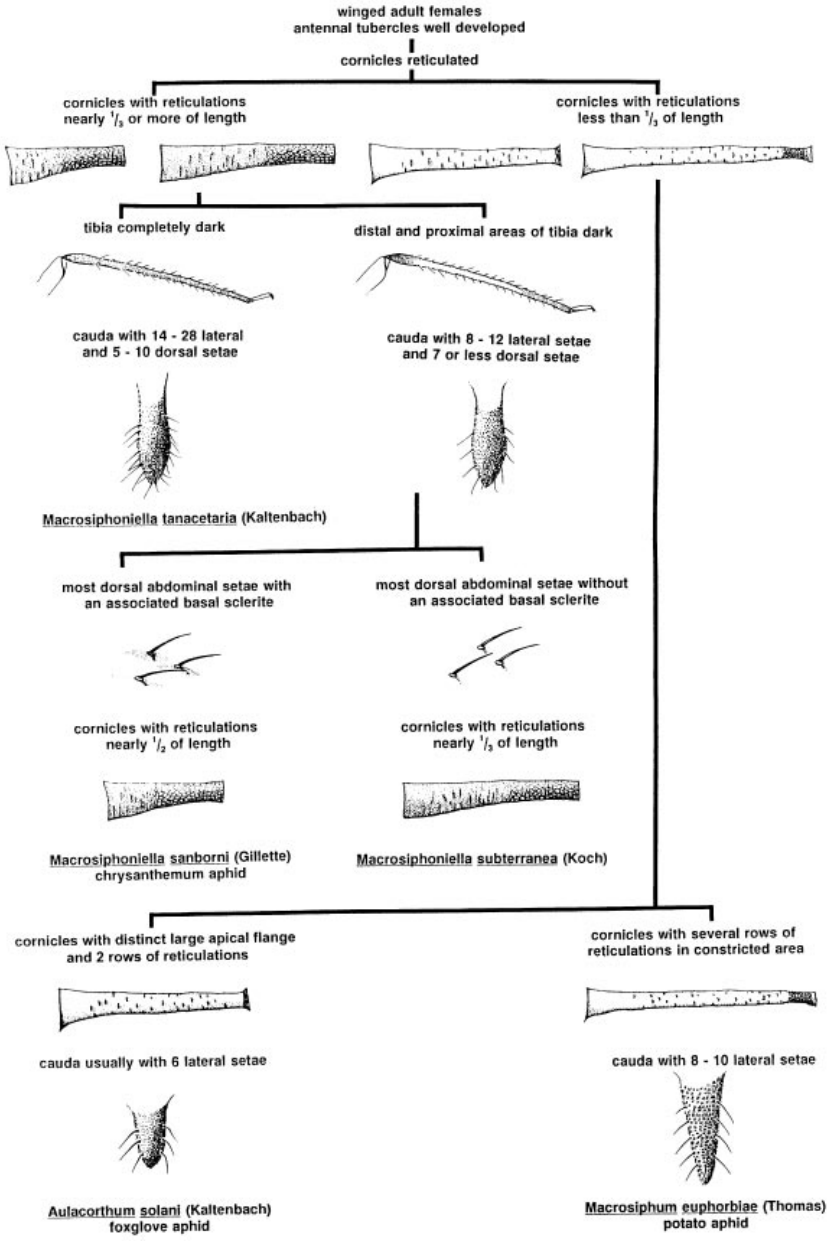

Fig. 5. Pictorial key to winged adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles well developed and cornicles reticulated.

as wide. Cauda pale, elongate with 4-6 (usually 6) lateral setae and a single dorsal preapical seta.

Hosts: Extremely polyphagous, occurring on many greenhouse and house plants, including *Chrysanthemum*.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Aulacorthum solani* transmits 45 plant viruses, including three viruses affecting chrysanthemums: chrysanthemum good news mosaic virus; chrysanthemum virus B; and tomato aspermy virus (Chan et al. 1991).

Brachycaudus cardui (Linnaeus 1758)
Figs. 1, 2, 3

Synonymy:

**Aphis cardui* Linnaeus
***Brachycaudus cardui* (Linnaeus)
ESA approved common name: thistle aphid
Other common names: none

Taxonomic characters: Wingless adult female.- In life, body color varying from yellow to green or red, abdomen with large dark dorsal patch; legs yellow with tarsi and tips of tibiae dark; apices of antennal segments dusky. Small to medium sized, body length 1.9-2.5 mm, pear shaped. Ultimate rostral segment more than three times as long as wide. Antennae 6 segmented; tubercles not developed; terminal process approximately 3¼-4½ times length of base of antennal segment VI; antennal segment III and IV without secondary sensoria. Cornicle dusky, cylindrical, slightly tapering to apical flange, approximately 2½-4 times as long as wide. Cauda dusky, stout, nearly as long as wide with 6 lateral setae.

Winged adult female.—In life, body shape and coloration similar to wingless adult female; antennal segments dark; small to medium sized, body length 1.7-2.5 mm. Ultimate rostral segment more than four times as long as wide. Antennae 6 segmented; tubercles not developed; terminal process approximately 2¾-4¼ times length of base of antennal segment VI; antennal segment III with 21-30 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle dusky, cylindrical, slightly tapering to apical flange, approximately 3-4¼ times as long as wide. Cauda dusky, stout with 6 lateral setae and 1 preapical seta.

Hosts: Principal hosts are *Prunus* spp., however, additional hosts include species of Asteraceae and Boraginaceae.

U.S. distribution: Throughout.

World distribution: Central Asia, Europe, India, Middle East, North Africa, North America.

Comments: *Brachycaudus cardui* transmits seven plant viruses but is not a known vector of the chrysanthemum viruses (Chan et al. 1991).

Brachycaudus helichrysi (Kaltenbach 1843)
Figs. 1, 2, 3

Synonymy:

**Aphis helichrysi* Kaltenbach
***Brachycaudus helichrysi* (Kaltenbach)
ESA approved common name: none

Other common names: leaf-curl plum aphid, leaf-curling plum aphid, plum leaf-curl aphid

Taxonomic characters: Wingless adult female.- In life, body color varying from green to yellow to nearly white or sometimes pink; legs pale; apex of antennal segments III-V and base of VI dusky on slide-mounted specimens. Small sized, body length 1.1-2.0 mm, pear shaped. Ultimate rostral segment less than three times as long as wide. Antennae 6 segmented; tubercles not developed; terminal process approximately 2-3¾ times length of base of antennal segment VI; antennal segment III without secondary sensoria. Cornicle apically dusky, cylindrical, slightly tapering to apical flange; approximately 1⅓-2 times as long as wide. Cauda dusky, stout, nearly as long as wide with 4-6 lateral setae and 1 preapical seta.

Winged adult female.—In life, body shape and coloration similar to wingless adult female with the addition of dark dorsal patch; antennal segments I-VI dusky on slide-mounted specimens; small sized, body length 1.5-1.9 mm. Ultimate rostral segment less than four times as long as wide. Antennae 6 segmented; tubercles not developed; terminal process approximately 3⅓-4 times length of base of antennal segment VI; antennal segment III with 14-28 secondary sensoria; antennal segment IV with 1-7 secondary sensoria. Cornicle completely dark, cylindrical, slightly tapering to apical flange; approximately 2-3 times as long as wide. Cauda dusky, stout with 4-6 lateral setae and 1 preapical seta.

Hosts: Principal hosts are *Prunus* spp., however, *B. helichrysi* is polyphagous on many additional hosts.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Brachycaudus helichrysi* transmits nine plant viruses but is not a known vector of the chrysanthemum viruses (Chan et al. 1991); it is however, an important pest of greenhouse chrysanthemums.

Coloradoa rufomaculata (Wilson 1908)
Figs. 1, 2, 3

Synonymy:

**Rhopalosiphum rufomaculatum* (Wilson)

***Coloradoa rufomaculata* (Wilson)

ESA approved common name: none

Other common names: pale chrysanthemum aphid, green chrysanthemum aphid

Taxonomic characters: Wingless adult female.- In life, body green. Small sized, body length 0.9-1.6 mm, pear shaped; dorsal body setae fan shaped. Antennae 6 segmented; tubercles not developed; terminal process approximately 1⅓-1¾ times length of base of antennal segment VI; antennal segment III without secondary sensoria. Cornicle dusky, cylindrical, slightly swollen apically; approximately 5-8⅓ times as long as wide. Cauda dusky, elongate with 4 lateral setae and a single dorsal preapical seta.

Winged adult female.—In life, head and thorax dusky, abdomen green; antennae, tarsi, and tips of tibiae dark; body shape similar to wingless adult female; small sized, body length 1.1-1.6 mm; dorsal body setae fan shaped. Antennae 6 segmented; tubercles not developed; terminal process approximately 1½-2 times length of base of antennal segment VI; antennal segment III with 8-15 secondary sensoria; antennal segment IV with 4-12 secondary sensoria. Cornicle dusky, cylindrical, slightly swollen apically; approximately 5⅓- 7 times as long as wide. Cauda dusky, elongate with 4 lateral setae and a single dorsal preapical seta.

Hosts: Principal hosts include cultivated chrysanthemums and *Artemisia* spp.

U.S. distribution: Throughout.

World distribution: Canada, Central Asia, Europe, India, Middle East, North Africa, and North America.

Comments: *Coloradoa rufomaculata* transmits three plant viruses including one affecting chrysanthemums: chrysanthemum virus B (Chan et al. 1991). *Coloradoa rufomaculata* can become problematic on greenhouse chrysanthemums.

Macrosiphoniella sanborni (Gillette 1908)
Figs. 1, 4, 5

Synonymy:

**Macrosiphum sanborni* Gillette
***Macrosiphoniella sanborni* (Gillette)

ESA approved common name: chrysanthemum aphid

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body color varying from light brown to nearly dark; most dorsal abdominal setae with associated basal scleroite; distal area of femur and proximal and distal areas of tibia dark. Small to medium sized, body length 1.7-2.6 mm, spindle shaped. Antennae 6 segmented, dusky (except segment III); tubercles well developed with inner faces divergent; terminal process approximately 4½-5 times length of base of antennal segment VI; antennal segment III with 11-24 secondary sensoria; antennal segment IV with 0-2 (usually 0) secondary sensoria. Cornicle dark, subconical with polygonal reticulation nearly ½ its length; approximately 2-3 times as long as wide. Cauda dark, elongate with 8-10 lateral setae and 3-7 dorsal setae.

Winged adult female.—In life, body coloration and shape similar to wingless adult female; most dorsal abdominal setae with associated basal scleroite; distal area of femur and proximal and distal areas of tibia dark; small to medium sized, body length 1.8-2.8 mm. Antennae 6 segmented; tubercles well developed with inner faces divergent; terminal process approximately 4¼-5¼ times length of base of antennal segment VI; antennal segment III with 18-30 secondary sensoria; antennal segment IV with 0-13 secondary sensoria. Cornicle dark, cylindrical, gradually tapering toward apex with polygonal reticulation nearly ½ its length; approximately 2-5 times as long as wide. Cauda dark, elongate with 8-10 lateral setae, 3-5 dorsal setae, and occasionally 1-6 ventral setae.

Hosts: Hosts include cultivated chrysanthemums as well as *Chrysanthemum leucanthemum* L., *Chrysanthemum maximum* Ramond, and other species of Asteraceae.

U.S. distribution: Throughout.

World distribution: Of east Asian origin, not distributed throughout the world.

Comments: *Macrosiphoniella sanborni* transmits five plant viruses including two viruses affecting chrysanthemums: chrysanthemum virus B and chrysanthemum virus B [chrysanthemum vein mottle virus strain] (Chan et al. 1991).

Macrosiphoniella subterranea (Koch 1855)
Figs. 1, 4, 5

Synonymy:

* & **not listed in Palmer (1952) or Blackman and Eastop (1984)

ESA approved common name: none

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body dark brown with a darker dorsal spot; femur and proximal and distal areas of tibia dark. Medium to large sized, body length 2.8-3.2 mm, spindle shaped. Antennae 6 segmented, dusky (except segment III); tubercles well developed with inner faces divergent; terminal process approximately 4-4¾ times length of base of antennal segment VI; antennal segment III with 8-15 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle dark, cylindrical, gradually tapering with polygonal reticulation nearly ⅓ its length; approximately 4½-7 times as long as wide. Cauda dark, elongate with 8-14 lateral setae and 4-9 dorsal setae.

Winged adult female.—In life, body coloration and shape similar to wingless adult female; femur and proximal and distal areas of tibia dark; medium to large sized, body length 2.7-3.2 mm. Antennae 6 segmented; tubercles well developed with inner faces divergent; terminal process approximately 5⅓-8¾ times length of base of antennal segment VI; antennal segment III with 26-32 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle dark, cylindrical, gradually tapering with polygonal reticulation nearly ⅓ its length; approximately 5⅓-8¾ times as long as wide. Cauda dark, elongate with 8-12 lateral setae and 2-7 dorsal setae.

Hosts: Hosts include cultivated chrysanthemums.

U.S. distribution: PA.

World distribution: Canada (Ontario), Europe.

Comments: *Macrosiphoniella subterranea* is not recorded as a known vector of any plant viruses (Chan et al. 1991).

Macrosiphoniella tanacetaria (Kaltenbach 1843)
Figs. 1, 4, 5

Synonymy:

***Macrosiphoniella tanacetaria* (Kaltenbach)

ESA approved common name: none

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body light grey green, covered with fine powder; legs dark. Large sized, body length 3.1-3.5 mm, spindle shaped. Antennae 6 segmented, dark; tubercles well developed with inner faces divergent; terminal process approximately 3¼-4⅓ times length of base of antennal segment VI; antennal segment III with 10-25 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle dark, cylindrical, gradually tapering with polygonal reticulation nearly ⅓ its length; approximately 4-8 times as long as wide. Cauda dark, elongate with 18-22 lateral setae and 8-12 dorsal setae.

Winged adult female.—In life, body coloration and shape similar to wingless adult female; legs dark; medium to large sized, body length 2.9-3.6 mm. Antennae 6 segmented; tubercles well developed with inner faces divergent; terminal process approximately 3-4 times length of base of antennal segment VI; antennal segment III with 30-42 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle dark, cylindrical, gradually tapering with polygonal reticulation nearly ⅓ its length; approximately 3¾-6 times as long as wide. Cauda dark, elongate with 14-28 lateral setae and 5-10 dorsal setae.

Hosts: Principle hosts include *Tanacetum* spp., however chrysanthemums, including *Chrysanthemum balsamita* L., also serve as occasional hosts.

U.S. distribution: DE, MA, NJ, NY, PA.

World distribution: Canada, Europe, Israel, Morocco, South America., and USA.

Comments: *Macrosiphoniella tanacetaria* transmits a single plant virus but is not a known vector of a chrysanthemum virus (Chan et al. 1991).

Macrosiphum euphorbiae (Thomas 1878)
Figs. 1, 4, 5

Synonymy:

**Macrosiphum solanifolii* (Ashmead 1882)
***Macrosiphum euphorbiae* (Thomas)

ESA approved common name: potato aphid.

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body usually of varying shades of green. Medium to large sized, body length 2.7-3.5 mm, pear shaped or elongate. Antennae 6 segmented; tubercles well developed with inner faces divergent; terminal process approximately 5-8⅓ times length of base of antennal segment VI; 3-6 secondary sensoria on basal half of antennal segment III; either entirely dark or only dark apically. Cornicle entirely pale or becoming increasingly dusky towards tip, cylindrical with slight apical constriction, several rows of polygonal reticulations in constricted area, reticulation less than ⅓ of length; 6-7½ times as long as wide. Cauda pale, elongate with 8-10 lateral setae and 1-2 dorsal preapical setae.

Winged adult female.—In life, body usually of varying shades of green, shape similar to wingless adult female; medium to large sized, body length 2.5-3.0 mm. Antennae 6 segmented; frontal tubercles well developed with inner faces divergent; terminal process approximately 5⅓-7 times length of base of antennal segment VI; 13-18 secondary sensoria of similar size on antennal segment III and in a straight row; no secondary sensoria on antennal segment IV; entirely dark except for segments I and II and base of III. Cornicle sometimes pale but usually progressively darker towards tip, cylindrical with slight apical constriction, several rows of polygonal reticulations in constricted area, reticulation less than ⅓ of length; 6¼-10 times as long as wide. Cauda pale, elongate with 8-10 lateral setae and 1-2 dorsal preapical setae.

Hosts: Principle hosts *Rosa* spp., however, *M. euphorbiae* is polyphagous and very damaging to many additional host plants of economic importance.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Macrosiphum euphorbiae* transmits 67 plant viruses, including two viruses affecting chrysanthemums: chrysanthemum virus B and tomato aspermy virus (Chan et al. 1991).

Myzus ascalonicus Doncaster 1946
Figs. 1, 6, 7

Synonymy:

***Myzus ascalonicus* Doncaster

ESA approved common name: shallot aphid

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body varying from yellow to green brown, dorsum of abdomen without spots and bands. Small to medium sized, body length 1.5-2.1 mm, spindle shaped. Antennae 6 segmented, pale except apex of

segment V and entire segment VI dark; tubercles well developed with inner faces parallel; terminal process approximately 2½-3¼ times length of base of antennal segment VI; antennal segments III-IV without secondary sensoria. Cornicle not reticulated, dusky, swollen apically with narrow medial constriction; approximately 5½-8 times as long as wide. Cauda elongate with 4-6 (usually 4) lateral setae.

Winged adult female.—In life, head and thorax dark, dorsum of abdomen with large dark patch; body shape similar to wingless adult female; medium sized, body length 2.0-2.6 mm. Antennae 6 segmented, dark; tubercles well developed with inner faces parallel; terminal process approximately 2½-3 times length of base of antennal segment VI; number of secondary sensoria on segments III-IV bimodal, antennal segment III with 25-35 secondary sensoria and antennal segment IV with 7-24 secondary sensoria or antennal segment III with 11-13 secondary sensoria and antennal segment IV with 0-1 secondary sensoria. Cornicle not reticulated, dusky, swollen apically with narrow medial constriction; approximately 5⅓-8 times as long as wide. Cauda elongate with 6-8 (usually 6) lateral setae.

Hosts: Polyphagous with preference for the Alliaceae, especially bulbs in storage.

U.S. distribution: Widespread.

World distribution: Antipodes, Auckland Isles, Australia, Europe, India, Japan, New Zealand, North America, South America.

Comments: *Myzus ascalonicus* transmits 16 plant viruses but none are recorded as affecting chrysanthemums (Chan et al. 1991).

Myzus ornatus Laing 1932
Figs. 1, 6, 7

Synonymy:

****Myzus ornatus*** Laing

ESA approved common name: ornate aphid

Other common name: violet aphid

Taxonomic characters: Wingless adult female.- In life, body varying from light yellow to green; dorsum of abdomen with dark green or brown spots and transverse bands. Small to medium sized, body length 1.6-2.0 mm, oval shaped. Antennae 6 segmented; tubercles well developed with inner faces convergent; terminal process approximately 1⅔-2⅓ times length of base of antennal segment VI; without secondary sensoria on antennal segment III. Cornicle not reticulated, dusky, cylindrical, constricted at tip, 4-6 times as long as wide. Cauda dusky, elongate with 6 lateral setae.

Winged adult female.—In life, dorsum of abdomen with a large dark patch; body shape similar to wingless adult female; small to medium sized, body length 1.6-2.3 mm. Antennae 6 segmented; tubercles well developed; terminal process approximately 1¾-2¼ times length of base of antennal segment VI; 7-11 secondary sensoria of similar size on antennal segment III; without secondary sensoria on antennal segment IV. Cornicle dusky, cylindrical, constricted at tip, 4-5¾ times as long as wide. Cauda dusky, elongate with 6 lateral setae.

Hosts: Polyphagous on many different hosts including cultivated chrysanthemums and *Chrysanthemum maximum*.

U.S. distribution: CA, NC, OR, PA, WA (probably found in all states).

World distribution: Widespread.

Comments: *Myzus ornatus* transmits 18 plant viruses but none are recorded as affecting chrysanthemums (Chan et al. 1991).

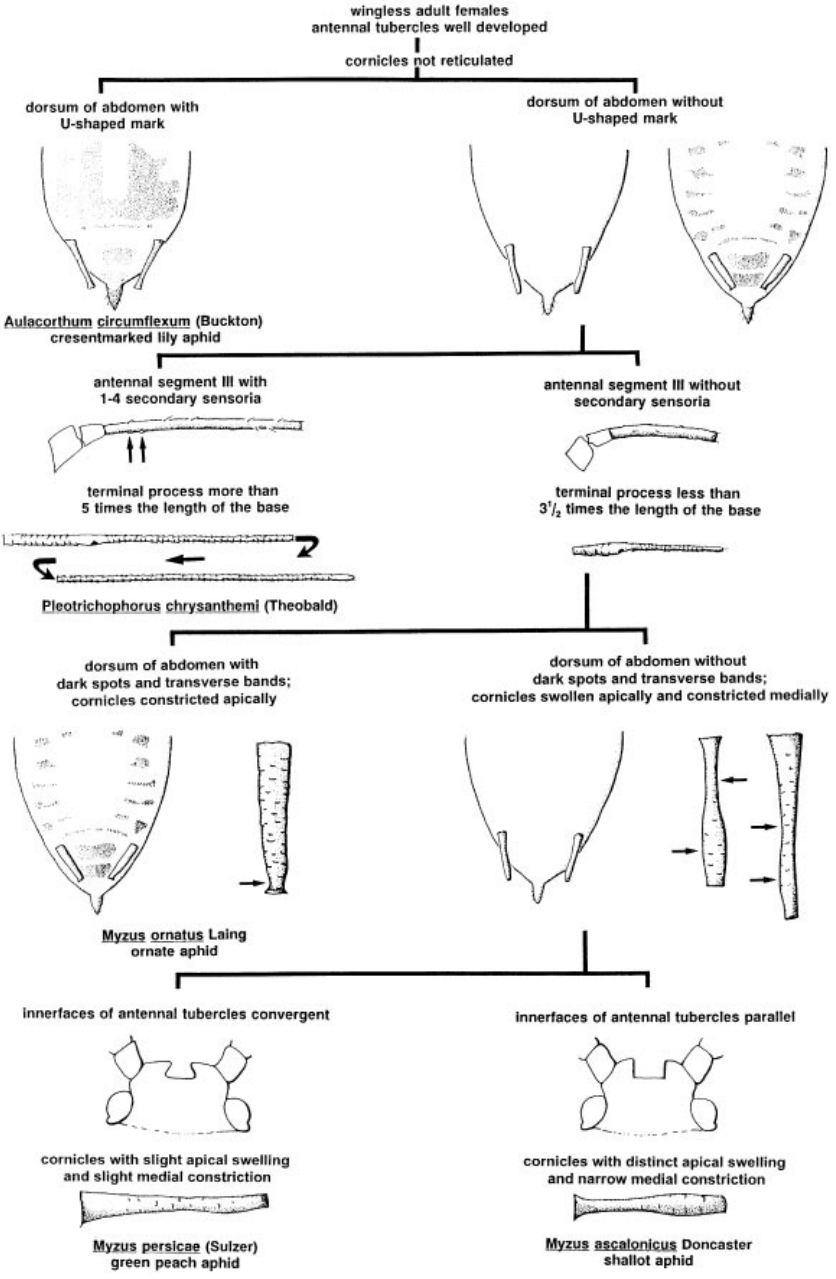

Fig. 6. Pictorial key to wingless adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles well developed and cornicles not reticulated.

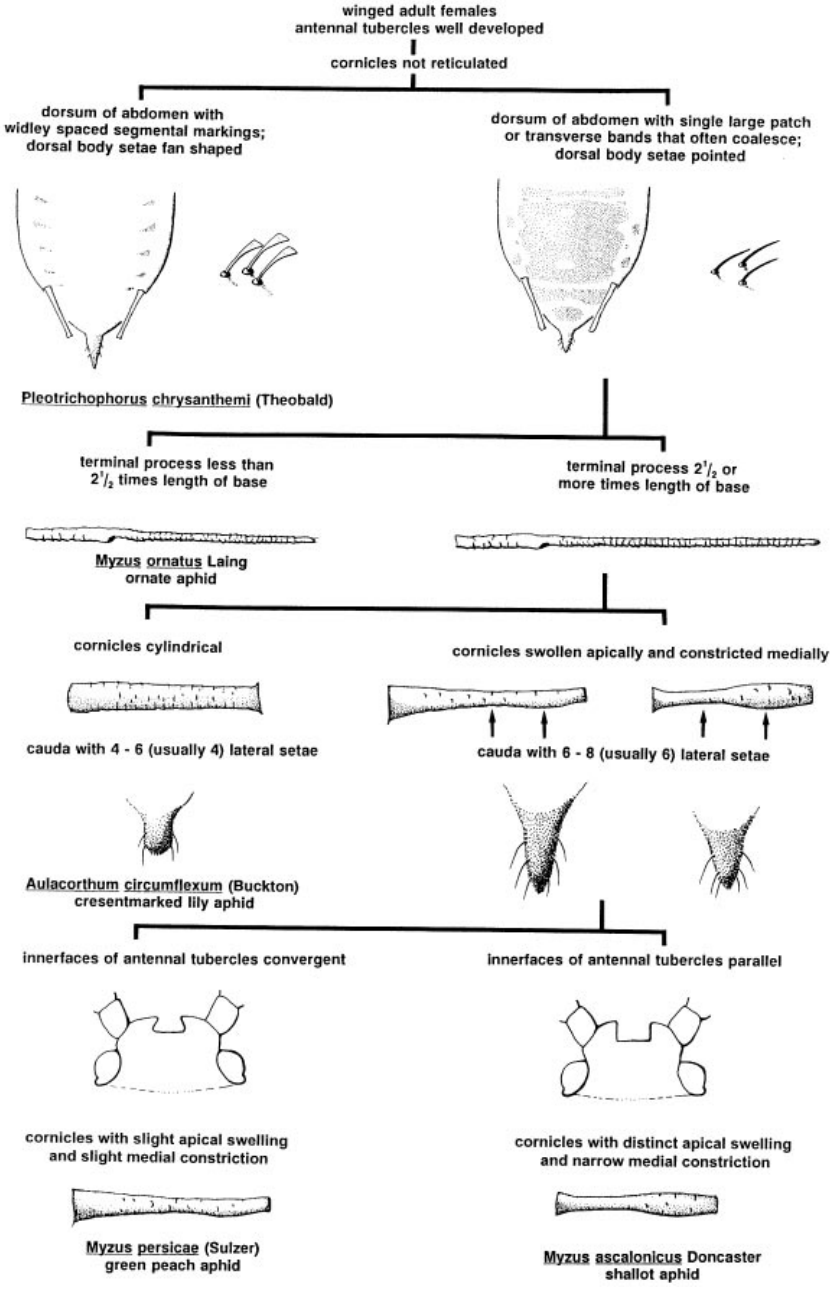

Fig. 7. Pictorial key to winged adult females of five aphid species that colonize chrysanthemum in the United States and have antennal tubercles well developed and cornicles not reticulated.

Myzus persicae (Sulzer 1776)
Figs. 1, 6, 7

Synonymy:

* & ***Myzus persicae* (Sulzer)

ESA approved common name: green peach aphid

Other common name: peach-potato aphid

Taxonomic characters: Wingless adult female.- In life, body varying from green to pale yellow, dorsum of abdomen without dark spots and transverse bands. Small to medium sized, body length 1.5-2.2 mm, pear shaped. Antennae 6 segmented; tubercles well developed with inner faces convergent; terminal process approximately 2¾-3¼ times length of base of antennal segment VI; without secondary sensoria on antennal segment III. Cornicle pale, usually with dark tip; 5-7 times as long as wide. Cauda pale to dusky, elongate with 6 lateral setae. Tarsi sometimes noticeably dark.

