RELEASE, ESTABLISHMENT AND SPREAD OF ASIAN NATURAL ENEMIES OF EUONYMUS SCALE (HOMOPTERA: DIASPIDIDAE) IN NEW ENGLAND

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ABSTRACT

Between 1990 and 1995, the USDA/APHIS National Biological Control Laboratory in Niles, MI, Texas A&M University, and the University of Massachusetts conducted a biological control introduction program against the Asian diaspidid scale insect *Unaspis euonymi* (Comstock), a pest of woody landscape plants. Two species of predators (*Chilocorus kuwanae* Silvestri, Coleop.: Coccinellidae and *Cybocephalus* sp. nr. *nipponicus* Enrody-Younga, Coleop.: Cybocephalidae) and three aphelinid parasitoids (*Encarsia* sp. nr. *diaspidicola* [Silvestri], *Coccobius* sp. nr. *fulvus* [Compere et Annecke], and *Aphytis* sp.) were collected near Beijing, China and released in southern New England. We report establishment of *C. kuwanae*, *C.* sp. nr. *nipponicus* and *Coccobius* sp. nr. *fulvus* in Massachusetts. *Chilocorus kuwanae* has spread throughout southern New England and the proportion of euonymus shrubs in landscape-level surveys bearing *C. kuwanae* stages was positively related to scale density, with the coccinellid present on 1.1%, 6.3%, 12.5%, and 26.3% of shrubs whose scale populations were classified as none, light, medium, and heavy, among 4843 plants examined from 1992-1994 in Massachusetts, Connecticut, and Rhode Island. *Cybocephalus* sp. nr. *nipponicus* and *C.* sp. nr. *fulvus*, while established at some release sites, have been observed to spread to new locations in only one and two instances, respectively. *Encarsia* sp. nr. *diaspidicola* was recovered at some release locations, but establishment is uncertain. No recoveries were made of the *Aphytis* sp. parasitoid, but this species was released later than the other species and further recovery efforts are needed.

Key Words: *Chilocorus kuwanae*, *Cybocephalus* sp. nr. *nipponicus*, *Coccobius* sp. nr. *fulvus*, biological control, establishment

RESUMEN

Entre 1990 y 1995 el Laboratorio Nacional de Control Biológico del USDA/APHIS en Niles, Michigan, la Universidad de Texas A&M, y la Universidad de Massachusetts dirigieron un programa de control biológico de introducción en contra de la escama asiática *Unaspis euonymi* (Comstock) (Diaspididae), una plaga que ataca arbustos leñosos utilizados en arreglos de jardinería. Dos especies de depredadores (*Chilocorus kuwanae* Silvestri, Coleop.: Coccinellidae y *Cybocephalus* sp. nr. *nipponicus* Endrody-Younga, Coleop.: Cybocephalidae) y tres parasitoides de Hymenoptera: Aphelinidae (*Encarsia* sp. nr. *diaspidicola* (Silvestri), *Coccobius* sp. nr. *fulvus* (Compere et Annecke), y *Aphytis* sp.), fueron colectados cerca de Beijing, China, y liberados en el sur de New England. Reportamos el establecimiento de *C. kuwanae*, *C.* sp. nr. *nipponicus* y *Coccobius* sp. nr. *fulvus* en Massachusetts. *Chilocorus kuwanae* se ha extendido por todo el sur de New England; las proporciones de arbustos de euonymus muestreados

en jardines con estadíos de *C. kuwanae* resultaron estar relacionados estadísticamente en forma positiva con la densidad de la escama, con la presencia de la coccinela en 1.1%, 6.3%, 12.5%, y 26.3% de los arbustos con poblaciones de escamas clasificadas como nula, ligera, mediana, y fuerte en 4,843 plantas examinadas en 1992-1994 en Massachusetts, Connecticut, y Rhode Island. *Cybocephalus* sp. nr. *nipponicus* y *C.* sp. nr. *fulvus*, aunque se establecieron en algunos sitios donde se realizaron liberaciones, han sido observados en otros sitios en sólo una y dos ocasiones respectivamente. *Encarsia* sp. nr. *diaspidicola* fué recolectada en varias localidades donde liberaciones fueron realizadas, pero su establecimiento no está confirmado. Recolectas del parasitoide *Aphytis* sp. no se han logrado, pero como esta especie fué liberada más tarde que las otras especies, es necesario que se realicen más esfuerzos de recolección en el futuro.

Euonymus scale, *Unaspis euonymi* (Comstock), is an exotic diaspidid scale of Asian origin that feeds on foliage and stems of woody landscape plants in the United States. In New England, the species overwinters as mated adult females, and eggs are produced in the spring. Three generations occur yearly. Major host plants are species of *Euonymus*, many of which were imported from Asia (Flint 1983) and are widely planted in urban areas (Gill et al. 1982). Effective natural enemies of euonymus scale were not present in North America before 1980, when USDA and state cooperating entomologists began the importation of predators and parasitoids from Korea (Drea & Hendrickson 1988, Hendrickson et al. 1991). From 1991-1994, collections of euonymus scale were made in the vicinity of Beijing, China and sent to M. Rose at Texas A&M University for quarantine and initiation of natural enemy cultures. Five species of scale natural enemies were recovered and released in New England: *Chilocorus kuwanae* Silvestri (Coleop.: Coccinellidae), *Cybocephalus* sp. nr. *nipponicus* Endrody-Younga (Coleop.: Cybocephalidae), two internal parasitoids, *Coccobius* sp. nr. *fulvus* (Compere et Annecke), *Encarsia* sp. nr. *diaspidicola* (Silvestri), and an external parasitoid, *Aphytis* sp. (all, Hymenoptera: Aphelinidae).

Chilocorus kuwanae is a multivoltine coccinellid that feeds on high density populations of various species of diaspidid scales (Nohara & Iwata 1989, Bull et al. 1993). *Cybocephalus* sp. nr. *nipponicus* is a much smaller predator that oviposits under individual scales, with the larva feeding sequentially on a small number of scales over the course of its development (Alvarez et al. in press). Of the three aphelinid parasitoids, only one, *Coccobius* sp. nr. *fulvus*, has received previous study. An internal parasitoid, this species parasitizes adult female scales, both before and after development of scale eggs (Takagi 1991).

Chilocorus kuwanae and *C.* sp. nr. *nipponicus* from Korea were established in the northeastern United States earlier (Drea & Carlson 1987, 1988). We report further releases of these predators in New England, releases of three species of parasitoids, establishment of *C. kuwanae*, *C.* sp. nr. *nipponicus*, and *C.* sp. nr. *fulvus* in Massachusetts, and estimates of rates of occurrence of *Chilocorus kuwanae* in southern New England on landscape euonymus plants in relation to scale density.

Materials and Methods

Collection and Laboratory Rearing

In 1990, adult *Chilocorus kuwanae* feeding on euonymus scale on *Euonymus* spp. near Beijing, China were collected and shipped to the USDA/ARS quarantine facility

in Newark, DE, where the coccinellid was identified and bred for one generation prior to release from quarantine. This colony was then used to make releases in southern New England starting in 1991.

Each year from 1991-1994, 3-5 shipments of *Euonymus* sp. branches infested with euonymus scale were sent by collectors in China to a quarantine laboratory at Texas A&M University. Collections were made in various locations within 200 km of Beijing, by Mr. Shen Zhicheng (1991), Mr. Du Yongjun (1992, 1993) and Mr. Zhao Youfou (1994). In each year, collections were made in late April-early May of overwintered adult female scales and then again in summer and early fall. In this manner, different life stages of scale predominated in different collections, allowing opportunity to encounter parasitoids associated with various life stages.

Four of the five species of natural enemies obtained could be reared under laboratory conditions on San José scale (*Quadraspidiotus perniciosus* [Comstock]) and field collected stock was used to initiate laboratory cultures on this alternate host. Both parasitoids emerging from field-collected scales and from laboratory rearing were used for field releases, except for *C.* sp. nr. *fulvus* which could only be reared on euonymus scale. All *C.* sp. nr. *fulvus* released were adults that emerged from immatures collected in China.

In addition to the euonymus scale natural enemies obtained from China, two species of natural enemies (*C. kuwanae* and *C.* sp. nr. *nipponicus*) originally collected in Korea were also obtained from USDA entomologists from earlier sites of establishment in the Washington, D.C. area. Releases of these predators were made in Massachusetts in 1988 and 1989. Subsequent collection of these same natural enemies in China was intended to find populations of these agents from areas more climatically similar to southern New England, as well as to locate new agents.

Field Releases

Releases were made in Massachusetts, Connecticut, and Rhode Island on *Euonymus fortunei* (Turz.) Hand.-Mazz. and *Euonymus europaeus* L. plants infested with medium to heavy populations of euonymus scale in urban or suburban locations from 1991 to 1995. Releases of *C. kuwanae* included adults, older larvae, and pupae. Mobile stages were allowed to crawl from opened 0.5 liter cardboard containers placed in euonymus plants. All other agents were released as adults by fixing open vials or cups containing parasitoids or *C.* sp. nr. *nipponicus* onto infested shrubs and allowing adults to walk or fly out.

Assessment of Establishment

For *C. kuwanae*, establishment was confirmed by visual inspection of shrubs at release sites to detect larvae, pupae, or adults, which were readily observed. *Chilocorus* adults were identified to species by examination of the pronotal punctation pattern to separate the released species from the native species *Chilocorus stigma* Say, which was occasionally encountered feeding on euonymus scale (Drea & Carlson 1987). Fifteen release sites (three each in western, central and eastern Massachusetts, Connecticut and Rhode Island) were visited every three weeks for 1-3 years, depending on survival of the shrub at each site, and the number of *C. kuwanae* life stages (larvae, pupae, adults) seen in three 5-min counts was recorded as an index of coccinellid population increase.

For *C.* sp. nr. *nipponicus*, establishment was confirmed by recovery of adult specimens, relying primarily on detection of males, which have a beige head and pronotum

and black body, and their comparison to voucher specimens. At some locations, establishment of *C.* sp. nr. *nipponicus* was detected by holding scale-infested twigs in cardboard cartons for three weeks and later noting the presence of adults or pupae in the rearing container.

Establishment of released parasitoid species was assessed by either rearing or dissection. Rearing of scales was done by holding cut twigs in 0.5 liter cardboard containers with ventilated tops at 21-27°C for three weeks. Material in the bottom of the rearing containers was then examined for dead adult parasitoids. Parasitoids were identified by comparison with voucher specimens.

In 1994, dissection of fully developed third stage female scale insects from 18 locations in Massachusetts was used to detect immature parasitoids. Samples were collected every three weeks from April through October. Larval and egg stages of *Encarsia* sp. nr. *diaspidicola* could not be separated from those of *Aspidiotiphagus* sp., a preexisting euonymus scale parasitoid in the United States that was common in southern New England, and therefore dissection was not useful in detecting this species. However, larvae of *Coccobius* sp. nr. *fulvus* were distinctively longer and more thread-like than larvae of either *Aspidiotiphagus* sp. or *Encarsia* sp. nr. *diapsidicola*, and could be reliably recognized. Pupae of *Coccobius* sp. nr. *fulvus* were black in contrast to the yellow-brown or striped pupae of *Encarsia* sp. nr. *diaspidicola* and *Aspidiotiphagus* sp. Pupal exuviae of *Coccobius* sp. nr. *fulvus* were completely black and easily distinguished from those of the other parasitoids. Therefore, *C.* sp. nr. *fulvus* could be reliably detected in samples from release sites by finding their larvae, pupae, or pupal exuviae. Rates of parasitism of the preexisting parasitoid *Aspidiotiphagus* sp. in these samples were also recorded and are reported to provide comparisons to future samples after introduced parasitoids have had sufficient time to reach their maximal levels of impact. Voucher specimens of all five natural enemies have been deposited in the insect collection of the U.S. Natural History Museum.

Rates of *C. kuwanae* Presence on Landscape Plants

To determine how widespread *C. kuwanae* had become following its establishment, a total of 4843 euonymus plants were examined in surveys conducted in Massachusetts, Connecticut, and Rhode Island from 1992 to 1994. Landscape euonymus plants (*E. fortunei* and *E. europaeus*) were located throughout each state. In Massachusetts, where three quarters of all surveyed plants were located, surveys were conducted yearly in an average of 54 towns in eleven counties. Each shrub was classified by scale infestation level category and the presence or absence of *C. kuwanae* life stages in 2 minute inspection periods was noted. Scale infestation categories were as follows: *none*—close inspection fails to reveal any scales; *light*—the shrub from one meter away appears uninfested but close inspection of the undersides of leaves reveals the presence of scattered second stage male scales (the most abundant, easily visible stage); *medium*—the shrub is visibly infested in casual inspection, but scales do not encrust stems, nor is die back of limbs present; and heavy-scales encrust stems and foliage and are immediately visible from a distance, die back of limbs is common.

Statistical Analysis

Chi square tests were performed on data to determine relationships between presence of *C. kuwanae* beetles and scale infestation levels on shrubs; and, for other data, to determine the relationship between the presence of the parasitoid *Aspidiotiphagus* sp. and scale infestation levels on shrubs (Daniel 1987). Simple linear regression was

used to assess the relationship between the post-release counts of the number of *C. kuwanae* and numbers released at sites to determine if numbers of beetles released or differences in site features were more important to *C. kuwanae* population growth.

RESULTS

Releases

In 1988 and 1989, 400 adults of a Korean population of *C. kuwanae* were released in Massachusetts at 15 sites. In 1991 and 1992, 2535 adults, larvae, or pupae of Chinese *C. kuwanae* were released at 25 sites in southern New England (Massachusetts, Connecticut, or Rhode Island). From 1991 to 1993, 675 adults of *C.* sp. nr. *nipponicus* from Korea and 945 from China were released at 17 sites in southern New England (Fig. 1b). From 1991 to 1994, 3862 adults of *C.* sp. nr. *fulvus* were released at 11 sites in Hampshire and Franklin Counties in Massachusetts (Fig. 1c, map shows towns used for releases; some towns had several release sites). From 1993 to 1995, a total of 12,966 adults of *E.* sp. nr. *diaspidicola* were released at 27 sites in eight counties in Massachusetts and one county in Connecticut (Fig. 1d). In 1994 and 1995, 801 adults of Aphytis sp. were released at five sites in two Massachusetts counties (Fig. 1e).

Establishments

Chilocorus kuwanae (Chinese strain) established at most release sites, but population increase at sites varied greatly. Of 15 sites followed in detail, the beetle established at all 15, following release of various numbers. Peak numbers of *C. kuwanae* life stages counted per five minute observation varied from 5 or fewer at three sites where the beetle scarcely persisted, to over 50 at five sites where beetle increased substantially. No relationship was observed in simple linear regression between numbers released per site and subsequent peak counts of beetles ($R^2 = 0.002$, $Y = 30.37 + 0.007X$, with X and Y as in Fig. 2), suggesting that site factors other than initial release rate were primarily responsible for beetle success at individual sites (Fig. 2).

Cybocephalus sp. nr. *nipponicus* was encountered at five of the seventeen release sites in the year following release, indicating successful establishment. Same-season reproduction of the beetle was observed at ten other sites (Fig. 1b).

Coccobius sp. nr. *fulvus* was recovered in 1994 from six of eleven release sites (from releases in either 1992 or 1993), indicating establishment (six sites, but only four towns, Fig. 1c). Same-season reproduction was observed at one additional location. Of 155 wasps obtained in rearing samples, 109 (70%) were female.

Encarsia sp. nr. *diaspidicola* was recovered in 1994 from two of ten 1993 release sites. Same-season reproduction was observed in 1993 or 1994 at twelve other sites (Fig. 1d—note, some locations marked on the distribution map include several sites). Establishment of this species remains uncertain.

Aphytis sp. releases were made later than those of other species. Recovery efforts in 1995, the last year of the study were unsuccessful and the status of this species is unknown.

Spread of Released Species

Of the five species released, *C. kuwanae* has achieved the most extensive range in southern New England (Fig. 1a). In 1992-1994 surveys of randomly selected land-

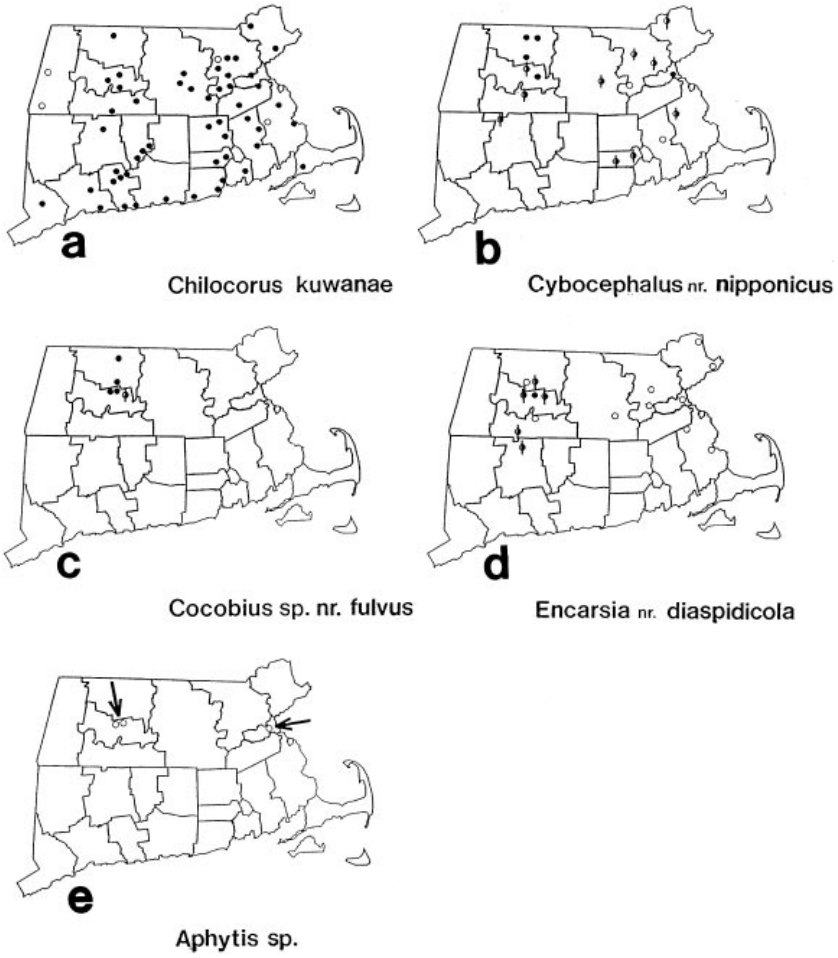

Fig. 1. Distribution in southern New England of *Chilocorus kuwanae* Silvestri (a); *Cybocephalus* sp. nr. *nipponicus* Enrody-Younga (b); *Coccobius* sp. nr. *fulvus* (Compere et Annecke) (c); *Encarsia* sp. nr. *diaspidicola* (Silvestri) (d); *Aphytis* sp. (e); open circles (releases with no recoveries), half filled circles with strike through lines (releases with recoveries, in the same year only) and filled circles (releases with recoveries one or more years after release).

scape euonymus plants in southern New England, the beetle was found on 14.1% of 3141 shrubs that were infested with euonymus scale, out of a total of 4843 plants examined. The proportion of shrubs with *C. kuwanae* present increased significantly with increasing scale density (Fig. 3) (df = 3, (χ^2 = 516.6).