Winged adult female.—In life, body varies from green to pale yellow with dorsum of the abdomen with a large dark patch, body shape similar to wingless adult female; small to medium sized, body length 1.7-2.3 mm. Antennae 6 segmented; tubercles well developed with inner faces convergent; terminal process approximately 3-3¾ times length of base of antennal segment VI; 10-13 secondary sensoria of similar size in a straight row on antennal segment III; without secondary sensoria on antennal segment IV. Cornicle pale, usually with dark tip, slight apical swelling and slight medial constriction; 4¾-8 times as long as wide. Cauda pale to dusky, elongate with 6 lateral setae. Tarsi may be noticeably dark.

Hosts: Principal hosts are *Prunus* spp., however, *M. persicae* is polyphagous and very damaging to many other host plants of economic importance.

U.S. distribution: Throughout.

World distribution: Widespread.

Comments: *Myzus persicae* transmits 182 plant viruses, including three viruses affecting chrysanthemums: chrysanthemum good news mosaic virus; chrysanthemum virus B; and tomato aspermy virus (Chan et al. 1991).

Pleotrichophorus chrysanthemi (Theobald 1920)
Figs. 1, 6, 7

Synonymy:

***Pleotrichophorus chrysanthemi* (Theobald)

ESA approved common name: none

Other common names: none

Taxonomic characters: Wingless adult female.- In life, body varying from light green to yellow with widely spaced dusky segmental markings. Medium sized, body length 2.1-2.9 mm, spindle shaped; dorsal body setae fan shaped. Antennae 6 segmented; tubercle well developed with inner faces divergent; terminal process approximately 5⅓-6 times length of base of antennal segment VI; antennal segment III with 1-4 secondary sensoria, antennal segment IV without secondary sensoria. Cornicle not reticulated, pale, cylindrical, flaring apically; approximately 7-10 times as long as wide. Cauda pale, elongate with 4 lateral and a single (occasionally 2) dorsal preapical seta.

Winged adult female.—In life, abdomen green to yellow with widely spaced dusky segmental markings. Medium sized, body length 2.0-2.6 mm, spindle shaped; dorsal body setae fan shaped. Antennae 6 segmented; terminal process approximately 5¾-6

times length of base of antennal segment VI; antennal segment III with 12-17 secondary sensoria; antennal segment IV without secondary sensoria. Cornicle pale, cylindrical, flaring apically, approximately 8-11⅔ times as long as wide. Cauda pale, elongate with 4 lateral and a single dorsal preapical seta.

Hosts: Principal hosts include *Chrysanthemum* spp.

U.S. distribution: CA, DC, NC, WA.

World distribution: Widespread.

Comments: *Pleotrichophorus chrysanthemi* is not recorded as a vector of any plant viruses (Chan et al. 1991).

KEY TO THE WINGLESS FEMALE APHID SPECIES COLONIZING CHRYSANTHEMUMS IN THE UNITED STATES

1. Antennal tubercles well developed 6
   Antennal tubercles not developed 2
2. Terminal process ≤2 times the base, cornicles slightly swollen apically ..... *Coloradoa rufomaculata* (Wilson)
   Terminal process ≥2 times the base, cornicles tapered or parallel sided, not swollen 3
3. Cauda stout in dorsal view, approximately as long as wide 4
   Cauda elongate in dorsal view, obviously longer than wide 5
4. Abdomen without large dorsal patch; cornicle 1⅓-2 times as long as wide; ultimate rostral segment <3 times as long as wide ..... *Brachycaudus helichrysi* (Kaltenbach)
   Abdomen with large dorsal patch; cornicle 2½-4 times as long as wide; ultimate rostral segment >3 times as long as wide ..... *Brachycaudus cardui* (L.)
5. Cauda with 10 or more total setae; cornicle and cauda both dark ..... *Aphis fabae* Scopoli
   Cauda with fewer than 10 total setae; cauda lighter colored than cornicles ..... *Aphis gossypii* Glover
6. Antennal segment III without secondary sensoria 7
   Antennal segment III with secondary sensoria, or if without secondary sensoria, then terminal process of antenna ≥4 times length of the base 9
7. Cornicle constricted apically; dorsum of abdomen with dark spots and transverse bands ..... *Myzus ornatus* Laing
   Cornicle swollen apically with medial constriction; dorsum of abdomen without dark spots and transverse bands 8
8. Cornicle with distinct apical swelling and narrow medial constriction; inner faces of antennal tubercles parallel ..... *Myzus ascalonicus* Doncaster
   Cornicle with slight apical swelling and slight medial constriction; inner faces of antennal tubercles convergent ..... *Myzus persicae* (Sulzer)
9. Dorsum of abdomen with distinct, dark, U-shaped marking ..... *Aulacorthum circumflexum* (Buckton)
   Dorsum of abdomen without distinct, dark, U-shaped marking 10
10. Cornicle subconical, approximately 2-3 times as long as wide at its base, with polygonal reticulation nearly ½ its length ..... *Macrosiphoniella sanborni* (Gillette)
    Cornicle cylindrical, >3 times the width at its base and without polygonal reticulation or polygonal reticulation less than ½ its length 11
11. Cornicle either completely pale, pale with dark tips, or completely dusky; cauda pale 12
    Cornicle dark; cauda dark or dusky 14

12. Dorsal abdominal setae pointed; cornicle with some rows of reticulations anterior to apical flange 13
    Dorsal abdominal setae fan shaped; cornicle without rows of striations anterior to apical flange ..... *Pleotrichophorus chrysanthemi* (Theobald)
13. Cornicle tapering gradually to a distinct large apical flange with 2 rows of reticulations anterior to flange ..... *Aulacorthum solani* (Kaltenbach)
    Cornicle cylindrical with slight apical constriction and several rows of polygonal reticulations in constricted area, no large flange ..... *Macrosiphum euphorbiae* (Thomas)
14. Tibiae with dark distal and proximal regions ..... *Macrosiphoniella subterranea* (Koch)
    Tibiae completely dark ..... *Macrosiphoniella tanacetaria* (Kaltenbach)

KEY TO THE WINGED FEMALE APHID SPECIES COLONIZING CHRYSANTHEMUMS IN THE UNITED STATES

1. Antennal tubercles well developed 6
   Antennal tubercles not developed 2
2. Terminal process ≤2 times the base, cornicles slightly swollen apically ..... *Coloradoa rufomaculata* (Wilson)
   Terminal process ≥2 times the base, cornicles tapered or cylindrical 3
3. Cauda stout, nearly as long as wide 4
   Cauda elongate, obviously longer than wide 5
4. Cornicle 2-3 times as long as wide; antennal segment IV with secondary sensoria; ultimate rostral segment <4 times as long as wide ..... *Brachycaudus helichrysi* (Kaltenbach)
   Cornicle 3-4½ times as long as wide; antennal segment IV without secondary sensoria; ultimate rostral segment >4 times as long as wide ..... *Brachycaudus cardui* (L.)
5. Abdomen usually with dark lateral areas and bands on dorsum; cornicle and cauda both dark; setae on antennal segment III longer than diameter of segment ..... *Aphis fabae* Scopoli
   Abdomen usually without dark lateral areas and bands on dorsum; cauda lighter colored than cornicle; setae on antennal segment III shorter than diameter of segment ..... *Aphis gossypii* Glover
6. Apical region of cornicle with several rows of polygonal reticulations; cauda usually with > 10 setae 7
   Apical region of cornicle with 3 or fewer rows of polygonal reticulations; cauda usually with < 10 setae 10
7. Cornicle entirely pale or becoming darker toward tip, slightly constricted in region of apical reticulation ..... *Macrosiphum euphorbiae* (Thomas)
   Cornicle completely dark, region of apical reticulation not constricted 8
8. Terminal process of antenna ≤4 times length of the base; antennae and legs completely dark ..... *Macrosiphoniella tanacetaria* (Kaltenbach)
   Terminal process of antenna > 4 times length of the base; antennae and legs with light and dark regions 9
9. Cornicle ≤5 times as long as wide; most dorsal abdominal setae associated with basal scleroite ..... *Macrosiphoniella sanborni* (Gillette)
   Cornicle >5 times as long as wide; dorsal abdominal setae without associated basal scleroite ..... *Macrosiphoniella subterranea* (Koch)

10. Dorsal body setae fan shaped; cornicle ≥8 times as long as wide ..... *Pleotrichophorus chrysanthemi* (Theobald)
    Dorsal body setae pointed; cornicle ≤8 times as long as wide 11
11. Cornicle with apical swelling and medial constriction 12
    Cornicle without apical swelling and medial constriction 13
12. Inner faces of antennal tubercles convergent; terminal process ≥3 times length of the base ..... *Myzus persicae* (Sulzer)
    Inner faces of antennal tubercles nearly parallel; terminal process ≤3 times length of the base ..... *Myzus ascalonicus* Doncaster
13. Terminal process <4 times length of the base; cornicle and cauda dusky ..... *Myzus ornatus* Laing
    Terminal process >4 times length of the base; cornicle entirely pale or pale with dusky tip and cauda pale 14
14. Dorsum with single large dark patch ..... *Aulacorthum circumflexum* (Buckton)
    Dorsum with several transverse pale to dark bands ..... *Aulacorthum solani* (Kaltenbach)

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INHIBITION OF FRUIT FLY (DIPTERA: TEPHRITIDAE) DEVELOPMENT BY PULSED ELECTRIC FIELD

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ABSTRACT

Pulsed electric field (PEF) has been studied as a means to inactivate microorganisms in liquid prepared foods to prolong shelf life and prevent food poisoning. PEF is thought to inactivate microbes by permeabilizing the cell membrane and has less adverse effects on nutritional quality and flavor of the food than traditional thermal pasteurization or sterilization methods. The goal of quarantine treatments are similar to the goal of food pasteurization in that any quarantined insects present in the commodity must be prevented from reproducing using techniques which are not significantly detrimental to the quality of the commodity. Traditional quarantine treatments include fumigation, heat, cold, and ionizing irradiation. PEF was applied to Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae), eggs and feeding third instars. The treatment disintegrated some of the eggs. Percentage egg hatch was progressively reduced to a minimum of 2.9% as voltage was increased to a maximum of 9.2 kV/cm^2 delivered in ten 50 µs pulses. Nevertheless, no first instars treated as eggs with ≥5.0 kV (ten 50 µs pulses) survived to the third instar. PEF did not kill third instars immediately; however, they displayed a variety of pathological symptoms including sluggishness, elongated, larviform, and partial pupariation, and de-

velopment of necrotic spots throughout the body. No third instars treated with >2.0 kV survived to the adult stage. Therefore, PEF has been shown to control insects, although considerable entomological and engineering work would be needed before a PEF-based treatment might become practical.

Key Words: pupariation, Mexican fruit fly, *Anastrepha ludens*

RESUMEN

Se ha estudiado el campo eléctrico pulsado (CEP) para inactivar microorganismos en alimentos líquidos preparados con el objetivo de conservar su calidad y prevenir intoxicación. Se postula que el CEP inactiva los microorganismos al permeabilizar la membrano de la célula. El CEP causa menos daño a la calidad nutritiva y sabor del alimento que métodos termales tradicionales. Los tratamientos cuarentenarios son similares a la pasteurización del alimento en que hay que inhibir la reproducción de todo insecto cuarentenado presente en la mercancía. Tratamientos cuarentenarios tradicionales incluyen fumigación, calor, frío, e irradiación. El CEP se aplicó a posturas y terceros ínstares de la mosca mejicana de las frutas, *Anastrepha ludens* (Loew) (Diptera: Tephritidae). El tratamiento disintegró algunos de las postucon. El porcentaje de eclosión fue el 2.9% el máximo voltaje usados (diez pulsos de 50 µs al 9.2 kV/cm^2). Sin embargo, ningún primer ínstar tratado con ≥5.0 kV llegó al tercer ínstar. El CEP no mató a los terceros ínstares de inmediato; no obstante, mostraron una variedad de síntomas patológicos incluyendo pereza, desarrollo de puntos necróticos, y pupariación alargada, larviforme, y parcial. Ningún tercer ínstar tratado con >2.0 kV sobrevivió al estado del adulto. Por eso, el CEP se ha sido capaz de controlar insectos, aunque falta mucho trabajo entomológico y de ingenería antes de poder ser práctico.

Insects inside harvested agricultural commodities must often be killed, prevented from completing development, or from reproducing without significantly harming the commodity or leaving residues of potentially harmful chemicals. Such treatments are needed not only to prevent continued increase of the pest population levels and associated losses of commodity quantity and quality, but also preclude the importation of exotic pests. This task has been made more difficult in recent years by the loss and pending loss of key fumigants. Use of ethylene dibromide was halted a decade ago because it was deemed a cancer risk. Methyl bromide is currently scheduled to be phased out within several years because it is considered a significant stratospheric ozone depleter. Other techniques for postharvest control of insects, such as exposure to extreme temperatures, are replacing these fumigants (Mangan & Hallman 1997, Mason & Strait 1997).

High voltage electric field pulses delivered in microseconds can deactivate vegetative stages of microorganisms (Grahl & Märkl 1996). Pulsed electric field (PEF) is being studied as a nonthermal means of fluid food preservation. The mode of action of PEF is thought to be related to increased permeability of the cell membrane due to compression caused by an electrical potential across the membrane when an external electrical field is applied. Electrical pulses of 25 kV or more may be needed to inactivate bacteria (Zhang et al. 1995). According to PEF theory, smaller voltages should suffice to inactivate organisms with larger cells, such as insects, because the electrical potential between the interior and exterior surfaces of the cell membrane, ΔV, is positively related to the size of the cell by the following equation:

$$\Delta V = \left(\frac{l}{l - 0.67a}\right) a \cdot E$$

where *l* is the length of the cell, *a* is the radius, and E is the external electric field applied. Hence, the greatest possible transmembrane potentials, ca. 1.5(a·E), occur to the largest cells of spherical shape [condensed from Grahl & Märkl (1996)]. Because of the presence of an electrically-influenced nervous system and complex multicellular organs in insects, it is conceivable that PEF may kill insects with a lower voltage than that needed to inactivate the insect cells by electropermeabilization.

The objective of this research was to determine if PEF could be used to kill insects; this is the first published record of the reaction of a multicellular organism to this treatment.

Materials and Methods

Pulsed Electric Field Generator

Experiments were conducted with a PEF generator at the Ohio State University, Department of Food Science & Technology. The PEF generator consists of a high voltage (≤15 kV DC) power supply (Cober Electronics 1450-4) which transmits voltage through a pulse generator (Cober Electronics Model 2829) to a static fluid treatment chamber containing the insects. The treatment chamber (a cylinder 1 cm long by 1 cm diameter or 0.8 cm^3) was bored out of a block of polycarbonate and placed between two stainless steel electrodes. Temperature of the electrodes was measured with type J, 20 gauge thermocouples and a data logger (John Fluke model 52).

Insects

Mexican fruit fly, *Anastrepha ludens* (Loew), originated in Montemorelos, Nuevo Leon, Mexico and were reared on a semi-artificial diet at Weslaco for 4-6 generations (Spishakoff & Hernandez-Davila 1968). Eggs (about half way through development) and feeding late-third instars were placed in the PEF treatment cylinder containing 0.05-0.2% NaCl in water. The insects were subjected to 1-10 pulses of 1.9-9.2 kV lasting 50 μs each with a lapse of about 30 seconds between pulses. Insects were treated in groups of about 100-200 eggs or ten larvae. Egg treatments were replicated twice and larval treatments 2 or 3 times. Controls were placed in 0.05-0.2% salt solution for a few minutes. After treatment eggs were placed on moist filter paper and larvae in petri dishes to observe development. First instar larvae emerging from eggs were placed on a semi-artificial diet; after seven days the diet was strained and large (third instar) larvae recovered.

Results

Eggs

Percentage egg hatch declined progressively to a low of 2.9% as voltage increased to the highest dose, 9.2 kV (Fig. 1). Some of the eggs disintegrated during treatment, and the number that disintegrated seemed to be directly related to the voltage. The contents of these eggs formed a brown gel several hours later. Probit analysis of egg mortality gave a y-intercept of -0.58 and a slope of 0.31. The estimate of $LD_{99.9968}$, a level of control often demanded of quarantine treatments against tephritids (Shannon 1994), was 14.7 kV with 95% fiducial limits of 10.6-31.4 kV. However, no third instars developed from first instars hatched from eggs treated with ≥5.0 kV and placed on diet, while only few developed from those treated with 4.0 kV.

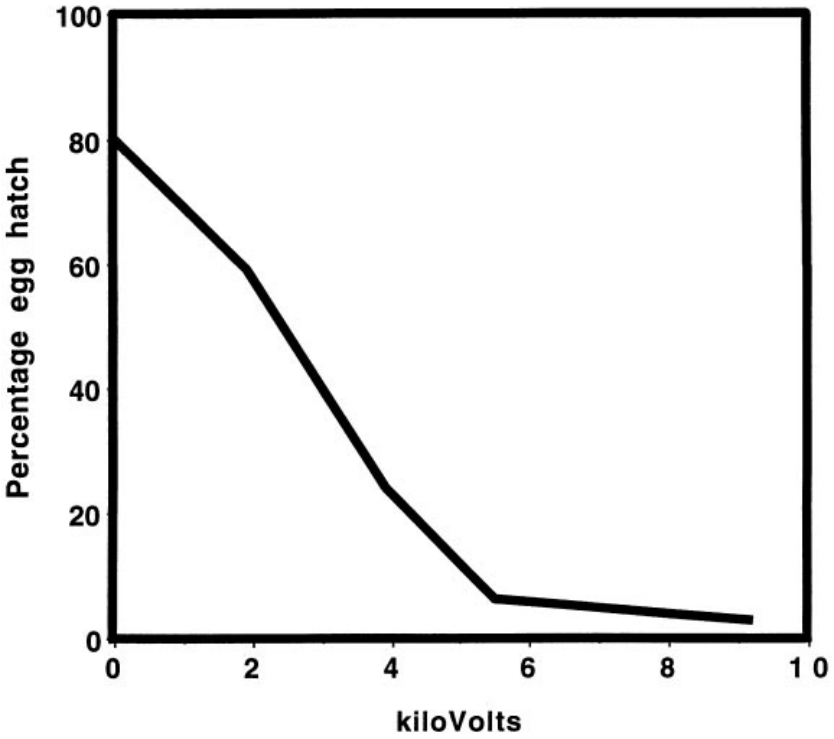

Fig. 1. Percentage Mexican fruit fly egg hatch as a consequence of voltage applied by pulsed electric field (ten 50 µs pulses per cm^2).

Larvae

Larvae contracted slightly but noticeably when the pulses passed through the treatment chamber. This reaction became less pronounced with each successive pulse. Treated larvae were very sluggish after the treatment; however, none were dead. Some of the larvae regained a measure of activity a few hours after treatment, but most remained sluggish. By about 10 hours after treatment, larvae were pupariating, and all of the control puparia were normal coarctate (Tables 1 and 2). Only 11 of 60 puparia treated as larvae with one or two 50-µs pulses at 2.0 kV, were normal (Tables 2). Nineteen of 90 puparia of larvae treated with one to three 50-µs pulses at 2.0 kV were of the elongated coarctate form (Fig. 2) as was one of the puparia treated at 1.9 kV for 10 pulses (Table 1). Most of the PEF-treated larvae formed larviform puparia (Fig. 3). Many others, especially those treated with ten 50-µs pulses at 7.4 or 8.0 kV, formed partial larviform puparia always commencing at the anterior end (Fig. 4). Many other treated larvae never began to pupariate but necrotic areas formed throughout the bodies, and eventually they died (Fig. 5). Some larvae were still moving after the entire body was black. The first treated insects to die did so about 24 hours after treatment. Although some treated insects lived several days, they were never as active as untreated larvae. Before 66 hours post-treatment, all larvae treated

TABLE 1. CONDITION OF *ANASTREPHA LUDENS* ABOUT 42 HOURS AFTER BEING SUBJECTED AS FEEDING THIRD INSTARS TO 10 PULSES OF 50 µS EACH AT VARIOUS VOLTAGES/CM^2.

	No. of insects of a total of 20 in each stage					
	Larvae		Puparial appearance			
Voltage (kV)	Normal	Necrotic	Normal	Elongated	Larviform	Partially pupariated
0	5	0	15	0	0	0
1.9	0	5	0	1	14	0
3.5	0	6	0	0	7	7
5.3	0	0	0	0	9	11
7.4	0	0	0	0	0	20
8.0	0	0	0	0	0	20

at 3.5-8.0 kV were dead. Forty-six of 50 control larvae developed into normal adults. Also, one male larvae treated with 1.9 kV developed first into a slightly elongated puparium and then into an apparently normal adult. From 30 larvae treated with one pulse of 2.0 kV, two apparently normal females emerged from seemingly normal puparia.

TABLE 2. CONDITION OF *ANASTREPHA LUDENS* ABOUT 46 HOURS AFTER BEING SUBJECTED AS FEEDING THIRD INSTARS TO 2.0 KV/CM^2 FOR 1-10 PULSES OF 50 µS EACH.

	No. of insects of a total of 30 in each stage					
	Larvae		Puparial appearance			
No. pulses	Normal	Necrotic	Normal	Elongated	Larviform	Partially pupariated
0	2	0	28	0	0	0
1	7	0	10	11	2	0
2	11	2	1	6	10	0
3	7	7	0	2	14	0
4[1]	4	3	0	0	22	0
5	9	6	0	0	15	0
6	3	7	0	0	20	0
7	3	8	0	0	17	2
8	1	8	0	0	19	2
9	0	8	0	0	19	3
10[1]	0	19	0	0	6	4

[1]Total number of larvae with 4 and 10 pulses was 29.

Fig. 2. Varying degrees of elongation of *Anastrepha ludens* puparia subjected as third instars to pulsed electric field (2 kV, one 50 µs pulse). Untreated puparium is shortest one (far left).

Fig. 3. One normal and eight larviform *Anastrepha ludens* puparia. Larviform puparia treated as third instars with pulsed electric field (2 kV, four 50 µs pulses).

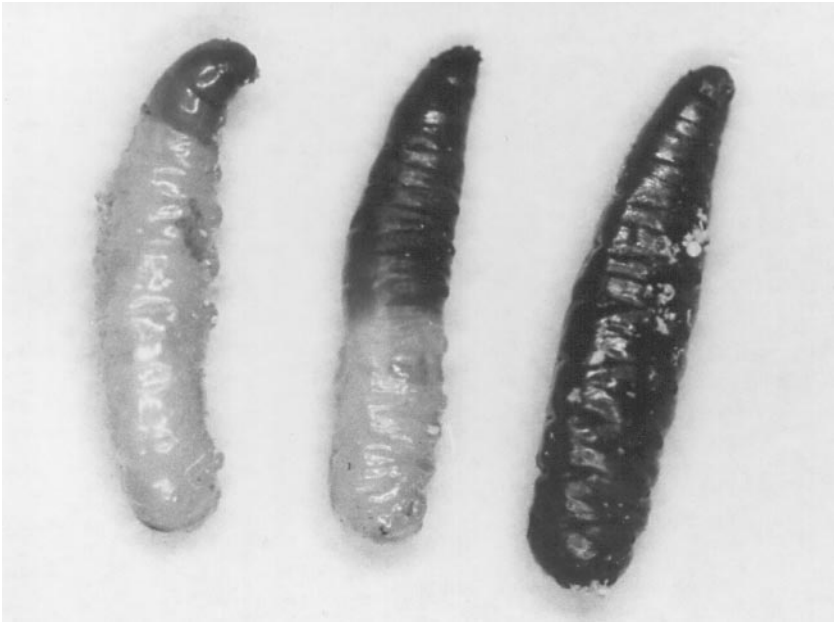

Fig. 4. Varying degrees of larviform pupariation by *Anastrepha ludens* treated with pulsed electric field (2 kV, ten 50 μs pulses) while third instars.

Temperature increase of the electrodes was never more than 0.1°C, confirming that PEF is a nonthermal treatment.

Discussion

Cumulative prevention of eclosion of *A. ludens* eggs by PEF was reduced only slightly after 3.8 kV and did not reach 100% at the highest dose, 9.2 kV. Although the estimated dose to achieve $LD_{99.9968}$ egg mortality was 14.7 kV, no late-instar larvae developed from eggs treated with ten pulses at ≥5.0 kV. Only larviform puparia formed from larvae subjected to 10 pulses at ≥3.5 kV or ≥4 pulses at 2.0 kV. Therefore, although acute mortality of *A. ludens* did not occur to any appreciable extent at the PEF doses used in this study, complete metamorphosis was stopped with much lower doses than those needed to inactivate microorganisms. A quarantine treatment need not cause acute mortality to be used commercially. Irradiation does not cause significant acute insect mortality at the doses used on fruits and vegetables, although completion of insect development can be averted (Burditt 1994). Consequently, PEF could be employed as a quarantine treatment under the same criteria used for irradiation. In fact, the efficacy of a PEF treatment would be easier to assess than that of irradiation. Irradiated third instar tephritids move normally and usually form normal puparia at the doses used on fruits. PEF-treated third instars, however, remain lethargic and, for the most part, do not pupariate normally.

Some of the pathological symptoms shown by the larvae were similar to those caused by irradiation of larvae of cyclorrhaphous flies. Irradiation at ≥25 Gy prevented inversion of the larval head of *Sarcophaga bullata* Parker (Diptera: Sarcoph-

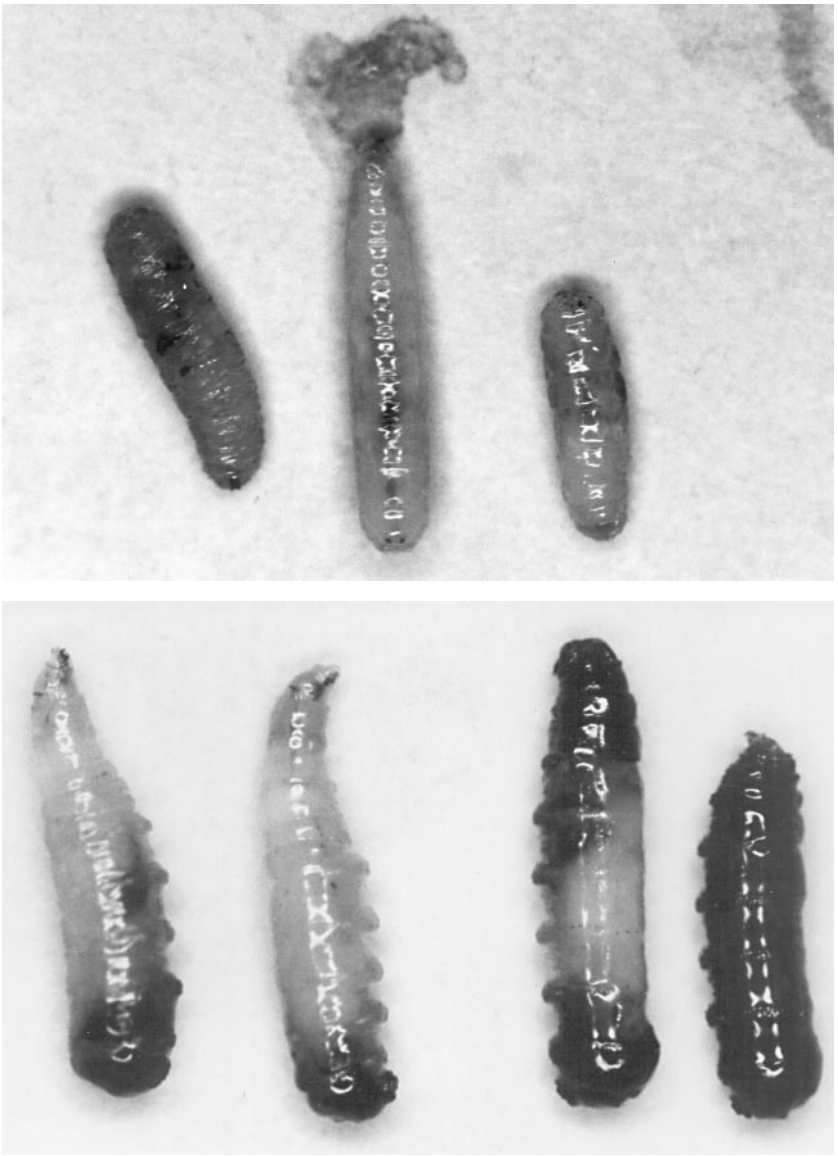

Fig. 5. Varying degrees of necrosis of third instar *Anastrepha ludens* 28 (a) and 46 (b) hours after treatment with pulsed electric field (2 kV, seven to ten 50 µs pulses).

agidae), resulting in the formation of a larviform puparium (Sivasubramanian et al. 1974). Ligation of postfeeding cyclorrhaphous larvae in the mid-body area before molting hormones were produced and tight enough to prevent translocation of the hormones from the anterior central nervous system to the posterior half of the body

produced normal pupariation in the anterior end while maintaining the posterior larval (Fraenkel & Zdarek 1970). We hypothesize that in those larvae which partially pupariated in the anterior end of the body, hormones initiating puparial sclerotization and melanization were not translocated but simply diffused from the central nervous system at the anterior end of the body. This was substantiated by our observation that in certain individuals the heart was not pumping.

Larviform puparia failed to retract the anterior prespiracular segments and contract longitudinally. This is consistent with a general paralysis of the musculature (Zdarek & Fraenkel 1987). The fact that larvae never recovered their former level of activity after PEF treatment denotes that the paralysis was permanent. Elongated puparia failed to retract the anterior prespiracular segments in varying degrees but were more successful at contracting longitudinally, indicating that PEF more easily paralyzed the former muscular system (retractors), which are also used in everting the anterior spiracles, than the latter (contractors), which are used in larval locomotion. In one case an adult with normal appearance emerged from a slightly elongated puparium (Table 1), confirming that normal puparia are not necessary for successful development of adult tephritids (Thomas & Mangan 1995).

Finally, because of the diverse reactions observed, PEF may prove to be a useful tool in the study of insect developmental biology.

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SELECTION FOR NON-RESPONSIVENESS TO METHYL EUGENOL IN MALE ORIENTAL FRUIT FLIES (DIPTERA: TEPHRITIDAE)

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ABSTRACT

An experiment was conducted to determine whether non-responsiveness of male *Bactrocera dorsalis* (Hendel) to methyl eugenol could be increased via selection. Of four select lines established, males of one line showed a persistent reduction in attraction to the lure over 12 generations in the two assays utilized. Implications of this result for male annihilation programs are discussed.

Key Words: *Bactrocera dorsalis,* methyl eugenol, male response

RESUMEN

Fue llevado a cabo un experimento para determinar si la falta de respuesta de los machos de *Bactrocera dorsalis* (Hendel) al methyl eugenol podria ser aumentada mediante selección. Los machos de una de las cuatro líneas establecidas seleccionadas mostraron una reducción persistente en la atracción por el cebo durante 12 generaciones en los dos ensayos realizados. Son discutidas las implicaciones de este resultado para los programas de aniquilación de machos.

Males of many economically important tephritid species are attracted to particular chemical compounds, termed parapheromones or lures, which either occur naturally in certain plants or are (presumed) synthetic analogues of plant-borne

substances (Metcalf & Metcalf 1992). Because of their powerful attractancy, parapheromones are frequently used in control programs for detecting and monitoring wild populations. In addition, traps baited with a lure-insecticide mixture are often used to eradicate males completely (a technique termed "male annihilation"; Metcalf & Metcalf 1992) or at least greatly reduce male abundance prior to the implementation of the sterile insect technique (SIT).

Although generally effective, prolonged use of lures in a male annihilation program could have a negative effect if it inadvertently selected for non-responsiveness to the lure. Cunningham (1989) reviewed data bearing on this issue and concluded that, although the development of a completely non-responsive strain has never been proven, selection for non-responsiveness is a possibility that should be avoided through quickly implemented and rigorous control methods. Two lines of evidence suggest that non-responsiveness could evolve. In a preliminary study, Ito & Iwahashi (1974) were able to decrease responsiveness of male *Bactrocera dorsalis* (Hendel) to methyl eugenol after only two generations of selection. Although this result could have reflected selection for overall reduction in male mobility (leading to decreased movement to the lure as well), tests were conducted in small cages where travel distances to the lure were negligible. In addition, it appears that a non-responsive strain of *B. dorsalis* may have existed on the remote Ogasawara Islands of Japan. Here, despite the low likelihood of immigration, an intensive two year program of male annihilation failed to eradicate the population (Ito & Iwahashi 1974, Habu et al. 1984).

The purpose of the present study was to determine whether non-responsiveness of *B. dorsalis* males to methyl eugenol could be increased through artificial selection. This work expands upon Ito & Iwahashi's (1974) pilot project by increasing the duration of the experiment (i.e., the number of generations followed) and the number of lines studied. As will be described, responsiveness was monitored in both cage and field tests over at least eight generations for four pairs of control and select lines, and reduced male attraction to the lure was observed in both tests for one of the select lines.

Materials and Methods

The flies used in this experiment were obtained from a laboratory colony established with 200-300 adults of each sex that emerged from mango (*Mangifera indica* L.) collected in Waimanalo, Oahu. At the start of the study, the colony had been maintained in the laboratory for approximately four months or about three generations. The colony was held in a large screen cage (1.2 m by 0.6 m by 0.6 m) and provided with food (protein/honey mixture) and water ad libitum. Ripe papayas (*Carica papaya* L.) were provided frequently for oviposition. Infested papayas were placed in buckets (5 liters volume) containing vermiculite, and larval and pupal development occurred in situ. Sexes were separated within five days of eclosion (well before sexual maturity at 14-21 days of age; T.E.S., unpublished data).

Select lines were initiated by mating males that failed to feed on methyl eugenol in two separate trials. Trials were run as follows. Groups of 15-20 males (21-25 days old) were placed into 10-12 screen cages (45 cm cubes) between 1100-1400 hours, and the cages were placed outside in the shade (26-32 C°). Approximately 10 min later, cotton wicks to which 1.5 ml of pure methyl eugenol had been applied were introduced into the cages. Two observers then monitored the cages continuously for 30 min, and males that landed on the wick were immediately removed and discarded. The remaining males were transferred to a holding container and supplied food and water ad libitum. Then, three days after the first trial, a second trial was conducted following the same procedure. Males that again failed to visit the wick were used as sires for select

lines. To start the lines, sires for control lines and dams (21-28 days old) for control and select lines were taken haphazardly from the colony. For all lines, sires (n = 52-66) and dams (n = 70-85) were placed in screen cages (45 cm cubes) with ample food and water, and papayas were supplied on alternate days for oviposition. Progeny were reared in situ as described above and separated by sex soon after eclosion. Four pairs of control-select lines were examined over the entire study; lines were maintained and tested concurrently.

For all lines, the responsiveness of male progeny (21-27 days old) to methyl eugenol was tested in two ways. First, I ran the double-test method described above to both score male response for all lines and obtain sires for the select lines (see below). Second, other males were used in a field test comparing capture probabilities of control vs. select males at Steiner traps baited with methyl eugenol (3% naled). Groups of 100 control and 100 select males (24-37 days old) were cooled on ice for 60-90 s and then marked by placing enamel paint on the thorax. The males were released the following day between 1000-1100 hours at a large grassy lawn on the campus of the University of Hawaii at Manoa. Ten Steiner traps were placed singly in trees in a circle (50 m radius) around a central point. Traps were checked 72 h after release, and flies were examined individually in the laboratory for markings. Daytime temperatures ranged from 24-33 C° during the releases. Ten releases were conducted per test.

Breeding cages were established as follows. For the select line, males that failed to respond to methyl eugenol in the double exposure test were used as sires for the next generation, and females (21-27 days old) were chosen haphazardly from the select stock. For the control line, sires (22-27 days old) and dams (23-27 days old) were chosen haphazardly from among untested individuals in the control stock. For all lines, sires (n = 55-70) and dams (n = 65-82) were placed in screen cages (45 cm cubes) and provided with unlimited food and water and papayas for oviposition. In all cases, progeny were separated by sex with five days of eclosion.

RESULTS

Results of the cage and field trapping tests are presented in Figs. 1 and 2, respectively. For the cage tests, the frequency of non-responders in control vs. select lines was compared for each generation using the G test with Yates correction (Zar 1974). For the field trapping, the number of captured males from control vs. select lines was compared for each generation using the Mann Whitney test (Zar 1974).

For two of the replicates (1 and 4, respectively), control and select males showed no consistent differences in responsiveness to methyl eugenol in either the cage or the field trapping tests. With only one exception (replicate 1, generation 1, $P < 0.001$), frequencies of non-responders in the cage tests were similar between control and select lines over all generations for both of these replicates ($P > 0.05$ in all cases). Likewise, field trap catches were similar between control and select lines over all generations for both replicates 1 and 4 ($P > 0.05$ in all cases) save one instance (replicate 4, generation 5, $P < 0.05$).

Consistent inter-line differences in responsiveness were, however, evident in the remaining two replicates. In replicate 3, decreased responsiveness of select males was evident in the cage test but not the field trapping test. Here, the mean proportion of non-responders in the cage tests was 24% for the select line compared to 5% for the control line (values based on generations 1-8; $P < 0.001$ in all tests). In contrast, field trap catches for replicate 3 were not statistically different between control and select lines for any generation ($P > 0.05$ in all tests). In replicate 2, select males exhibited reduced responsiveness to methyl eugenol in both cage and field tests. For select males, the proportion of non-responders in the cage test increased rapidly and remained con-

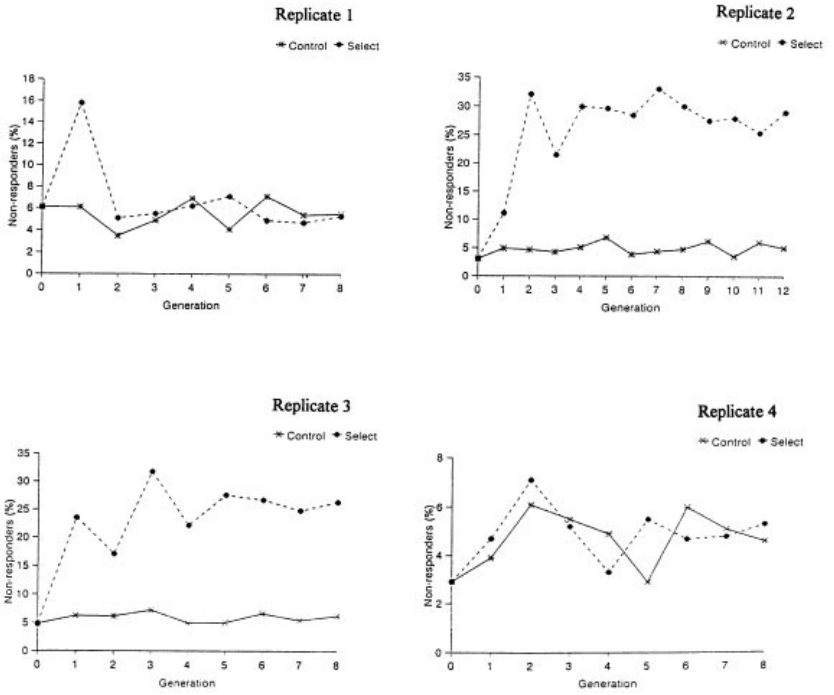

Fig. 1. Proportion of males (n = 602-777 for control, n = 405-1569 for select) that did not land on a methyl eugenol-treated wick during two exposure periods (30 min each) in laboratory cages spaced three days apart plotted against time (generation) since the onset of the experiment. Note differences in the scaling of axes.

sistently high (22%-32%) between generations 2-12 (when the experiment was terminated). In contrast, only a consistently small proportion (3%-6%) of control males failed to respond ($P < 0.001$ for generations 2-12). In the field test, over generations 2-12 an average of 41-54 control males was captured per test compared to only 18-33 select males ($P < 0.001$ in all cases).

Discussion

The present study confirms Ito & Iwahashi's (1974) preliminary data that responsiveness of male *B. dorsalis* to methyl eugenol can be reduced via artificial selection under laboratory conditions. Owing to the relatively large size of the colonies, it is unlikely that the changes observed in responsiveness were the result of genetic drift (Falconer 1981). Reduced responsiveness was not, however, a certain outcome as in only two of the replicates did the select lines differ from control lines. These differences may have reflected the initial presence of rare "non-responder" males in only two of the four select lines (i.e., replicates 2 and 3).

Even between these two replicates, the response to selection was different. In replicate 2, decreased responsiveness was noted in both field and cage tests, whereas in replicate 3 reduced responsiveness was noted in the cage tests only. It is not known why (for this replicate) a lowered response was not observed in the field test as well.

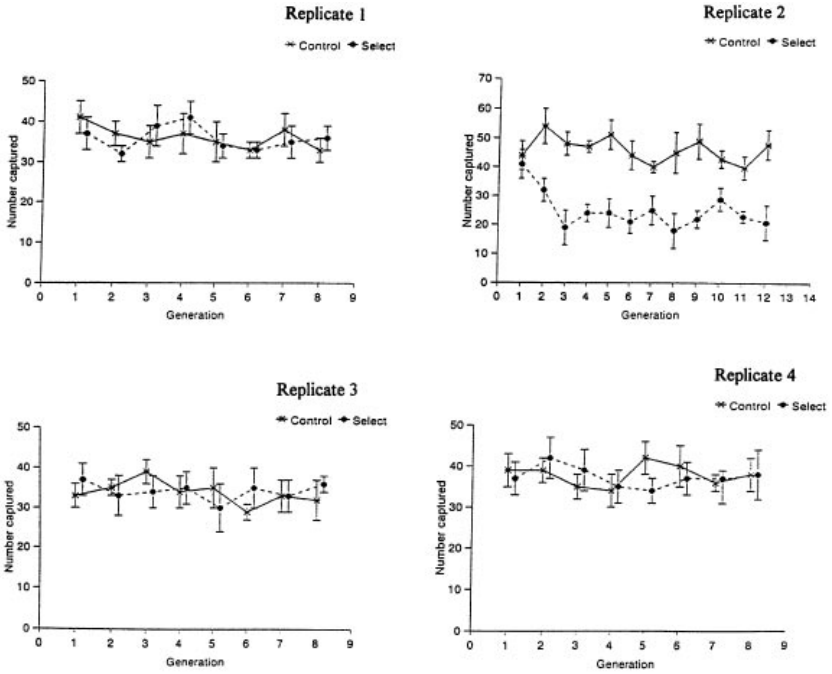

Fig. 2. Number of control and select males captured in Steiner traps baited with methyl eugenol (and naled). Each value represents average of 10 replicates; bar represents ± 1 SD.

It is possible that "responsiveness" to methyl eugenol is a composite trait that involves variable thresholds for physiological and/or behavioral responses with varying distance (concentration) to the lure. Perhaps the selection protocol effectively inhibited the mechanisms associated with close-range attraction in this line without concurrently affecting factors involved with long-range attraction. However, why such differential selection might occur in one select line (replicate 3) but not another (replicate 2) remains unclear.

Even where evident, selection did not result in the complete disappearance of male attraction to methyl eugenol. Although lowered through selection, male responsiveness in replicates 2 and 3 was stable (and not continually decreasing) though 8 and 12 generations, respectively. Still, the rapid (and persistent) response to selection reinforces Cunningham's (1989) recommendation that programs of male annihilation be implemented vigorously and decisively to avoid protracted costs associated with the eradication of unresponsive males. Interestingly, the same recommendation holds for SIT as well, as wild females may evolve "behavioral resistance" to sterile males in protracted release programs (McInnis et al. 1996).

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HABITAT ASSOCIATIONS OF GRASSHOPPERS AT THE MACARTHUR AGRO-ECOLOGY RESEARCH CENTER, LAKE PLACID, FLORIDA

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ABSTRACT

Grasshopper populations of the MacArthur Agro-Ecology Research Center at Lake Placid, in south-central Florida were monitored during the period 1993-1995. Samples were taken monthly during the spring, summer, and autumn months from 3 discrete habitats: citrus groves, improved pastures, and weedy margins of irrigation ditches. The grasshopper species assemblage at the Research Center consisted of 16 species in the family Acrididae, 7 species in the family Tettigoniidae, and 3 species in the family Tetrigidae. Family and species dominance varied among habitats. Grasshopper abundance was highest in citrus groves and ditch margins, and these habitats had proportionally more acridids. Pastures were inhabited by fewer grasshoppers, and were dominated by tettigoniids. The nymphal tettigoniid population was relatively high, and adult population relatively low, in pastures. Tetrigids were infrequent in all habitats. The most abundant grasshoppers were *Dichromorpha viridis* (Scudder) and *Conocephalus fasciatus* (DeGeer), grass-feeding species that were abundant in all habitats sampled. Collection of *Melanoplus bispinosus* Scudder is a new state

record. Potential effects of grasshoppers and land management on avifauna are discussed.

RESUMEN

Las poblaciones de saltamontes del MacArthur Agro-Ecology Research Center en Lake Placid, Florida, fueron muestreadas durante los años 1993-95. Fueron tomadas muestras mensualmente durante la primavera, verano y otoño en tres habitats discretos: campos de cítricos, pastos mejorados, y márgenes enyerbadas de embalses de riego. El conjunto de especies de saltamontes consistió de 16 especies de la familia Acrididae, 7 especies de la familia Tettigoniidae y 3 especies de la familia Tetrigidae. La dominancia de familias y especies varió entre los habitats. La abundancia de saltamontes fue más alta en los campos de cítricos que en las márgenes de los embalses y estos habitats tuvieron proporcionalmente más acrídidos. Los pastos fueron habitados por pocos saltamontes, y fueron dominados por los tetigónidos. La población ninfal de tetigónidos fue relativamente alta y la población de adultos relativamente baja en los pastos. Los tetrígidos fueron infrecuentes en todos los habitats. Los saltamontes más abundantes fueron *Dichromorpha viridis* (Scudder) y *Conocephalus fasciatus* (DeGeer), las especies que se alimentan de hierba fueron abundantes en todos los habitats muestreados. La colecta de *Melanoplus bispinosus* Scudder es un nuevo record para el estado. Son discutidos los efectos potenciales en la avifauna de los saltamontes y el manejo de la tierra.

Grasshoppers are usually the dominant aboveground invertebrates in pastures and natural grasslands, at least when judged by biomass (Scott et al. 1979, Risser et al. 1981). By any measure, they usually are central to the conversion of plant matter into animal matter and in nutrient cycling. They also are critical elements in the food supply of many birds and mammals. Most birds, even those normally considered to be granivorous, rely on insects for part of their diet, and for rearing their young (McEwen 1987). Thus, resource management that impinges on grasshopper population dynamics potentially affects several trophic levels.

Much of south Florida is experiencing major change in land use, but not without considerable controversy. One of the most frequent forms of land conversion is replacement of grazing land with citrus groves. Debate continues as to the most appropriate use for land. The debate would be clarified considerably if data were available on actual impacts of land conversion. The MacArthur Agro-Ecology Research Center (MAERC) was established in 1988 to foster study of the ecological relationships among cattle ranching, citrus production, and the native environment. Herewith we report results of a study designed to obtain baseline data on the effects of land management practices on grasshoppers at MAERC.

MATERIALS AND METHODS

Research Site

MacArthur Agro-Ecology Research Center is adjacent to, and administered by, Archbold Biological Station, near Lake Placid, in Highlands County, Florida. MAERC is a 4,170 ha working cattle and citrus ranch, consisting principally of cabbage palm savannas, and wet and dry prairies. Most of the property is used to support cattle grazing, although there is a citrus grove on the property. The area is dissected by ditches to drain excess water from the pastures and grove.

The vegetation varies, but bahiagrass, *Paspalum notatum* (Poaceae), occurs abundantly in all habitats sampled. The improved pastures were nearly bahiagrass monocultures. The citrus groves were also invaded by weeds such as beggar-tick, *Bidens alba* (L.) DC (Asteraceae); dayflower, *Commelina diffusa* Burm. (Comelinaceae); marsh pennywort, *Hydrocotyle umbellata* L. (Apiaceae); West Indian chickweed, *Drymaria cordata* (L.) Willd. ex Roem. & Schult. (Caryophyllaceae); and Indian hemp, *Sida rhombifolia* (L.) (Malvaceae). The ditchbanks included the vegetation found in the groves, and also additional flora such as the umbrella sedge, *Cyperus brevifolius* (Rottb.) Hassk. (Cyperaceae); tropical carpetgrass, *Axonopus compressus* (Sw.) Beauv. (Poaceae); and the madder *Richardia braziliensis* (Moq.) Gomez (Rubiaceae). Emergent vegetation is found in some ditches, and consists of such flora as cattail, *Typha* spp.(Typhaceae); rushes, *Juncus* spp. (Juncaceae); arrowhead, *Sagittaria* sp. (Alismataceae) and primrose willow, *Ludwigia peruviana* (L.) Hara (Onagraceae). Ditch vegetation is quite variable, because ditches periodically are dredged or treated with herbicide.

Sampling

Selected sites were sampled monthly during spring, summer, and autumn months (March-October) for the years 1993-1995 except when adverse weather prohibited access to the sites. Two replicate sites of improved pasture (bahiagrass; at least 50 ha each), mature (>10 years old) orange grove (bahiagrass and weed understory; 60 ha), and ditchbank (various weeds and grasses) were sampled. Because there is only one citrus grove on the MAERC property, a commercial grove (80 ha) immediately adjacent to the MAERC, and an associated ditch area, were included to obtain 2 replicates for each habitat type. The commercial grove occupied a higher, drier site, and also differed in that insecticides were sometimes applied. The bahiagrass pastures were randomly selected from, and immediately adjacent to, 16 other bahiagrass pastures measuring 50-130 ha in area. The citrus groves also exceeded 50 ha in area. Thus, the size of the plots alleviates problems with edge effects.

Sampling was conducted using a standard 40 cm diameter sweepnet. We assumed that vegetation did not greatly influence our ability to capture a representative proportion of grasshoppers at each sampling location, but this is an imperfect assumption because the heavier vegetation of the ditchbanks sometimes impeded sampling. Each site was swept for a 3 min period in each of 6 locations; these subsamples were pooled and the grasshoppers were counted and identified to species. Some immature grasshoppers are very difficult to identify, principally acridids in the subfamily Cyrtacanthacridinae (Melanoplinae), so immatures were reared to the adult stage to facilitate identification. A single sampler collected grasshoppers from all pastures and sampling dates during each year of the study, but different samplers were employed in each year.

Results and Discussion

We observed 26 species of grasshoppers at the research site: 16 species in the family Acrididae, 7 species in the family Tettigoniidae, and 3 species in the family Tetrigidae (Table 1). These pasture, citrus, and ditchbank habitats contained about 22, 11, and 23% of the species in the families Acrididae, Tettigoniidae, and Tetrigidae, respectively, known to inhabit Florida (Peck et al. 1992). They also represent 59, 18, and 43% of the species in the families Acrididae, Tettigoniidae, and Tetrigidae, respectively, known to inhabit south Florida. *Melanoplus bispinosus* Scudder was heretofore not known from Florida, although recently we have also collected it from Quincy, in

TABLE 1. INVENTORY OF GRASSHOPPERS FOUND AT MACARTHUR AGRO-ECOLOGY RESEARCH CENTER, LAKE PLACID, FLORIDA, AND THEIR RELATIVE ABUNDANCE AND HOST PREFERENCE DURING 1993-1995.

Taxa (family, subfamily, species)	Abundance[1]	Habitat[2]
Acrididae: short-horn grasshoppers		
Crytacanthacridinae (Melanoplinae): spur-throated grasshoppers		
Aptenopedes aptera Scudder	+	P
Aptenopedes sphenarioides Scudder	+	G
Melanoplus bispinosus Scudder	+	D
Melanoplus propinquus Scudder	+++	G,D
Paroxya atlantica Scudder	++	D
Paroxya clavuliger (Serville)	+	D
Schistocerca americana (Drury)	+++	G,D
Schistocerca obscura (Fabricius)	+++	G,D
Stenacris vitreipennis (Marschall)	++	P,G
Gomphocerinae: slant-face grasshoppers		
Achurum carinatum (F. Walker)	+	P,D
Amblytropidia mysteca (Saussure)	++	P,G
Dichromorpha elegans (Morse)	++	P,G,D
Dichromorpha viridis (Scudder)	+++	P,G,D
Orphulella pelidna (Burmeister)	++	P,G,D
Oedipodinae: banded-wing grasshoppers		
Chortophaga australior (Rehn and Hebard)	+++	G,D
Romaleinae: lubber grasshoppers		
Romalea guttata (Houttuyn)	+	G,D
Tettigoniidae: long-horn grasshoppers		
Conocephalinae: meadow grasshoppers		
Conocephalus fasciatus (DeGeer)	+++	P,G,D
Orchelimum agile (DeGeer)	++	D
Copiphorinae: cone-headed grasshoppers		
Neoconocephalus triops (Linnaeus)	++	D
Phaneropterinae: katydids		
Amblycorypha floridana Rehn and Hebard	+	G,D
A. rotundifolia (Scudder)	+	G
Scudderia furcata Brunner	++	G,D
Scudderia texensis Saussure and Pictet	+	D
Tetrigidae: pygmy and grouse locusts		
Batrachideinae		
Tettigidea lateralis (Say)	++	G,D

[1](+ indicates rare; ++ indicates occasional; +++ indicates frequent)
[2](P indicates pasture; G indicates citrus grove; D indicates irrigation ditch)

TABLE 1. (CONTINUED)INVENTORY OF GRASSHOPPERS FOUND AT MACARTHUR AGRO-ECOLOGY RESEARCH CENTER, LAKE PLACID, FLORIDA, AND THEIR RELATIVE ABUNDANCE AND HOST PREFERENCE DURING 1993-1995.

Taxa (family, subfamily, species)	Abundance[1]	Habitat[2]
Tetriginae		
Neotettix femoratus (Scudder)	+	G,D
Paratettix mexicanus (Saussure)	++	G,D

[1](+ indicates rare; ++ indicates occasional; +++ indicates frequent)
[2](P indicates pasture; G indicates citrus grove; D indicates irrigation ditch)

northwest Florida, and it has long been known from Alabama (Dakin & Kirby 1970). Certainly more species would be found with additional collection, or collection from nearby xeric pine and oak-dominated habitats.

Nymphs predominated in the early collections, but by June most of the acridids and tetrigids were adults, whereas the tettigoniids were predominantly nymphs. A mixture of nymphal and adult tettigoniids could be found until October, but the proportion of nymphs was consistently higher in the pastures than elsewhere. There are several possible explanations for the high proportion of nymphs in pastures, including: (1) pastures may be more, or less, favorable for growth and reproduction of the tettigoniids; (2) avian predation may be higher in the pastures, with the birds feeding principally on the larger, more visible adults; and (3) adults may disperse from pastures to more preferred feeding or oviposition sites.

Family and species dominance varied among habitats. Figure 1 shows the abundance of acridids and tettigoniids at the various sample sites for 1994; the other 2 years exhibited very similar trends. Grasshopper abundance was highest in citrus groves and ditch margins, and these habitats had proportionally more acridids. Pastures supported fewer grasshoppers, and they were principally tettigoniids. Tetrigids were infrequent in all habitats.

Grasshopper populations in the citrus grove adjacent to MAERC were suppressed in mid-summer, following application of insecticides, during all years of the study. Chemical applications were particularly frequent in 1994 because a new insect pest, citrus leaf miner, *Phyllocnistis citrella* Stainton, had been introduced to Florida. The grove in MAERC did not receive insecticide applications, and grasshopper abundance remained high throughout the year.