Spread of other released species of natural enemies was rarely observed. One case of recovery at a nonrelease site was noted for *C.* sp. nr. *nipponicus* and two for *C.* sp. nr. *fulvus*.

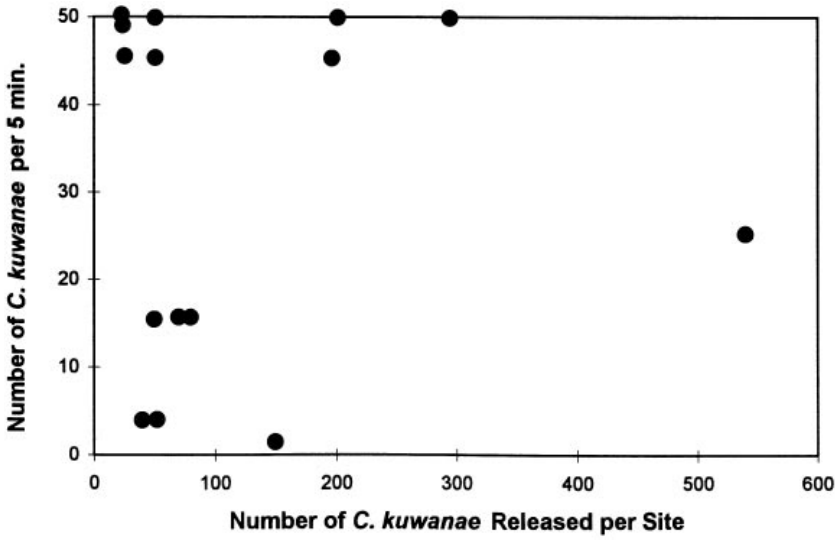

Fig. 2. Relationship between number of *Chilocorus kuwanae* Silvestri released at a site and the peak number of the coccinellid counted per five minutes subsequently at the same location, over the course of 1-3 years of observations every three weeks (April through October) ($R^2 = 0.002$, where $Y = 30.37 + 0.007X$).

Occurrence of Nonreleased Parasitoid Species

Aspidiotiphagus sp. was a preexisting aphelinid found parasitizing euonymus scale at 44% of 79 sites in southern New England from which euonymus scales were collected and reared in 1991 (Table 1). The presence of the parasitoid was not significantly related to the level of the scale infestation at a site ($df = 2, \chi^2 = 5.991$). Parasitism of third stage female euonymus scales, pooled by generation, for scales dissected in 1994 from 18 locations in Massachusetts was 13.4% (n = 2174 scales) for the overwintered spring adults, 33.6% (n = 1271 scales) for the summer generation, and 31.2% (n = 933 scales) in the fall generation.

Discussion

The coccinellid *C. kuwanae* is now widespread throughout southern New England on euonymus scale plants infested with euonymus scale. Establishment of *C. kuwanae* at release sites was not related to numbers released. Likely influences were host density, bush size and degree of sunniness at sites. The later two factors were not, however, quantified. Coccinellids were recovered at sites ranging from shrubs at cool, moist sites surrounded by lawn, to hot, dry sites such as shrubs at shopping malls, where plants were often surrounded by concrete and bark mulch. Most sites examined were urban or suburban in nature and no attempt was made to assess rates of discovery by coccinellids of shrubs at isolated properties in non-urban areas. Rates of recovery of *C. kuwanae* on shrubs examined in the statewide surveys of euonymus scale were unlikely to have been influenced by proximity to release sites because release sites were few (45 over a five year period) and the number of shrubs in surveys was

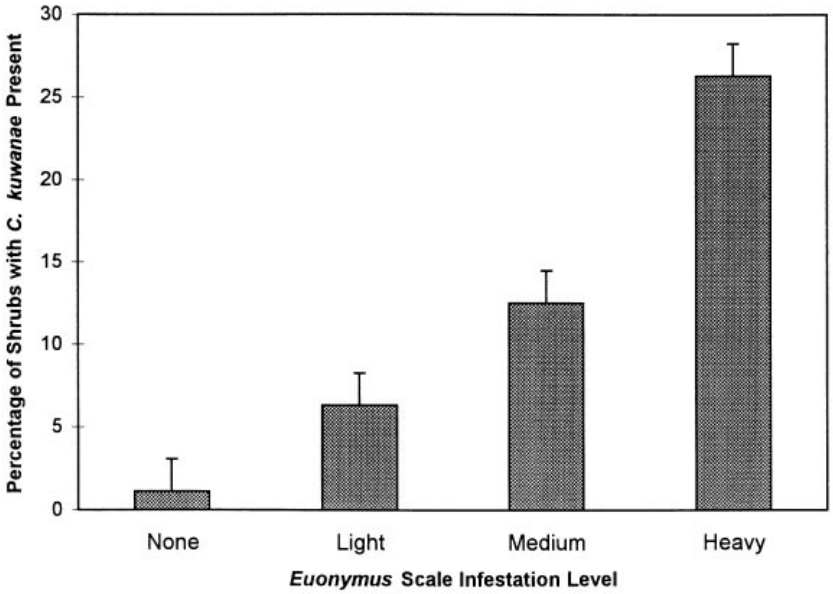

Fig. 3. Percentages (and SE values) of euonymus plants in various categories of scale density on which *Chilocorus kuwanae* Silvestri was present in surveys in southern New England in 1992-1994, where sample sizes by category were 1702 (N), 1401 (L), 745 (M), and 995 (H), and divided by state were 3220 (Massachusetts), 1076 (Connecticut), and 547 (Rhode Island).

large (4843) and shrubs were distributed widely over the three state area. Thus, while a few sites may by chance have been close (under 5 km) to release sites, most were not.

Chilocorus kuwanae life stages were most commonly encountered on plants with medium or heavy scale infestations, suggesting that the principal effect of this coccinellid will be to suppress scales at sites where scale densities are at or approaching damaging levels, rather than acting when scale densities are light. Because *Cybocephalus* sp. nr. *nipponicus* and *Coccobius*. sp. nr. *fulvus* require fewer hosts for repro-

TABLE 1. PRESENCE OF *ASPIDIOTIPHAGUS* SP. ON EUONYMUS PLANTS WITH DIFFERENT EUONYMUS SCALE DENSITIES IN SOUTHERN NEW ENGLAND IN 1991.

Scale Inf. Level	Samples with *Aspidiotiphagus*	Samples without *Aspidiotiphagus*
light	7 (64%)[a]	4
medium	7 (35%)	13
heavy	21 (44%)	27
total	35 (44%)	44

[a]Percentage samples with parasitoids was not significantly associated with scale density in a χ^2 test (df = 2, χ^2 = 5.991).

duction, these species may be more effective in causing mortality to low density scale populations. Establishment of these agents in Massachusetts makes possible a future evaluation of their effects on survivorship of scales in low density populations. The remaining parasitoids (*E*. sp. nr. *diapidicola* and *Aphytis* sp.) have not yet been shown to have established; future assessment of their status will be needed.

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A NEW SPECIES OF *MYODOCHA* (HEMIPTERA: LYGAEIDAE: RHYPAROCHROMINAE: MYODOCHINI) FROM THE WEST INDIES

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ABSTRACT

Myodocha froeschneri n. sp. is described based on specimens from Dominican Republic, Haiti, and Jamaica.

Key Words: West Indies, *Myodocha*, new species

RESUMEN

Se describe *Myodocha froeschneri* n. sp. basada en especímenes de la República Dominicana, Haití, y Jamaica.

The genus *Myodocha* is characterized by elongate body and appendages. The head is especially elongate with the postocular region produced into a narrow stalk-like neck. The seven previously described species are primarily Neotropical with one species, *M. serripes* Olivier, broadly distributed in the Nearctic. *M. froeschneri*, named for Dr. Richard Froeschner of the United States National Museum, is described in advance of a revision of the genus to make the name available for a faunal work on the West Indies by R. M. Baranowski and J. A. Slater.

Myodocha froeschneri A. Slater, **New Species**

Structure.—Head: vertex evenly convex, shiny, with obscure, barely perceptible texturing; juga rounded, not carinate, nearly glabrous, no hairs longer than least diameter of neck; ocelli just behind line connecting hind margins of compound eyes; lateral margin behind eye evenly rounded to neck. Labium: segment I not surpassing posterior margin of compound eye; II not reaching prosternum; IV reaching, not surpassing, fore coxa. Pronotum: dull; collar and anterior lobe impunctate; posterior lobe shallowly punctate, punctures ranging from contiguous to separated by twice puncture diameter. Scutellum: dull; sparsely, obscurely punctate; indistinct Y-shaped median carina. Thoracic sterna: dull dark brown except mesosternum shiny. Hemelytra: not reaching apex of abdomen. Legs: shiny; fore femur lightly incrassate, hairs short, sparse, spines in two ranks restricted to about apical third, three small spines in anterior rank, two small and one large (basal) spine in posterior rank; fore tibia unarmed.

Measurements.—All in mm. Total length 9.0. Head: length 2.6, preocular 0.7, postocular including neck 1.4, width across eyes 1.2, interocular 0.6. Antennal segment length: I 1.1, II 2.1, III 1.9, IV 2.3. Labial segment length: I 1.0, II 1.2, III 1.1, IV 0.5. Pronotum: length collar plus anterior lobe 0.8, posterior lobe 0.7, greatest width anterior lobe 1.1, posterior lobe 1.7. Scutellum: length 0.9, width 0.7. Hemelytra: length corium 3.5, claval commissure 0.8, membrane 2.8 (to corial apex 1.6, beyond corial apex 1.2).

Color.—Head dark reddish brown becoming darker ventrally, clypeus lightest, neck darkest. Antennal segment I reddish brown, II creamy white, III creamy white except apical third pale brown, IV creamy white except basal seventh and apical third pale brown. Pronotum dark brown fading to dark reddish brown on apical half posterior lobe. Scutellum dark brown. Corium dark brown except extreme base, extreme apex, basal half costal margin, claval margin, two small elongate discal spots level with middle of clavus, large subapical spot from costal margin almost to membranal margin, and indistinct discal spot opposite basal angle of membrane off-white. Clavus dark brown; veins lightest, subbasal and larger subapical spot darkest. Membrane dark brown, veins subbasally and indistinct elongate apical spot lighter, off-white opposite corial apex. Coxae dark brown; femora light reddish brown except pale basally; tibiae pale brownish yellow, tarsi yet paler brownish yellow. Abdomen reddish brown, segments V-VIII becoming darker apically, lateral margin segment V and basal half lateral margin segment VI off-white.

Types: Holotype male. HAITI: Enneri, nr. 1000 ft., Sept. 6-11-34, Darlington. Deposited in the American Museum of Natural History. Paratypes. HAITI: 1 female, Enneri, no date, Mann; 1 female, Etang Lachaux, S. W. Peninsula (sic), under 1000 ft., Oct. 26-27, 1934, Darlington. DOMINICAN REPUBLIC: 1 male, S.R. [San Rafael ?], 4 km. S.W. Stgo Rodriguez, May 28, 1978, C. W. & L. B. Obrien & Marshall; 1 male, Barahona, 9.2 km N.W. Paraiso, confluence of Rio Nizso and Rio Coltico, 18-03N, 71-12W, 230 m., 9-10 Aug 1990, J. Rawlins, S. Thompson; 1 male, La Vega, 1.5 km. N Jarbacoa, 240 m., 21 July 1987, J. Rawlins, R. Davidson. JAMAICA: 1 female, St. Andrews, 9/17 and JA20, at light, A. M. Richie; 1 female, Balaclava, 15 April 1909, A. S. Wright; 1 female, same data but 1 May 1909. In collections of the American Museum of Natural History, Carnegie Museum, Snow Entomological Museum, British Museum (Natural History), J. A. Slater.

Variation.—The holotype male is fairly light in overall color. The darkest specimens examined are almost uniformly dark chocolate brown on head and body except for the pale areas on abdominal segments V and VI. On these darker specimens the light areas on clavus and corium are more distinct except the discal dorial spots and the light areas on the membrane except at the corial apex are obscured. The color pattern of legs and antennae remains constant except that the darker areas are more distinct and antennal segment II becomes pale reddish brown apically. The femoral spines range from 3-5 in the anterior rank and from 2 to 4 in the posterior rank. Three spines in each rank is most common. In only one case is a short spine located basal of the long basal spine of the posterior rank. In one case the posterior rank bears 2 about equally long basal spines. Total length varies from 8.0-9.0 mm in males and from 9.0-9.6 mm in female.

Etymology.—Named for Dr. Richard C. Froeschner, United States National Museum.

Identification: The combination of smooth head vertex and lack of elongate hairs on the "neck" separate *M. froeschneri* from all other members of the genus except the Cuban *M. fulvosa* Barber. That species is castaneous or fulvous in color, has unicolored fore femora, and typically has at least one small spine basal to the long subapical spine.

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DISTRIBUTION AND DISPERSAL OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE), AN EXOTIC *OPUNTIA*-FEEDING MOTH, IN FLORIDA

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ABSTRACT

The recent arrival of *Cactoblastis cactorum* Berg in Florida has raised concern for Florida's native *Opuntia* cacti. Moreover, the potential for movement of the moth across the gulf states and into the southwestern United States may endanger cacti in the *Opuntia*-rich areas of Texas, Arizona, New Mexico, and Mexico. However, the spread of the moth northward through Florida has either slowed since the invasion or the rate of spread for the first two years was over estimated. The mortality rate of pads and the distribution of egg sticks at six sites in Florida were recorded on *O. stricta* Haworth, the most common host in Florida. While the percentage of cactus pads with *C. cactorum* damage is as high as 60%, the data indicates that most mature cacti are not being reduced in size. However, small cacti and new growth pads are particularly susceptible to mortality by *C. cactorum*, thus, over time we may expect to see a reduction in the number of plants as a result of an increase in the mortality rate of recruits.

Key Words: pest, biological control, herbivory, moth, cactus

RESUMEN

La reciente introducción a la Florida de *Cactoblastis cactorum* Berg a causado preocupación en cuanto a los cactos indígenas de la Florida de la especie *Opuntia*. Además, la posibilidad de que la palomilla avance a través de los estados del Golfo hacia el suroeste de los Estados Unidos amenaza áreas con abundancia de *Opuntia* en Texas, Arizona, Nuevo México, y México. Sin embargo, la expansión de la palomilla hacia el norte a traves de Florida desde que la invasión empezó ha disminuido o el cálculo de la tasa de expansión durante los dos primeros años fué exagerado. La tasa de la mortalidad de las pencas de cacto y la distribución de grupos de huevos en seis localidades en Florida fueron registrados en *O. stricta* Haworth, que es el hospedero más común dentro de Florida. Aunque el porcentaje observado de pencas dañadas por *C. cactorum* es tan alto como el 60%, los datos indican que los cactos más maduros no están siendo reducidos en tamaño. Sin embargo, cactos pequeños y pencas nuevas son particularmente susceptibles a mortalidad causada por *C. cactorum*; en consecuencia, en un futuro podríamos contar con una reducción del número de plantas debido al aumento de la tasa de mortalidad de cactos jóvenes.

In 1957, the moth *Cactoblastis cactorum* Berg was introduced onto the Caribbean island of Nevis as a biological control agent for pest *Opuntia* spp. and in 1960 was introduced onto Montserrat and Antigua (Simmonds & Bennett, 1966). The moth dispersed to other islands such as Cuba, Puerto Rico, Hispaniola, the Bahamas, and Cuba (Habeck & Bennett, 1990).

A Florida Keys record for *C. cactorum* in October, 1989, was a new record for the continental United States (Habeck & Bennett, 1990). The moth likely arrived in Florida by one of two methods: (1) natural dispersal via flight/wind from the Caribbean or (2) via shipments of cacti to Miami from the Caribbean (Pemberton, 1995). This species may disperse beyond Florida, and eventually reach the *Opuntia*-rich desert southwest. The moth successfully dispersed several times from one island to another in the Caribbean; thus, spread across long distances is possible. The moth may have already invaded the Yucatan (Pemberton, 1995), thus, the moth also may disperse to the southwestern United States via Mexico.

Florida has six species of native *Opuntia* (*O. stricta* Haworth, *O. humifusa* (Rafinesque) Rafinesque, *O. spinosissima* (Martyn) Miller, *O. triacantha* (Willdenow) Sweet, *O. cubensis* Britton & Rose, and *O. pusilla* (Haworth) Haworth) (Benson, 1982). *Cactoblastis cactorum* has been found on all of the natives except *O. pusilla* (Bob Ehrig, The Nature Conservancy, pers. comm.; pers. obs.). The United States ranges of three of these cacti, *O. spinosissima*, *O. triacantha*, and *O. cubensis*, are limited to local populations in the Florida Keys. Only 12 *O. spinosissima* plants remain in one location in the Florida Keys and *O. triacantha* and *O. cubensis* are rare.

This study focuses on the attack of *C. cactorum* on *O. stricta*. *O. stricta* is a common cactus throughout coastal Florida, growing in sandy soils and shell mounds. We investigated the rate of the moth's spread throughout Florida, distribution of egg sticks and larval damage, and extent of damage to *O. stricta*. This information, coupled with the information from oviposition and larval choice experiments (Johnson & Stiling, 1996), could be useful in setting future management goals for *C. cactorum* in the continental United States.

Materials and Methods

Damage and Egg Stick Distribution

We repeatedly visited ten sites throughout south and central Florida (Fig. 1). Upon each visit to every site, we counted the total number of cactus pads on 20 to 100 *O. stricta* plants, the number of pads with old *C. cactorum* damage (those that had been fed upon but the larvae had since abandoned them), the number of pads with new larval damage (pads with larvae currently feeding on them), and the number of egg sticks per plant. The same population of plants was surveyed at every census. From October, 1991 to November, 1992, each site was sampled approximately monthly. The sites were sampled less frequently in 1993.