The most abundant grasshoppers were the acridid *Dichromorpha viridis* (Scudder) and the tettigoniid *Conocephalus fasciatus* (DeGeer), grass-feeding species that were abundant in all habitats sampled. In the pastures, these were sometimes the only species collected. *Dichromorpha viridis* is the most common grasshopper associated with bahiagrass and St. Augustine grass throughout the state, whether the grass is used for forage or as turfgrass. *Conocephalus fasciatus* tends to be associated with these grasses, and other grasses, when they are taller, and not regularly cut, because grass seedheads are a preferred food (Gangwere 1961). Tettigoniids are common elements of eastern meadows (Osborne 1939), but infrequent in western grasslands where most grasshopper research has been conducted (Capinera & Sechrist 1982a).

Additional species that were found frequently were *Melanoplus propinquus* Scudder and *Chortophaga australior* Rehn and Hebard. These two species are present in Florida wherever broadleaf weeds occur, and are common in agricultural fields and other disturbed sites (Blatchley 1920). Thus, they were found in the citrus groves and

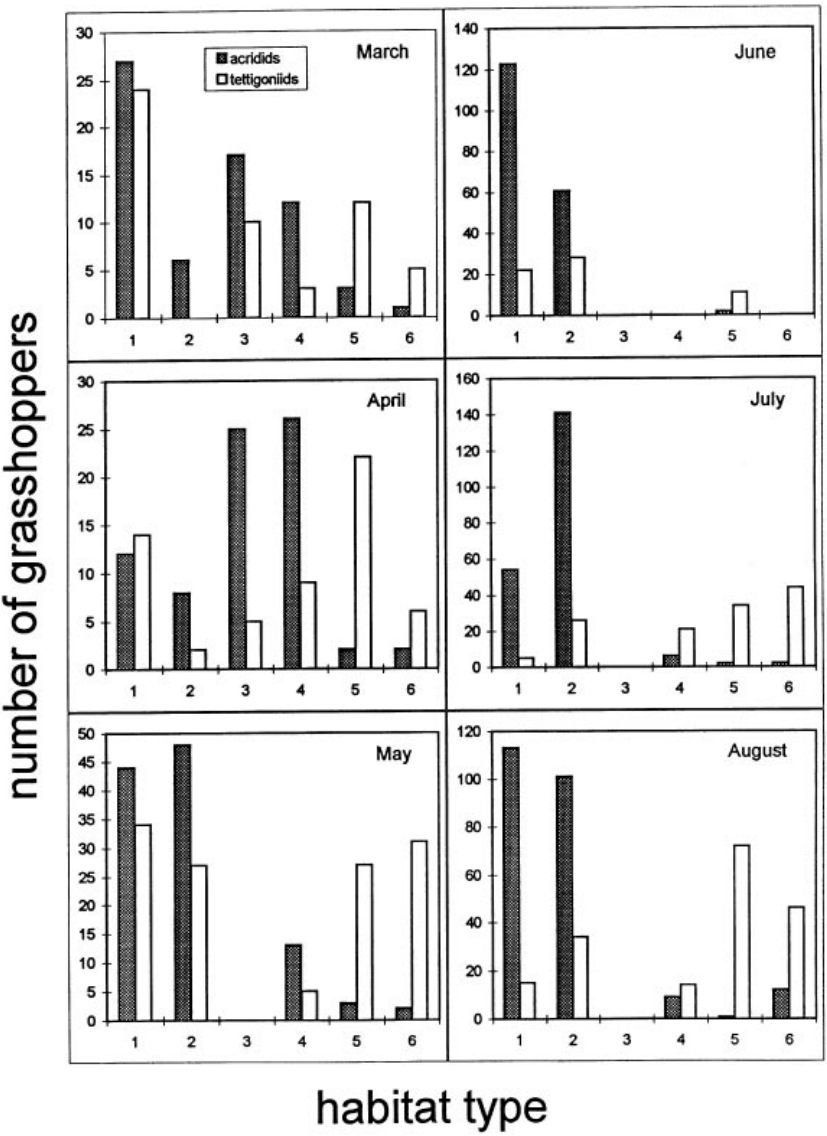

Fig. 1. Distribution pattern and abundance of acridid and tettigoniid grasshoppers at MacArthur Agro-Ecology Research Center (MAERC), summer 1994. Habitat designations are: 1 = understory of MAERC citrus grove; 2 = vegetation of MAERC irrigation ditch; 3 = understory of commercial citrus grove adjacent to MAERC; 4 = vegetation of irrigation ditch adjacent to commercial citrus grove; 5 = bahiagrass pasture 1; 6 = bahiagrass pasture 2.

ditchbank areas, but were absent from the bahiagrass pastures. The other abundant species were *Schistocerca americana* (Drury) and *S. obscura* (F.). These are polyphagous species that generally prefer broadleaf plants. They also tend to be arboreal in perching behavior. These species also were limited to citrus groves and ditchbanks in this study, but *S. americana* nymphs are sometimes found in pastures (Capinera 1993).

Habitat associations of some of the less abundant grasshoppers are also noteworthy. *Stenacris vitreipennis* (Marschall) and *Paroxya atlantica* (Drury) are found in wet habitats, often associated with emergent vegetation (Blatchley 1920). Although they were commonly found in the ditchbank areas, they also were recovered from groves. This is somewhat indicative of the moist environs of the MAERC, where standing water was not infrequent in both pastures and grove. However, it also reflects the highly dispersive nature of the grasshoppers. Without the moist habitat provided by irrigation ditches to serve as a source of inoculum, the citrus groves probably would not contain these species. Similarly, *Paratettix mexicanus* (Saussure) is found only in wet habitats, although *Tettigidea lateralis* (Say) inhabits a wide range of environments (Rehn & Grant 1961).

There is a rich literature documenting the effects of resource availability and land management on grasshopper populations. In arid and tropical environments grasshopper population density increases in proportion to rainfall and plant biomass (Capinera & Horton 1989, Fielding & Brusven 1990, Joern & Gaines 1990). The principal exception is when a shift in plant suitability is effected. For example, if a plant that is a relatively unsuitable host for grasshoppers, such as bluestem, *Andropogon* spp., is replaced by a more suitable plant, such as broadleaf weeds, grasshopper numbers may increase markedly despite the lack of change in biomass (Capinera & Sechrist 1982b, Capinera 1987, Olfert et al. 1994). This information has been used to promote vegetation replacement in weedy roadsides and fence rows with perennial grasses that are relatively unsuitable for grasshopper growth and reproduction and thereby reduce breeding by grasshoppers that disperse to nearby crops (Davis 1949, Olfert et al. 1994). The data collected from MAERC are consistent with these general observations about grasshopper population dynamics. However, the trends in abundance and diversity would have been even more pronounced were it not for the abundance of tettigoniids in pastures. The phenomenon of tettigoniid abundance is not usually observed in western grasslands except when decticine tettigoniids such as Mormon cricket, *Anabrus simplex* Haldeman, occur. Conocephaline tettigoniids, which were quite abundant in these studies, are an eastern phenomenon. The MAERC data also reflect the benefits of a rich floral understory. Some citrus producers keep their groves weed-free, or planted to bahiagrass; such groves would have a relatively depauperate grasshopper species assemblage, and relatively low abundance of grasshoppers.

The agroecosytems most common in south Florida, pastures, citrus groves, and accompanying drainage ditches, all were found to support abundant grasshopper populations. Grasshopper species assemblages were richer in citrus groves and drainage ditchbanks, which is undoubtedly related to the more diverse flora and greater biomass found in these habitats. On average, grasshopper populations were lower in pastures, but it is not certain whether this habitat is less suitable for grasshoppers, or more suitable for foraging by avian predators. Several bird species, including eastern meadowlark, *Sturnella magna magna* (L.); redwing blackbird, *Agelaius phoeniceus phoeniceus* (L.); cattle egret, *Bulbulcus ibis* L.; northern bobwhite, *Colinus virginianus virginianus* (L.); and northern mockingbird, *Mimus polyglottos polyglottos* (L.); frequent pastures at MAERC during the breeding season (Champe 1993). It remains to be determined whether birds make effective use of the grasshopper food resource available to them in the more diverse floral communities of the citrus groves and

ditchbanks, or whether they are deterred from feeding there by the density and architecture of the flora. Research conducted at MAERC by Champe (1993) suggests that birds take advantage of the food resources in citrus groves. Her studies showed that the most abundant birds in citrus groves are northern cardinal, *Cardinalis cardinalis*; cattle egret; mourning dove, *Zenaida macoura*; redwing blackbird; white-eyed vireo, *Vireo griseus*; and common yellowthroat, *Geothlypis trichas*. In addition to supporting a greater diversity of avifauna than pastures, Champe's (1993) studies showed that citrus groves supported a bird density more than twice that of pastures, and nearly as great as that occurring in natural forest. Thus, properly managed (minimal insecticide use, diverse understory) groves introduce habitat that increases insect and bird biodiversity in the south Florida grazing ecosystem.

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MORTALITY INDUCED BY *BACILLUS POPILLIAE* IN *CYCLOCEPHALA PARALLELA* (COLEOPTERA: SCARABAEIDAE) HELD UNDER SIMULATED FIELD TEMPERATURES

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ABSTRACT

The bacterium, *Bacillus popilliae* Dutky, causes milky disease in numerous species of scarabs around the world. *Bacillus popilliae* induced mortality in naturally infected grubs (third instars) of *Cyclocephala parallela* Casey was measured when held under simulated field temperatures. Our data show that visual examination in the field underestimates the percentage of grubs actually infected by *B. popilliae*. 5.6 to 8.2 times as many milky disease infected grubs died during the first 60 days of incubation under simulated field temperatures than did uninfected grubs. These data show that the widely used prevalence value underestimates the total mortality which this bacterium ultimately causes to *C. parallela*.

Key Words: white grubs, milky disease, sugarcane pests, natural infection

RESUMEN

La bacteria *Bacillus popilliae* Dutky, causa la enfermedad lechosa en numerosas especies de escarabajos alrededor del mundo. La mortalildad inducida por *B. popilliae*

en larvas (tercer instar) de *Cyclocephala parallela* Casey fue medida bajo condiciones simuladas de temperatura de campo. Nuestros datos muestran que el examen visual en el campo subestima el porcentaje de larvas realmente infestadas por *B. popilliae*. De 5.6 a 8.2 veces más larvas infestadas que no infestadas murieron durante los primeros 60 dias de incubación bajo temperaturas de campo simuladas. Estos datos muestran que el valor aplilamente usado de prevalencia subestima la mortalidad total que esta bacteria causa a *C. parallela*.

White grubs of the family Scarabaeidae are important insect pests of agricultural crops, horticultural plants, and turf world wide. The bacterium, *Bacillus popilliae* Dutky, causes milky disease in many scarab species and is one of the most widely known pathogens in biological control of insects (Klein & Jackson 1992). Infection with milky disease is synonymous with eventual grub death (Warren & Potter 1983). Prevalence of a disease in insect populations is the most commonly used parameter in epizootiology and is defined as the number of hosts afflicted with that disease at a given point in time (Fuxa & Tanada 1987). Many studies such as those of Harris (1959), Hutton & Burbutis (1974), Boucias et al. (1986), Kaya et al. (1992, 1993), and Redmond & Potter (1995) have reported on the prevalence of *B. popilliae* in different grub species. In many of these studies, it is either stated or implied that a high prevalence of infection indicates that *B. popilliae* is effective in controlling grub populations. Conversely, a low prevalence suggests that the bacterium is ineffective. However, grubs infected with *B. popilliae* would be expected to die more quickly under field conditions and be removed from future samples. Hence, prevalence data will underestimate the cumulative mortality of the insects over time. This would especially be true in a warm climate where milky diseased grubs will die more quickly due to faster development of *B. popilliae* at high temperatures (Milner et al. 1980; Cherry & Boucias 1989), and thus these grubs will be removed from prevalence estimations. Numerous studies have been conducted on *B. popilliae* in different grub species (Klein 1992). However, no studies have attempted to determine if prevalence data underestimate the impact of *B. popilliae* in controlling grub populations. In this study, we report on *B. popilliae* induced mortality in naturally infected grubs of *Cyclocephala parallela* Casey held under simulated field temperatures. The relevance of these data to the use of prevalence data of *B. popilliae* in grub populations is discussed.

Materials and Methods

Third instar larvae (grubs) of *C. parallela* were collected by digging under sugarcane plants in commercial fields in southern Florida. *Cyclocephala parallela* larvae were collected from October to March when the predominant life stage in Florida sugarcane fields is the third instar (Cherry 1985). Approximately 70 grubs were collected each month from October 1993 to March 1994 (354 grubs) and October 1994 to March 1995 (326 grubs). Grubs were collected in the morning and held 2 to 3 h in plastic buckets filled with soil. Physical damage to grubs caused by digging became apparent during the 2 to 3 h period after collection and these bruised grubs were removed from the tests. After the damaged grubs were discarded, milky appearing grubs were noted, and the grubs were placed individually into petri dishes. Each petri dish (9 cm diam) contained a piece of raw carrot for food and moist soil. The soil was obtained from a field which had been in rice production for several years. This soil was selected since we believed it would contain few, if any, *B. popilliae* spores due to the absence of

scarab populations in this cropping system. Hence, we felt that we were evaluating naturally infected grubs in all stages of infection directly from the sugarcane fields and not infecting them while they were being held in the lab.

Grubs were held in the petri dishes in a temperature cabinet in constant darkness and at simulated field temperatures. Simulated field temperatures were obtained by holding the grubs at the mean monthly soil temperatures (Cherry 1991) at 10 cm, which is where most grubs are found (Cherry 1984). Daily temperatures at that depth in Florida sugarcane fields do not fluctuate greatly during the time the tests were conducted. The temperature was changed each month to match the field temperature of that month. Cabinet temperatures were 26.0, 26.0, 22.8, 18.3, 20.2, 21.3, and 23.3°C for the October through April test period. Grub survivorship was checked every 3-4 days by opening the petri dish to examine the grub. This procedure also allowed fresh carrot and/or water for soil moisture to be added. Grubs which were inactive and did not move when prodded were considered dead and were frozen for later examination for *B. popilliae* spores. All grubs still alive 60 days after the start of the tests were killed by freezing and held for later examination. Since these grubs were alive at 60 days, and they would have lived longer than 60 days if we had not frozen them, they were recorded as dying at >60 days. Frozen grubs were thawed out later and bled middorsum onto individual microscope slides. These slides were examined with phase contrast microscopy for the presence of *B. popilliae* spores. Mortality data were grouped into four time intervals of 0-20, 21-40, 41-60, and >60 days. Thereafter, these data were put into a 4×2 contingency table (Steel & Torrie 1980) using Chi-square analysis to determine if the mortality rate was independent of *B. popilliae.*

Results and Discussion

A total of 354 grubs were observed from October 1993 to March 1994. Four of these grubs appeared milky at field collection and hemolymph examination later showed *B. popilliae* present in all four. *B. popilliae* was found in a total of 23 grubs. Hence, only 17.4% of the grubs with *B. popilliae* were actually seen as milky at field collection.

A total of 326 grubs were observed from October 1994 to March 1995. Fourteen of these grubs appeared milky at field collection and hemolymph examination later showed *B. popilliae* present in all 14. *B. popilliae* was found in a total of 39 grubs during the second year. Hence, 35.9% of the grubs with *B. popilliae* were actually seen as milky at field collection.

Harris (1959) used a visual examination for milky appearing grubs in the field to estimate the disease incidence of *B. popilliae* in *C. paralella* populations. Our data show that visual examination in the field for milky grubs seriously underestimates the percentage of grubs actually infected by *B. popilliae.* These data support the findings of Kaya et al.(1992, 1993) for *B. popilliae* in *C. hirta* LeConte in California turf.

Mortality data for *C. parallela* grubs held from October 1993 to March 1994 are shown in Table 1. Chi-square analysis showed that mortality rate was dependent (Chi-square = 106.3, $P < 0.005$) upon the presence of *B. popilliae.* During 0 to 59 days after field collection, 69.6% of grubs with *B. popilliae* died. In contrast, 8.5% of grubs without *B. popilliae* died during that time frame. Hence, in this test, 8.2 times more grubs which were infected with *B. popilliae* died during the first 59 days under simulated field temperatures than did uninfected grubs.

Mortality data for *C. parallela* grubs held from October 1994 to March 1995 are also shown in Table 1. Chi-square analysis again showed that mortality rate was dependent (Chi-square =74.6, $P < 0.005$) upon the presence of *B. popilliae.* During 0 to 59 days after field collection, 64.1% of grubs with *B. popilliae* died. In contrast, 11.5% of grubs without *B. popilliae* died. Hence, in this test, 5.6 times more milky disease in-

TABLE 1. MORTALITY OF THIRD INSTAR *CYCLOCEPHALA PARALLELA* AFTER FIELD COLLECTION FROM OCTOBER 1993 TO MARCH 1994, AND OCTOBER 1994 TO MARCH 1995.

	Number Dying During Interval (Days)[a]			
	0-20	21-40	41-60	>60
October 93-March 94				
+*Bacillus popilliae*	3(1.4)	8(1.0)	5(0.5)	7(20.2)
–*B. popilliae*	18(19.6)	7(14.0)	3(7.5)	303(289.9)
October 94-March 95				
+*B. popilliae*	10(3.2)	5(1.8)	10(1.9)	14(32.2)
–*B. popilliae*	17(23.8)	10(13.2)	6(14.1)	254(235.8)

[a]Number in parentheses = Expected via Chi-square analysis. The contingency table (Steel and Torrie 1980) shows that the mortality rate is dependent (Chi-square = 106.3, P < 0.005 [93-94], and = 74.6, P < 0.005 [94-95]) upon the presence of *Bacillus popilliae.*

fected grubs died during the first 59 days under simulated field temperatures than did uninfected grubs.

C. parallela has a one year life cycle with the third larval instar being the predominant stage during nine months of the year (Cherry 1985). *B. popilliae* is found in all three larval instars (Cherry and Boucias 1989). Data in Table 1 show that percent prevalence taken at any one time underestimates the total mortality to *C. parallela* caused by *B. popilliae.* This underestimation is simply due to *B. popilliae* infected grubs dying more rapidly under conditions in the fields than healthy grubs and hence infected grubs are removed from future samples.

In summary, our data show that the impact of *B. popilliae* upon *C. parallela* may be underestimated for two reasons. First, field observation of visually obvious milky appearing grubs indicates only a proportion of the total infected grubs. Second, and more important, the widely used percent prevalence method underestimates the total mortality which the bacterium ultimately causes to *C. parallela* over time.

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A NEW SPECIES OF *ARRHOPALITES* FROM CHINA (COLLEMBOLA: SMINTHURIDAE)

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ABSTRACT

A new species of *Arrhopalites* is described from China. It is distinguished by lack of eyes and absence of short spines on anogenital segment.

Key Words: Collembola Sminthuridae, *Arrhopalites*, China

RESUMEN

Una nueva especie de *Arrhopalites* es descrita de China. La especie se distingue por la falta de ojos y la ausencia de espinas cortas en el segmento anogenital.

A number of authors have described species of *Arrhopalites* from Asia (Nayrolles 1990, Yosii 1954, 1966a, 1966b, and 1970) but no species of *Arrhopalites* have previously been recorded or described from China. We describe the first Chinese species below. In the descriptions and figures we follow the system of tibiotarsal and third antennal segment chaetotaxy developed by Nayrolles (1987 & 1991) and the system of circumanal chaetotaxy shown in Christiansen & Bellinger 1996.

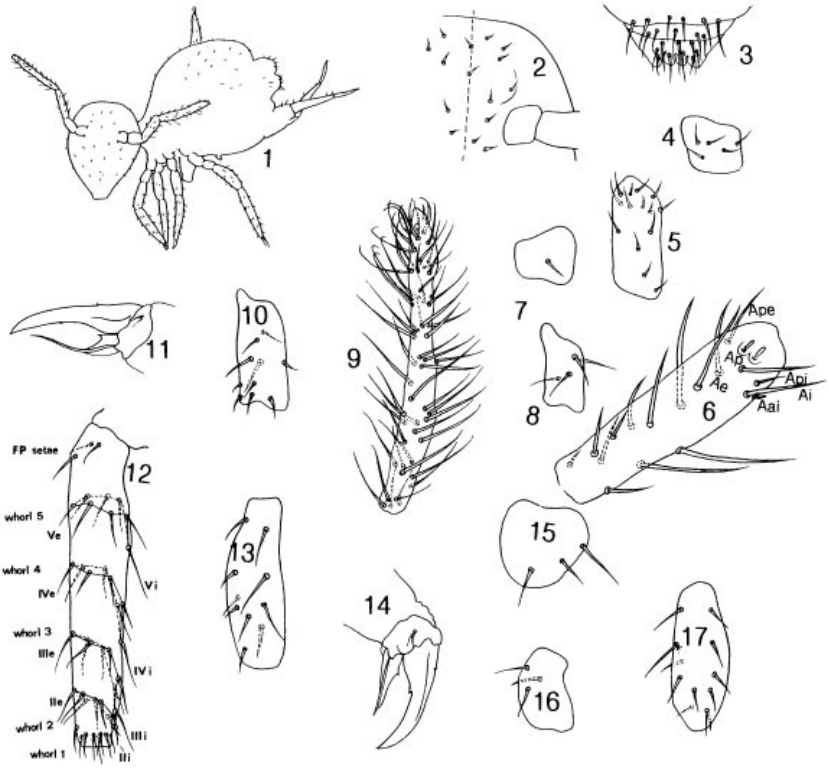
Arrhopalites pukouensis, sp. nov. (Figs. 1-27)

Length up to 1.30 mm.

Pigment completely absent (Fig. 1).

Eyes absent. Vertical setae slender and short (Fig. 2). Labral setal pattern 6, 5, 5, 4 (Fig. 3). Average ratio of antenna to head 4: 3; antennal ratios 1: 1.63-1.73; 2.44-2.53; 4.88-5.2. Ant. I with 5 dorsal setae (Fig. 4); Ant. II with 14 setae, mostly on distal half (Fig. 5); Ant. III with setae Ai, Api, Ae, and Ape similar and acuminate with Ape only slightly smaller than others, seta Api short and acuminate, seta Aai short blunt and rod like (Fig. 6); Ant. IV not subsegmented; distal half thinner with setae verticillate from 3 or 4 slight thickenings; outer setae of distal 1/4 with tips strongly curved apically towards antennal axis; dorsally with a subapical paddle-shaped organ (Fig. 9). All antennal setae smooth.

All leg setae smooth and acuminate. First coxa with 1 anterior seta (Fig. 7). Trochanter with 2 anterior and 2 posterior setae (Fig. 8). Femur with 8 anterior and 2 posterior setae (Fig. 10). Pretarsus with 1 anterior and 1 posterior setulae, 1 outer and 1 inner tooth; unguiculus with 1 tiny corner tooth, acuminate subapical filament, not reaching apex of unguis (Fig. 11). Tibiotarsus with 3 FP setae, 8 setae in whorls 2 - 5 and 9 in whorl 1 (Fig. 12).



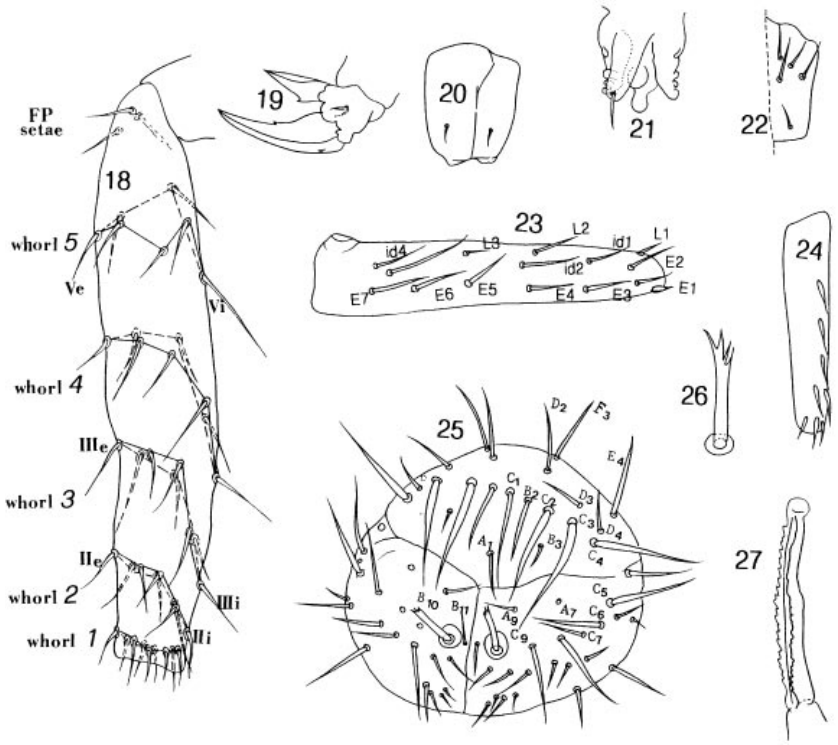
Arrhopalites pukouensis n. sp.

Fig. 1. Habitus; 2. Setae of vertex; 3. labral setae; 4. ant. I, dorsal view; 5. ant. II, dorsal view; 6. ant. III, dorsal view; 7. fore coxa, anterior view; 8. fore trochanter, anterior view; 9. ant. IV, dorsal view; 10. fore femur, anterior view; 11. fore pretarsus; 12. fore tibiotarsus, anterior view; 13. Mesofemur, anterior view; 14. middle pretarsus; 15. metacoxa, anterior view; 16. metatrochanter, anterior view; 17. metafemur, anterior view.

Middle coxa and trochanter each with 3 anterior setae. Femur with 8 anterior and 2 posterior setae (Fig. 13). Tibiotarsus similar to hind leg. Pretarsus similar to that of foreleg except subapical filament of unguiculus is much shorter (Fig. 14).

Hind coxa with 3 anterior setae (Fig. 15). Trochanter with 2 anterior and 1 posterior setae (Fig. 16). Femur with 9 anterior and 3 posterior setae (Fig. 17). Tibiotarsus with 3 FP setae, 7 setae in whorl 5, 8 setae in each of whorls 2-4 and 9 setae in whorl 1 (Fig. 18). Pretarsus as in fore leg. Unguiculus without subapical filament and broader than those of fore and middle pretarsus (Fig. 19).

Ventral tube with 1+1 subapical setae (Fig. 20). Corpus of tenaculum with 1 setula; ramus with 3 teeth and 1 basal appendix (Fig. 21). Manubrium with 5+5 dorsal smooth setae (Fig. 22). Dorsum of dens with setae E1-7, d1-3, id1 - 4 & L1-3 present. Only seta E1 is spinelike, L1,3 very short (Fig. 23); Ve setae on ventral dens as 3, 2, 1, 1, 1, (Fig. 24). Mucro with both dorsal edges irregularly serrated; distal part abruptly narrowed with tip rounded (Fig. 26). Circumanal setae C2-5 swollen basally,



Arrhopalites pukouensis n. sp.

Fig. 18. metatibiotarsus, anterior view; 19. hind pretarsus; 20. ventral tube; 21. tenaculum; 22. manubrium, right half, dorsal view; 23. left dens, dorsal view; 24. left dens, ventral view; 25. anogenital segment; 26. left mucro; 27. female subanal appendage.

C1 slightly swollen; C6, D2- 4, E4 and F4 setaceous (Fig. 25). Female subanal appendage 4-forked apically (Fig. 27).

Known only in type locality: in soil at depth of 10-15 cm beneath surface.

Types: Holotype female; paratypes 1 female & 1 male. P. R. China: Jiangsu Province: Nanjing: Pukou: Longwangshan (Longwang Hill), IV-23-1995, locality No. 8449, Guo Jian-Ying coll. Deposited in Department of Biology, Nanjing University.

Etymology. Named after type locality: Pukou.

Arrhopalites pukouensis is found in soil at the depth of 10-15 cm beneath the surface rather than on surface or in caves as most known species in the genus. It is the second record of an eyeless Asian species of *Arrhopalites*. It differs from the eyeless Japanese cave-dwelling species *A.* (*Coecarrhopalites*) *antrobius* (Yosii 1954) in lacking the short spines on the valves of anogenital segment as well as in the shape of the subanal appendages.

This species has the 5 rows of heavy Ve setae characteristic of the group of species usually included in the subgenus *Coecarrhopalites* but as Ellis & Bellinger (1973) have pointed out this is an objective synonym of *Arrhopalites* and therefore not an available name. *A. pukouensis* lacks the short anal valve spines which has generally

been considered diagnostic for this group of species. This, along with conflicting characteristics of other recently described species, indicates that if this subgenus is to be resurrected (and renamed) it must be redefined.

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ATTRACTION OF *ANASTREPHA SUSPENSA* (DIPTERA: TEPHRITIDAE) TO VOLATILES FROM AVIAN FECAL MATERIAL

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ABSTRACT

Flight tunnel bioassays confirmed attraction of female Caribbean fruit flies, *Anastrepha suspensa* (Loew), to volatiles from aqueous solutions of avian fecal material and methanol extracts of avian fecal material. Attraction was highest to freshly prepared and 72-h-old solutions of crude material. In direct comparisons between aqueous solutions of crude material and weight-equivalent amounts of methanol extract, more females were captured in response to volatiles from crude material in tests of 0-, 24- and 72-h-old solutions. Ammonia release rate was greater from the crude material than from the methanol extract in tests of 0-, 24- and 48-h-old solutions, The greatest amount (± sd) of ammonia was released from freshly prepared aqueous solutions of crude material (777 ± 250 µg/h from 75 mg of crude material) but dropped within 24 h (288 ± 96 µg/h from 75 mg of crude material) and then stayed close to that level. The greatest amount of ammonia released from methanol extracts was obtained from freshly prepared solutions (229 ± 70 µg/h from 75 mg crude material weight equivalent), also dropped within 24 h (98 ± 12 µg/h from 75 mg crude material weight equivalent) and then stayed fairly constant. Numbers of flies captured by either solution were directly correlated with ammonia release within the first 48 h of testing only, indicating that ammonia was partially or wholly responsible for attraction to the crude material during the first 48 h of testing. An increase in capture of females by volatiles from avian fecal material after 72 h in aqueous solution, which was observed in all tests, indicates that some chemical(s), other than ammonia, remain to be identified that are involved in fruit fly attraction.

Key Words: Caribbean fruit fly, attractants, ammonia, avian fecal material

RESUMEN

Los bioensayos en túneles de vuelo confirmaron la atracción de las hembras de la mosca frutera del Caribe, *Anastrepha suspensa* (Loew), por volátiles de soluciones acuosas de material fecal de aves y por extractos en metanol del mismo material. La atracción fue más alta por las soluciones de material crudo frescas y de 72 horas de preparadas. En comparaciones directas entre las soluciones acuosas de material crudo y las cantidades equivalentes en pesos de extracto de metanol, más hembras fueron capturadas en repuesta a volátiles de material crudo en pruebas con soluciones de 0, 24 y 72 horas de edad. La tasa de liberación de amonio fue mayor en el material crudo que en el extracto de metanol en pruebas de 0, 24 y 48 horas. La mayor cantidad (± sd) de amonio fue liberada de las soluciones acuosas frescas de material crudo (777 ± 250 µg a partir de 75 mg de material crudo), pero cayó dentro de las 24 horas (288 ± 96 µg/h a partir de 75 mg de material crudo) y entonces permaneció cercana a ese

nivel. La mayor cantidad de amonio liberado de los extractos de metanol fue obtenida de soluciones frescas (229 ± 70 µg/h a partir de 75 mg de material crudo por equivalente en peso), también cayó en 24 horas (98 ± 13 µg/h a partir de 75 mg material crudo por equivalente en peso) y entonces permaneció medianamente constante. Los números de moscas capturados directamente en cualquier solución estuvieron directamente correlacionados con la liberación de amonio dentro de las primeras 48 horas de prueba solamente, indicando que el amonio fue parcial o totalmente responsable de la atracción hacia el material crudo durante las primeras 48 horas de prueba. Un aumento en la captura de las hembras por los volátiles de material fecal de aves en solución acuosa después de las 72 horas, el cual fue observado en todos los tests, indica que algunas sustancias, diferentes del amonio, están pendientes de ser identificadas como envueltas en la atracción de moscas fruteras.

Many adult insects require protein meals to ensure reproductive success. This requirement has been the basis for the successful use of protein-based liquid baits for detecting adults of pest Tephritidae (Anonymous 1989). McPhail traps, which are bell-shaped glass traps with a water reservoir (Newell 1936), baited with torula yeast (TY)-borax pellets (ERA Int., Freeport, NY) are currently used for detection and delineation of the Caribbean fruit fly, *Anastrepha suspensa* (Loew), in Florida (Anonymous 1989). These traps have low efficiency (Calkins et al. 1984) and improved lures are needed for these and other pest Tephritidae currently monitored with protein-baited traps (Calkins 1993). Food-based synthetic attractants have been developed for the Mexican fruit fly, *Anastrepha ludens* (Loew), and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Robacker & Warfield 1993, Heath et al. 1995, Robacker 1995). These synthetic attractants, which include ammonia in combination with 1,4 diaminobutane (putrescine), are based on volatiles emitted from liquid protein baits. Adult tephritids have been observed feeding on plant exudates, rotting fruits, decaying insects and bird dung (Christenson & Foote 1960), substances that provide sources of protein. Identification of volatile chemicals from natural food sources, such as bird dung, may provide additional components that could improve the effectiveness of the food-based synthetic attractants.

Adults of C. *capitata* and the apple maggot, *Rhagoletis pomonella* (Walsh), feed on bird dung in the field (Hendrichs & Hendrichs 1990, Hendrichs & Prokopy 1990). Droppings that were held for 24-48 h before testing were more attractive than droppings that were tested before 24 or after 48-72 h, and avian fecal material was more attractive than liquid protein bait in field cage trials (Prokopy et al. 1992, Prokopy et al. 1993a). We report herein the results of laboratory trials that were conducted to evaluate the attraction of Caribbean fruit fly females to volatiles from avian fecal material. Change in attractiveness of avian fecal material over a 4 d period and attraction of flies to volatiles from avian fecal material partially purified by solvent extraction were also tested. Ammonia is one of the volatile chemicals produced by avian fecal material (e.g., Beard & Sands 1973), and ammonia is a known attractant for fruit flies (reviewed in Econompoulos 1989). Therefore, the role of ammonia in attraction was investigated by measuring the release rate of ammonia and correlating female preference with ammonia release from avian fecal material and from methanol extractions.

Material and Methods

Caribbean fruit flies used in this study were obtained as pupae from the Florida Department of Agriculture and Consumer Services, Division of Plant Industry in

Gainesville, Florida. Flies were given water and adult food (3:1 mixture of refined cane sugar:brewer's yeast), and were maintained in screen cages (30× 30 × 30 cm) in a laboratory with a photoperiod of 12:12 (L:D) h at room temperature and ambient humidity. Females were 4-10 d post-eclosion and were protein-starved for 24 h before testing.

Avian fecal material was obtained as droppings from housed chickens (Prokopy et al. 1993a). Droppings were collected within 24 h of deposition and placed in storage at 4°C. Fecal material was removed from storage and incubated at room temperature and ambient relative humidity for 24 h before use. This incubation time was found to be important for attractiveness (Prokopy et al. 1993a). Fecal material was tested as aqueous solutions of crude material (mg/ml) and as aqueous solutions of methanol extract (µl/ml) in tap water. Aqueous solutions were used to prevent desiccation of the sample during the bioassay. Previous studies indicated that only water and methanol extracts of crude material retained biological activity for apple maggot attraction (B. D. D., C. R. L. & R. J. P., unpublished data). Methanol extracts of the avian fecal material were made by mixing two parts methanol (volume) to one part crude material (weight). After mixing for 20 min, the particulate material was removed by filtration through a 70-100 µ (micron) sintered glass filter. The filtrate was concentrated to 50% of the original volume under vacuum. Weight equivalents (1 mg/µl) were used for comparisons with crude materials. Fresh solutions were made for each replicate, and solutions were tested over a 4-d-time period (0, 24, 48 and 72 h after preparation) to test for change in attractiveness over time.

Bioassays were conducted using a two-choice volatile attractant bioassay system (Heath et al. 1993). The test insects were released in a flight tunnel (122 × 30.5 × 30.5 cm plexiglass chamber). Two horizontally-mounted traps, with orange sticky paper (Atlanta Paste and Glue, Brooklyn, NY) on the front to retain responding flies, were suspended inside the tunnel. Test substrates (100 ml) were placed in narrow mouth flasks (500 ml), and entrained volatiles from the test substrate were introduced into the bioassay test chamber. Volatiles from the test substrates were vented through the flight tunnels for at least one hour before addition of flies to allow volatile release to stabilize. There were 20-25 females tested per bioassay, and numbers of flies per trap were recorded after approximately 20 h.

Preliminary tests, which evaluated a range of two-fold dilutions (6, 3, 1.5, 0.75 and 0.38 mg/ml) of crude material in tap water, were used to determine appropriate concentrations for the bioassays. These tests indicated that 0.38-1.5 mg/ml was the optimal range for fruit fly capture in the laboratory bioassay. Capture decreased at concentrations greater than 1.5 mg/ml, indicating that test volatiles were repellent at these higher concentrations. Three experiments were conducted to evaluate attractiveness of avian fecal material for *A. suspensa*. In experiment 1, females were exposed to volatiles from 0.38, 0.75 or 1.5 mg/ml of aqueous solutions of crude material or a water blank with 4, 3 and 3 replicates, respectively, of each concentration. In experiment 2, females were exposed to volatiles from 0.38 or 1.5 µl/ml methanol extract in water or a water blank with an equivalent amount of methanol, with 5 replicates of each concentration. In experiment 3, females were given the choice of aqueous solutions of crude material and methanol extract (0.75 mg/ml and 0.75 µl/ml), and there were 13 replicates. In the last 4 replicates of experiment 3, release rates of ammonia from the test substrates were determined each day before the substrate was used in the bioassay. Ammonia release rates were determined using an ammonia-specific ion-selective electrochemical probe (Orion, Boston, MA) following the procedure of Heath et al. (1995).

Number of flies captured by test substrate versus blank and by crude material versus extract were analyzed by two sample *t*-tests (Proc TTEST, SAS Institute, 1985). Effects of other factors were analyzed using a mixed model with interaction (Proc

GLM, SAS Institute 1985). These factors included test solution concentration and time period. Data were assessed by the Box-Cox procedure (Box et al. 1978) and were square-root ($x + 0.5$) transformed to stabilize the variance before analyses. Correlations between ammonia release rate and number of females trapped for each time period were tested using Proc CORR (SAS Institute 1985).

Results and Discussion

More flies responded to the test solution than to the associated blank in all tests in experiments 1 and 2 (Table 1). Concentration of test substrate had no effect on fly capture, so data from all concentrations were grouped. Separate analyses were conducted on the effect of time period (age of test substrate) on response to crude material and to methanol extract. For these analyses, number responding to the control subtracted from number responding to test substrate, and the difference was used as the response variable (Table 1). Time period affected capture in response to volatiles from crude material ($F = 3.15$; df = 3, 36; $P = 0.0366$), but not from methanol extract. The highest capture was obtained with volatiles from fresh solutions and from 72-h-old solutions of crude material.

In experiment 3, more females were captured by crude material for all but the 48-h old test substrates (Table 2). Average ammonia release rates from the test substrates in the last 4 replicates are given in Table 3. The highest amount of ammonia was obtained from the freshly prepared crude material. There was a 37% drop in release rate within 24 h of testing, and ammonia remained at that level throughout the remainder of the study. Ammonia release from the crude material was higher than release from the methanol extract for the first 48 h testing. After 72 h, although the release rate of ammonia from crude avian fecal material was still higher on average, the ammonia release was more variable among the samples and the difference was not significant. Numbers of flies trapped were correlated with ammonia release rate for 0-h ($r = 0.69$, $P = 0.05$) and 24-h ($r = 0.63$, $P = 0.05$) old test substrates. The number of flies trapped was also indirectly related to presence of methanol, which could indicate that the methanol was repellent. There was methanol in the extract test solution that was not in the crude material test solution. However, the amount of methanol was small (75 µl in 100 ml of water), and preliminary tests indicated that, if anything, the small amount of methanol was attractive.

No correlation between ammonia release and number of flies trapped was found in tests with 48-and 72-h-old substrates. Although there was a significant difference in ammonia released from crude material and methanol extracts in 48-h-old test substrates (Table 3), there was no difference in fly capture (Table 2). The reverse was observed in tests of 72-h-old test substrates, that is, that although there was no difference in ammonia release rates, more flies were captured in response to volatiles from the crude material. Thus, it appears that some attractive chemicals other than ammonia are released from the crude material after 72 h in aqueous solution, Prokopy et al. (1993a, 1993b) found that reducing microbial activity by the addition of antibiotics to avian fecal material reduced attractiveness to fruit flies. The 72 h time lag observed in our studies may indicate that microorganisms, which are utilizing breakdown products from earlier microbial action, may be responsible for the production of these late-appearing volatile chemicals.

The results of this study confirm that volatile chemicals released from avian fecal material are attractive to female Caribbean fruit flies. Ammonia was released in high amounts and there was a direct correlation between ammonia release from and capture of female flies by freshly prepared aqueous solutions of avian fecal material. Thus, ammonia appears to be partially or wholly responsible for fruit fly attraction to

TABLE 1. AVERAGE ± SD NUMBER OF FEMALE *ANASTREPHA SUSPENSA* TRAPPED IN LABORATORY BIOASSAYS OF RESPONSE TO VOLATILES FROM AQUEOUS FORMULATIONS OF TEST SUBSTRATE VERSUS CONTROL IN TESTS CONDUCTED OVER A FOUR DAY TIME PERIOD (FRESHLY PREPARED SOLUTIONS TESTED DURING 0 H).

	Time Period (h)			
Test Substrate	0	24	48	72
Crude material	10.1 ± 0.7*	7.3 ± 0.8*	8.5 ± 0.8*	11.7 ± 1.1*
Water control	1.4 ± 0.3	1.4 ± 0.3	1.5 ± 0.5	1.0 ± 0.5
Crude material minus control	8.7 ± 2.5	5.9 ± 2.6	7.0 ± 3.4	10.7 ± 4.4
Methanol extract	9.5 ± 1.0*	10.0 ± 0.7*	9.7 ± 1.0*	8.5 ± 0.9*
Methanol/water control	2.7 ± 0.5	2.3 ± 0.6	1.2 ± 0.2	1.9 ± 0.4
Methanol extract minus control	6.8 ± 3.7	7.7 ± 3.3	8.5 ± 2.9	6.6 ± 2.8

*Significant difference in number trapped by treatment odor source and paired control odor source (*t*-test, $P < 0.001$).

TABLE 2. AVERAGE ± SD NUMBER OF FEMALE *ANASTREPHA SUSPENSA* TRAPPED IN LABORATORY BIOASSAYS OF RESPONSE TO VOLATILES FROM AQUEOUS FORMULATIONS OF AVIAN FECAL MATERIAL VERSUS METHANOL EXTRACT OF AVIAN FECAL MATERIAL.

Time period (h)	Number of females trapped		*t*-test comparisons		
	Avian fecal	Methanol extract	*t*	df	*P*
0	7.0 ± 2.82	3.9 ± 2.06	3.17	24	0.0044
24	8.1 ± 2.88	4.3 ± 1.70	4.14	24	0.0004
48	6.8 ± 3.98	6.1 ± 2.61	0.47	24	ns*
72	7.1 ± 2.72	4.5 ± 2.63	2.49	24	0.0201

*not significant.

TABLE 3. AVERAGE ± SD RELEASE RATE OF AMMONIA FROM AQUEOUS SOLUTIONS OF AVIAN FECAL MATERIAL VERSUS METHANOL EXTRACT (MG EQUIVALENTS) OF AVIAN FECAL MATERIAL. AMMONIA MEASUREMENTS WERE MADE AT THE START OF THE TIME PERIOD.

Time period (h)	Ammonia release rate (μg/h)		*t*-test comparisons		
	Avian fecal	Methanol extract	*t*	*df*	*P*
0	778 ± 250	229 ± 70	4.22	6	0.0055
24	288 ± 96	98 ± 12	4.37	8	0.0024
48	250 ± 108	93 ± 30	3.12	8	0.0142
72	244 ± 232	93 ± 41	1.27	6	ns*

*not significant.

fresh bird dung. Methanol extracts maintained some activity, but were less attractive than equal amounts of the crude material and did not show an increase in attractiveness with aging as was observed with crude material. It is hypothesized that microbial activity in the aqueous solutions of avian fecal material is responsible for the production of the late-appearing attractive compounds. Methanol extracts may not provide substrates needed for this microbial activity. Volatiles from microorganisms found associated with fruit flies or larval-infested fruit have been shown to be attractive to various fruit flies (e.g., Courtice & Drew 1983, Jang & Nishijima 1990, Robacker et al. 1991, MacCollom et al. 1992). Studies on the microbial profile of avian fecal material over this time period are underway to identify microorganisms that may be responsible for production of additional chemical attractants.

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MORTALITY OF THE LARVAL ROOT WEEVIL *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE) IN SIMULATED FLOODING

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ABSTRACT

Larvae of the weevil *Diaprepes abbreviatus* L. can cause substantial damage to sugarcane and citrus. To test the feasibility of managing *Diaprepes* populations by flooding canefields for extended periods of time, larval mortalities were recorded after submerging larvae under water in soil filled trays at temperatures from 18 to 27°C for up to 5 weeks. Mean mortality exceeded 90% by 3 weeks of submergence at 24 and 27°C and after 5 weeks at 21°C, but was only 46% after 5 weeks at 18°C. A model was derived by multiple regression analysis, describing the response of mortality to time and temperature. The model accounted for 84% of the variation in larval mortality. Levels of O_2 and pH were monitored in selected trays during the experiment; only pH correlated significantly with larval mortality but contributed only 20% of total variation.

Key Words: citrus root weevil, drowning, sugarcane, statistical modeling

RESUMEN

Las larvas de *Diaprepes abbreviatus* L. pueden causar daño sustancial a la caña de azúcar y los cítricos. Para probar la posibilidad de manejar poblaciones de *Diaprepes* mediante la inundación de campos de caña durante largos períodos, las mortalidades

larvales fueron registradas después de sumergir las larvas en agua en bandejas con suelo a temperaturas de 18-27°C hasta 5 semanas. La mortalidad promedio excedió el 90% antes de las 3 semanas de submersión a 24 y 27°C, y después de 5 semanas a 21°C, pero fue solamente del 46% después de 5 semanas a 18°C. Fue derivado un modelo que describe la respuesta de la mortalidad al tiempo y a la temperatura, mediante análisis de regresión múltiple. El modelo respondió por el 84% de la variación en la mortalidad larval. Los niveles de O_2 y pH fueron muestreados en bandejas seleccionadas durante el experimento; sólo el pH se correlacionó significativamente con la mortalidad larval pero contribuyó solamente en un 20% a la variación total.

Diaprepes abbreviatus has infested citrus and various ornamental and wild host plants in Florida since 1964 (Woodruff 1964, Beavers & Selhime 1975, Schroeder et al. 1979). In the Caribbean Basin, the weevil is called the West Indian sugarcane rootstock borer weevil and infests both sugarcane and citrus. The impact of *D. abbreviatus* on sugarcane has long been recognized in Puerto Rico, where it is the primary insect pest of citrus and sometimes a primary pest of sugarcane as well. Since its discovery in Florida, *D. abbreviatus* has spread from northwestern Orange County, Florida, into at least 18 counties, including some within the Florida sugarcane production area. The Florida sugarcane industry has been concerned for many years that *D. abbreviatus* could become a significant pest of sugarcane. Although no infestations have yet been documented in sugarcane, such infestations are imminent, especially since an introduced host plant, the Brazilian pepper tree (Schroeder et al. 1979), is widespread in the sugarcane growing areas.

The adult weevil lays its eggs on cane leaves, and neonate larvae fall to the soil and burrow down to begin feeding on roots. As a larva develops, it moves along a root toward the tree trunk or the crown of a cane stool. As larvae mature, they grow to at least 2 cm in length and sometimes tunnel into the base of cane stalks. Larval development may last 8 to 10 months or longer and results in extensive feeding damage to cane. Symptoms of damage to roots include the desiccation and death of leaves, stool lodging, and stunted stalk growth. Mechanical harvesting of infested cane is difficult, as damaged stalks can snap over.

Cane growers may be able to avoid or reduce the risk of weevil infestations by controlling or employing alternate host plants such as the Brazilian pepper tree (Cassani 1986). Adults are weak fliers, and consequently their spread may be limited by eliminating host plants that bridge infested and uninfested areas. The importance of host plants other than cane is indicated by the avoidance of some cane varieties in Puerto Rico except as foliar egg laying sites. Cane fields in Puerto Rico are sometimes infested primarily along edges of fields near alternate host plants. Such alternate host species are numerous (Simpson et al. 1996). If sugarcane in Florida becomes heavily infested, growers may have no choice but to disk and replant, since application of pesticides to soil is governmentally regulated. Control of populations by flooding might prove a useful alternative to replanting, which may do little for control, anyway. Depending on factors such as water availability, legal considerations, and environmental regulations, flooding is sometimes used as a pest management strategy in southern Florida sugarcane fields for insects such as grubs of the scarab *Ligyrus subtropicus* (Cherry 1984) and larvae of the wireworm *Melanotus communis* (Hall & Cherry 1993). This report presents results of laboratory research on the susceptibility of the larvae of *D. abbreviatus* to submergence when exposed to varying temperatures for varying periods of time in flooded soil.

MATERIALS AND METHODS

Insects

Neonate *D. abbreviatus* larvae were obtained from a laboratory colony collected from Florida field populations and maintained in Orlando for over 4 yr (approximately 8 generations) in isolation. Larvae were collected within 2 days of hatching and about 10 larvae per cup were added to 30-ml cups containing 20 ml of a commercial citrus root weevil diet (Bio-Serve, Frenchtown, NJ). Rearing was as described by Beavers (1982). Larvae were reared on diet for approximately 6 weeks, then transferred to individual cups with fresh diet and reared approximately 10 more months before the test was begun. The mean weight ± SD of all larvae used in the tests (n = 1,296) was 427 ± 125 mg. Larvae of *D. abbreviatus* molt indeterminately and asynchronously, so the stage of development of these large larvae could not be accurately determined.

Soil

Soil was collected from a sugarcane field located about 0.4 km from a *D. abbreviatus* infestation in citrus in Glades County near Moore Haven, Florida. Analysis identified the soil as an Immokalee sand characterized by 7% organic content, 4% mineral content, and 89% silica content. Soil analysis using a 0.7 N NH_4OAc test at pH 4.8 indicated extractable contents of 45.4 kg/acre phosphorous, 88.0 kg/acre potassium, 3,995 kg/acre calcium, and 177.4 kg/acre magnesium. The soil averaged 11.9% moisture by weight prior to submergence of soil and larvae.

Polyethylene trays with hinged lids were used in the study. Each tray contained 18 individual compartments, each $5.1 \times 5.1 \times 5.1$ cm. One or two 3-mm holes were drilled into the floor and ceiling of each compartment to allow influx of water; they remained open through the study. Each compartment of each tray (1 tray = 1 replicate) was filled with the field-collected soil, one larva per compartment was placed into a 1.5-cm χ 1-cm diam depression made in the soil with a wooden dowel, and larvae were covered with soil. Each tray of 18 larvae was closed and submerged in water purified by reverse osmosis and deionization, tilted, and tapped to completely fill all larval compartments and eliminate air pockets. A few small bubbles remained in some compartments beneath the lid, a situation comparable to that in the field, where air bubbles may persist around roots and crown of a stool. Two of the three closed replicate trays were placed together in a single water-filled $22.9 \times 35.6 \times 7.6$-cm polystyrene storage box and one replicate tray was placed alone in the water-filled box. The two polystyrene boxes were covered by loose-fitting lids and placed into controlled-temperature cabinets with three unsubmerged (control) polyethylene trays.

The following durations and temperatures of submergence were studied: non-submerged control larvae (in soil with no water added) were maintained at 18, 21, 24, and 27°C; submerged larvae were maintained for 1, 2, 3, 4, or 5 weeks at 18, 21, 24, and 27°C. Three replicate trays of each duration and temperature of submergence plus three control trays at each temperature were included, with 18 larvae per replicate tray. Submergence of all replicates was initiated simultaneously. The dissolved oxygen contents of water in each of two boxes (but outside the submerged trays) at each temperature were measured weekly with an oxygen meter; the pH was measured in each of three boxes at each temperature (except at week 5, when only two boxes remained) with a pH meter.

One set of three replicate trays at each temperature was removed and examined at the end of each week. The soil and larva were removed from each compartment, the

box was dried, and larvae were replaced in their respective cells and checked for survival 24 hours later. Larvae in soil within the three unsubmerged trays at each temperature were spot-checked for survival and returned to the controlled temperature chamber. Soil from all compartments in all control trays was removed and mortalities were recorded at the end of 5 weeks.

Statistical Analysis

To define a model correlating temperature and time with mortality, multiple regression was employed using the Multiple Regression module of Statistica (StatSoft 1995). Values of the dependent variable, Mortality, were arcsine-transformed (arcsin $\sqrt{\text{mortality}}$). The independent variables Time and Temperature were progressively included in their linear, quadratic, cubic, and combined linear forms until further addition of terms yielded no appreciable increase in r^2. To test the significance of changes in pH and O_2 with time and the effects of pH and O_2 on mortality, regressions followed by ANOVA of the regression were performed using the Multiple Regression module of Statistica (StatSoft 1995).

RESULTS

Mortality of submerged larvae increased with both time and temperature (Fig. 1). Since sampling was destructive (individual trays were dismantled when examined), mortalities were not cumulative with time, but represent replicates of trays unique to each individual time point and temperature. Mortality was therefore sometimes lower than the week before (as from 4 to 5 weeks at 18°C), due to variability. By week

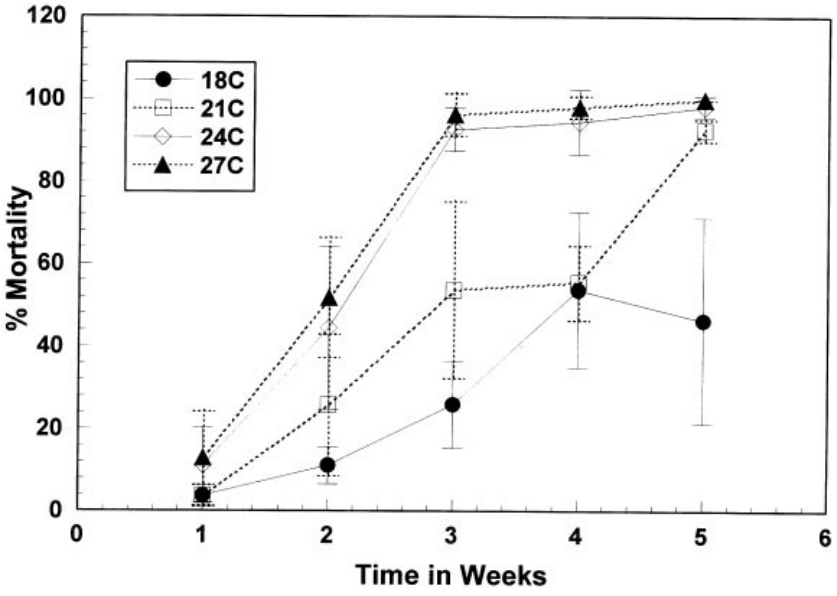

Fig. 1. Mortalities of larvae submerged 1-5 weeks at four temperatures. Standard deviations are indicated by vertical error bars.