We are confident that the vast majority, if not all, of old damage, new damage, and egg sticks measured at the eight sites were attributable to *C. cactorum* and not the native cactus-feeding moth, *Melitera prodenialis* Walker, for the following reasons. First, at all sites where *C. cactorum* larvae were not detected, the percentage of pads with old damage was less than one percent, while within a year after *C. cactorum* larvae were detected, old damage increased to over ten percent. Secondly, cactus pads with new damage were randomly cut open and the larvae were identified. All Pyralidae larvae encountered at the sites were *C. cactorum*. Lastly, the widths of *C. cactorum* egg sticks are narrower than *M. prodenialis* egg sticks and the ranges of width are non-overlapping (DMJ, unpublished data). Three-hundred eighty-two hatched egg sticks were collected from the sites and compared to egg sticks known to be laid by *C. cactorum* and *M. prodenialis*. All of the egg sticks were determined to be laid by *C. cactorum*. Thus, while we can not be certain that *M. prodenialis* was always absent, we are confident that its contribution was insignificant.

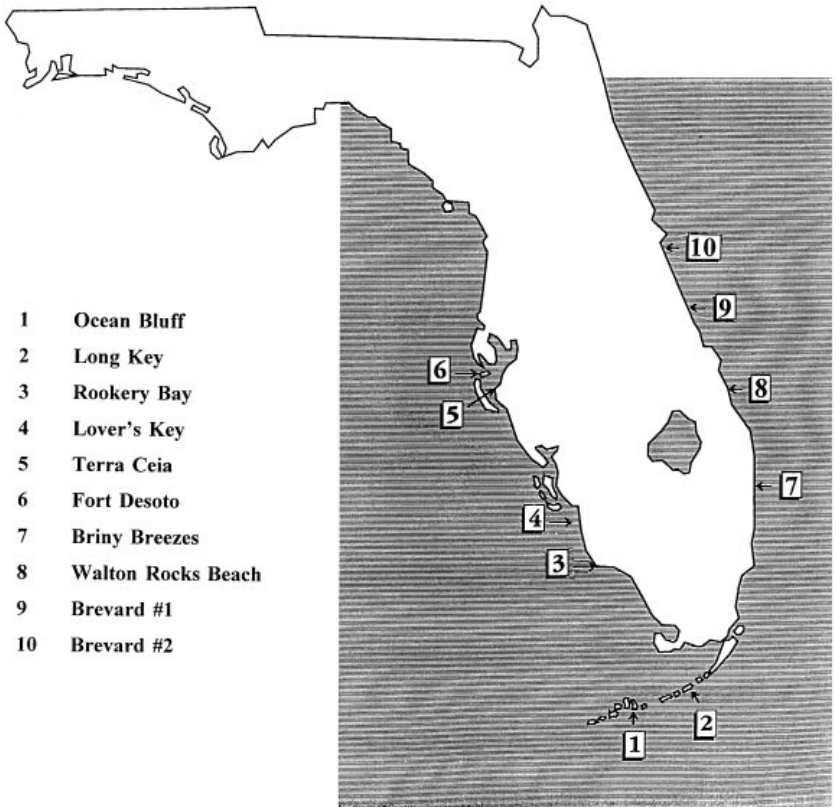

Fig. 1. *Opuntia stricta* populations surveyed for *Cactoblastis cactorum* from October 1991 to October 1993.

The distribution of egg sticks on cacti was measured by using the Morisita Index of Dispersion (Krebs, 1989). The Kruskal-Wallis test (Sokel & Rohlf 1981) was used to determine whether the number of egg sticks on a plant and the number of egg sticks per pad was related to plant size (as measured by the total number of pads). The Kruskal-Wallis test was also used to determine whether the percent damage was related to the size of the plant.

In addition, all reports of *C. cactorum* detected in new locations around Florida were examined to determine when the moth extended its known range northward along both the east and west coastlines. These reports included personal observations, reports to the Florida Department of Agriculture and Consumer Services (FDACS), and other sources.

Growth and Mortality of *Opuntia stricta*

From January to March 1992 all individual pads on 10 *O. stricta* plants at the Walton Rocks Beach site were marked. In 1993 10 additional plants were marked. Each pad was numbered using permanent ink. Upon every subsequent visit, once per

month in 1992 and less frequently in 1993, pad mortality and the number of new growth pads were recorded. These data were used to determine net growth of the attacked plants. The Rank Sum Test (Ambrose & Ambrose 1987) was used to determine whether smaller cacti had a significantly higher mortality. The Wilcoxon Signed Ranks Test (Sokel & Rohlf 1981) was used to determine whether new pads suffered a higher mortality caused by *C. cactorum* than did old pads.

RESULTS

Damage and Egg Stick Distribution

Peaks in new larval damage and percentage of pads with egg sticks varied temporally and spatially (Figs. 2 and 4). No *C. cactorum* was recorded at Lover's Key or Rookery Bay. Larval activity was generally highest from May to September, but larval activity also heightened in late fall and early winter of 1991 at most sites. Larval damage measurements, the percentage of pads with both old and new damage, increased at every site from the fall of 1991 to the fall of 1992. Overall, measurements of damage decreased slightly from the fall of 1992 to the fall of 1993 at all of the sites except Ocean Bluff, Terra Ceia and Brevard #2. Over the 2 year period, the percentage of dead or damaged pads increased (range 9-37%) at all 6 sites (Fig. 3). Percent damage and plant size were not significantly related ($p > 0.05$).

Egg sticks were clumped among plants (Table 1). At two of the six sites tested, significantly more egg sticks were laid on either medium or large-sized plants (Table 1). At the other four sites with a sufficient number of egg sticks the trend was present but not significant. The number of egg sticks per pad was not significantly different between small, medium, and large plants at any of the sites ($p > 0.10$) (Table 1).

At the peak of old *C. cactorum* damage, 90% of the plants with over 10 pads had old damage (Table 2). Excluding plants at the Terra Ceia site, which had a lower percentage of old damage than the other sites, 172 out of 173 plants (99.4%) with over 10 pads showed evidence of previous larval damage as compared to 14 of 28 plants (50%) with 10 pads or fewer having previous larval damage.

The Spread of *Cactoblastis cactorum*

The spread of *C. cactorum* up Florida's east coast, assuming that the moth first colonized the lower Florida Keys and migrated north, has been relatively well documented as compared to Florida's west coast. The moth was first discovered in the United States on Big Pine Key in October, 1989 (Habeck & Bennett, 1990). In less than a year, the moth was discovered at Key Biscayne State Park in Miami (FDACS, unpublished), approximately 200 km east northeast of Big Pine Key. One year later, in August, 1991, the moth was discovered at Brevard #1 (FDACS, unpublished), approximately 240 km north of Key Biscayne. The most northerly record of *C. cactorum* was at Brevard #2 (Patrick Air Force Base), 50 km north of Brevard #1 (pers. obs.). The moth arrived at this site in June 1992 and has established there.

The spread of *C. cactorum* up the west coast of Florida has not been so well documented. The first west coast record was in Terra Ceia, Manatee County, in May 1991 (FDACS, unpublished), one year and seven months after its discovery in the Florida Keys and approximately 360 km north. Six months later, the moth was discovered at Fort Desoto State Park in Pinellas County (pers. obs.), approximately 16 km north of Terra Ceia. The most northerly record of *C. cactorum* on the west coast of Florida was at Upper Tampa Bay Park in Hillsborough County, February, 1992 (pers. obs.). This site is approximately 50 km north of Fort Desoto.

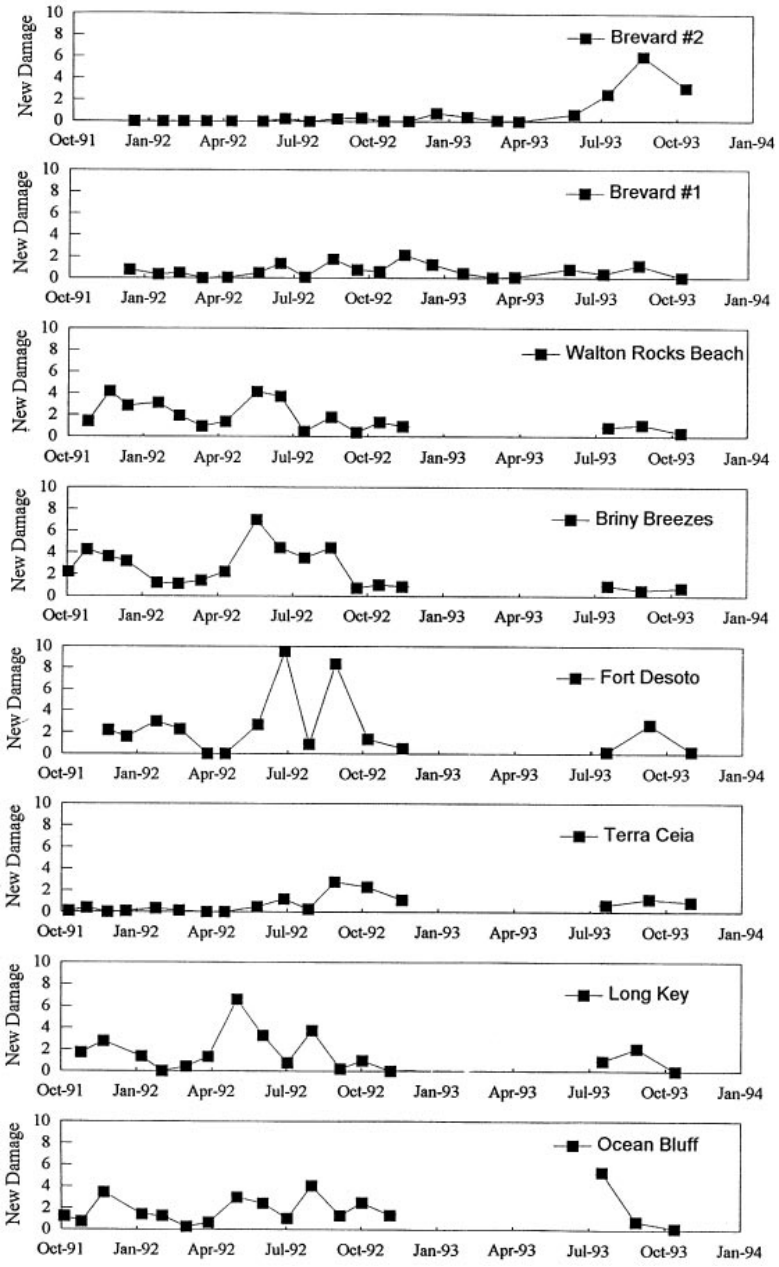

Fig. 2. Percentage of *Opuntia stricta* pads with new damage due to *Cactoblastis cactorum* larval feeding at eight sites in central and south Florida (see Fig. 1 for locations).

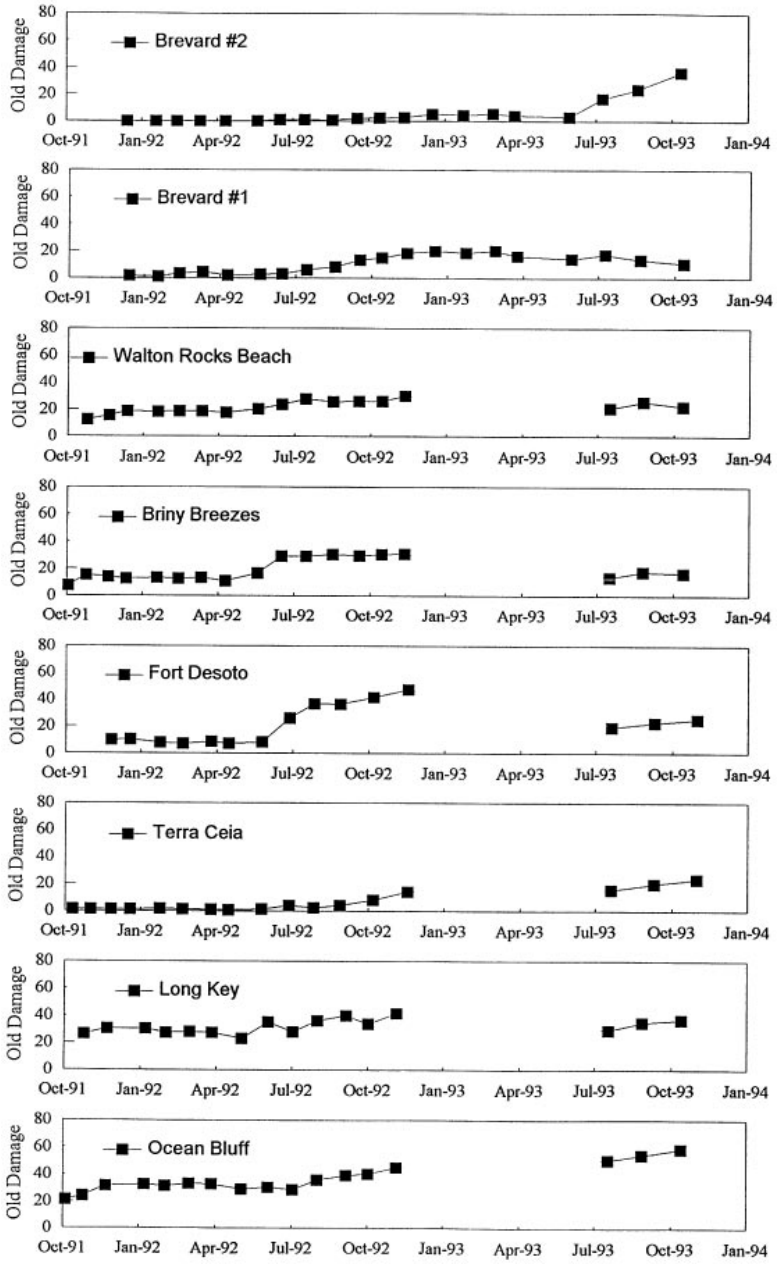

Fig. 3. Percentage of *Opuntia stricta* pads with old damage due to *Cactoblastis cactorum* larval feeding at eight sites in central and south Florida (see Fig. 1 for locations).

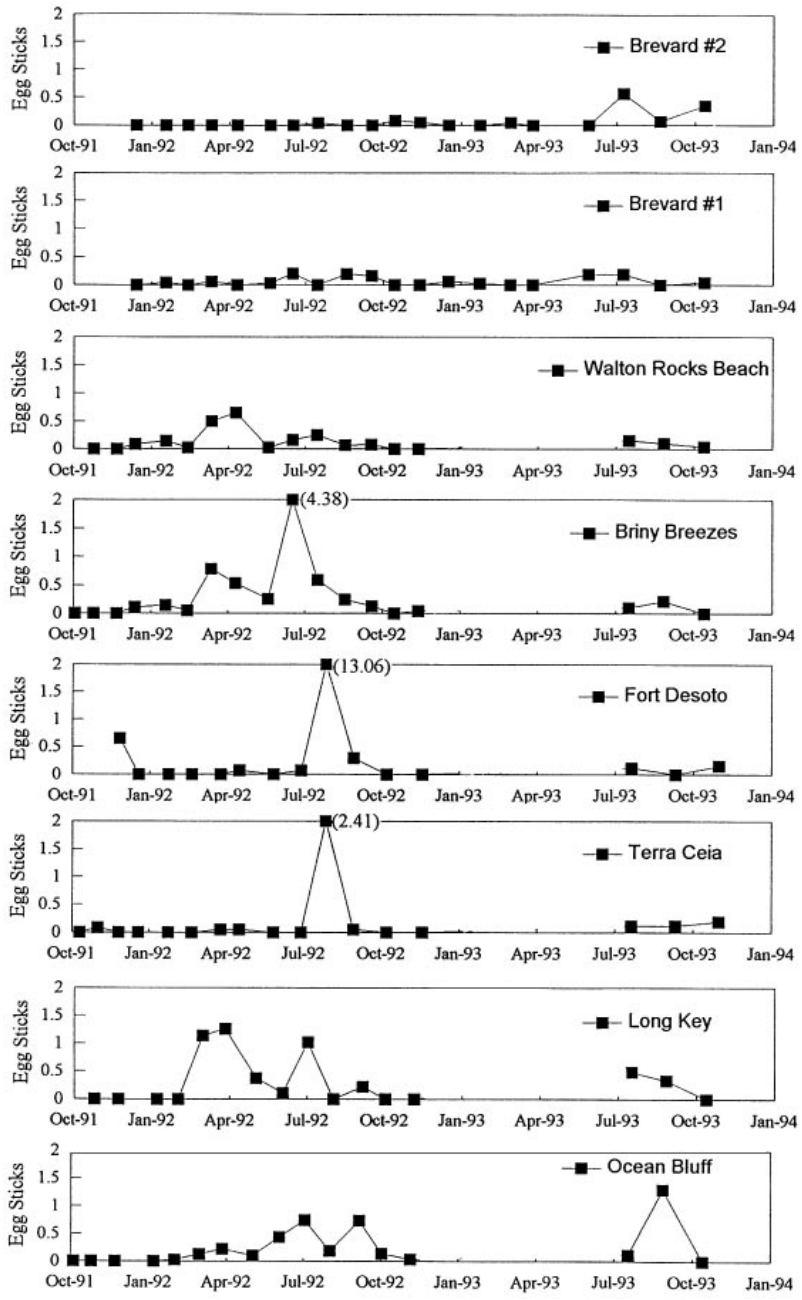

Fig. 4. Percentage of *Opuntia stricta* pads with *Cactoblastis cactorum* egg sticks at eight sites in central and south Florida (see Fig. 1 for locations).

TABLE 1. *CACTOBLASTIS CACTORUM* EGG STICK DISTRIBUTIONS ON SIX POPULATIONS OF *OPUNTIA STRICTA*.

Site	Egg Stick Distribution			
	Among Plants[a]	By Plant Size[b]	Plant Size Preferred	Egg Sticks per Pad by Plant Size[b]
Ocean Bluff	Clumped	N. S.	—	N. S.
Long Key	Clumped	Signif., $p < 0.05$	Medium	N. S.
Briny Breezes	Clumped	N. S.	—	N. S.
Walton Rocks Beach	Clumped	N. S.	—	N. S.
Terra Ceia	Clumped	Signif., $p < 0.01$	Large	N. S.
Fort DeSoto	Clumped	N. S.	—	N. S.

[a]Tested using the Morisita index of dispersion (significant at $p < 0.05$).
[b]Tested using the Kruskal-Wallis test (significant at $p < 0.05$).

There has been almost no confirmed records of inland movement of over a few of kilometers by *C. cactorum* in Florida. The discovery of the moth in Loxahatchee, Palm County in June of 1992 (FDACS, unpublished), 24 km inland from the Atlantic Ocean, is the most inland of confirmed records.

Growth and Mortality of *Opuntia stricta*

Growth in nine plants marked in 1992 ranged from a loss of 100% of the pads to an increase of 87%. One of the 10 plants marked in 1992 was not located until 1 year later. Some of the marks had worn off of the pads, so this plant was omitted from analysis. Two of the nine plants died from larval feeding during 1992. These were two of the three smallest marked plants (each having nine pads). The net growth of all of the plants in 1992 was +5%.