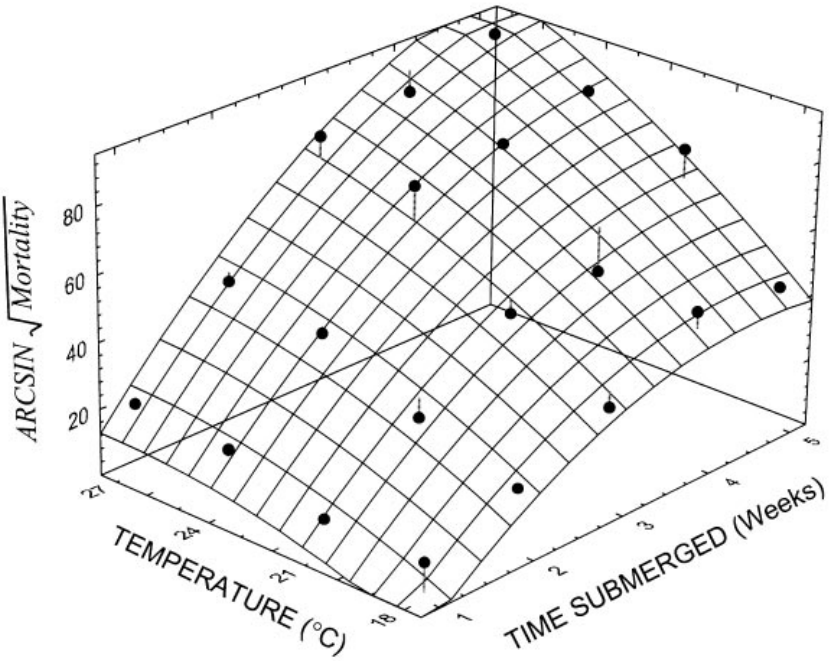

Fig. 2. Response surface derived from regression model. Mean mortalities (•) are also shown. Equation: $z = -2.725 + 0.2258x + 0.1935y - 0.0413x^2 - 0.0038y^2 + 0.0097xy$, where z = Mortality (proportion), χ = Time (weeks), and y = Temperature (°C). Circles represent the transformed means (N = 3) of actual measurements.

3, mortality exceeded 90% at 24°C and 27°C, while only 44% and 33% had died at 21°C and 18°C, respectively. At 21°C, 94% had died by the fifth week. Larvae at 18°C exhibited low, variable mortality rates (46 ± 24%) after 5 weeks of flooding. Control mortalities (% ± SD; N = 3) at the end of 5 weeks were 0 at 18°C; 11.1 ± 5.6 at 21°C; 16.7 ± 14.7 at 24°C; and 18.5 ± 3.2 at 27°C.

A model was developed by multiple regression, yielding excellent correlation of Time and Temperature (independent variables) with Mortality (dependent variable). The best fit, shown graphically in Fig. 2, was obtained using the linear and quadratic forms of the independent terms Time and Temperature, plus their linear interaction, in the form of the equation:

$$z = -151.766 + 12.696x + 10.772y - 3.338x^2 - 0.214y^2 + 1.004xy$$

where × = time (weeks), y = temperature (°C), and $z = \arcsin\sqrt{\text{mortality}}$, with mortality as a proportion. The model strongly correlated with the observed results ($P < 10^{-6}$; $r^2 = 0.843$; $F(5,54) = 57.82$), as can be seen from comparisons between observed mortality and mortality calculated from the model (Table 1).

The biophysical microenvironments in the boxes that contained sample trays varied with time, based on representative sampling. Perhaps due to variation and small sample size, changes in O_2 concentration with time at specific temperatures (Fig. 3) were not significant. Mortality also did not significantly correlate with oxygen levels.

However, pH did increase significantly with time at all temperatures (Fig. 4; $P < 0.007$ in all cases), especially at higher temperatures, up nearly one pH unit at 27°C

(Fig. 4). When a regression of mortality vs. pH was run, mortality significantly correlated with pH ($P = 0.002$, $r^2 = 0.163$) if temperature was not considered as a variable. When mortality at individual temperatures was considered, however, correlation between mortality and pH was significant only at 18°C ($P = 0.003$, $r^2 = 0.538$) and 24°C ($P = 0.006$, $r^2 = 0.433$).

DISCUSSION

The regression model of larval mortality with time and temperature accurately described the results (Table 1). Eighty-two percent of observed variation in mortality was explained. The model does not address all factors that could govern the success of flooding as a control strategy. Larval behavior of grubs may modify susceptibility to environmental conditions (Villani & Wright 1990). For example, in cane fields larvae may move to avoid moisture, but such behavior was precluded in the laboratory. Since our experimental matrix did not include plant material, interactions of larvae with plants—e.g. crown stem tunneling activity—were also precluded. It may be difficult to entirely flood all areas inhabited by larvae. Developmental state can also have a significant effect. Larval size or age could have a dramatic effect on the success of flooding. In fact, general information on behavioral and biochemical interactions of root-

TABLE 1. COMPARISON OF OBSERVED MORTALITIES WITH MORTALITIES CALCULATED FROM THE ARCSIN-TRANSFORMED MODEL.

Time (Wks.)	Temp (°C)	Mortality, from Model	Mortality, Observed
1	18	0.00	0.04
2	18	0.13	0.11
3	18	0.33	0.26
4	18	0.46	0.54
5	18	0.47	0.46
1	21	0.03	0.04
2	21	0.32	0.22
3	21	0.61	0.54
4	21	0.78	0.56
5	21	0.83	0.93
1	24	0.09	0.11
2	24	0.48	0.44
3	24	0.81	0.93
4	24	0.95	0.94
5	24	0.99	0.98
1	27	0.11	0.13
2	27	0.58	0.52
3	27	0.91	0.96
4	27	1.00	0.98
5	27	0.98	1.00

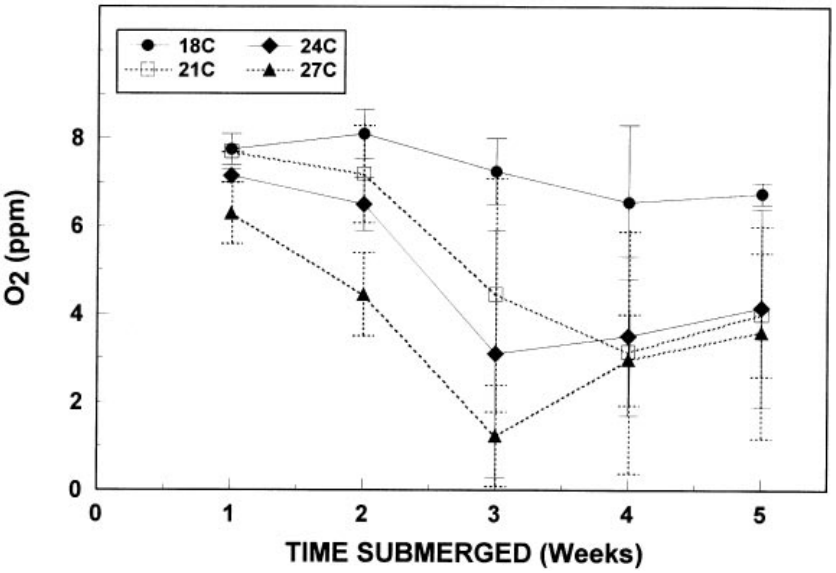

Fig. 3. Oxygen content (ppm) of water in representative containers at each temperature.

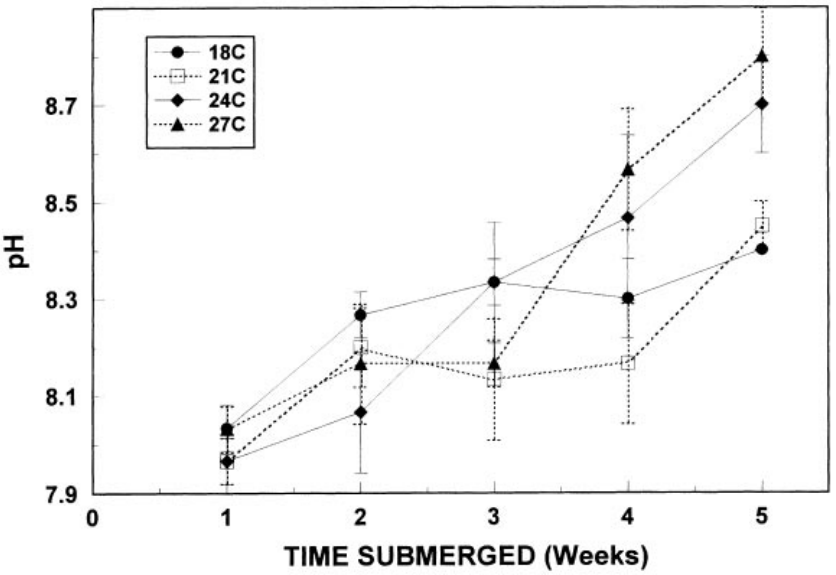

Fig. 4. pH of water in representative containers at each temperature.

feeding insects with hosts, host-derived phytochemicals, and the abiotic environment is extremely limited due to the difficulty of study of subterranean root-feeders (Shapiro 1991, Shapiro & Gottwald 1995, Villani & Wright 1990). In short, the success of flooding as an emergency control tactic for *Diaprepes abbreviatus* in sugarcane needs to be evaluated under field conditions.

In comparison to our findings on *Diaprepes*, wireworms (*Melanotus communis*), sustained less than 80% mortality after six weeks of submergence, even at 27°C (Hall & Cherry 1993). At the other extreme, first through third instar grubs of the scarab *Ligyrus subtropicus* sustained 100% mortalities after 5-10 days of submergence (Cherry 1984).

The cause(s) of observed mortality of submerged *Diaprepes* larvae is not clear. Mortality may have been due to drowning or suffocation (asphyxiation) due to decreasing oxygen and increasing carbon dioxide levels, or to sepsis from the growth of microorganisms in the stagnant water. The two possibilities are difficult to differentiate, since temperature could interact with either. If increased temperature results in increased metabolic rate, lower oxygen content may very well cause suffocation. However, carcasses of dead larvae were found to have deteriorated substantially. In many cases, only some thin outer cuticle remained intact, the internal organs entirely removed, apparently by microbial growth. Thus, sepsis may have been at least partly responsible for mortality, offering possible ramifications for the biological control of larval *Diaprepes*.

Results presented here suggest that flooding of sugarcane fields may be useful in the control of larval *Diaprepes*, though only during the summer or fall months when temperatures of water in flooded fields reach their reported maximum of 27°C (Hall & Cherry 1993).

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A NEW SUBGENUS OF BOURLETIELLIDAE (COLLEMBOLA) FROM QUINTANA ROO, MEXICO

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ABSTRACT

A new subgenus and new species of Bourletiellidae are described and illustrated. The subgenus is part of the genus *Stenognathriopes* and it is characterized by the presence of lamellar expanded tenent hairs. This new taxon seems to be endemic of the Sian Ka'an Biological reserve.

Key Words: *Tenentiella*, taxonomy, Stenognathriopes, Collembola

RESUMEN

Un nuevo subgénero y una nueva especie de Bourletiellidae son descritos e ilustrados. El subgénero es parte del género *Stenognathriopes* y se caracteriza por la presencia de "tenent hairs" expandidos en forma de lamela. Este nuevo grupo parece ser endémico de la Reserva de la biosfera de Sian Ka'an.

The Symphypleona is the subclass of Collembola least studied in Mexico. Only about 50 species of the family Sminthuridae s. l. have so far been recorded from Mexico.

During our study of the diversity of soil fauna in the Biological Reserve of Sian Ka'an, we have found specimens belonging to the new subgenus and new species herein described.

Stenognathriopes (*Tenentiella)* **subgen. nov.**

Bourletiellidae having 2-3 very modified clavate tenent hairs (one laminar), arranged parallel to the long axis of each tibiotarsus. Antennal segment IV with 13 sub-

divisions. Tibiotarsi with four dorsal oval organs. Dental chaetotaxy reduced. Mucro with both edges smooth.

This new subgenus is very similar to *Stenognathriopes*, but differs in the lamellar shape of one of the tenent hairs. It also differs in the presence of 4 oval organs dorsally on tibiotarsi. Neither of these characteristics is found in any other genus of the Family Bourletiellidae. *Tenentiella* has a subdivided fourth antennal segment as do other genera of the family and shares a reduction of ventral chaetotaxy of dens with the members of the genus *Deuterosminthurus* (Palacios-Vargas and V. González, 1995).

Type species: *Stenognathriopes* (*Tenentiella) siankaana* sp. nov. from Quintana Roo, Mexico.

Stenognathriopes (*Tenentiella) siankaana* **sp. nov.**
(Figs. 1 - 8)

Description

Body yellow; head, antennae and legs purple. Eyepatch black. Some small spots of purple in the body. Furcula light blue. Body with spinelike macrosetae, acuminate mesosetae and bothriotrichia (Fig. 1).

Eyes 8 + 8. Two oval organs on each side of the mouth. Antennal segments ratio (from holotype) 1:2.2;2.2; 5.5. Ant. IV with 14 subsegments and no apical bulb. Each subsegment has a single circlet of setae and sensillae (Fig. 2). Ant. I with 6 setae, Ant. II with 16 setae varying in size (Fig. 3). Ant. III with 19 setae, 4 spiniform (Fig. 4). Sense organ of Ant. III with two microsensillae, two guard sensillae and one external microsensilla (Fig. 5). Ratio head-antenna: 1: 1.5. Labral chaetotaxy with 4/5,3,4 setae. Thoraxic segmentation not distinct. Metatrochanters without oval organs. Femora with one internal spine each (reduced in femur III).

Leg setation as follows from coxa to tibiotarsi: leg I: 1,4, 13+ spine, 40 + 4 oval organs; leg II: 3, 6, 13 + spine, 40 + 4 oval organs; 3, 5, 13 + spine; 42 + 4 oval organs. Tenent hairs 3, 3 and 2 (Figs. 6 and 7). Ventral setae of tibiotarsi are thick, the spinelike setae are weakly serrate. Pretarsus without microsetae. Ungues thick and short, with one external tooth, without tunica or pseudonychia. Unguiculus slender and pointed, a slightly longer than ungues on Leg III. Sacs of ventral tube tuberculate. Rami of tenaculum tridentate (Fig. 1), corpus with three apical setulae. Manubrium with 7 dorsal setae and one ventral. Dens with 7 ventral setae, 6 external and 13 lateral and dorsolateral setae. Mucro with both edges smooth. Ratio mucro: dens = 1: 2.3. Maximum size (n = 8): 1.2 mm. Spiniform dorsal macrochaetae of head and body as shown in Fig. 1.

Female subanal appendix palmate. Male genital plate with seven pairs of setae.

Type Locality

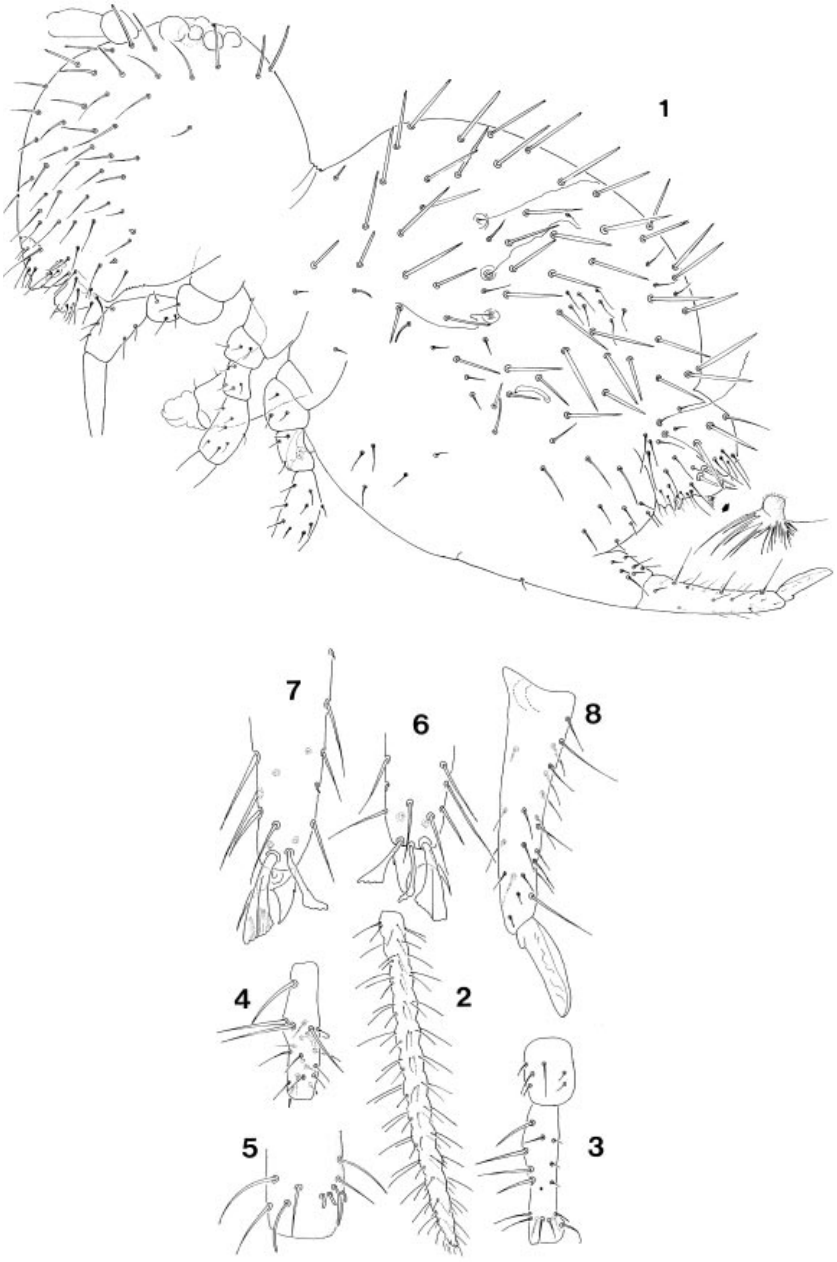
MEXICO: Quintana Roo, Biological Reserve of Sian Ka'an. Low tropical forest. Soil and litter, 17-V-95, 8-VII-95, 7-VII-95. M. M. Vázquez coll.

Type Material

Holotype female on slide; 2 female paratypes, 2 male paratypes and 3 juveniles on slides. Two paratypes will be kept in senior author institution, holotype and other paratypes in junior author institution.

Variation

Some variation in the number of the mesosetae on abdominal chaetotaxy was observed.



Figs. 1-8. *Stenognathriopes* (*Tenentiella) siankaana* gen. et sp. nov.
1. Body Chaetotaxy in lateral view; 2. Antennal segment IV; 3. Antennal segment I and II; 4. Antennal segment III; 5. Magnification of sensorial organ of Ant. III; 6. Foot complex I; 7. Foot complex III; 8. Dens and mucro in lateral view.

Etymology

The species is named after the type locality: Sian Ka'an.

DISCUSSION

The only genus known in the Family with very modified tenent hairs is *Stenognathriopes* (Betsch & Lasebikan, 1979), originally described with one species from Nigeria. The new subgenus is very similar or identical to the other members of the genus in the structure of the ungues, lack of pretarsal setae, the 14 subsegments of the fourth antennal segment, labral structure and dorsal chaetotaxy of the body. The differences in the new subgenus *Tenentiella* are that the tibiotarsal spines are less strongly serrate, the unguiculus apical filament is short on legs I and II and the ungues with clear external teeth. One tenent hair on each foot is lamellate rather than swollen and clavate as in *Stenognathriopes* s. s. Head with 2 oval organs on each side which are not mentioned in Betsch & Lasebikan (1979). Leg III with four oval organs. Tenaculum is tridentate with three rather than four setae on the corpus.

The occurrence of this highly modified genus in Africa and Mesoamerica is of considerable biogeographic interest.

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BIOLOGY AND DEVELOPMENT OF *LESPESIA ALETIAE* (DIPTERA: TACHINIDAE) IN TWO LEPIDOPTERAN SPECIES IN THE LABORATORY

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ABSTRACT

The tachinid *Lespesia aletiae* (Riley) was obtained from parasitized larvae of *Syntomeida epilais* (Walker), which is an arctiid pest of oleander, *Nerium oleander* (L.). Development of *L. aletiae* in fifth and sixth instars of *S. epilais* and of a noctuid, the fall armyworm, *Spodoptera frugiperda* (Smith) was determined in laboratory studies. Female *L. aletiae* flies lived an average of approximately 24 d, 14 days longer than males, and were observed to oviposit membranous eggs directly on the host body. First instars cut their way out of the egg and into the host within 2 min of oviposition. The percent of successful parasitism in laboratory assays ranged from 36% in fifth instar *S. epilais* to 65% in sixth instar fall armyworms. Puparial size was found to increase with increasing host instar and to decrease with increasing number of maggots per host. The time between exposure to parasitoids and host death was longer in fifth than sixth instars of the same host, and was significantly longer in fifth instar *S. epilais* than in any other combination of host instar and species tested. The parasitoid puparial stage was approximately one day longer for females than it was for males. Both the fifth and sixth instars of the fall armyworm and *S. epilais* were suitable for the parasitoid's development, however, parasitism levels and parasitoid survival were higher in fall armyworms.

Key Words: tachinid fly, parasitoid, biocontrol, Lepidoptera host, rearing

RESUMEN

El tachinido *Lespesia aletiae* (Riley) fué encontrado parasitando larvas de *Syntomeida epilais* (Walker), un arctiido plaga del narciso, *Nerium oleander* (L.). El desarrollo de *L. aletiae* en quinto y sexto estadios de la palomilla del narciso, *Syntomeida epilais*, y del gusano soldado, *Spodoptera frugiperda* (Smith) fué evaluado bajo condiciones de laboratorio. Las hembras del *L. aletiae* vivieron un promedio de 24 días, 14 días más que los machos, y fueron observadas depositando huevos membranosos directamente sobre el hospedero. El primer estadío del parasitoide cortó su camino fuera del huevo y hacia dentro del hospedero en menos de dos minutos después de ser depositados. El porcentaje de parasitismo, en los ensayos de laboratorio, varió desde 36% en el quinto estadío de *Syntomeida epilais*, hasta 65% en el sexto estadío de *Spodoptera frugiperda*. Se observó que el tamaño de las pupas tendió a aumentar en relación al estadío del hospedero, y a disminuir en relación al número de larvas por hospedero. El tiempo transcurrido entre la ovoposición de los parasitoides y la muerte del hospedero fue más largo para el quinto que para el sexto estadío dentro del mismo hospedero, y fue significativamente más largo para el quinto estadío de *Syntomeida epilais* que para las otras combinaciones de estadío/hospedero evaluadas en este estudio. La duración de lestadío de pupa fue aproximadamente un día más largo para

las hembras que para los machos. Ambos, quinto y sexto estadios de *Spodoptera frugiperda* y *Syntomeida epilais* demostraron ser buenos hospederos para el desarrollo de *L. aletia*; sin embargo, el porcentaje de parasitismo y la tasa de sobrevivencia del parasitoide fueron más altas en *Spodoptera frugiperda*.

Lespesia aletiae (Riley) (Tachinidae) is recorded from most states of the continental USA, and from southern Canada. It has been found parasitizing species in the lepidopteran families Arctiidae, Hesperiidae, Lasiocampidae, Lymantriidae, Megalopygidae, Noctuidae, Notodontidae, Nymphalidae, Pieridae, Pyralidae and Sphingidae, and the coleopteran family Coccinellidae (Benneway 1963). Reported hosts include agricultural pests such as the salt-marsh caterpillar, *Estigmene acrea* (Drury), *Helicoverpa* and *Heliothis* spp., the fall armyworm, *Spodoptera frugiperda* (J. E. Smith); the cabbage looper, *Trichoplusia ni* (Hübner) and the imported cabbageworm, *Pieris rapae* (L.). It has also been reported to parasitize *Syntomeida epilais* (Walker) (Patton 1958, Benneway 1963, McAuslane & Bennett 1995), a serious pest of oleander, *Nerium oleander* (L.), which is a flowering ornamental shrub that is grown in much of Florida.

The distribution of *S. epilais* extends from south Florida and Mexico in North America to northern South America (Bratley 1932). Oleander is the primary host for the immature stages of *S. epilais* in Florida, although *Echites umbellata* (Jacquin) was earlier reported as its native host (Grossbeck 1917). Except for one specimen of *Chetogena* (=*Euphorocera*) *floridensis* (Townsend), *L. aletiae* was the only larval parasitoid recovered from field collections of *S. epilais* caterpillars made in Gainesville and Tampa, Florida. Although *L. aletiae* has been reported as a parasitoid of the larval stages of *S. epilais*, no studies have been made on the biology and immature development of this tachinid.

Studies were initiated to obtain information on the potential use of fall armyworm larvae as a laboratory host for *L. aletiae*. Oviposition activity of adult flies was observed, and longevity of adult flies reared from fall armyworms was determined. Comparative laboratory studies were conducted on parasitoid development in fifth and sixth instars of the original host, *S. epilais*, and in fifth and sixth instars of the laboratory host, the fall armyworm.

Materials and Methods

The colony of *L. aletiae* was initiated from parasitized *S. epilais* larvae collected from oleander bushes in Tampa, Florida, in January 1994. Adults were maintained in screen cages (25 by 25 by 25 cm) and were provided with water, an aqueous sucrose solution (20% wt/vol) and hydrolyzed brewer's yeast as a protein source. Subsequent generations were reared on sixth instar fall armyworms obtained from a laboratory colony maintained at the Center for Medical, Agricultural and Veterinary Entomology, USDA/ARS, Gainesville, Florida. All stages of the *L. aletiae* colony were maintained in laboratory rearing conditions with a photoperiod of 12:12 (L:D) h at 25°C and 80% relative humidity. Flies were provided with fall armyworms twice a week for oviposition (Bryan et al. 1968). Caterpillars were exposed for twenty minutes and then set individually in plastic cups (25 ml) half filled with pinto bean diet as food for the hosts, and were maintained throughout parasitoid development until puparia appeared. Fly puparia were placed in plastic cups (25 ml) within a screen cage for adult emergence. Additional *L. aletiae* maggots were obtained from *S. epilais* larvae collected from oleander bushes in Gainesville, Florida during the fall of 1994, and adult flies were added to the laboratory colony.

After ill-fated attempts to rear *S. epilais* on artificial diet, larvae used for the parasitoid development studies were field-collected in Gainesville during October - December 1994 as third, fourth and fifth instars. All rearing was conducted in a greenhouse under natural light conditions. Larvae were reared on potted oleander bushes until the last instar, and then were transferred to plastic containers with screened lids (either 18 by 13 by 9.5 cm or 30 by 22 by 9.5 cm) and given freshly cut oleander leaves. Leaves were replaced every other day.

Parasitoid Oviposition and Adult Longevity

Sixth instar fall armyworm larvae were introduced individually into a cage with five adult female flies for observations on host-parasitoid interactions. The introduced host was watched continuously from time of introduction and was removed immediately after oviposition contact by a female fly. The larva was then observed under a stereo microscope at 10-30× magnification to confirm oviposition, and to determine the time periods from oviposition to egg hatch and host penetration by the first instar maggot. This was repeated for 20 host larvae.

Adult longevity was determined by placing ten flies (5 females and 5 males) that emerged within a 24-h time period into a screen cage with food and water as above. Flies were provided with fall armyworms twice a week for oviposition. The number and sex of dead flies were recorded daily and the adult longevity determined. The experiment was replicated five times.

Parasitoid Development

Sexually mature male and female *L. aletiae* (10-25 d old) were placed in acrylic cages (15 by 15 by 15 cm) with a wire screen (15 mesh) top and provided with food and water as above. Host larvae were confined under the lid of a petri dish (15 cm diam.) placed on the screened top of a cage containing six female flies for 10-20 min. The *L. aletiae* females have long ovipositors, so they were able to reach and parasitize the caterpillars through the mesh. After exposure to the parasitoids, fall armyworm larvae were placed individually in plastic cups (25 ml) containing pinto bean diet, and *S. epilais* caterpillars were placed together in a plastic container and given fresh oleander leaves daily. Host larvae were exposed in separate groups of 20 fifth or 20 sixth instars for the fall armyworm and *S. epilais*. Since *S. epilais* were field-collected, control groups of ten non-exposed fifth and sixth instar *S. epilais* were placed under the same conditions as the parasitoid-exposed caterpillar groups for each replicate. When *S. epilais* died or pupated, they were moved from collective containers to individual plastic cups. The experiment with fifth instar *S. epilais* was replicated four times. There were five replications of each of the other instar/host combinations.

Host larvae were checked daily. Fly maggots and puparia were placed individually in dry microcentrifuge tubes with a hole in the cap to facilitate ventilation, and the microcentrifuge tubes were checked daily. The following data were recorded: date of host death and host stage at death, date of maggot emergence from the host, date of maggot pupariation, date of adult fly emergence and sex of adult fly. Within 24 h of pupariation, puparial length and width were measured under a stereomicroscope with an ocular micrometer, and puparial weight determined. Number of maggots per host cadaver, parasitoid sex ratio and percent parasitism were recorded.

Statistical Analysis

Longevity of female and male adult *L. aletiae* was compared with a two sample *t*-test using Proc TTEST (SAS Institute 1985). Chi-square analysis using Proc Freq (SAS Institute 1985) of a contingency table of number parasitized was used to compare

percentage parasitized for each host and host instar combination. Time period for parasitoid development from initial host exposure to adult emergence was divided into three separate response variables for statistical analysis. These developmental response variables were time until host death, time from host death until maggot emergence from the host cadaver, and time from maggot emergence until adult emergence. Effect of host and host instar on developmental response variables and puparial size were tested with two-way analysis of variance (ANOVA) with interaction using Proc GLM (SAS Institute 1985). Significant ANOVAs were followed by Tukey's mean separation tests ($P = 0.05$). Data were assessed by the Box-Cox procedure (Box et al. 1978) and were transformed when necessary to stabilize the variance prior to analysis. Differences in the developmental response variables and puparial size between male and female parasitoids were tested with two sample *t*-tests. Separate comparisons were conducted within each host species and host age group. Finally, correlations among the puparial size parameters were tested using Proc CORR (SAS Institute 1985).

RESULTS

Parasitoid Oviposition and Adult Longevity

Adult flies mated within the first day after emerging. However, females did not begin ovipositing until 5-10 d after emergence. After host larvae were introduced into a cage of adult flies, the flies became very active. Females moved aggressively and flew in circles around the host until physical contact was made. They then extended the ovipositor and laid several eggs along the host body. Females attached membranous, macrotype eggs to the host body. First instar maggots cut their way out of the egg and into the host within 2 min of oviposition. Female flies lived longer than males ($t = 7.19$, df = 48, $P < 0.0001$). Adult longevity (± SD) averaged 23.9 (± 7.27) d for females and 10.3 (± 6.03) d for males.

Parasitoid Development

Parasitized hosts became increasingly sluggish prior to death. Approximately 95% of parasitized hosts died as larvae. Percent parasitism was higher in fall armyworm than in *S. epilais* regardless of instar exposed to the parasitoid (Table 1). There was 23 and 16% parasitism in control (field-parasitized) fifth and sixth instar *S. epilais*, respectively. An effort was made to differentiate between field- and laboratory-parasitized *S. epilais* caterpillars by comparing the time periods until host death. Time until host death ranged from 5 to 14 d and from 2 to 12 d for laboratory-exposed fifth and sixth instar *S. epilais*, respectively; and from 5 to 12 d and from 1 to 12 d for control fifth and sixth instar *S. epilais*, respectively. Because of the overlap in the time periods, no further attempt was made to separate field-parasitism from lab-parasitism in laboratory-exposed *S. epilais*. Therefore, all data from *L. aletiae* obtained from laboratory-exposed *S. epilais* were assumed to be due to laboratory parasitism and were used for statistical analysis.

There was a significant interaction between host and host instar for both the time period from exposure to the parasitoid until host death and the time period from host death until maggot emergence ($F = 65.39$; df = 1, 381; $P = 0.0001$; $F = 6.20$; df = 1, 381; $P = 0.0132$, respectively). Therefore, the two two-level factors of host and host age were combined to a single four-level factor of host-host age combination and the effect was tested with oneway ANOVA. The time period from exposure to parasitoids until host death was the shortest in sixth instar fall armyworm and the longest in fifth instar *S. epilais* (Table 1). Time period from host death until maggot emergence, however, was longer in sixth instar fall armyworms than in any other host-host age group (Table 1). After the host's death, maggots developing in fall armyworms were found

TABLE 1. PARASITISM LEVEL AND PARASITOID DEVELOPMENTAL TIMES (MEANS ± SD) IN LEPIDOPTERAN LARVAE EXPOSED TO *L. ALETIAE* IN LABORATORY TRIALS[1].

Host and Host Instar	No. of Hosts Exposed	No. of Hosts Parasitized (%)[1]	Time Period from Parasite Exposure to Host Death (d)[2]	Time Period from Host Death until Maggot Emergence (d)[2]	No. of Maggots per Host[2]
S. frugiperda					
5th instar	100	62 (62%)b	6.2b ± 1.78	1.8a ± 0.93	1.7ab ± 0.89
6th instar	100	65 (65%)b	5.5a ± 2.08	2.4b ± 0.94	2.0b ± 1.45
S. epilais					
5th instar	80	29 (36%)a	11.2c ± 1.64	1.9a ± 1.09	1.5a ± 0.41
6th instar	100	49 (49%)a	5.9ab ± 3.64	1.8a ± 1.18	1.5a ± 1.37
		$\chi^2 = 18.597$ df = 3 $P < 0.001$	$F = 73.88$ df = 3, 382 $P = 0.0001$	$F = 10.75$ df = 3, 382 $P = 0.0001$	$F = 3.53$ df = 3, 183 $P = 0.016$

[1]Means within a column followed by the same letter are not significantly different (2 × 2 contingency tables [df = 1] of 2-at-a-time comparisons within host or instar, $P < 0.05$).
[2]Means within a column followed by the same letter are not significantly different (Tukey's mean separation test; $P = 0.05$).

associated with respiratory funnels and/or the host's spiracles. No such association was observed in parasitized *S. epilais*.

Parasitoids formed puparia within three to six hours after exiting the host's cadaver, whether they emerged from the fall armyworm or from *S. epilais*. The number of maggots per host ranged from one to seven, and about 48% of the hosts had more than one parasitoid maggot. Average number of maggots per host was higher in sixth instar fall armyworm than in either instar of *S. epilais* (Table 1).

Puparia from sixth instar hosts were larger than puparia from fifth instar hosts for both host species (Table 2). There were positive correlations between puparial weight and both length (r =0.88, P = 0.0001) and width (r = 0.78, P = 0.0001). Therefore, weight could be used as a single indicator of puparial size. Puparial weight decreased as the number of maggots per host increased (Fig. 1). Survival percentage to adult was greater for parasitoids from sixth instar hosts than for those from fifth instar hosts for both host species (Table 2), and there was no difference in the weight of puparia of individuals that survived to adult versus those that did not (t =0.9792, df = 384, P = 0.3281). Information on parasitoid progeny from field-parasitized *S. epilais* is presented for comparative purposes (Table 3). Only one maggot per host was obtained from field-parasitized sixth instar *S. epilais*. The puparia from sixth instars tended to be larger than those obtained in laboratory parasitism of either host, but this was not the case for puparia from fifth instars.

Puparial stadium was affected by host (F = 180.34; df = 1, 261; P = 0.0001) but not by host instar (F = 1.57; df = 1, 261; P = 0.2109), and the interaction between those factors was not significant. Time from maggot emergence until adult emergence from *S. epilais* was longer than from fall armyworm (12.9 ± 1.72 d versus 10.2 ± 1.02 d). The sex ratio of parasitoid adults ranged from 1:0.8 female:male from 5th instar *S. epilais* to 1:1.7 female:male from 6th instar *S. epilais* (Table 2).

For individuals that successfully completed development to the adult stage, developmental response variables and puparial size of males versus females could be compared. Puparial stadium for females was one day longer than for males for parasitoids from fifth instar fall armyworms (17.7 ± 2.24 versus 16.7 ± 2.1, respectively; t = 2.2943, df = 126, P = 0.0234). No other differences were found in the developmental times of male versus female flies within any of the host-host instar combinations. The puparial width of males that emerged from fifth instar *S. epilais* was greater than for females from that host (3.1 ± 0.36 versus 2.8 ± 0.37, respectively; t = 2.0868, df = 25, P = 0.0473), but there were no other differences in puparial size.

Although most of the parasitized hosts died as larvae, ten hosts were able to pupate. All of these hosts had been parasitized as late sixth instars. In each case, a single robust maggot emerged from the host pupa. Nine of these hosts died as pupae and parasitoids from those hosts became adults. The remaining pupa, an *S. epilais*, completed development to the adult stage after parasitoid emergence. However the adult emergence was not completely successful as pupal exuviae remained on the host abdomen. The parasitoid from this host died in the pupal stage.

DISCUSSION

The *L. aletiae* females readily accepted fall armyworms for oviposition after a 5-10-d pre-oviposition period. Pre-oviposition periods, similar to that of *L. aletiae*, have been reported for other tachinid parasitoids including *Drino munda* (Wiedemann) (Chauthani & Hamm 1967), *Lespesia archippivora* (Riley) (Bryan et al. 1968), *Voria ruralis* (Fallen) (Elsey & Rabb 1970), *Panzeria ampelus* (Walker) (Arthur & Powell 1990) and *Winthemia fumiferanae* (Clemens) (Hebert & Cloutier 1990). We found that *L. aletiae* females lived an average of 14 days longer than males. Hughes (1975) ob-

TABLE 2. *LESPESIA ALETIAE* PUPARIAL SIZE (MEAN ± SD) AND SURVIVAL TO ADULT IN LABORATORY TRIALS[1].

Host and Host Instar	n	Weight (mg)	Length (mm)	Width (mm)	No. Surviving to Adult (%)	Female:Male Ratio
S. frugiperda						
5th instar	108	31.5a ± 14.17	5.9a ± 0.80	2.9a ± 0.44	54 (50)	27:27 (1:1)
6th instar	159	35.4b ± 13.48	6.1b ± 0.72	3.0b ± 0.42	128 (81)	65:59 (1.1:1)
S. epilais						
5th instar	43	31.2a ± 13.90	6.0a ± 0.71	2.9a ± 0.51	27 (63)	15:12 (1.2:1)
6th instar	76	36.4b ± 12.21	6.3b ± 0.70	3.2b ± 0.51	56 (75)	21:35 (0.6:1)
		F = 10.52 df = 1, 382 P =0.0013	F = 6.98 df = 1, 382 P =0.0086	F = 10.84 df = 1, 382 P =0.0011		

[1]Means within a column followed by the same letter are not significantly different (Tukey's mean separation test; P = 0.05). Host age was the only significant factor from two-way analysis of variance on host and host age, and those statistics are presented.

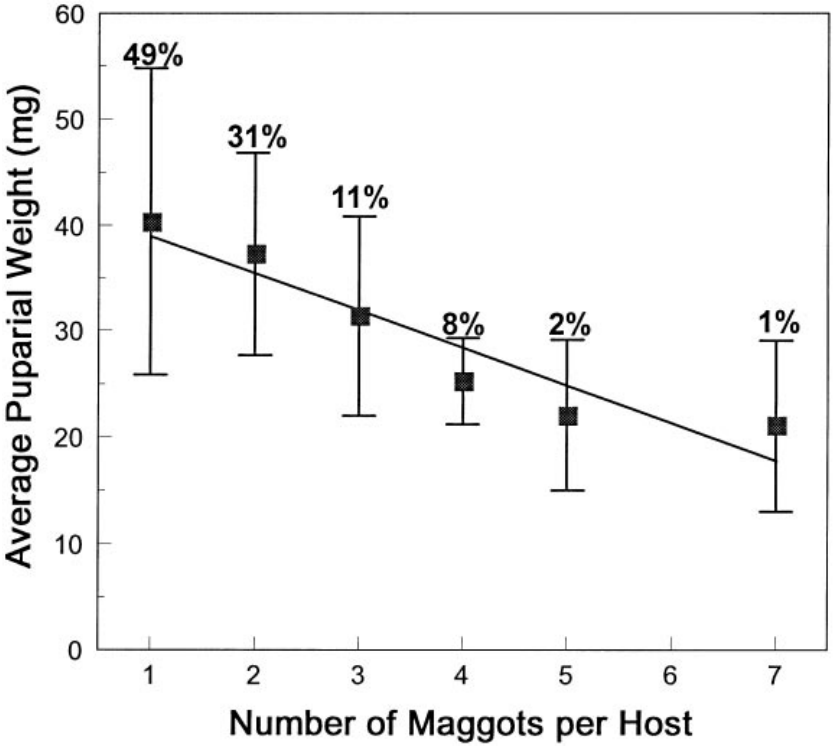

Fig. 1. Average and standard deviation of puparial weight of parasites from hosts with 1-7 maggots per host (n = 209). Number above each mean indicates the percentage of hosts parasitized at each number of maggots per host level. Regression was determined from average puparial weight for each number of parasitoids per host (r^2 = 0.89, y = 42.5 - 3.53 [± 0.608]x).

served that *Archytas marmoratus* (Townsend) females lived approximately twice as long as the males. It has been suggested that temperature, crowding, superparasitism and host suitability may influence adult lifespan and reproductive capacity (Salt 1941, Bryan et al. 1969, Mason et al. 1991). No efforts were made during this experiment to evaluate the effect of any of these factors on the longevity of adult flies.

Oviposition of membranous macrotype eggs along the host body has been previously reported for the genus *Lespesia* and other genera of Tachinidae (Benneway 1963). Time period between larval hatch and penetration into the host has been reported to occur immediately in *D. munda* (Chauthani & Hamm 1967) and in *V. ruralis* (Elsey & Rabb 1970), which is similar to the time period observed for *L. aletiae* maggots in our study. *Athrycia cinerea* (Coquillet) eggs hatched after 10 min of oviposition and entered their host within 1 min after hatching (Arthur & Powell 1989) and Bryan et al. (1968) reported that the eggs of *L. archippivora* hatched within 20 minutes postoviposition.

Syntomeida epilais larvae remained motionless when approached by parasitoid adults. Fall armyworm larvae, however, moved aggressively from side to side and tried to remove the flies and eggs by grooming them off their bodies and by covering

TABLE 3. PUPARIAL SIZE (MEAN ± SD) AND SURVIVAL TO ADULT FOR *L. ALETIAE* FROM FIELD-PARASITIZED *S. EPILAIS*.

Host Instar	n	No. of Maggots per Host	Weight (mg)	Length (mm)	Width (mm)	No. Surviving to Adult (%)
5th instar	12	1.3 ± 0.52	28.2 ± 13.18	5.9 ± 0.92	2.9 ± 13.18	5 (42)
6th instar	8	1.0 ± 0.00	46.9 ± 11.08	6.7 ± 0.46	3.6 ± 0.51	6 (75)

themselves with regurgitated substances. Grooming interactions, in which caterpillars would bite parasitoid eggs off each other, were also noted on several occasions. Danks (1975) observed similar responses by *H. zea* and *H. virescens* (F.) towards the attack of *Winthemia rufopicta* (Big.). Miles and King (1975) observed that *Lixophaga diatraea*e (Townsend) maggots showed a tendency to enter through their host's intersegmental membranes. We observed no oviposition preference when *L. aletiae* flies had to lay eggs through the wire mesh and eggs were laid wherever physical contact was made. However, when host larvae were introduced into a cage of flies and direct contact was possible, there was a clear preference for the intersegmental and ventral regions of the host's body. The observation that *L. aletiae* females prefer specific sections of the host's body contrasts with the reports on its congene, *L. archippivora* (Bryan et al. 1968).

Fall armyworms appeared to be better hosts for *L. aletiae* than *S. epilais*. The overall parasitoid developmental cycle was shorter and the parasitism and parasitoid survival levels were higher for individuals that parasitized fall armyworms versus *S. epilais*. *Syntomeida epilais* were reared on oleander foliage, which contains cardiac glycosides (Harborne 1982), and the caterpillars have the aposematic coloration typical of chemically defended organisms. Allelochemicals in host food may be deleterious to parasitoid development if the chemicals are present in host tissue (Thurston & Fox 1972). Fall armyworms were reared on artificial diet, which has a higher nutrient content than plant foliage, and this may also contribute to improved parasitoid development (House & Barlow 1961, Beach & Todd 1986). There are nutritional differences between larvae that consume artificial diet versus larvae that consume plant foliage (Cookman et al. 1984).

When parasitizing fall armyworms, *L. aletiae* maggots were observed to be associated with spiracles and/or respiratory funnels approximately one day after host death. Miles and King (1975) noticed that *L. diatraeae* maggots either attached directly to the host's spiracles or to the tracheal trunks nearby. Ziser and Nettles (1978) observed that when *Eucelatoria* spp. maggots attached themselves directly to the host cuticle there was no formation of a respiratory funnel, and the same was true when maggots penetrated the host's tracheal system. This could have been the case of *L. aletiae* maggots developing in *S. epilai*s where no respiratory funnel or spiracle association was observed.

The level of parasitism by *L. aletiae* and parasitoid survival as well as puparial size tended to increase directly with host instar, whereas developmental time tended to decrease with increasing host instar. Similar results have been found with other tachinids (e.g., Miles & King 1975, King et al. 1976, Beland & King 1976). When given the choice, *L. aletiae* flies exhibited no preference between the fifth and the sixth instars of either the fall armyworm or *S. epilais* (Y. J. C., unpublished data). Female *W. fumiferanae* showed a clear preference for sixth instars over fifth instars of the spruce budworm, *Choristoneura fumiferana* (Clemens), and survival from egg until pupariation was five times higher in sixth than in fifth instars (Hebert & Cloutier 1990). Maggots of *L. diatraeae* were more efficient seeking fourth and fifth instars of the sugar cane borer, *Diatraea sacharalis* (F.) (Miles & King 1975), and the early fifth instar was the most suitable host for parasitoid development (King et al. 1976).

The number of maggots per host had an adverse effect upon puparial weight. Ziser et al. (1977) found that the average puparial weight of *Eucelatoria spp.* decreased as number of maggots per host increased. Similar results were found for puparial weight of *L. diatraeae* (King et al. 1976). Miles and King (1975) observed that female *L. diatraeae* had longer maggot and puparial periods than their male counterparts; however in our study females differed from males only by having a longer puparial period. Mason et al. (1991) observed that older *Lydella thompsoni* (Herting) males tended to

mate with newly emerged females. Thus, it may be advantageous for males to have a shorter puparial period than females. This was also observed in the parasitoids *D. munda* (Chauthani & Hamm 1967) and *A. marmoratus* (Hughes 1975).

The information presented herein on the biology and development of *L. aletia*e may provide the basis for the consideration of this parasitoid as an environmentally safe tool for use in insect pest management. However, rearing in other hosts or under other rearing conditions should be investigated to further evaluate the potential for mass-rearing of this insect. Further experiments are needed to assess the effect of natural parasitism by *L. aletiae* on populations of *S. epilais* and the fall armyworm, and to evaluate the potential use of laboratory-reared *L. aletiae* for control of these and other pest lepidopterans.

Acknowledgments

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CATOLACCUS HUNTERI (HYMENOPTERA: PTEROMALIDAE), A PARASITE OF *ANTHONOMUS MACROMALUS* (COLEOPTERA: CURCULIONIDAE) IN SOUTH FLORIDA

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Acerola or Barbados Cherry, *Malpighia glabra* (L.) (= *punicifolia* L.), is a tropical fruit native to the West Indies, Central America, and South America (Stahl et al. 1955, Phillips 1991). The genus *Malpighia* is present from south Texas to Peru (Asenjo 1980). Recently, it has received world-wide attention as an exceptionally high natural source of ascorbic acid (vitamin C) found in the cherry-like fruit, and its cultivation has extended throughout the subtropics and tropics (Ledon 1958). Estimated commercial acreage in the Caribbean region is over 400 acres with a potential crop value of several million dollars (Melendez 1968, Gonzalez-Ibanez 1983). In Florida, acerola is grown in the southern part of the state in homeowner's yards and as a commercial crop. Flowering and fruit set occur almost continuously from April through November in Florida, and fruits mature in approximately 30 days (Stahl et al. 1955, Ledon 1958).

The major insect pests of acerola are comprised of a complex of weevils known collectively as acerola weevils; *Anthonomus sisyphus* Clark identified from Mexico, *A. acerolae* Clark from Brazil, *A. tomentosus* (Faust) from Trinidad and Venezuela, and *A. macromalus* Gyllenhal (= *A. flavus*, = *A. bidentatus*, = *A. malpighia*) reported from several islands in the Caribbean region and Florida (Clark & Burke 1985, Clark 1992). A. macromalus was first reported in Dade County, Florida, in 1972 (Stegmaier & Burke 1974). This species appears to be native to the Neotropics, with reports from Dade County, Florida (USA) and from many of the islands of the Caribbean Region (The Dominican Republic, Puerto Rico, US Virgin Islands, Tortola, Guadeloupe, St. Kitts, St. Lucia, Antigua, Martinique, the Grenadines, and Trinidad) (Clark & Burke 1985).

The biology of *A. macromalus* was reviewed by Stegmaier & Burke (1974), and Ballof (1993). Adults deposit eggs on the anthers of flower buds or in immature fruits. Acerola weevil larvae develop in the flowers and fruit causing extensive damage to floral reproductive structures and to the flesh of the fruit. This damage results in reduced yields. To our knowledge, parasitoids have not been reported from this weevil.

Acerola fruit were collected in Dade County as part of a population dynamics study to determine the presence and importance of natural enemies as mortality factors of the acerola weevil. Collection sites were established at the University of Florida Tropical Research and Education Center, Homestead, and at two commercial sites. One commercial site was located 3.4 km west of the Education Center and the other was adjacent to the east side of the Center. Random samples of immature (green) and ripe fruits from each site were collected weekly from 7 April through 31 August 1995. The mean number of fruit collected per site per date was 75.86 (S.E. 13.03, range 6-333). Fruits were immediately placed in plastic bags and transported to the laboratory where they were held in 30 cm^3 plastic cages at 26 ± 1°C. The cages were checked daily and insect emergence was recorded. When parasitoids were recovered, the percentage parasitism was calculated as the ratio of the number of emerged parasitoids/(number of emerged parasitoids + the number of emerged weevil adults) × 100.

The first parasitoid was observed on 21 April 1995 from Education Center acerola fruit. This wasp was identified by S. Heydon (Bohart Museum of Entomology, UC, Davis) as *Catolaccus* (*Heterolaccus*) *hunteri* Crawford (Hymenoptera: Pteromalidae). To the best of our knowledge, this is a new host for this species. No additional specimens of *C. hunteri* emerged from subsequent fruit collections from this site (Fig. 1). The percentage parasitism for the Research Center site was 0.042% (n = 1).

Catolaccus hunteri was recovered again from samples collected on 12 June 1995, and 26 June 1995, from the second and third sites, respectively. *Catolaccus hunteri* was continually collected from these sites during July and August (Fig. 1). Percentage parasitism was 0.986% (n = 17) and 0.603% (n = 42) from the second and third sites, respectively. It is probable that an extensive survey in Florida and the Caribbean Region would contribute new parasitoid records for *A. macromalus* and perhaps other species of *Anthonomus*.

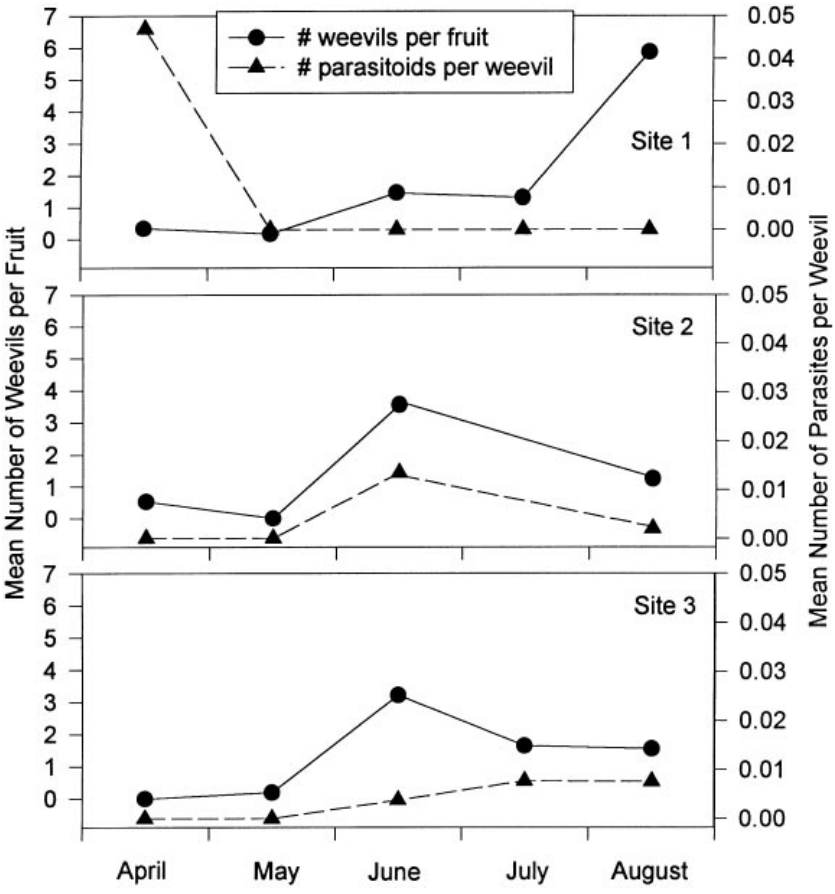

Fig. 1. Monthly emergence of *A. macromalus* and *C. hunteri* from three sites in South Florida. Site 1 (Tropical Research and Education Center), sites 2 and 3 (commercial orchards).

The highest incidence of *C. hunteri* coincided with high host densities during the months of June and August (Fig. 1). This parasite acts as an ectoparasitoid of acerola weevil larvae (personal observation) and is a known larval ectoparasitoid of several anthonomids (Pierce 1908, 1910). *Catolaccus hunteri* is one of the major parasitoids of the cotton boll weevil, *Anthonomus grandis grandis* Boheman (Cate et al. 1990, Ramalho & Wandeley 1996). This parasitoid has a known host range of at least 13 other species of *Anthonomus* in the New World and occurs in Delaware, throughout the southern US (including Arizona and California), Mexico, Guatemala, Peru, Ecuador, Colombia, Brazil, and Hawaii (Townsend 1913, Muesebeck et al. 1951, Ramalho & Wanderley 1996). The biology of *C. hunteri* is described by Pierce et al. (1912) and Berry (1947).

Based on these findings, *C. hunteri* hold promise as a biological control agent against the acerola weevil. However, further studies such as the efficacy and timing of augmentive releases of *C. hunteri* need to be conducted.

We thank R. Irwin for collecting fruit and L. Miller for the use of his orchards. Thanks go to S. Heydon (Bohart Museum of Entomology, University of California, Davis, CA) and L. Stange (Florida Dept. of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL) for the indentification of the pteromalid. Thanks also to A. Castineiras, M. Joyner, D. Seal, and R. Giblin-Davis for critical reviews of an earlier version of this manuscript. This is Florida Agricultural Experiment Station Journal Series No. R-05471.