During the second year of monitoring, plant growth ranged from -100% to +56%. The net mean growth of all of the plants was +6%. The smallest of the original nine plants, having eight pads, was the only plant in this group to die (killed by *C. cactorum*) during 1993. Thus, over the two year period the three smallest plants died. Plants with nine or fewer pads had a higher mortality rate than plants with greater than nine pads (Rank Sum Test; $p < 0.05$).

The 10 plants that were marked and monitored in 1993 had a much higher growth rate. Only 1 of the 10 plants decreased in number of pads (-27%) and the highest growth rate was +170%. The mean net growth of the 10 plants was +86%. In 1992 and 1993 combined, new growth pads sustained a higher mortality rate due to larval damage than did old growth pads on 22 out of 25 plants (Wilcoxon Signed Ranks Test; $n = 25$, $p < 0.05$) (Fig. 5).

DISCUSSION

Cactoblastis cactorum in Florida is more active in the spring and summer. The distribution and spread of the moth largely has been restricted to the coastal regions of south and central Florida. The lack of inland reports of the moth may be because *O.*

TABLE 2. RELATIONSHIP BETWEEN THE SIZE OF *OPUNTIA STRICTA* AND DAMAGE BY *CACTOBLASTIS CACTORUM*.

Site	Damage	Size of plant	
		0-10 pads	11-more pads
Ocean Bluff	Present	3	39
	Absent	1	0
Long Key	Present	2	18
	Absent	6	0
Briny Breezes	Present	2	24
	Absent	4	0
Walton Rocks Beach	Present	6	61
	Absent	2	1
Terra Ceia	Present	6	42
	Absent	30	22
Fort Desoto	Present	1	33
	Absent	1	0
Total	Present	20	217
	Absent	44	23
Percentage of plants with damaged pads		31%	90%

stricta is more common in coastal areas (Benson 1982) or because of other biotic and abiotic factors. Future work should address why *C. cactorum*'s distribution is mainly coastal so we can determine whether it will, in time, invade inland populations of *Opuntia*.

Previous studies in Australia and South Africa found that the females lay their egg sticks in a clumped distribution based on plant size, plant color, and shelter from the wind (Myers et al., 1981; Robertson, 1987). Similarly, egg sticks were clumped at all of our sites and more were laid on medium or large-sized plants at two of the sites. There was no difference, however, in the number of egg sticks per pad among plants of different sizes. Thus, pads on large plants are no more likely to have egg sticks laid on them than pads on small plants. This is consistent with our finding that there is no relationship between *C. cactorum* damage and plant size.

The moth is doing significant damage to *O. stricta* individuals in Florida, but is the moth reducing the populations? Overall, the number of pads on marked individual cacti at Walton Rocks Beach increased in 1992 and 1993. However, while fewer small plants received moth damage than did medium or large-sized plants, small cacti with moth damage were most susceptible to mortality. Thus, *C. cactorum* could strongly reduce the survivorship of maturing *O. stricta*. We may reach a scenario in Florida whereby large *O. stricta* can withstand the attack, but, in the ensuing years, as these plants die, there are fewer individuals to replace them. Only then would the total adverse effect of *C. cactorum* become noticeable. Forecasting such a process necessitates a more detailed study in which recruitment as well as the fates of the plants are measured. Also, *O. stricta* populations in Australia partially recovered a few years after

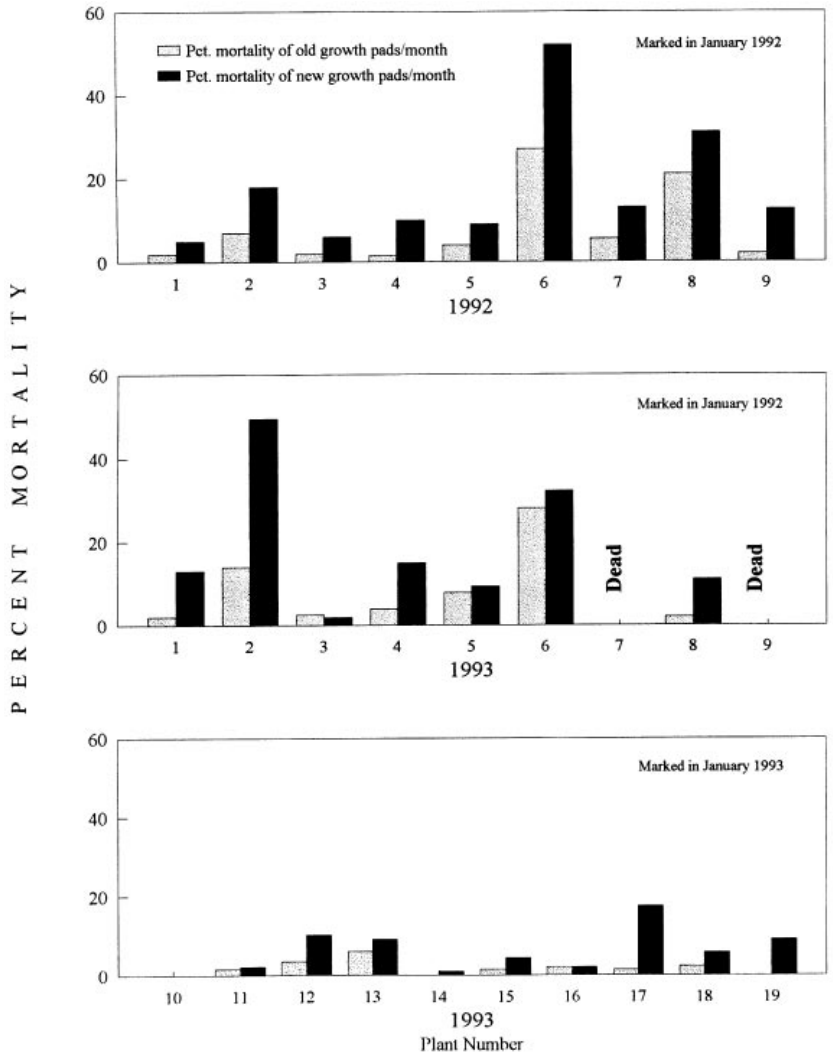

Fig. 5. Percent mortality of old growth vs. new growth pads on marked *Opuntia stricta* in 1992 and 1993.

the introduction of *C. cactorum*, only to be decimated greater within the next few years (Dodd 1940).

Soon after *C. cactorum* was discovered in Florida, its rapid invasion northward prompted concern not only for native Florida cacti but for those native to the rest of the North American continent (especially the *Opuntia*-rich desert southwest). The movement of the moth northward through Florida from 1989 to 1991, assuming it dispersed from the lower Florida Keys, averaged over 160 miles per year. From 1991 to

1993, however, the spread averaged only 24 miles per year. Recent information (Pemberton, 1995) indicates that *C. cactorum* may have invaded Florida via imported cacti through Miami rather than natural dispersal, in which case the dispersal rate reported for 1989 to 1991 is an over estimate. Determining the true rate of spread of *C. cactorum* and which biotic and/or abiotic factors affect this rate, would be valuable because then we could determine if and when the moth may be expected to attack *Opuntia* in other regions of North America (barring accidental introduction on imported cacti).

ACKNOWLEDGEMENTS

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EFFECT OF MALE MESADENE SECRETIONS ON FEMALES OF *CANTHON CYANELLUS CYANELLUS* (COLEOPTERA: SCARABAEIDAE)

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ABSTRACT

This study determined the effect of male mesadene secretions on females of *Canthon cyanellus cyanellus* LECONTE, both when they were inseminated normally and when the secretions were transplanted to virgin females. In the first case, mating took place when the ovary was immature, triggering ovarian maturation, egg laying and nest building. In the second case, the transplantation of male mesadene secretions to virgin females initiated ovarian maturation, but neither egg laying nor nest building took place. Virgin females that did not receive the secretions had no ovarian maturation and did not lay eggs or build nests. It is therefore possible that male mesadene secretions induce ovarian maturation. In the present study, this inducement was greater in inseminated females than in those receiving transplanted secretions.

Key Words: Mesadene secretions, Transplant, Ovarian maturation, Scarabaeinae

RESUMEN

En este trabajo se determinó el efecto que tienen las secreciones de las mesadenias del macho sobre las hembras de *Canthon cyanellus cyanellus*, cuando son inseminadas normalmente, o cuando las secreciones son trasplantadas a hembras vírgenes. En el primer caso la cópula tuvo lugar cuando el ovario estaba inmaduro, desencadenando la maduración ovárica, la oviposición y la construcción del nido. En el segundo caso, el trasplante de las secreciones de las mesadenias a hembras vírgenes inició la maduración ovárica, pero no la oviposición ni la construcción del nido. Las hembras vírgenes que no recibieron las secreciones no maduraron el ovario ni hubo oviposición o construcción del nido. Es posible que las secreciones mesadénicas del macho induzcan la maduración ovárica. Esta inducción fue mayor en las hembras inseminadas que en las que recibieron el trasplante de las secreciones.

In various species of Scarabaeinae (Scarabaeidae), mating takes place shortly after the female emerges (Monteith & Storey 1981; Klemperer 1982) or before egg laying (Halffter & López 1977; Halffter et al. 1980; Huerta et al. 1981; Monteith & Storey 1981; Anduaga & Huerta 1983; Sato & Hiramatsu 1993). In the above-mentioned cases, mating is necessary for egg laying and nesting to begin.

In the dung beetles, *Canthon indigaceus chevrolati* HAROLD and *Copris incertus* SAY, the first mating, which occurs during the pre-nesting period, when the ovary is still immature, is indispensable for ovarian maturation, egg laying and nesting to occur (Martínez & Cruz 1990; Martínez et al. 1996).

In *Canthon cyanellus cyanellus* LECONTE, the first mating is at 10 days after female emergence. This occurs half way through the pre-nesting period, which lasts about 20 days. During this period ovarian maturation occurs, only food balls are pro-

duced and there is no nesting. Afterwards, during the nesting period, other matings may occur (Martínez 1992).

During mating, the male of *C. c. cyanellus* produces a spermatophore containing abundant seminal fluid which consists principally of the secretions of the accessory glands (mesadenes). Most of this seminal fluid has a high concentration of proteins, although it also contains glycogen and acid mucopolysaccharides (Cruz & Martínez 1992). This is also the case in other Coleoptera (Anderson 1950; Landa 1960; Gerber, et al. 1971; Gundevia & Ramamurty 1977; Huignard et al. 1977; Peferoen & de Loof 1983; Black & Happ 1985).

The objective of this study was to determine the effect of male mesadene secretions in *C. c. cyanellus* upon ovarian maturation and female reproductive behavior.

MATERIALS AND METHODS

This study was carried out on adult *Canthon cyanellus cyanellus*, of known age and raised in the laboratory. Insects were kept at 27°C, 70% RH, a photoperiod of 14:10 hours and were fed beef.

Females were tested in one of four manners: 1) a female was kept together with a male from the time of emergence (n = 63), 2) virgin females were isolated from the time of emergence (n = 57), 3) virgin females received transplants of mesadene secretions from mature males at 10 days old (n = 31), and 4) virgin females had sterile Ringer-Ephrussi solution injected at 10 days old (n = 25).

The females in categories 1 and 2 were sacrificed at 5, 10, 15, 20, and 25 days of age, with approximately 10 females per age group. At 10 days of age the females in categories 3 and 4 received the secretion transplant or the injection of Ringer solution. It was allowed to take effect for 5, 10 or 15 days. The females in these last two categories were sacrificed at 15, 20 and 25 days of age. The were about 5 females in these age groups.

To carry out mesadene transplantation, the reservoir, a structure in which glandular secretions are stored, was obtained from 20-30 day-old males. Females were anaesthetized with ethyl acetate for 3 minutes, which allowed them to recover without complications. The elytra and wings of anaesthetized females were lifted carefully, and the reservoir was placed in the dorsal region of the abdomen. Using an entomological pin, a dorsal puncture was made through which glandular secretions were introduced into the abdominal cavity. It was not necessary to use sealer, as the wound healed quickly on its own. Females recovered in about 5-10 minutes. After a 24-hours period they were put inside a terrarium (Cruz 1994).

The reproductive systems from all four groups were dissected out in Ringer-Ephrussi solution. Each ovary was measured and drawn to scale with the aid of a camera lucida. The ovary and vaginal frotis together with the spermatheca from each female were obtained and dyed *in toto* using the Feulgen-green light technique. The presence of the spermatophore in the vagina or of spermatozoids in the spermatheca indicated that the female had been inseminated.

The length of the basal oocyte was analyzed in each age group and the different categories were compared. Sample sizes were 5 to 17 females per age group. Since these were small samples, a 95% confidence interval was calculated using the formula $\bar{x} \pm \alpha_{n-1}/\sqrt{n}$ (1.96), where $\bar{x}$ is the sampling median and α_{n-1} is the standard deviation. Analysis of variance (ANOVA) was used to compare means.

Female reproductive behavior was categorized according to the following factors: if they were inseminated, if they laid eggs, and either made food or nest balls.

RESULTS

The female reproductive system in *C. cyanellus cyanellus* is similar to that of other Scarabaeinae: it consists of a single left ovary with one ovariole, an oviduct, vagina and spermatheca with its accessory gland.

Females with Males

In these females, the first basal oocyte measured 0.7 mm 5 days after eclosion. By the 10th day it had more than doubled in size to 1.5 mm. By the 15th day it had again doubled in size. After 20 days, it was almost egg-laying size, which in this species is 3 mm (Fig. 1; Table 1). Females in this group copulated between 10 and 15 days of age. Spermatozoids were observed in the spermatheca, and the spermatophore was in the vagina. By 15 days after eclosion, all of the females dissected had been inseminated but had not yet begun to nest. By 20 days, most of the females had already laid a first egg, and the second basal oocyte was close to egg-laying size. At the age of 25 days, all females were making their first nest with 1 to 7 nest balls, corresponding at 1 to 7 eggs laid.

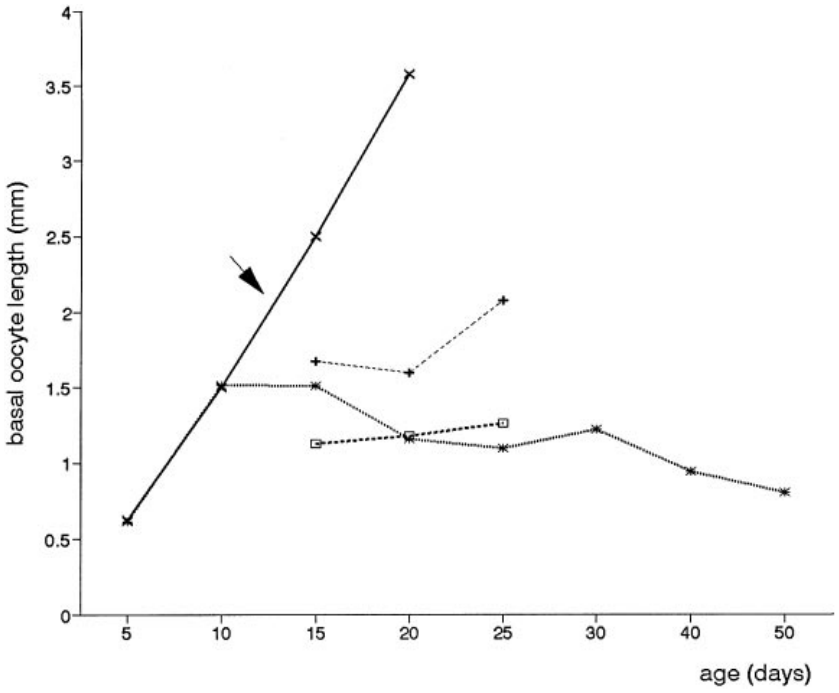

Fig. 1. First basal oocyte development in *Canthon cyanellus cyanellus* females. (X) Females with male since emergence, the arrow shows the age at which first copula occurs; (✻)Virgin females; (+) Virgin females with transplant from 10 days of age on; (□) Virgin females injected with Ringer's solution.

TABLE 1. BASAL OOCYTE MATURATION IN FEMALES OF *CANTHON CYANELLUS CYANELLUS* KEPT WITH A MALE SINCE EMERGENCE (F-M), VIRGIN FEMALES (VF), VIRGIN FEMALES WITH TRANSPLANT (VF-T) AND VIRGIN FEMALES INJECTED WITH RINGER'S SOLUTION (VF-R). ($\bar{x}$ ± SE)(N) NUMBER OF FEMALES PER AGE.

Age (days)	Basal oocyte length (mm)			
	F-M	VF	VF-T	VF-R
5	0.72 ± 0.10(10)	0.61 ± 0.17(11)	—	—
10	1.50 ± 0.12(14)	1.52 ± 0.15(12)	—	—
	mating			
15	2.50 ± 0.15(17)	1.51 ± 0.09(12)	1.68 ± 0.15(10)	1.13 ± 0.17(10)
20	3.58 ± 0.10(10)	1.16 ± 0.10(10)	1.60 ± 0.13(10)	1.18 ± 0.08(10)
25	2.65 ± 0.21(12)	1.10 ± 0.10(12)	2.08 ± 0.17(11)	1.26 ± 0.31(5)

Virgin Females

Until the 10th day, the development of the first basal oocyte in these females was similar to that of females of the same age that had been kept with males. On the 15th day, the size of the basal oocyte remained almost identical to that observed at 10 days. From day 20 to 25, however, it gradually diminished in size, and was reabsorbed in females more than 50 days old (Fig. 1: Table 1).

The ovaries of virgin females did not fully mature, and the oocytes entered into reabsorption. Virgin females only made food balls, and did not construct nest balls or nest.

Virgin Females with Male Mesadene Secretion Transplant

The transplant of secretions was performed at 10 days of age due to our observation that the first mating tends to occur around this age. At day 15 the first basal oocyte measured an average approximately 1.6 mm; this size did not change by 20 days of age. However, at 25 days of age, the first basal oocyte became substantially larger (Fig. 1; Table 1). All females in this group initiated first basal oocyte maturation, but oocytes did not reach egg-laying size even at 25 days.

Although they initiated ovary maturation, these females did not lay eggs, make nest balls or nest; their only activity was the production of food balls.

Virgin Females Injected with Ringer's Solution

In these females, first basal oocyte size did not noticeably increase (Fig. 1; Table 1); furthermore, neither egg laying, ovary maturation or nest making took place. Activity was limited to making food balls which they did not turn into nest balls.

DISCUSSION

In *Canthon cyanellus cyanellus* the development of the first basal oocyte in virgins was compared with those of females kept together with the male since the time of emergence. After 15 days, the size of the first basal oocyte was no longer comparable

between the two groups ($F_{(1,27)}$: 26.8; $p < 0.01$). In females which were inseminated by a male, the ovary was bigger than in individuals kept alone. This difference was greatest at 20 days of age ($F_{(1,19)}$: 210; $p < 0.01$) even compared to 25-day-old females ($F_{(1,22)}$: 41.8; $p < 0.01$).

These results demonstrate that the first mating triggers the final maturation of the basal oocyte and the ovary, and, in some yet unknown way, induces egg laying and nesting. This has also been demonstrated to be true in *Canthon indigaceus chevrolati* and *Copris incertus*. In these two beetles, virgin females neither finish ovary maturation, lay eggs, nor make nests (Martínez & Cruz 1990; Martínez et al. 1996).

A comparison of the size of the first basal oocyte in females which were inseminated and in those which received male mesadene transplant showed marked differences from the age of 15 days ($F_{(1,25)}$: 14.0; $p < 0.01$) until 20 days ($F_{(1,18)}$:136; $p < 0.01$), but differences were non significant at 25 days ($F_{(1,21)}$: 4.1); the effects of mating and glandular secretions are, therefore, not comparable. The slow increase in basal oocyte size in females that received the transplant suggests that egg laying size could be reached at a more advanced age, although this was never confirmed through observation.

When virgin females were compared with those that received the transplant of male mesadene secretions, it became clear that the secretions do have a positive effect on ovarian maturation. After 20 days of age, the basal oocyte size was larger in the females receiving the transplant than in virgins ($F_{(1,18)}$: 6.4; $p < 0.05$). The greatest difference was observed during the period between 20 and 25 days of age ($F_{(1,21)}$: 24.6; $p < 0.01$): the ovary continued to mature up to an advanced stage, but oviposition did not take place during the period of observation. In females over 30 days old, basal oocyte size diminished in unaltered virgins but not in those that had received the secretion transplant.

An analysis of females with the transplant compared to those with Ringer's solution injections at various ages yielded the following data: the only significant difference observed was between treatments ($F_{(1,4)}$: 14.4; $p < 0.05$) regardless of age ($F_{(4,50)}$: 1.4; non significant). Virgin females which received male mesadene transplants had greater oocyte size than virgin females injected only with Ringer's solution.

When *C. c. cyanellus* virgin females received the transplant of male mesadene secretions, the ovary matured up to an advanced stage, but oviposition never took place. Females can receive the stimulus that induces ovarian maturation either during copulation or through the transplant of secretions. We do not yet know which of the components in these secretions act directly upon the ovary to induce vitellogenesis and ovary maturation, but the abundance of certain proteins may indicate that they are responsible.

In the weevil *Acanthoscelides obtectus* SAY (Huignard 1984) and in the mosquito *Aedes taeniorhyncus* (WIEDEMANN) (Borovsky 1985), vitellogenesis is induced by proteins called paragonial substances found in secretions of the male glands. In *A. obtectus* these substances are distributed through the haemolymph to the female's head, thorax and abdomen soon after mating and induce ovarian maturation (Huignard 1978). In other species of flies, and a grasshopper in which virgin females received secretions or male accessory gland extracts, ovarian maturation and egg laying resulted (Merle 1968; Leahy 1973; Burnet et al. 1973; Ramalingan & Craig 1976). Egg laying in various species of Orthoptera is also controlled by the paragonial substances (Pickford et al. 1969; Leahy 1973; Friedel & Gillott 1976) and in one butterfly (Santhosh-Babu & Prabhu 1987). In various species of Diptera, these substances control not only oviposition but the sexual receptiveness of females after mating (Burnet et al. 1973; Baumann 1974; Ramalingan & Craig 1976; Young & Downe 1987; Ohashi et al. 1991; Spencer et al. 1992).

In various species of insects, after lysis of the spermatophore into the vagina, the spermatozoids and part of the seminal fluid pass into the spermatheca. The remainder of the seminal fluid enters the haemolymph, where it subsequently reaches target sites directly or via a hormone that controls reproductive output (Raabe 1986).

Although it has been confirmed that the first mating is necessary for ovarian maturation and egg laying in *Canthon indigaceus chevrolati*, *Copris incertus* and *Canthon c. cyanellus*, only in *C. c. cyanellus* has it been show that the male mesadene secretions induce ovarian maturation and egg laying. However, in the dung beetle genus *Sisyphus* LATREILLE, virgin females sometimes make a few brood balls that contain infertile eggs or no eggs at all (Paschalidis 1974), suggesting that in this group the male mesadene secretions is not necessary to induce ovarian maturation and egg laying.

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NATURAL PARASITISM OF *PHYLLOCNISTIS CITRELLA* (LEPIDOPTERA:GRACILLARIIDAE) AT CUITLAHUAC, VERACRUZ, MEXICO

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ABSTRACT

The Citrus Leafminer *Phyllocnistis citrella* (CLM) was reported from Mexico for first time in September 1994. This insect spread rapidly over the main citrus-growing areas and it became a serious threat to the citrus industry in Mexico. The options for controlling this pest include chemical control and natural biological control. The objective of this investigation is to identify the parasitoids associated with the CLM and the variation in their populations in Persian lime, *Citrus aurantifolia cv.* 'Tahiti', at Cuitlahuac, Veracruz, Mexico. The species found are: *Cirrospilus* sp. n.1, *Cirruspilus* sp. n.2, *Horismenus* sp., *Galeopsomyia* sp. and *Elasmus tischeriae.* From November to March of 1995-96, parasitism of the CLM was more than 70% and the most abundant parasitic species were *Galeopsomyia* sp. and *Cirrospilus* sp. n.1 and sp. n. 2.

Key Words: *Phyllocnistis citrella, Citrus aurantifolia,* parasitoids, citrus

RESUMEN

El minador de la hoja de los cítricos *Phyllocnistis citrella* (MHC) se registró por primera vez en México en septiembre de 1994. El insecto se extendió rápidamente por las principales áreas citrícolas y se ha convertido en una seria amenaza para la citricultura mexicana. Las tendencias para el control de la plaga señalan el uso del control químico y el control biológico natural. A este respecto, el objetivo del presente trabajo es conocer los parasitoides asociados con el MHC y su fluctuación poblacional en limón Persa, *Citrus aurantifolia cv.* 'Tahiti', en Cuitláhuac, Veracruz. Las especies encontradas son: *Cirrospilus* sp. n.1, *Cirrospilus* sp. n. 2, *Horismenus* sp., *Galeopsomyia* sp. y *Elasmus tischeriae.* Durante los meses de noviembre a marzo de 1995-96 se observó

un parasitismo de MHC mayor del 70%, y las especies más abundantes fueron: *Galeopsomyia* sp. y *Cirrospilus* sp. n.1 y sp. n.2.

The Citrus Leafminer (CLM) *Phyllocnistis citrella* Stainton (Lepidoptera:Gracillariidae) was found first in 1993 in Florida USA, (Heppner 1993) and in September 1994 in Tamaulipas and Veracruz, Mexico (Ruíz and Coronado 1994) from these points of introduction, it spread rapidly through the main citrus-producing areas of Mexico. At the present time it is difficult to locate an area free of this pest, which now threatens citrus production in Mexico. In the southern part of Veracruz State, where Cuitlahuac is located, the problem is especially serious because Persian lime, *Citrus aurantifolia* (Christm.) Sweet *cv.* 'Tahiti', is severely damaged by this insect. Other insect species such as the mealybug *Planococus citri* and snow scale *Unaspis citri* also contribute to the pest problems in the area.

The CLM has its origin in South Asia, where it was observed in Calcuta, India, for the first time in 1865 (Sponagel and Diaz 1994). In this century the pest has spread to many countries through shipments of plant materials and by migration. This insect damages the young tender leaves of all species of the genus *Citrus*. In addition, Clausen (1931) reported that the pest also damages *Aeple marmelos*, *Murraga koenigii* and *Jasminium sombae*, and Quayle (1941) mentioned that CLM feeds on species of *Loranthus*. CLM reduces possibly the photosynthetically active leaf area of its host both by destroying mesophyll cells and by rolling the leaves during pupation. The pest is most destructive in young plantations, where it may cause total defoliation if it is not controlled. Furthermore, as Guerout (1994) pointed out, the mine built by insect favors the development of citrus canker, *Xanthomonas citri*, and other fungus pathogens such as *Alternaria*.

At present, CLM control practices consist of the application of chemical products as well as natural biological control. Classical biological control is another option, using the non-native parasitoid *Ageniaspis citricola* (Hymenoptera:Encyrtidae), which has reduced significantly damage by the CLM in Australia (Knapp et al. 1995).

In Mexico, various species of native parasitoids, principally members of the family Eulophidae, have been reported (Table 1). Most of these are ectoparasites and attack not only lepidopteran leafminers, but also those belonging to other orders.

The main objective of this work is to identify the species of parasitoids associated with the CLM at Cuitlahuac and to learn about their effectiveness in controlling the pest at this location.

Materials and Methods

Field work was conducted from August, 1995, to September, 1996, at Cuitlahuac, Veracruz (Fig. 1). This area is located at 18°50' North latitude, 96°55' West longitude and is 420 meters above sea level. Total precipitation in 1995 was 2, 200 mm, with a temperature that varied from 12°C to 36°C. The rainy season is from June to November (Fig. 2) (Bautista et al. 1996).

The collections were made mainly from Persian lime but some were made from sweet orange (*Citrus sinensis* (L.) Osbeck) and tangerine (*C. reticulata* Blanco). Every week 10 flushes less than eight centimeters long, in five different trees (50 flushes in total) were examined to determine the level of infestation by CLM. Parasitism of the CLM was detected by collecting a total of 1609 infested leaves located at or below the

TABLE 1. PARASITOID SPECIES ASSOCIATED WITH THE CLM IN MEXICO (RUIZ & MATEOS 1996, MARTÍNEZ & RUIZ 1996, PERALES ET AL. 1996).

Taxon	Locality
Cirrospilus quadristriatus	Tecoman, Colima.
Cirruspilus sp	Tecoman, Colima. northern Veracruz central Tamaulipas
Closterocerus sp	Tecoman, Colima.
	Tecoman, Colima. northern Veracruz central Tamaulipas
Horismenus sp	Tecoman, Colima. northern Veracruz central Tamaulipas
Pnigalio sp	central Tamaulipas
Tetrastichus sp	Tecoman, Colima. northern Veracruz
Zagrammosoma sp	Tecoman, Colima. central Tamaulipas

middle of flushes 20 cm length. These leaves were placed in paper bags and taken immediately to the laboratory where the relative humidity was between 65 to 75% and the temperature varied between 18 and 25°C. The leaves were placed in Petri dishes, three per dish, with their petioles wrapped in moist cotton, and observed daily until emergence of the adult CLM or its parasitoids. It was necessary to control the humid-

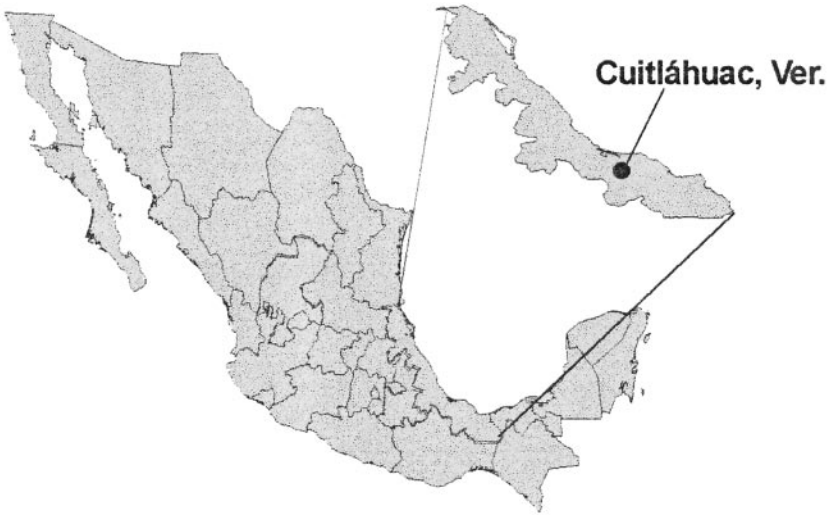

Fig. 1. Location of the area of study of the CLM.

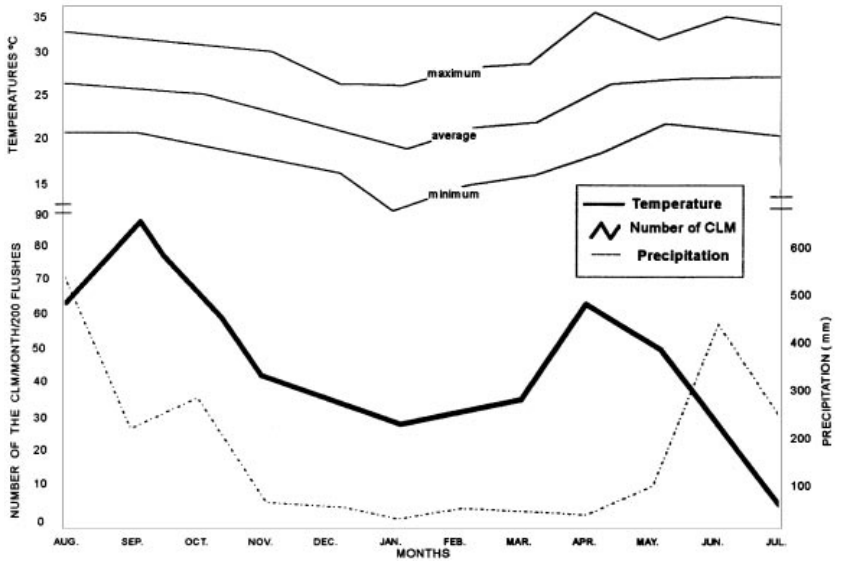

Fig. 2. Variation in temperature, precipitation and the number of citrus leafminers between August, 1995, and July, 1996, at Cuitlahuac, Veracruz.

ity because dehydration of the leaves or contamination by saprophytic fungi due to excess humidity can affect the emergence of the insects. Some of the wasps that emerged were placed in 70% alcohol and others were dehydrated with a critical point drier and pinned for identification. Another procedure that was used to collect parasitoids consisted of selecting infested leaves and enclosing them is small bags of organdy, without removing them from the tree. They were examined every day until emergence of the adult insects. A total of 312 leaves from 39 flushes were treated this way.

The parasitoids were identified using the keys of Schauff and LaSalle (1996). In addition, the eulophids were sent to the Centro Nacional deReferencia de Control Biológico in Tecomán, Colima, Mexico and to Dr. John LaSalle, at the International Institute of Entomology, in London, England, for confirmation. To confirm the determinations of the elasmids, specimens were sent to Dr. Lonny D. Coote, at the Royal Ontario Museum, in Canada.

Results and Discussion

The highest population levels of the CLM were observed in September, October, April and May while the lowest incidence occurred in the months of January and July (Fig. 2). Incidence of the CLM was not closely related to the development of new flushes. In January and July most of these flushes were free from the pest (Table 2). In addition a high level of parasitism, above 70%, was observed from November to March. In June and July a high percentage of parasitism was observed on the few leafminers collected (Fig. 2).

Five species of parasitoids in the superfamily Chalcidoidea (Table 3) were reared from the 1609 infested leaves that were taken to the laboratory for this purpose. The first four species belong to the family Eulophidae (Hymenoptera). *Cirrospilus* 1 and 2

TABLE 2. VARIATION IN THE INCIDENCE OF THE CLM AND ITS PARASITOIDS AT CUITLAHUAC, VERACRUZ IN 1995-96.

Month	Leaves examined	CLM larvae and/or pupae found	CLM larvae and/or pupae parasitized	Percent parasitized
Aug.	225	207	68	32.8
Sep.	291	301	148	49.1
Oct.	229	158	92	58.2
Nov.	191	148	107	72.2
Dec.	95	18	15	83.3
Jan.	63	7	6	85.7
Feb.	94	11	9	81.8
Mar.	111	31	22	70.9
Apr.	201	104	71	68.2
May.	109	62	29	46.7
Jun.	67	12	9	75
Jul.	45	4	4	100

and *Galeopsomyia* sp yet have not been described. The neotropical genus *Horismenus* is very difficult taxonomically, so it is not possible to be sure if the species collected is undescribed or not (LaSalle 1997, personal communication). *Elasmus tischeriae* is in the family Elasmidae, species of which generally attack species in the orders Diptera and Coleoptera.

In the months of August and September the parasitoids population on the CLM were reduced considerably, possibly because they were attacking other species of leafminers.

Cirrospilus

LaSalle (1996) reported fifteen species of *Cirrospilus* associated with the CLM, including the undescribed species collected in this study. The same author states that

TABLE 3. PARASITOIDS OF THE CLM AND THEIR RELATIVE IMPORTANCE AT CUITLAHUAC, VERACRUZ.

Species	Percent parasitized	Biological phase attacked[1]
Cirrospilus sp 1	22.6	Larvae III (2) and prepupae(7)
Cirrospilus sp 2	25.1	Larvae III(2), prepupae(1) and pupae(9)
Horismenus sp	19.3	Prepupae(1) and pupae(13)
Galeopsomyia sp	27.6	Larvae II(1), III(1), prepupae(4) and pupae(7)
Elasmus tischeriae	5.4	Larvae II(2), III(1) and pupae(2)

[1]() number of individuals observed.

this is a cosmopolitan and polyphagous genus although it prefers to parasitize insects in the family Gracillaridae. Sometimes the members of *Cirrospilus* act as hyperparasitoids (LaSalle 1996), even though this the species collected at Cuitlahuac, Veracruz were not observed doing this. The two *Cirrospilus* species found at Cuitlahuac are ectoparasitic, the pupae remaining in the mines of the host.

Galeopsomyia

The collection at Cuitlahuac is the first record of the genus for Mexico (Bautista et al. 1996). This species, which is being described by LaSalle, is ectoparasitic on the CLM in the larval phases II and III and prepupae. In one case it was observed as a facultative solitary hyperparasitoid. The highest incidence of this species was observed in October and November. According to LaSalle (1994), the species of this genus generally attack Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera).

Horismenus

This ectoparasitoid of the CLM, can be confused with *Galeopsomyia*. LaSalle (1996) reported two species of *Horismenus* associated with the CLM which have not yet been described. It is very common to find species of this genus acting as hyperparasitoids (Coffelt and Sehultz 1993).

Elasmus

Of the five species of parasitoids associated with the CLM, *E. tischeriae* Howard was the least abundant at Cuitlahuac; only about 5% of the parasitoid individuals were of this species. LaSalle (1994) reports three species attacking the CLM, *E. tischeriae, E. zenhtneri* and an undescribed species. To date, *E. tischeriae* is the only one that has been found in Mexico. Some authors place this species in the family Eulophidae instead of the monotypic Elasmidae. It is the capable of parasitizing lepidopteran borers, but it also has been frequently found parasitizing species of *Polistes* (Hymenoptera: Vespidae) (Borror *et al.* 1989). In the study area this species was observed in the months of August and September.