Summary

The parasite *Catolaccus hunteri* Crawford (Hymenoptera: Pteromalidae) is reported for the first time on *Anthonomus macromalus* Gyllenhal (Coleoptera: Curculionidae) in Florida. Percentage parasitism was found to be as high as 0.986% in acerola fruit.

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BOOK REVIEWS

SYMONDSON, W. O. C., AND J. E. LIDDELL (eds.) 1996. The Ecology of Agricultural Pests. Biochemical Approaches. Chapman and Hall, London. xiv + 517 p. ISBN 0-412-621909-8. Hardcover. $138.95.

This symposium proceedings volume makes it clear that modern agricultural and medical entomologists had better learn some molecular genetic and biochemical methods. The book contains 21 chapters that illustrate the types of problems that can be resolved using some of the newer (and older) molecular techniques. Because the book also includes chapters on mosquitoes and tsetse flies, the title is somewhat misleading. The book should be, in fact, of interest to taxonomists, ecologists, and evolutionary biologists, as well as applied entomologists in both agricultural and medical/veterinary entomology.

The first chapter points out that agricultural pest management has changed dramatically in the past fifteen years. Because we no longer can rely primarily on pesticides to suppress pests, we must understand the pests' ecology, behavior, and diversity, as well as their population structure and dynamics. Frequently the role of natural enemies and their interactions with pests must also be understood if we are to effectively employ multitactic integrated pest management practices.

Many fascinating examples are provided that illustrate how biochemical and molecular genetic methods can be used. For example, Hemmingway et al. describe the efforts to identify mosquito species in the *Anopheles gambiae* species complex, to detect pesticide resistance status, to identify the source of the mosquito's blood meal, and to calculate the rate of infection of the mosquitoes with malaria parasites. In the Gambia, pyrethroid-impregnated bednets are being used for malaria control. The program depends on the mosquito vectors remaining susceptible to the pesticide. A sentinel site for monitoring pesticide resistance in mosquitoes was set up and molecular methods were used to discriminate between three morphologically indistinguishable sibling species, which are not all equally effective vectors of malaria. Bioassays also were conducted to detect low levels of resistance to pyrethroid, organophosphate, and carbamate pesticides among insects from the different sites. Sample mosquitoes were identified to species using the polymerase chain reaction (PCR) using species-specific ribosomal DNA primers.

A chapter by Hsiao unravels some of the interactions between "the alfalfa weevil", *Hypera postica* (Gyllenhal), its *Wolbachia* endosymbionts, and its parasitoids. There has long been confusion about the species status of this insect in the USA. The alfalfa weevil invaded the USA on three different occasions and the different populations were identified as "western", "Egyptian", and "eastern" populations and given different species names. Strain hybridization, cytogenetic analysis, and allozyme analysis had previously indicated that all North American populations are strains of the same species. More recent analyses of mitochondrial DNA and nuclear ribosomal DNA by the PCR and by DNA sequencing confirmed the earlier conclusion and led to estimates of the relatedness of the three strains and to diagnostic markers for distinguishing between them. The DNA sequence data suggested the origins of the populations in the USA based on comparisons with sequences from weevils from Egypt, Europe, and China.

Another mystery was cleared up by using molecular methods to examine the reproductive incompatibility between North American weevil strains. Giemsa staining, immunoblotting, and PCR analyses demonstrated that the western strain contains a rickettsia-like endosymbiont (*Wolbachia*) while the eastern and Egyptian weevil

strains do not. The western strain could be made compatible with these two strains by eliminating the *Wolbachia*.

The *Wolbachia* story has implications for classical biological control efforts against the alfalfa weevil in North America. Again molecular methods have provided an answer to a puzzling problem. One parasitoid, *Bathyplectes curculionis* (Thomson), became established and effective as a natural enemy of the western weevil strain, but is ineffective against the Egyptian and eastern weevils because most of its eggs are encapsulated, which prevents the development of the parasitoid. The parasitoid *Microctonus aethiopoides* Loan became established in the eastern USA and is effective there, but it has failed to establish in regions where the western weevil occurs. The failure of *M. aethiopoides* to develop normally in the western weevil is due to the presence of *Wolbachia*. The *Wolbachia* provide protection to the western weevil against the parasitoid. Hsiao concluded that these results reconfirm the importance of matching biotypes of pests and parasitoids in classical biological control programs. The interactions between alfalfa weevil strains, *Wolbachia*, and parasitoids are surprisingly complex and suggest that studies such as this could aid in developing more effective pest management programs.

The development of insecticide resistance is both an evolutionary and practical problem. Daly and Trowell show how DNA-based methods or immunological techniques can allow one to examine a broad range of problems including separating sibling *Heliothis* species, detecting and monitoring resistant individuals, and monitoring the distribution of resistance genes in populations. They also point out that the molecular methods will not replace the more imprecise bioassay techniques, because bioassay tests are quick to devise and are relatively independent of the mechanism of resistance. Daly and Trowell conclude that "Development of molecular techniques to monitor resistance, though costly, will be justified for some major insect pests of agriculture, livestock and human health."

More than a third of the book, 8 of 21 chapters, is devoted to using immunological or electrophoretic approaches to understanding arthropod predation and parasitism. Greenstone reviews "Serological analysis of arthropod predation: past, present and future", Stuart and Greenstone describe a method "Serological diagnosis of parasitism: a monoclonal antibody-based immunodot assay for *Microplitis croceipes* (Hymenoptera: Braconidae)", Symondson and Liddell contribute "Polyclonal, monoclonal and engineered antibodies to investigate the role of predation in slug population dynamics", Liddell and Symondson describe "The potential of combinatorial antibody libraries in pest-predator relationship studies", Sigsgaard describes "Serological analysis of predators of *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) eggs in sorghum-pigeonpea intercropping at ICRISAT, India: a preliminary field study", Hagler and Naranjo describe "Using gut content immunoassays to evaluate predaceous biological control agents: a case study", Sunderland reports on "Progress in quantifying predation using antibody techniques". Finally, Solomon, Fitzgerald and Murray report on "Electrophoretic approaches to predator-prey interactions".

While this book includes many entomological problems, ranging from brown planthoppers to tsetse flies and mosquitoes, it also includes a chapter on risk analysis of a microsporidium, *Nosema pyrausta* (Paillot), as a control agent of European corn borer, *Ostrinia nubilalis* (Hübner), and a chapter on identifying the genetic basis of resistance to the aphid *Brevicoryne brassicae* in wild brassica plants.

If you want to learn about biochemical and immunological techniques for evaluating interactions between pests, their hosts, their predators and other organisms, their population genetics, dynamics and systematics, this book provides some useful case studies and discussions of the virtues and limitations of the different methods. Discussions include an analysis of the benefits and detriments of enzyme electrophoresis,

polytene chromosome analysis, various DNA analysis methods [ribosomal DNA analysis by the polymerase chain reaction (PCR), DNA dot blots, DNA fingerprinting, DNA sequencing, nuclear and mitochondrial DNA analysis, restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR), microsatellite analysis], biochemical assays for insecticide resistance detection, and immunological assays.

The book is not a manual that will provide details of methods, nor is it an introductory text. If you want to learn how to use the methods described, then other sources will have to be consulted. This book does provide abundant examples of the value of using molecular methods to solve problems of interest to applied entomologists as well as an entry into the published literature.

All graduate students beginning entomological careers should read this book. If they are not already convinced that molecular and biochemical approaches provide useful tools for entomologists, this book **should** convince them that any graduate student in entomology who graduates without learning at least the basics of the PCR will be seriously handicapped.

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DENT, D. R. (ed.) 1995. Integrated pest management. Chapman & Hall; London. xii + 356 p. ISBN 0-412-57370-9. Hardback. $94.95.

The small size of this tome belies its rich information content. Dent has done a marvelous job at bringing together the essential elements of IPM—historical, philosophical, theoretical, and practical—in an uniquely readable and understandable way. In a field that has long been known as multidisciplinary and interdisciplinary, Dent has effectively broadened and redefined the essential elements for an IPM text. This book offers instructors an excellent tool on which to base an introductory course, or even a capstone course after students have taken disciplinary courses in the protection sciences. Long-time IPM practitioners would also benefit greatly from reading this book.

Integrated pest management contains 8 chapters, all authored by Dent, that consider the theoretical and ecological basis pest management; the organizational and management elements of IPM; and the paradigms or approaches to IPM implementation. This is complemented by 4 additional chapters contributed by 6 other authors who describe IPM systems in olives, wheat, cotton, and protected crops (greenhouses). Dent clearly strove for a balanced approach by including philosophy, terminology, and examples from the fields of plant pathology and weed science as well as entomology. In addition, he provides and unusually good treatment of systems analysis, organizational behavior, and personnel management. Remarkably, he succeeded in weaving this all together into a seamless, instructive treatise that is marked by both brevity and readability.

The content of this book appears to be fairly conventional, but it is not. Dent has interjected a strong social science element into his book, rather than the preponderance of biological and technological information usually found in such texts. Yes, we all acknowledge the contributions of economists and other social scientists, but rarely is social science presented in such a central role. What other IPM text contains dis-

cussion of the personality types needed for program planning and implementation? What other IPM text contains detailed discussion of IPM educational programs, including the methodologies used by extensionists? Although the principles underlying IPM are the focus of the book, the breadth of the treatment imparts a "how to" flavor, leaving the reader with the feeling that he or she is prepared to commence the planning, implementation, and evaluation of IPM programs. This is a remarkable achievement for any book, and especially for such a brief treatment of the subject.

I highly recommend this book to any practitioner of IPM. Its value may not be immediately apparent for researchers whose focus is the component elements of IPM, but anyone who has ever tried to implement IPM will recognize its elegance and utility. Anyone teaching an IPM course **must** review this book.

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SCHAEFER, C. W. (ed.) 1996. Studies on Hemipteran Phylogeny. Entomological Society of America (Thomas Say Publications in Entomology); Lanham, MD. iii + 244 p. ISBN 0-938522-54-X. Paperback. $13.20 ESA members, $22.00 non-members, from ESA Sales, 9301 Annapolis Rd., Lanham, MD 20706-3115. Add $2.50 per volume for postage and shipping ($3.50 to foreign addresses).

This book evolved from a symposium on hemipteran phylogeny at the Eighteenth International Congress of Entomology held in Vancouver in 1988. It is a collection of eleven independent papers that present the ideas of scholars from Canada (K. G. A. Hamilton), Czech Republic (P. Štys), Japan (H. Mori), Poland (J. Koteja), Russia (Y. A. Popov and D. E. Shcherbakov), United Kingdom (R. J. Wootton), and United States (J. R. Aldrich, H. D. Blocker, C. W. Schaefer, M. H. Sweet, and D. B. Thomas, Jr.), who are studying evolutionary relationships and higher systematics in Hemiptera. Cladistics permeate this book, as stated by Schaefer in his introduction, even if cladistic techniques are not explicitly used. Schuh's (1986) article on the Influence of Cladistics on Heteroptera Classification is a good introduction to many of the terms used in this book to those uninitiated in hemipteran cladistics. The glossary in Schuh & Slater's (1995) book is also helpful.

I would consider the Introduction as a true chapter since, aside from a helpful summary and analysis of the following 11 chapters, it presents information not included in them. Specifically, Schaefer discusses recent research papers on analysis of molecular (18S rDNA) data and proposes a classification for Hemiptera based on both these papers and this book. He expects vigorous discussion of both the classification and the names of the Hemiptera suborders that he proposes to substitute for Homoptera and Heteroptera, which are the following: Sternorrhyncha (for Psylloidea, Coccoidea, Aleyrodoidea, and Aphidoidea), Clypeorrhyncha (for Cicadoidea), Archaeorrhyncha (for Fulgoroidea), and Prosorrhyncha (for both Peloridiidae and Heteroptera).

The first two chapters summarize a long-term study of the insect collections in the Paleontological Institute in Moscow. Cladograms, phylograms (including extinct groups), geographic distribution maps, black and white illustrations, and photographs of existing species and of fossils extensively illustrate the text. The following chapter presents a synthesis of ideas on the origin and radiation of the suborder now called Auchenorrhyncha (for Fulgoroidea, Cicadoidea, Cercopoidea, and Cicadel-

loidea), the classification of which is still not agreed upon. The fourth chapter discusses the morphological and structural evolution of coccids based on 130 scale insect characteristics (morphological, genetic, developmental, and other), introduces a coccid phylogenetic tree and includes several drawings of wing venation and sculpture. Hamilton presents in his chapter on fossil Homoptera from Brazil the classification of Hemiptera that Schaefer adopts, although with different names (Psyllomorpha, Cicadomorpha, Fulgoroidea, and Heteropteroidea), based on cladistic data derived both from fossil and recent morphology as well as DNA analysis that demonstrate that the suborders are monophyletic; he recommends adopting the names proposed by Sorensen et al. (1995), which were presented in the introduction of this book.

Štys presents and supports the hypothesis that Enicocephalomorpha (for Enicocephalidae and Aenictopecheidae) is a sister group to the rest of Heteroptera but at the same time encourages exploration into the possibility that Enicocephalomorpha may not be a natural taxon. His paper discusses four character complexes in trying to present the components of a heteropteran ground plan: male genitalia, first abdominal sternite, forewing venation, and abdominal and thoracic scent glands. Sweet surveys the external morphology of the abdomen, excluding the genital segment, in Hemiptera and in other insect orders and discusses how the various forms of the abdomen and its structures serve the insects in their various habitats. Based on abdominal morphology he supports the division of Hemiptera into four instead of two suborders, but not the same as Hamilton and Schaefer support: Sternorrhyncha, Auchenorrhyncha, Coleorrhyncha, and Heteroptera; he also proposes a new heteropteran infraorder, Aradomorpha, to be added to the generally-accepted other seven infraorders (known as suborders by those who consider Heteroptera an order). An extensive reference list (241 entries) makes this an important source of information on hemipteran morphology. Thomas's chapter reports on autosomal polyploidy in Heteroptera; he concludes that polyploidy has not been a major speciation mode in Heteroptera, but that it has probably been significant at the macroevolutionary levels, and presents five dendrograms based on chromosome numbers, one for Heteroptera, the others for some infraorders.

The remaining chapters do not propose or analyze hemipteran phylogenies. Instead, they discuss some characters important for sorting phylogenetic relationships in Hemiptera in the future. For example, Wootton discusses the functional significance of front wing design in Hemiptera, the morphology of which is a compromise between the conflicting needs of flight efficiency and protection, venation variations reflecting differences in flexibility. Wootton cautions that too many conclusions in phylogenetic studies have been drawn from superficial resemblances, which can be due to convergence, a widespread phenomenon in Hemiptera. Numerous illustrations of wings and of a cercopid in flight make this a very interesting paper. Aldrich reviews the sex pheromone systems of eight terrestrial hemipteran families: Margarodidae, Diaspididae, Pseudococcidae, Aphididae, Miridae, Reduviidae, Pentatomidae, and Scutelleridae and illustrates his text extensively with drawings, photographs, chemical formulae, walking tracks, and gas chromatograph tracings of the pheromone components. He also reviews some aspects of acoustical communication in Hemiptera. The 172 references are a good source of information on hemipteran volatile secretions. Mori suggests that phylogenetic reconstructions could be based on embryonic structures instead of on structures only seen in the adult insects. He believes that distribution patterns at the family level of embryonic ventral nerve masses and of the convolution in the posterior part of the midgut are useful characters for analyses of phylogeny in Heteroptera.

This book is primarily for the very specialized entomologist, in part because a glossary is not included and many terms go unexplained. Both a glossary and a subject in-

dex are missing. The addition of the first one would make this book more accessible and the second one would make it more useful to all readers. This book is important for all hemipterists and systematic entomologists because it updates the higher classification of this order, presents new ways to study some characters, has extensive reference lists, and gives new ideas and directions for research in the phylogeny of Hemiptera.

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JERVIS, M. A., AND N. A. C. KIDD (eds.). 1996. Insect natural enemies. Practical approaches to their study and evaluation. Chapman and Hall; London, x + 491 p. Hardback. ISBN 0-412-39900-8. $138.95.

This book is about the behavior and ecology of insect parasitoids and predators. The subjects (the parasitoids and predators) and the objects (hosts of the parasitoids and prey of the predators) are insects. Its 7 authors are from Wales, the Netherlands, and England. In 6 long chapters, mostly with 2 authors, they write about many of the things that a specialist in biological control needs to know. The chapters are thus aimed at graduate students and professionals in biological control. I think the book will also be very useful to ethologists and ecologists who study insect parasitoids and predators from a purely academic viewpoint (as contrasted with biological control's applied viewpoint) because biological control research is at the forefront of studies in insect behavior and ecology. The book will be of very little use to systematists because the information is **not** organized order by order and family by family and is **not** a replacement for Clausen's **Entomophagous insects**.

The 6 chapters are: (1) Foraging behavior [with emphasis on Hymenoptera], (2) The life cycle [which includes sections on female and male reproductive systems with emphasis on Hymenoptera], (3) Mating behavior [with emphasis on Hymenoptera], (4) Populations and communities [including a section on field sampling techniques], (5) Population dynamics [including a section on selection criteria for biological control agents], and (6) Phytophagy. The chapters are not like those in Annual Review of Entomology. First, they are longer. Second, they offer their authors' viewpoint, documented and illustrated by selected examples, rather than attempting to review at least the highlights of everything published. This is not detrimental. Third, they emphasize the "parasitic" Hymenoptera, although this is reasonable in the context of biological control because these insects have played such a prominent role. Fourth, the

author's perspective and the examples they cite are mainly European. Undoubtedly it makes a better book when authors write about examples familiar to them; North American readers can learn by reading it even if they find the examples unfamiliar. Fifth, the literature cited is almost entirely in English, most likely because most of the literature these days **is** published in English (there could be other explanations).

The chapter on populations and communities includes a 35-page section on field sampling techniques. I found inclusion of this section to be a little curious because the authors **should** have been able to omit it, and refer to a standard textbook on entomology for the methods. Yet, I do not know a standard textbook on entomology which includes a comprehensive review of this subject. Then again, the section seems to have been included only halfheartedly because it is about sampling techniques for insects on the ground surface, on plants, and in flight: it does not include methods for sampling aquatic insects, has little about subterranean insects, and omits many techniques. Perhaps there is a market for an entire book on sampling techniques for all groups of insects.

The chapter on phytophagy is much the shortest and deals almost entirely with feeding by adult parasitoids and predators on floral nectar and pollen. Most of the information is about Syrphidae, and the reader might reasonably hope for a more complete synthesis of knowledge on other insect families. The reader might also wish for more insight into saprophagy, and phytophagy on plant materials other than nectar and pollen, by parasitoids and predators.

Overall, the book is a very useful supplement to textbooks on biological control (for example, Van Driesche & Bellows, 1996, reviewed in Florida Entomologist 79: 269-270), but its price is likely to deter purchase by students. The line drawings and standard of editing are good. The photographs are all in black and white, and some lack contrast. The book emphasizes the "parasitic" Hymenoptera, as perhaps it must, but to the detriment of other taxa of biological control agents, especially predators. It is the first of its kind and was needed: the editors should be congratulated.

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DURDEN, L. A., AND J. E. KEIRANS. 1996. Nymphs of the Genus *Ixodes* (Acari: Ixodidae) of the United States: Taxonomy, Identification Key, Distribution, Hosts, and Medical/Veterinary Importance. Entomological Society of America (Thomas Say Publications in Entomology); Lanham, MD. iv + 95 p. ISBN 0-938522-57-4. Paperback. $13.20 (ESA members), $22.00 non-members, from ESA Sales, 9301 Annapolis Rd., Lanham, MD 20706-3115. Add $2.50 per volume for postage and shipping ($3.50 to foreign addresses).

There are about 670 species of hard ticks (Ixodidae) belonging to 13 genera. Out of those, more than a third—234 species—belong to a single genus—*Ixodes*. Members of this genus are distributed world-wide and include documented and suspected vectors of an extensive list of viral, bacterial and protozoan agents of human and animal diseases. Also, several species of this genus can cause tick paralysis in their hosts. All *Ixodes* ticks that have been tested so far appear to be capable of acquiring and transmitting agents of animal and human diseases. Therefore, one can say that the genus *Ixodes* have the highest epidemiological and veterinary significance among Ac-

ari. It attracted profound attention by the medical and scientific communities in the late 1930's, at the time of the discovery of Russian spring-summer tick-borne encephalitis. Our knowledge about the importance of diseases transmitted by *Ixodes* spp. to public health has grown greatly since then. Concurrently, it has been recognized that closely related species of ticks possess markedly different susceptibility to certain tick-borne pathogens, and play different roles in their natural circulation. Yet, those species that are capable of acquiring and transmitting pathogens in turn differ in their aggressiveness toward humans, and therefore have dissimilar significance as a source of infection for humans and domestic animals.

In the late 1950's, it was found that one of the major vectors of Russian tick-borne encephalitis (TBE), previously considered to be a single species, indeed presented a complex group. There are several species of ticks phylogenetically close to *Ixodes persulcatus* which dwell in a huge territory of Southern Siberia, Far East, and Middle Asia. One of those species—*I. pavlovskyi*—appears to have a wide geographical range, and sometimes reaches a high abundance in active foci of TBE. Still, because of its ecological peculiarities *I. pavlovskyi* plays a notably different role in epidemiology and epizootiology of TBE than *I. persulcatus*. In the USA, ticks *I. dentatus*, *I. spinipalpis*, and *I. neotomae* are competent vectors of the Lyme disease spirochete. However, they rarely attack humans, and therefore pose a lot lesser threat to human health than *I. scapularis* or *I. pacificus*. These are just a few of the available examples of the importance of careful identification of tick species for both practical and scientific purposes.

The reviewed book presents the first practical guide for identification of the *Ixodes* spp. nymphs since 1945. It includes all 34 species of the genus *Ixodes* considered to be resident in the United States. The authors introduce their book with a short morphological description of an *Ixodes* sp. nymph which makes the usage of the guide possible for an inexperienced person. The following comprehensive key to nymphal stages of all U.S. species contains references to scanning electron micrographs for further help with the identification. In the species accounts, the authors have included micrographs of characteristic features of each species, chronological listings of synonymies, geographical distribution, and known host records. They also provide synopses of the known medical and veterinary importance in the United States of each species. The 148 cited references alone present valuable information to those interested in learning about tick distribution, and tick-borne diseases in the U.S. The format and concise information included in this book make it useful to medical and veterinary practitioners, as well as to specialists studying ectoparasites of vertebrates.

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A. T. BARRION, AND J. A. LITSINGER. 1995. Riceland spiders of south and southeast Asia. Centre for Agriculture and Biosciences International, Wallingford, Oxon, England. xix + 700 pages + 16 color plates; 414 text-figures and 339 maps included in the text. Hardback, 22.1 x 28.2 cm. ISBN 0-85198-96-5. US $225.

I have seen two very thorough reviews of this book by John Dalingwater (Newsletter of the British Arachnological Society, Number 76) and Norman Platnick (The Journal of Arachnology, Volume 24, Number 2). Rather than attempting to redo their

reviews, I will summarize their comments, then address the book from a more personal perspective. I feel qualified to do this because I spent three weeks in the Philippines with other colleagues and the first author in December 1993, and I had the opportunity to review the chapter on the family Salticidae subsequent to my visit.

Positive aspects of the book include: (1) Descriptions of new genera and species are detailed. (2) It is lavishly illustrated and most of the illustrations are of high quality, thanks to the efforts of the illustrator, Danilo Amalin. (3) It is well typeset and very well printed on high quality paper, and it has a strong and attractive hard binding. (4) The combination of a description of external anatomy and a glossary provide enough information that a novice could use the book (but not with ease). (5) A discussion of spider diversity in Philippine ricelands is included, along with lists of collecting sites and trapping methods, as well as discussions of some other arachnid groups. (6) It has a more comprehensive coverage than any similar volume which has been published from Southeast Asia.

Negative aspects of the book, which unfortunately outnumber the positive aspects, include: (1) The title is misleading, since over 95% of the records occur in the Philippines. (2) the editing stage was apparently skipped over, as there are numerous "typos" and assorted inconsistency errors (probably averaging more than one per page), as well as poor organization of accessory categories in the descriptions (some categories, e.g., Natural History and Material Examined, should have been combined to save space). (3) The distribution maps are superfluous, as they almost invariably show either only one or two records, or numerous records showing a species occurs throughout the Philippines. (4) A classification for Philippine spiders is provided which does not even include all the families listed in the volume, much less all families known from the Philippines. (5) The bibliography is scanty and does not even include some of the most relevant literature from the same geographic region. (6) Many scientific names of species are outdated and the authors' knowledge of modern spider nomenclature seems minimal; even when they show evidence of knowing otherwise, they still use names that are incorrect; furthermore, they apply generic names to species that are clearly unrelated to the genera in which they place them. (7) Adequate diagnoses are generally lacking, and, for the most part, newly described species and genera are not compared to previously described related taxa; in fact, there is no evidence that the authors looked at the types of any of the described Philippine species prior to describing new species or genera. (8) Males and females of what are probably the same species are described as different species on several occasions. (9) Some of the new names are combinations of Tagalog names that are excessively long and difficult to pronounce (at least for a person not of Philippine origin). (10) Apparent new synonyms are not noted as such, but in at least one case a new synonym inadvertently sinks a generic name (!). (11) Terminology used (e.g., the use of holotype and paratype to designate additional specimens of previously described species) is suspect. (12) Some new species do not have the genitalia adequately illustrated, and in one case, not illustrated at all. (13) Some illustrations are unnecessary (e.g., when two specimens of the same sex are illustrated, or a species is only illustrated by an immature specimen). (14) Keys are of limited value, being based in many cases on measurements of a few specimens (often one or two) per species. (15) The cost is so great that the people most likely to find the book useful will be unlikely to be able to afford it.

Mitigating circumstances: (1) The authors were instructed by their supervisors, authorities at the International Rice Research Institute, to cover all spiders occurring in Philippine ricelands; this by itself, in one of the tropical areas of the world where the spider fauna is most poorly known, verged on the impossible. (2) The authors' background was more in spider ecology than in spider systematics, yet they have put nearly 20 years worth of effort into this enormous task; even well-known specialists

on the various spider families would have some difficulty with the fauna of this region of the world as it is now known. (3) The editors apparently neglected to do any editing or find any qualified referees; could the 700+ page manuscript have been too daunting a task?

The authors made corrections when a review was provided for them. At least 90% of the minor corrections in my review of the family Salticidae were fixed. I did have concerns that of the 36 species of salticids covered, 28 were described as new species. Undoubtedly there are synonyms of previously described species among these new descriptions. Probably the male and female *Simaetha*, which were described as two new species, belong together (a similar situation exists for *Telamonia*). Unfortunately, the person with the best knowledge of the salticid fauna of the region who might know which would be synonyms, Fred Wanless at the British Natural History Museum, is no longer allowed to work on spiders. It is therefore most ironic that this book was published in this condition by a noted British entomological institution.

I have seen the collections, reprint files, and other resources at IRRI, worked in the laboratory facilities, and become aware of a little of the politics of creating such a project. Based on what I observed, the resources did not exist during most of the time dedicated to this project to properly create this book. Neither was it clear that the authors had sufficient taxonomical background to undertake such a project. Although their descriptive technique was reasonable, their inconsistencies reflect a lack of understanding of the minimum conditions necessary to support the description of new taxa, as well as a lack of familiarity with modern spider systematics. One wonders why in nearly 20 years they haven't maintained better contact with spider specialists who might have been able to help them with nomenclature and literature. Were they so isolated that they were not completely aware of the resources available to them? If aware, did they not have the ability to acquire these resources? Were there cultural conditions or politics involved which prevented them from seeking assistance, or from receiving it? Were their other job responsibilities so time-consuming that they could not spend the time to do all the extras required to make this book what it should have been? Perhaps a little of all the above reflects the true situation.

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