Other predators

Several other predatory arthropods associated with the CLM were observed at Cuitlahuac. These include syrphid flies, common lacewings, spiders (Table 4) and the ant species, *Crematogaster aff-brevispinosa* and *Conomyrma bicolor* (Hymenoptera:Formicidae).

TABLE 4. SPIDER SPECIES ASSOCIATED WITH CLM, AT CUITLAHUAC, VERACRUZ.

Family	Species
Araneidae	*Araneus* sp
	Leucauge argyra Walckanaer
	Argiope argentata Fabricius
Salticidae	*Habronatus* sp
Theridiidae	*Thymoites unimaculatum*

CONCLUSIONS

The highest population levels of the citrus leafminer occurred in September and October, then in April and at the beginning of May. The lowest incidence of the pest was observed in January and July. The parasitoid species with the highest percentage; of parasitism were *Cirrospilus* and the *Galeopsomyia*. In the period from November to March, the level of parasitism was very high, about 70%.

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A REVIEW OF THE LITERATURE ON *TOXOPTERA CITRICIDA* (KIRKALDY) (HOMOPTERA: APHIDIDAE)

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ABSTRACT

Literature is reviewed on the brown citrus aphid (BCA), *Toxoptera citricida* Kirkaldy, a serious pest of citrus recently introduced to Florida. Information is summarized on the aphid's distribution, host range, biology, population ecology, natural enemies, entomopathogens, transmission of plant viruses, and management.

Key Words: citrus tristeza virus, coccinellidae, control, parasitoids, predators, syrphidae

RESUMEN

Es revisada la literatura sobre el pulgón pardo de los cítricos, *Toxoptera citricida* Kirkaldy, una plaga de cítricos recién introducida en la Florida. La información está resumida en cuanto a la distribución del áfido, sus plantas hospederas, biología, ecología, enemigos naturales, entomopatología, transmisión de virus, y control.

The brown citrus aphid, *Toxoptera citricida*, (BCA) was first discovered in Florida in November, 1995 in Broward and Dade Counties. BCA is a major concern to citrus growers throughout the state because of its high efficiency in transmitting citrus tristeza virus (CTV). In view of the current interest in this insect, the purpose of this manuscript is to summarize information available on its biology, ecology, and management, and its role as a vector of CTV. The volume of literature on CTV warrants a separate review and I have therefore referenced only review articles and those specifically concerned with CTV transmission by the BCA.

The BCA, a.k.a. the oriental citrus aphid, was formerly called "*Aphis citricidus*" (1935-1960) and then *Toxoptera citricidus* before the species name was changed to its present form to agree in gender with the genus name (Stoetzel 1994a). In earlier literature (prior to 1940) it was commonly referred to as "*Aphis tavaresi*". Other synonyms include "*Myzus citricidus*" and "*Paratoxoptera argentiniensis*", but usage of these names is rare. Essig (1949) lists "*Aphis citricola*" Van der Goot as synonymous with *T. citricida*, but Hille Ris Lambers (1975), upon re-examination of the original material collected by Van der Goot in Chile (Van der Goot 1912), concluded that *A. citricola* is synonymous with *Aphis spiraecola* Patch, the green citrus aphid, and this was later confirmed by Eastop and Blackman (1988). *A. citricola* has been used as a synonym for *A. spiraecola* in some literature (e.g. Komazaki 1982, 1988), although in pre-1950 publications it often appears as a synonym for BCA. Further confusion arises in studies where the BCA has been mistaken for its close relative *T. aurantii* Kirkaldy, and such cases are difficult to identify.

Many of the large number of publications which refer to BCA make only passing reference to it, or report it as one of many species collected in a general survey of citrus insects. I have therefore reviewed in detail only those articles which I felt provided original data, useful observations, or novel insights. The information has been organized under subject headings to provide readers with quick access to particular areas of interest.

Description & Distribution

Toxoptera citricida was first described by Kirkaldy (1907) who placed it in the genus *Myzus*. Good descriptions can also be found in Essig (1949), Stroyan (1961), Bänziger (1977), Denmark (1978), Stoetzel (1994b), and Halbert and Brown (1996). The latter provides a detailed description complete with drawings and a key for distinguishing other aphids common in Florida citrus. The cytotaxonomy of the Genus *Toxoptera*, including BCA, has been described by Kurl (1980).

The BCA is thought to have originated in Southeast Asia (Kirkaldy 1907; Rocha-Peña et al. 1995) and is common throughout Asia, including China, Cyprus, India, Japan, Laos, Taiwan, Viet Nam (Essig 1949), Sumatra (Takahashi 1926; Mason 1927), Nepal (Knorr & Moin Shah 1971), Sri Lanka (Van Der Goot 1918; Peiris & Bertus 1958), Malaysia (Ting 1963; Ting & Arasu 1970), the Philippines (Gavarra & Eastop 1976) and Thailand (Bänziger 1977). Pacific islands with records include Hawaii (Kirkaldy 1907), Fiji (Lever 1940), Mauritius (D'Emmerez De Charmoy 1918; Mamet 1939), Réunion (Moreira 1967), Samoa (Laing 1927), and Tonga (Carver et al. 1994). BCA has been present in Australia for many years, possibly since the last century (Hely 1968) and can also be found in New Zealand (Cottier 1935).

Specimens of BCA collected by J. S. Tavares in Zambezi were described by Del Guercio in 1908 who named it "*Aphis tavaresi*" (Del Guercio 1917). Anderson (1914) and Theobald (1915) both reported collections of BCA from British East Africa. Other african countries with records include Cameroon, Congo, Ghana, Kenya, Morocco, South Africa, Tanzania, Uganda, Zaire, Zimbabwe (Essig 1949), Ethiopia (Del Guercio 1917; Abate 1988; Godfrey-Sam-Aggrey & Balcha 1988), Mozambique, (Saraiva 1929; Annecke 1963) Somalia (Theobald 1928; Chiaromonte 1933), and Tunisia (Halima et al. 1994). It is still absent from Israel (Bar-Joseph & Loebenstein 1973; Raccah & Singer 1987). Essig (1949) reported BCA as present in Italy, Malta and Spain, but these reports are questionable and remain unconfirmed. Although apparently present in Turkey (Yumruktepe & Uygun 1994) the BCA is still absent from much of mediterranean Europe (Mendel 1956; Jamoussi 1967).

Accidental introductions of BCA (and CTV) to South America are thought to have been made in either Brazil or Argentina during the 1920's when these regions were expanding their citrus production and importing material from Australia and South Africa (Rocha-Peña et al. 1995). Since that time it has spread to Bolivia (Squire 1972; Timmer et al. 1981), Peru (Roistacher 1988), Uruguay, Chile, and Colombia, (Rocha-Peña et al. (1995). It has even been found in jungle regions of the Peruvian Amazon (Ortiz 1981). BCA was first reported in Venezuela in 1976 (Geraud 1976), although it had been present in neighboring Guyana since at least 1968 (Bisessar 1968) and in Surinam since 1961 (van Hoof 1961). BCA first appeared in the Caribbean islands in Trinidad in 1985 (Yokomi et al. 1994). In 1991 it was found in Guadeloupe, Martinique and St. Lucia (Aubert et al. 1992) and in 1992, in Puerto Rico and the Dominican Republic (Lastra et al. 1992). It is now also present in Jamaica and Cuba (Yokomi et al. 1994). The BCA had spread into Central America as far north as Costa Rica by 1989 (Lastra et al. 1991, Voegtlin and Villalobos 1992), to Nicaragua and El Salvador in 1991 (Lastra et al. 1992, Lee et al. 1992), and to Belize in the fall of 1996 (Halbert 1996). In the fall of 1995, the BCA arrived in Florida in the Ft. Lauderdale area and, within one year, spread as far north as Melbourne on the east coast and Ft. Meyers on the west (Halbert 1997). By the summer of 1997, BCA was widely distributed throughout southern central and coastal regions of Florida, although it remained absent from much of the ridge citrus north of Highlands county.

HOST RANGE

The host range of the BCA is largely restricted to the Genus *Citrus*, although there are many reports of it colonizing other rutaceous plants. A list of the host plants from which BCA has been reported is provided in Table 1. The majority are woody shrubs, although some are perennial vines and annual herbs. Symes' (1924) report of a single infestation on cotton was from Rhodesia. Tao & Tan (1961) collected their specimens in Taiwan. Collections by Mondal et al. (1976) are from India and those of Carver (1978) are all from Australia. Van Harten & Ilharco (1975) and Remaudiere et al. (1985) reported collections from Africa. Ghosh & Raychaudhuri (1981) reported finding the BCA feeding on rosaceous fruit trees in India (apple, cherry, peach etc.—species names not provided), although I suspect this to be a possible mis-identification of *T. aurantii*. The record from white yam, *Dioscorea rotundata*, (Reckhaus 1979) is from Togo and that for *Passiflora* sp. (Bakker 1974), from Kenya. All collections reported by inspectors of the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, are from Florida.

Most non-rutaceous plants are not normally suitable hosts for the BCA and it should be noted that collections from these plants do not imply they are suitable for development and reproduction of the aphid. These may be colonized occasionally by variant individuals when suitable citrus foliage is unavailable, or alates may be collected that are resting rather than feeding. Several generations of BCA were reared successfully in the laboratory on seedlings of West Indian cherry (a.k.a. acerola), *Malpighia punicifolia*, in Puerto Rico, although natural colonization of this plant could not be elicited by placing flushed seedlings adjacent to infested citrus (Michaud 1996). Halbert et al. 1986 has been erroneously cited as a host record for BCA on soybean, *Glycine max*, (Stibick 1993) but this work examined only transmission of soybean mosaic virus by BCA. Many of the anomalous occurrences (e.g. cotton) probably represent isolated events or colonizations by variant populations that are atypical of the species' normal host range, although others probably represent mis-identifications (Stoetzel 1994b).

TABLE 1. HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

Anacardiaceae
Mangifera sp. (Carver 1978)
Mangifera indica (Stibick 1993)
Rhus sp. (Mondal et al. 1976)
Bombaceae
Bombax ceiba (Tao & Tan 1961)
Burseraceae
Commiphora mollis (Remaudière et al. 1985)
Camelliaceae
Camellia japonica (Tao & Tan 1961)
Caryophyllaceae
Dianthus sp. (Mondal et al. 1976)
Dioscuraceae
Dioscorea rotundata (Reckhaus 1979)
Ebenaceae
Diospyros kaki (Essig 1949)
Diospyros sp. (Carver 1978)
Ericaceae
Azalea sp. (Essig 1949)
Rhododendron sp. (Stibick 1993)
Euphorbiaceae
Bridelia monoica (Tao & Tan 1961)
Bridelia ovata (Tao & Tan 1961)
Clutia abyssinicam (Remaudière et al. 1985)
Fagaceae
Quercus sp. (Mondal et al. 1976)
Flacouatiaceae
Xylosna congestum (Tao & Tan 1961)
Juglandaceae
Engelhardtia spicata (Mondal et al. 1976)
Leguminoceae
Cassia absus (Mondal et al. 1976)
Cassia sp. (Mondal et al. 1976)
Lauraceae
Cinnamomum camphora (Tao & Tan 1961)
Litsia polyantha (Mondal et al. 1976)

TABLE 1. (CONTINUED) HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

Malpighiaceae
Malpighia punicifolia (J. P. Michaud unpublished)

Malvaceae
Gossypium hirsutum (Symes 1924; Carver 1978)

Moraceae
Cudrania triscuspidata (Essig 1949)
Ficus carica (Essig 1949)
Ficus ingens (Remaudière et al. 1985)
Ficus retusa (Tao & Tan 1961)
Malclura cochinchinensis (Carver 1978)

Mysinaceae
Maesa chisea (Mondal et al. 1976)
Maesa sp. (Mondal et al. 1976)

Nyctaginaceae
Bougainvillea spectabilis (Remaudière et al. 1985)

Oxalidaceae
Oxalis pes-caprae Carver (1978)

Passifloraceae
Passiflora foetida (Mondal et al. 1976)
Passiflora sp. (Bakker 1974)

Rosaceae
Cottoneaster sp. (Carver 1978)
Crataegus sp. (van Harten & Ilharco 1975)
Eriobotrya sp. (Tao & Tan 1961)
Malus domestica (van Harten & Ilharco 1975)
Malus sylvestris (Mondal et al. 1976)
Pyrus communis (Essig 1949; van Harten & Ilharco 1975; Mondal et al. 1976)
Pyrus sp. Carver (1978)

Rubiaceae
Lasianthus chinensis (Tao & Tan 1961)

Rutaceae
Calodendrum capense (Carver 1978)
Choisya ternata (Carver 1978)
Citrifortunella floridana (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
Citrifortunella microcarpa (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
Citrus spp.
Clausena lanisum (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)

TABLE 1. (CONTINUED) HOST RECORDS FOR THE BROWN CITRUS APHID. NOTE: ALL PLANTS IN THE GENUS CITRUS ARE HOSTS AND ARE NOT LISTED BY SPECIES.

Eremocitrus glauca (Carver 1978)
Evodia hupehensis (Meneghini 1948)
Geijera parviflora (Carver 1978)
Flindersia xanthoxyla (Carver 1978)
Fortunella sp. (Stibick 1993)
Fortunella maragarita (Carver 1978)
Murraya exotica (Stibick 1993)
Murraya paniculata (Tao & Tan 1961; Carver 1978)
Poncirus trifoliata (Essig 1949; Tao & Tan 1961; Carver 1978)
Severinia buxifolia (Carver 1978)
Toddalia asiatica (Essig 1949)
Triphasia trifolia (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
Vepris undulata (Carver 1978)
Zanthoxylum fagara (Fla. Dept. Agr. & Cons. Serv., D.P.I., Gainesville, FL.)
Zanthoxylum ornatum (Mondal et al. 1976)
Zanthoxylum sp. (Mondal et al. 1976)
Ternstroemiaceae
Schima wallichii (Mondal et al. 1976)
Ulmaceae
Ulmus procera (Carver 1978)
Trema orientalis (Essig 1949)
Urticaceae
Boehmeria sp. (Mondal et al. 1976)

BASIC BIOLOGY

The BCA feeds only on newly expanded shoots, leaves and flower buds of its host plants. Newly expanding terminals are suitable for BCA growth and reproduction for usually a period of only 3-4 weeks, depending on environmental conditions. Therefore, a BCA colony has a relatively narrow time window within which to mature and produce alates prior to the demise of its food resource. This is an important consideration in the development of management strategies since only those colonies exporting alates are of importance in terms of the secondary transmission of CTV. In this context it is unfortunate that no laboratory studies have yet examined the environmental conditions that induce the production of alate morphs in BCA. Crowding of nymphs seems to induce alate formation (J. P. Michaud unpublished), but declining food quality and temperature may also play a role. However, once shoot hardening progresses beyond some threshold point, BCA nymphs either fail to mature or leave the terminal in search of new flush on other branches.

Despite the fact that the BCA can apparently move long distances in a short period, it is not clear to what extent this results from natural dispersal as opposed to accidental movement by man. My own observations indicate that the majority of alates

probably do not fly far from their nascent colony. This is borne out by the fact that foci of BCA infestations are often localized in citrus groves and can be observed to expand more slowly than those of *Aphis gossypii* (Gottwald et al. 1995). Furthermore, suction and yellow-trap catches often underestimate the number of active BCA colonies in a particular vicinity (e.g. Yokomi et al. 1997). Consequently, BCA infestations tend to be endemic in citrus groves, surviving at low density on bits of asynchronous flush and root sprouts until a new flush cycle provides sufficient food for a population outbreak. Weather conditions such as thermal updrafts or tropical storms may play some role in dispersal. For example, the discovery of BCA in Jamaica in 1993 was preceded by the passage of a strong tropical depression (Lee et al. 1995, p. 209). However, long-range dispersal by alates is probably rare and movement of infested plant material by humans may be a more important mechanism. Gottwald et al. (1993) estimated very low probabilities for colonization of Florida citrus by BCA through arial dispersal from the Carribean, specifically Cuba, but the true mechanism by which it ultimately arrived in Florida was never established.

The earliest detailed study of the biology and life history of the BCA is by Symes (1924) in Southern Rhodesia. The author reported as many as 30 generations per year, depending on availability of citrus flush. The time for development to adult was estimated to range from 8 to 21 d. The BCA is anholocyclic (without sexual generations) throughout most of its range in tropical and subtropical regions. In New Zealand, Cottier (1935) observed the anholocyclic apterae to overwinter, although their development was greatly retarded. Komazaki et al. (1979) observed a holocyclic generation of BCA under temperate conditions in Japan. However, the authors found very few overwintering eggs of BCA on trees compared to the numbers of *A. gossypii* and *A. spiraecola* eggs. Furthermore, although hatching rates were similar across species, the survival rate of hatched BCA nymphs was very low and surviving adult fundrices produced no second generation. In the laboratory, Komazaki (1990) compared the development and reproduction of BCA fundrices hatched from eggs with that of subsequent viviparous generations and found that the former took longer to mature at all temperatures tested, and had a lower reproductive rate. Because of low overwintering populations, the BCA is the last of the citrus aphids to appear on spring flush in Japan (Komazaki 1988).

Takanashi (1989) compared the reproductive rates of alate and apterous morphs of the BCA feeding on *Citrus natsudaidai* in the laboratory. The pre-reproductive period was longer for alatae than for apterae at both 20° and 25°C, and estimates of both age-specific fecundity and net reproductive rate were higher for apterae at both temperatures. Komazaki (1982) determined that the maximum intrinsic rate of increase for the BCA occurred at a constant temperature of 27°C, even though the fecundity and net reproductive rate of individual apterous females was maximal at 21.5°C. In general, the pre-reproductive period, post-reproductive survival, and longevity were all shortened as temperature increased.

Galatoire (1983) calculated life table statistics for 3 cohorts of BCA grown in outdoor enclosures in Argentina. She reported mean life expectancies for apterous females ranging from 28 to 48 d; the shorter life expectancies correlated with higher mean daily temperatures and reduced duration of the third and fourth nymphal instars. Age-specific mortality rates varied among cohorts, presumably in response to the different ambient conditions they experienced, although >80% of individuals survived to become adults in all 3 cohorts. Daily fecundity of adult apterae averaged between 5 and 6 nymphs per female per day, and total fecundities ranged between 73 and 81 nymphs. The highest mean replacement rate (59 females/female) was observed in a cohort which experienced a moderate regime of daily temperatures, but the highest instantaneous rate of increase was observed in the cohort experiencing the highest

mean daily temperatures. This result was attributed to reduced generation time under the warmer conditions.

There is also evidence that the performance of BCA varies on different species of citrus. Komazaki (1982) observed differences between BCA reared on *Citrus unshui* and those reared on *C. aurantium*. He also discovered a temperature-host plant interaction effect on development. *C. unshui* yielded aphids with shorter pre-reproductive periods and greater longevities and fecundities than did *C. aurantium*. The threshold temperature for BCA development was also lower on *C. unshui* (8.0°C) than on *C. aurantium* (8.4°C). However, the survival rate on *C. unshui* was 0% at 29.7°C, but 60% on *C. aurantium* at 29.9°C.

Komazaki (1984) succeeded in rearing 4 generations of BCA on an artificial diet of 20% sucrose at pH7, but the growth rate, fecundity, and longevity of these aphids were reduced relative to those fed on citrus.

Population Dynamics

Given that the BCA feeds only on tender new citrus terminals, many authors have observed population outbreaks to occur about 2 wk following heavy rainfall that induces citrus flush (Schwarz 1965a; Klas 1979). Typically, there are two BCA population peaks per year in subtropical regions, one in the spring and another in the fall. This has been observed in Argentina (Nickel & Klingauf 1985), Australia (Khan 1976; Carver 1978), Brazil (Chagas et al. 1982), Kenya (Seif & Islam 1988), Puerto Rico (J. P. Michaud unpublished), Taiwan (Tao & Tan 1961), and Japan (Nakao 1968; Shindo 1972). Komazaki (1981) reported three annual population peaks in Japan during one year's observations.

Geraud (1979) studied the life cycle and population dynamics of BCA in Venezuela, but I was unable to obtain a copy of this thesis. Nickel & Klingauf (1985) studied BCA population dynamics for a 2-yr period in Misiones, Argentina. They compared the longevity of exposed colonies with those in exclusion cages and others growing under climate-controlled conditions indoors. The maximum longevity of exposed outdoor colonies was only 12 d (mean = 7.5) compared with a range of 16-26 d in the exclusion cages and 19-33 d under temperature-controlled conditions. The improved survival of colonies in the exclusion cages was attributed, in part, to their protection from natural enemies, primarily *Cycloneda sanguinea* (Coleoptera: Coccinellidae) and, in part, to physical protection afforded by the enclosures. Periods of heavy rain and hot dry weather were both correlated low BCA population densities. Heavy rainfall appeared to impede flight activity as measured by catches in yellow bowl traps. Anderson (1914) also noted a popular belief that BCA populations are checked by heavy showers. However, Nickel & Klingauf (1985) concluded that temperature is an important determinant of BCA population trends and that temperature extremes in winter and summer had a negative impact on development and flight activity. A negative effect of high temperatures on BCA populations was also inferred by Hall (1930).

Natural Enemies

The BCA is unusual as an aphid species with few effective parasitoids throughout its range (Stary 1970). One exception may be Japan where *Lysiphlebia japonica* Ashmead (Hymenoptera: Aphidiidae) reportedly exerts some level of control (Kato 1969, 1970; Takanashi 1990, 1991). This species was imported to Florida in 1996 and released at 29 sites throughout the state, and to Puerto Rico where it was released at 2 sites. To date (Aug, '97) there no have been no recoveries of this insect from Puerto

Rico. In April 1997, a few weeks after releases were made, a number of specimens of *L. japonica* were recovered at several sites in St. Lucie County, Florida. This would indicate at least one generation of *L. japonica* was successful under field conditions in Florida. However, it is still uncertain whether permanent establishment of this species will occur and, if so, whether any significant control of BCA will result.

Symes (1924) reports collecting a single unidentified Braconid (probably an Aphidiid) parasitoid from BCA in South Africa, although Abate (1988) found no parasitoids of BCA in his survey of citrus disease vectors in Ethiopia. *Lysiphlebus testaceipes* Cresson attacks BCA in Venezuela (Stary & Cermeli 1989) and in Brazil (Gallo et al. 1978), although Murakami et al. (1984) did not recover this or any other species of parasitoid from BCA during their survey in the Cerrados region. *L. testaceipes* is frequently observed parasitizing the BCA in Puerto Rico, but fewer than 5% of mummies yield viable adults (Yokomi & Tang 1996). In Cuba, *L. testaceipes* frequently parasitizes *T. aurantii* but is only rarely found on BCA (Batista et al. 1995). Carver (1984) found that *L. testaceipes* (imported to Australia) readily oviposited in BCA but rarely completed development. Similarly, Carver & Woolcock (1985) reported incomplete parasitism of BCA by *Aphelinus asychis* Walker in Australia. *L. testaceipes* is frequently found parasitizing BCA in most citrus-growing regions of Florida, although very few mummies can be found with emergence holes (J. P. Michaud unpublished).

Nickel & Klingauf (1985) reported that, in Argentina, *Aphidius colemani* Viereck parasitized up to 50% of BCA in some colonies in the fall, although no information is presented on the survival of the parasitoid in this host. Stary & Cermeli (1989) made collections of *A. colemani* from 10 spp. of aphids in Venezuela, but did not find it attacking BCA. Valencia & Narciso Cárdenas (1973) reported collection of *Aphidius matricariae* Haliday from BCA in Peru. De Huiza & Ortiz (1981) collected 4 spp. of aphidiid wasps from aphids in Peru, including *A. colemani* and *A. matricariae*, but only *L. testaceipes* emerged from BCA. Carver (1978) noted parasitism of BCA by *A. colemani* in Australia, although she noted that such mummies were rare in the field. Messing & Rabasse (1995) observed that *A. colemani* from Réunion Island oviposited in various aphid species in which the wasp did not complete development. Newman (1924) reports *Aphelinus mali* (Aphelinidae) emerging from BCA in Western Australia. Flanders & Fisher (1959) reported collections of *Lipolexis* sp., *Trioxys* sp., and two *Aphelinus* spp. from BCA in Kwantung Province, China. Yokomi et al. (1993) reported a collection of *Lipolexis scutellaris* and *L. gracilus* from BCA in Malaysia and Tang et al. (1996) report *Aphelinus spiraecolae* Evans and Shauff attacking BCA in China.

In most studies of the natural enemies of BCA, emphasis has been placed on predatory insects, primarily ladybeetles (Coleoptera: Coccinellidae), and hoverflies (Diptera: Syrphidae) as species causing the greatest mortality to BCA populations. Kato (1968) reported *Eristrophe balteatus* de Geer, *Paragus quadrifasciatus* Meigen, *Sphaerophoria cylindrica* Say, and *Syrphus serarius* Wiedemann as hoverfly species feeding on BCA in Japan. Symes (1924) reported *Xanthogramma aegyptium* Wiedmann as the most common syrphid preying on BCA in Rhodesia. Catling (1970) reported *Allograpta pfeiferi* Bigot and *Baccha* sp. as syrphid predators of BCA in South Africa. Abate (1988) found *Sphaerophoria rueppellii* Wiedmann attacking BCA in Ethiopia, as well as *Leucopis* spp. (Diptera: Chamaemyiidae). Lever (1946) lists *Xanthogramma* (Ischiodon) *scutellare* F. and *Syrphus corollae* var. *vitiensis* Bez. as the important syrphids attacking aphids, including BCA, in Fiji. Goncalves & Goncalves (1976) collected 10 species of syrphids from aphids in São Paulo and Rio de Janeiro states in Brazil. Those attacking BCA included *Allograpta exotica* (Wiedmann.), *Ocyptamus gastrostactus* (Wiedmann) (= *Baccha gastroctacta*) and *Pseudodorus clavatus* (F.) (= *Baccha clavata*). Bartoszeck (1980) also reported the latter two spp. as predators of BCA in the state of Maranhao, Brazil. Leal et al. (1976) reported *O. gas-*

troctactus to be the most abundant syrphid on BCA in Pernambuco, Brazil and concluded it was the only predator affording any control. *P. clavatus* and *Ocyptamus fuscipennis* Say are the most abundant syrphids attacking BCA in Puerto Rico, although *Allograpta exotica*, *A. radiata*, and *Ocyptamus cubanus* have also been collected (J. P. Michaud unpublished). Valencia and Nárciso Cardenas (1973) collected *P. clavatus* and *Allograpta* spp. in their survey of aphid natural enemies in Peru, but did not find them feeding on BCA. *P. clavatus* is also abundant on BCA in Cuba (Batista et al. 1995) and in Trinidad where O. gastroctactus is also important (White 1995). Collections from Florida suggest that *P. clavatus* is by far the most abundant and ubiquitous syrphid on BCA, but *Toxomerus geminatus* (Say) and *Leucopis* sp. (Diptera: Chamaemyiidae) have also been recorded (J. P. Michaud unpublished).

Michaud (1996) observed relatively good biological control of BCA in Puerto Rico throughout the summer months of 1996. Fewer than 5% of suitable citrus terminals were infested with BCA in most citrus groves between May and August, largely due to the activities of various species of coccinellids, the adults and larvae of which destroyed many colonies in their early stages. The following species of coccinellids have been collected from BCA in Puerto Rico: *Chilocorus cacti* (L.), *Cladis nitidula* (F.), *Coelophora inaequalis* (F.), *Coleomegilla innotata* (Mulsant), *C. sanguinea limbifer* (L.), *Diomus* sp., *Egius platycephalus* Mulsant, *Hippodamia convergens* (Guerin), *Hyperaspis* sp., *Olla v-nigrum* (Mulsant), *Procula feruuginea* (Oliver), and *Scymnus* (*Schymnus*) *floralis* (F.) (J. P. Michaud unpublished). The most abundant species were *C. inaequalis* and *C. sanguinea*. Small species such as *Diomus* sp., *Hyperaspis* sp. and *S. floralis* prey only on early instars of BCA and appear to have only minimal impact on aphid populations. *C. sanguinea* is the most common coccinellid on BCA in the Dominican Republic (Borbón et al. 1992) and Cuba (Batista et al. 1995). It is also abundant feeding on BCA in Venezuela (Morales & Burandt 1985) and Brazil (Lara et al. 1977; Bartoszeck 1980). Additional coccinellid spp. recorded from BCA in Brazil include *Cleothera* sp., *Diomus* sp., *Exoplectra* sp., and *Scymnus* sp. (Bartoszeck 1980). Chagas et al. (1982) concluded that the coccinellids *C. sanguinea*, *Nephaspis* sp., *Stethorus* sp. and *Scymnus* sp. in particular, were the most important predators of BCA in São Paulo state and provided data on their seasonal abundance in citrus. Other coccinellids collected from BCA in this study included *Cleothera* sp., *Cycloneda conjugata*, *Delphastus* sp., *Hyperaspis* sp. *Lindorus lophanthes*, *Neaporia* sp., and *Pentilia* sp. Valencia and Narciso Cárdenas (1973) reported *C. sanguinea* and *H. convergens* as predators of BCA in Peru. Coccinellid species attacking BCA in Florida include *Brachiacantha decora* (Casey), *Brachiacantha dentipes* (F.), *C. cacti*, *Chilocorus stigma* (L.), *Coccinella septmpunctata* L., *C. ineaqualis*, *Curinus coeruleus* (Mulsant), *C. s. sanguinea*, *Harmonia axyridis* (Pallas), *H. convergens*, *Hyperaspis ornatella* Gordon, *O. v-nigrum*, and *Scymnus* sp. (J. P. Michaud unpublished).

Kato (1969) listed *Scymnus hilaris* Motschulsky, *Coccinella septepunctata bruckii* Mulsant, *H. axyridis*, *Propulaea japonica* (Thunberg), *Chilocorus kuwanae* Silvestri and *Hyperaspis japonica* (Crotch) as coccinellid species attacking BCA in Japan. Komozaki (1981) reported that *S. hilaris* was an important predator of BCA in Japan and that its numerical response to increasing BCA populations was relatively good. Nakao (1968) reported *Stethorus japonica* Kamiya as another coccinellid species preying on BCA in Japan, although *Telsimia nigra* Weise and *C. kuwanae* were the most abundant species in that study.

Maelzer (1978) states that *Leis conformis* (Boisduval.) is an important predator of BCA in South Australia. *Cheilomenes propinqua* is listed by Catling (1970) as a coccinellid feeding on BCA in South Africa. Symes (1924) lists *Chilomenes lunata* F., *Alesia bohemani* Mulsant, *A. geisha* Gorh., *Halyzia exiguenotata* F., *Lotis* sp., and *Scymnus trepidulus* Weise as coccinellids feeding on BCA in Rhodesia, noting that the

first two species were most common. Abate (1988) lists *Exochomus* sp., *Hyperaspis senegalensis* (Mulsant), *Pharoscymnus madagassus* (Weise) and *Pharoscymnus* sp. as coccinellid predators of BCA in Ethiopia. Lever (1946) listed *C. inaequalis* and *Coccinella repanda* var. *transversalis* F. as important predators of aphids in Fiji, including BCA.

A study by Nickel & Klingauf (1985) in sub-tropical Argentina indicated that *C. sanguinea* was the most important predator in that particular region. They measured predator-prey ratios varying between 1-40 and 1-10, suggesting relatively good levels of biological control which they attributed to the semi-natural conditions surrounding their study sites. Recruitment of predators from outside citrus groves was judged to be an important factor. The relatively low numbers of predators present in winter months (May-August) was attributed to low rates of recruitment resulting from low BCA population densities.

Lacewings (Neuroptera) are also predators of aphids that may contribute to suppression of their populations. Nakao (1968) reports *Micromus novitus* Navás and *Eumicromus numerosus* Navás (Hemerobiidae) as lacewings feeding on BCA in Japan. Valencia and Narciso Cárdenas (1973) collected *Chrysopa* sp. (now *Chrysoperla* sp. chrysopidae) feeding on BCA in Peru. Chagas et al. (1982) reported the seasonal abundance of *Chrysopa* sp., *Hemerobius* sp. and *Megalomus* sp. found feeding on BCA in São Paulo state, Brazil. *Nusalala uruguaya* (Hemerobiidae) has been recorded from BCA in Brasil (Souza et al. 1989) and a *Ceraeochrysa* sp. (Chrysopidae) occurs on BCA in Puerto Rico (J. P. Michaud unpublished), although it is rare. Abate (1988) reported *Anisochrysa boninensis* (Okamoto) as a Chrysopid predator of BCA in Ethiopia. White (1995) reported *Chrysopa silvana* Naval from BCA in Trinidad, although it was not deemed a significant source of mortality. To date, *Ceraeochrysa lineaticornis* (Fitch), and *Micromus posticus* (Walker) have been collected from BCA in Florida (J. P. Michaud unpublished).

Several studies have suggested that BCA may be toxic to certain predators, or nutritionally inadequate for their successful development. Tao & Chiu (1971) reported that 5 of 13 coccinellid species fed BCA, including *C. repanda*, suffered injury or death, while the others remained unaffected. Souza et al. (1989) reported that larvae of *N. uruguaya* fed BCA did not survive to pupation and Tao & Chiu (1971) reported similar findings for two species of *Chrysopa*. However, Venzon & Carvalho (1993) found *Toxoptera* spp. (BCA?) to be a suitable diet for *Cereaochrysa cubana* (Hagen) in Brasil and *Ceraeochrysa* sp. in Puerto Rico has been successfully reared to adult stages on BCA (J. P. Michaud unpublished). Parker & Singh (1973) found that the coccinellids *Chilocorus politus* Muls., *Coccinella arcuata* F. and *Micraspis* (*Alesia*) *discolor* (F.) all expressed a non-preference for BCA in feeding trials, although *Menochilus* (*Cheilomenes*) *sexmaculatus* (F.) did not. Morales & Burandt (1985) found that *C. sanguinea* collected in Venezuela and fed BCA in the laboratory failed to complete development. On the other hand, *C. sanguinea* and *C. inaequalis* collected in Puerto Rico developed normally and had good survival on an exclusive diet of BCA (J. P. Michaud unpublished), suggesting that there may exist regional differences between biotypes of predator species with respect to their ability to utilize BCA as food. Interestingly, no studies have found any indication of BCA toxicity to syrphids.

Ants are notorious for interfering with the beneficial activities of aphid predators and/or parasites and BCA may sometimes benefit from a mutualistic association with certain ant species. Observing ant and aphid populations in a citrus orchard in Japan, Shindo (1972) concluded that the ant *Pristomyrex pungens* Mayr interfered with the behavior of BCA predators (syrphids and coccinellids). Tao & Wu (1968) recommended the removal of ant nests in the vicinity of BCA-infested trees in conjunction with chemical treatments for control of the aphid. Bartoszeck (1980) recorded the ants *Eu-*

cryptocerus placidus (F. Sm.) and *Camponotus godmani* Forel in association with BCA in Brazil. Fire ants, *Solenopsis invicta* Buren, are often observed tending BCA in Florida and Puerto Rico (J. P. Michaud unpublished) and are known to remove parasitized aphids and mummies of L. testaceipes from aphid colonies (Vinson & Scarborough 1991). They have also been observed removing predatory larvae and dead aphids from BCA colonies, and carrying live aphids to fresh, uninfested terminals (J. P. Michaud unpublished). Other ant species observed tending BCA in Puerto Rico include *Brachymyrmex obscurion* Ford, *Monomorium ebeninum* Ford, *Paratrechina longicornis* (Latrielle), *Pheidole fallax* Mayr, *Solenopsis globularia* (F. Smith), and *Wasmannia auropunctata* (Roger) (J. P. Michaud unpublished). In Florida, *B. obscurion*, *Camponotus sexguttatus* (F.), and *Pseudomyrmex ejectus* (F. Smith) have been collected at BCA colonies (J. P. Michaud unpublished).

ENTOMOPATHOGENS

Rondon et al. (1981) found the entomophagous fungus *Verticillium lecanii* (Zimm.) Viégas to be the most important biological control agent during population outbreaks of the BCA in the Carabobo and Yaracuy states of Venezuela in 1979 and 1980. The predators reported as important in this study were *C. sanguinea*, *O. gastrostactus* and *Zelus* spp. The authors noted that ideal ambient conditions for sporulation and germination of the fungus (temperatures ranging from 18-24°C at a high relative humidity) were prevalent during the 2-yr period of the study. The fungus was reported to survive unsuitable conditions in dried aphid mummies, and on aphid cadavers that occur on suckering shoots growing in the interior of the tree where they are protected from direct sunlight. The most suitable nutrient media for growing the fungus in the laboratory were 523, nutrient agar, malt-agar, and PDA. These workers stated that "the elevated pathogenicity on nymphs of different instars, adults, apterous and alate, for which there was >80% mortality in the first 2 wk, prevented culmination of the insect's life cycle". However, the infection rate of 1.2% of colonies reported by White (1995) in Trinidad is probably a more typical value for the natural occurrence of this fungus on BCA. *V. lecanii* has also been recovered from BCA in Puerto Rico, where it appears to be a sporadic and localized source of aphid mortality (J. P. Michaud unpublished). De Romero and Romero (1985) evaluated mycelial growth and conidia yield of *V. lecanii* collected from BCA in Argentina on 2% potato agar. Batista et al. (1995) reported satisfactory results with applications of both *V. lecanii* (Micotal-1 & Y-57 strains) and *Paecilomyces fomosoroseus* (INISA V strains) against the BCA in Cuba, despite the fact that they observed no natural attacks by entomopathogenic fungi. Samways & Grech (1986) found that the fungus *Cladosporium oxysporum* (Berk. and Curt.) had considerable impact on BCA populations in field trials in South Africa, which they attributed to the action of an unidentified toxin, rather than direct hyphal growth. Other fungi are currently under evaluation for pathogenicity to BCA.

CTV TRANSMISSION

CTV is a closterovirus which causes multiple disease syndromes in citrus. The most important are quick decline of trees on sour orange rootstock and stem-pitting in susceptible scions irrespective of rootstock. Tristeza is possibly the most serious virus disease of citrus world-wide and yet it is poorly understood. It is not yet possible to attribute particular symptoms on a particular citrus cultivar to specific viral sequences, nor is it known which sequences influence transmissibility by its most efficient insect vector, the BCA. Meneghini (1946) in Brazil presented the first evidence of CTV transmission by the BCA. Meneghini (1948) showed semi-persistent transmis-

sion of CTV; viruliferous BCA starved for 48 h lost their ability to transmit the virus, while a 24 h starvation period did not affect the percentage of trees infected. This was later confirmed by Costa & Grant (1951). Kennedy et al. (1962) suggested that tristeza virus was probably stylet borne. Retuerma & Price (1972) claimed that both acquisition and transmission of CTV by BCA can occur within a few seconds of feeding and concluded this was proof that CTV was stylet borne, a conclusion subsequently questioned by others. Singh (1978) successfully achieved CTV transmission feeding leaf and bark extracts to BCA through a stretched parafilm membrane and suggested that CTV may not be a typical stylet-borne virus, but may also be transmitted in a circulative, non-propagative manner. Such bimodal transmission was also suggested by Lim & Hagedorn (1977) but this explanation is not generally accepted and further evidence of short probing transmission is required (Bar-Joseph et al. 1979). The fact that CTV is phloem-limited makes transmission by brief probing less likely. The current consensus is that CTV transmission best fits the semi-persistent mode (Bar-Joseph et al. 1979; Raccah & Singer 1987) in which the virus is acquired and transmitted by aphids with feeding times ranging from several minutes to several hours, but usually not by brief probing.

Historically, introduction of the BCA has invariably resulted in the accelerated spread of CTV throughout entire citrus growing regions, the best example being the virtual destruction of the citrus industry in Brazil and Venezuela during the 1970's, most of which was rooted on sour orange (Lee et al. 1995). A number of studies have shown that the BCA is a relatively efficient vector of CTV when compared with other aphids that feed on citrus. Schwartz (1965b) observed that infections of trap plants with BCA were closely correlated with the numbers of BCA collected from the plants. In the Philippines, Celino et al. (1966) showed that BCA was a more effective vector than either *T. aurantii* or *A. gossypii*. Sharma (1989) tested 20 isolates of CTV and found that 12 were most efficiently transmitted by BCA, 5 by *A. gossypii*, and 3 by *Myzus persicae*. Yokomi and Damsteegt (1991) quantified the efficiency with which the BCA transmitted CTV in comparison to *A. gossypii* and found the former species to be significantly more efficient. Balaraman & Ramakrishnan (1979) showed that BCA was more efficient than either *A. gossypii* or *T. aurantii* at transmitting the 2 strains of CTV they tested, and that higher percentage transmission occurred with the severe strain than with the mild strain. The authors found that a minimum of 15 viruliferous aphids/plant were required for 100% transmission when feeding periods were 24 h each for acquisition and transmission.

A number of studies have shown that variant strains of CTV differ in their transmissibility by aphids (Bar-Joseph & Loebenstein 1973; Raccah et al. 1978; Raccah et al. 1980). Sharma (1989) showed that severe strains of CTV he tested were transmitted by BCA with higher efficiency than the mild strains; acquisition periods were shorter and retention periods were longer. The fact that citrus varieties vary with regard to their suitability for CTV acquisition by BCA further complicates the picture (Bar-Joseph et al. 1979).

A concise review of the literature on CTV transmission by aphids, including a list of infectivity studies on BCA and *A. gossypii*, is provided by Roistacher & Bar-Joseph (1987) (reproduced in Roistacher & Bar-Joseph 1989). Bar-Joseph et al. (1983) provide a review of the epidemiology and control of CTV, as does Lee (1994). Bar-Joseph et al. (1989) and Lee & Rocha-Peña (1992) are both comprehensive reviews of the history of CTV, its host range, diagnosis, and molecular characterization.

In addition to CTV, the BCA has been implicated in vectoring other plant viruses, although some reports are questionable and lack confirmation. Potyviruses transmitted by BCA include yam mosaic virus (Thouvenel & Fauquet 1979), soybean mosaic virus (Halbert et al. 1986), sugar cane mosaic virus (reported as mosaic of abacá,

Musa textilus, by Gavarra & Eloja (1965)) and chili veinal mottle virus (Ong et al. 1979). BCA did not transmit potato virus Y or pepper veinal mottle virus, other viruses infecting chilli peppers, *Capsicum annum* (Gowda & Reddy 1989). In the same series of experiments, BCA failed to transmit cucumber mosaic cucumovirus, which, although not a potyvirus, is non-persistently transmitted by many aphid species.

Using electron microscopy, Maharaj & da Graca (1988) found virions of citrus vein enation virus, a probable luteovirus, in the hindgut lumen and accessory salivary glands of BCA and subsequently (Maharaj & da Graca 1989), showed transmission by the aphid. Persistent transmission of citrus vein enation virus has been demonstrated in both *A. gossypii* and *M. persicae* (Hermoso de Mendoza et al. 1993). Portillo & Beñatena (1986) claimed that BCA was capable of transmitting citrus psorosis virus to various *Citrus* spp. in Argentina. However, the assays were based primarily on symptoms and this conclusion has yet to be confirmed by molecular studies. Protacio (1965) reported that BCA can potentially transmit the agent of cadang-cadang disease to coconut palms, but this disease is now thought to be caused by a viroid and there is no evidence for insect transmission of viroids.

Broadbent & Fraser (1976) concluded that BCA was not responsible for vectoring the organism that causes citrus dieback in Australia. Similarly, BCA was shown not to be responsible for vectoring citrus leaf mottle disease in the Philippines (Salibe & Cortez 1967), or the greening disease of citrus that is vectored by *Trioza erytreae* (McLean & Oberholzer 1965).

Monitoring and Control

Sticky traps and pan traps have both been used for monitoring flight activity of the BCA, and are more economical than suction traps in terms of capital outlay. However, sticky traps are attractive to many insects and must be replaced frequently. Furthermore, aphids caught in such traps inevitably require special solvents to remove and are usually badly damaged, making identification difficult. Pan traps yield specimens in better condition but also need to be emptied on a regular basis and are prone to flooding during periods of heavy rain. Furthermore, it should be kept in mind that traps only monitor the flight activity of alates, provide little information on the survival or location of aphids in citrus groves, and are not a substitute for effective survey techniques, i.e. physically searching groves for established colonies.

Alate BCA are not strong fliers and few fly far from their parent colony (Gottwald et al. 1995). Gavarra & Eastop (1976) obtained better catches of BCA in yellow Moericke trays at 152 cm height than they did in trays at ground level. Consequently, optimal placement of traps is probably above ground level, but lower than the height of surrounding trees. Lara et al. (1976) used water traps to compare the attractiveness of various colors to a number of different insects in citrus. In general, they found yellow and white to be the most attractive to all species, including the BCA and its predators *C. sanguinea* and *Chrysopa* sp. However, Schwarz (1965c) found that the relative attractiveness of yellow and green to BCA changed seasonally, and varied from year to year.

The decision whether or not to apply an insecticide to a BCA infestation will be affected by many factors, primarily the type of trees infested. These can be arranged in order of tolerance (lowest to highest): (1) budwood sources, (2) nursery stock, (3) newly-planted saplings and, (4) mature, producing trees (Knapp et al. 1996). Given the Budwood Certification Program presently in effect in the state of Florida which regulates the maintenance of budwood sources free of severe strains of CTV, the first two categories demand a very low tolerance of BCA infestations. Such trees are best protected either by screened enclosures, soil applications of systemic insecticides, or a combination of both. Alternatively, geographic isolation of budwood groves in non-

citrus producing areas might provide a more permanent solution. Heavy infestations on young trees may impede their growth (Hely 1968) and the tolerance level for BCA on saplings is consequentially lower than that for mature trees. There is some indication that BCA infestations can reduce flowering and fruit set (Hall 1930; Smit 1934; Hely 1968), and occasionally lead to dropping of flower buds and young fruit on a large scale (Symes 1924), although good quantitative data is lacking. This suggests that a lower injury threshold may exist for trees in flower and early stages of fruit set. Apart from these circumstances, tolerance levels for BCA infestations on producing trees will likely vary with the local incidence of severe CTV strains capable of producing decline on sour orange-rooted trees or stem-pitting on scions of orange or grapefruit, and with their proximity to susceptible trees. Otherwise, there is little indication of direct damage to mature trees, even under heavy feeding pressure.

The earlier reports of successful chemical control of BCA usually recommended foliar sprays of lime-sulphate, nicotine sulphate, or soap and nicotine. Hall (1930) recommended spraying winter colonies to reduce populations prior to spring flush. Tao & Tan (1961) recommended chemical treatment of CTV-infected trees, which tend to bloom and flush early, in order to prevent migration of aphids to healthy trees which flush later. Young resets typically flush earlier than mature trees and could be inspected for BCA prior to the flush of mature trees and spot-treated as required to preclude outbreak populations when flush availability increases. Ideally, growers should attempt to prevent BCA infestations developing on CTV-infected trees, as opposed to CTV susceptible, uninfected trees, as there is no evidence to suggest that even the best systemic compounds can protect against CTV transmission. In practise, this will only be possible for growers with good information on the location of CTV infections in their groves. Foliar formulations of various insecticides can be used to kill aphids on contact, but they can also be expected to have greater impact on non-target and beneficial insects than systemic materials. Consequently, their use should be limited to spot applications of heavily infested areas only.

Calza et al. (1968) evaluated 9 organphosphate and carbamate compounds against BCA in São Paulo, Brazil. Tao & Wu (1968) painted tree trucks with a 30% aqueous solution of the systemic insecticide monocrotophos (Azodrin) and found it more effective against BCA than dimethoate, vamidothion, or formothion when applied in this manner. In a later study (Tao & Wu 1969) they found that 2 spring applications of monocrotophos at 12.5% a.i. gave good control of BCA and had minimal impact on natural enemies in the grove. Buitendag & Bronkhorst (1986) found monocrotophos to be without phytotoxicity to citrus trees and calculated application rates for control of BCA on trees of different sizes. These authors also calculated rates for trunk applications of Dicrotophos against BCA (Buitendag & Bronkhorst 1984) and described a method for injecting systemic insecticides directly into trees (Buitendag & Bronkhorst 1980). While systemic compounds may generally have lower impact on natural enemies, their use as granular formulations or soil drenches on producing trees is often narrowly restricted to particular seasons to minimize contamination of ground water runoff. Foliar applications should be considered a last resort, unless compounds can be selected which minimize impact on beneficial insects within the grove. For example, Portillo (1977) showed that various concentrations of pirimicarb were effective against BCA in laboratory tests, and relatively low in toxicity to *C. sanguinea*. In addition, spot treatments of heavily infested trees or blocks, as opposed to blanket treatment of entire groves, would provide refuges for natural enemy populations and speed their recolonization of treated areas.

Koli et al. (1978) tested 0.05% sprays of 6 insecticides against BCA on citrus seedlings in India and found that phosphamidon gave the best initial knockdown and the most prolonged activity. Trevizoli & Gravena (1979) compared trunk and foliar sprays

of ethiofencarb, dimethoate, malathion and pirimicarb and found that all methods and materials were effective against BCA. However, they found that trunk sprays of pirimicarb and dimethoate had less impact on predator populations (*C. sanguinea* and *Chrysopa* sp.) than did foliar sprays.

Milne & de Villiers (1977) determined application rates for delivery of dimethoate by microjet and drip irrigation that gave season-long control of BCA and other homopterans. Milne (1977) protected bagged nursery seedlings from BCA for a period of 5-6 wk with a single soil-drench application of dimethoate (40% EC, 1.0 ml/bag). Buitendag & Bronkhorst (1983) describe a method for using bands to hold Temik© granules against the trunks of trees. This method provided good control of BCA on young citrus trees, but its effectiveness declined when trunk diameter increased above 125 mm. Shevale et al. (1987) found that foliar applications of phosphamidon, dimethoate, methyl demeton, monocrotophos and quinalphos (each at 0.025% conc.) all provided >95% reduction of BCA within 24 h of treatment, although phosalone did not. Significant recolonization by BCA was evident in all treatments by day 15. Under the particular conditions of this study, phosphamidon and dimethoate were judged to be the most cost-effective.

Jothi et al. (1990) obtained control of BCA on lime in India with foliar application of botanical insecticides. They found that oils of Mahua (*Bassia latifolia*) and pongamia (*Pongamia pinnata*) at 1% and seed extracts of pongamia and neem (*Azadirachta indica*) at 2% applied early in the flush cycle gave adequate control, and resulted in BCA populations significantly lower than controls after 7 days. Field trials conducted in Puerto Rico by Yokomi et al. (1995) indicate that foliar treatments of ethion (2.5 lb ai/A) + oil (5 gal), ethion + abamectin (2.5 lb and 1.1 gal ai/A, respectively) + oil (5 gal), and pirimicarb (0.25 lb ai/A), and acephate (1.0 lb ai/A) all produced close to 100% mortality of BCA, whereas chlorpyriphos (2.5 lb ai/A) yielded 88% mortality. Knapp et al. (1996) provide current recommendations for management of BCA in Florida citrus, (budwood sources, nurseries, and producing trees), and include a list of currently approved materials.

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FORAGING AND NESTING ECOLOGY OF *ACROMYRMEX OCTOSPINOSUS* (HYMENOPTERA: FORMICIDAE) IN A COSTA RICAN TROPICAL DRY FOREST

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ABSTRACT

Leaf-cutting ants (*Acromyrmex* sp. and *Atta* sp.) in Costa Rica show many intra- and interspecific differences in ecology. Recent taxonomic studies question whether the *Acromyrmex octospinosus* populations on the Pacific and Atlantic slopes of Costa Rica are a single species. We therefore examined the foraging and nesting ecology of *A. octospinosus* in the tropical dry forest of Palo Verde National Park on the Pacific slope of Costa Rica and compared our findings with published data on the ecology of *A. octospinosus* in the tropical moist forest of La Selva Biological Station on the Atlantic slope. The Pacific *A. octospinosus* foraged primarily on the leaves of herbs and other small plants, fallen leaves, fruit, flowers, and insect frass, but does not cut the leaves of large trees. Worker size distribution within colonies was bimodal with only

the larger workers leaving the nest to forage. Nests were shallow and generally under a few centimeters of organic debris at the base of trees and woody shrubs or in crevices. The foraging and nesting ecology of the Pacific *A. octospinosus* appeared to be very similar to that of the Atlantic *A. octospinosus*, except that the Pacific ants collected considerable amounts of insect frass (11% of all loads), whereas the Atlantic ants had no recorded loads of frass. This difference in selectivity, however, may have been due simply to seasonal differences in availability of frass at the sites.

Acromyrmex octospinosus was the only species of leaf-cutting ant found at Palo Verde. The vertisol soil of the area, which has very poor drainage when wet and cracks deeply when dry, may not be suitable for major pest species of leaf-cutters in Costa Rica, *Atta cephalotes* and *Atta colombica*, which excavate nests deep underground.

Key Words: *Atta*, foraging selectivity, Palo Verde, pest ants

RESUMEN

Las hormigas podadoras (*Acromyrmex* sp. y *Atta* sp.) en Costa Rica muestran muchas diferencias intra- e interespecíficas en ecología. Estudios taxonómicos recientes ponen en duda la noción que poblaciones de *Acromyrmex octospinosus* en los flancos Orientales y Occidentales de Costa Rica sean una sola especie. Por lo tanto, nosotros examinamos la ecología de alimentaciùn y anidamiento de *A. octospinosus* en el bosque seco tropical del Parque Nacional Palo Verde en el flanco occidental de Costa Rica, y comparamos nuestros resultados con datos previamente publicados sobre la ecología de *A. octospinosus* en el bosque húmedo tropical de la Estación Biológica La Selva en el flanco oriental. La alimentación de *A. octospinosus* en el lado occidental consistió principalmente de hojas de hierbas y otras plantas pequeñas, hojas caídas, frutas, flores y excrementos de insectos, pero no cortan hojas de árboles grandes. La distribución del tamaño de las obreras en la colonia es bimodal, y sólo las obreras grandes salen de la colonia para recoger alimentos. Los nidos son poco profundos y por lo general están bajo unos cuantos centímetros de materia orgánica al pie de árboles y arbustos, o en grietas. La ecología de alimentación y anidamiento de *A. octospinosus* en el lado occidental parece ser muy similar a la de *A. octospinosus* en el lado oriental, excepto que las hormigas en el lado occidental recogen cantidades considerables de excremento de insectos (11% de todas las cargas), mientras que las hormigas en el lado oriental no han sido observadas cargando excremento de insectos. Esta diferencia en selectividad, sin embargo, puede ser causada por diferencias en disponibilidad de excremento de insectos en diferentes estaciones entre las localidades. *Acromyrmex octospinosus* fue la única especie de hormiga podadora encontrada en Palo Verde. El suelo vertisol de esa área, que tiene muy mal drenaje cuando está mojado y que forma rajaduras hondas cuando está seco, puede no ser adequado para otras especies dañinas de hormigas podadoras en Costa Rica, *Atta cephalotes* y *Atta* colombica, las cuales excavan nidos profundos.

Fungus-growing ants (Myrmicinae; Attini) are unique among ants in their habit of cultivating a symbiotic fungus for food. All attine ants are obligately dependent on their fungus. In other aspects of their ecologies, however, different species of attines vary greatly (Weber 1972, Hölldobler & Wilson 1990). Ants of the nine "lesser" genera (*Cyphomyrmex*, *Mycetosoritis*, *Mycetophylax*, *Mycocepurus*, *Mycetarotes*, *Myrmicocrypta*, *Apterostigma*, *Sericomyrmex*, and *Trachymyrmex*) typically collect insect frass, dead insects, or small pieces of fallen plant material to use as substrate for their fungal gardens. They tend to have small and inconspicuous colonies (fewer than 5000 individuals), with relatively monomorphic workers. In contrast, ants belonging to two

genera of attines, *Acromyrmex* and *Atta*, often depend on harvesting leaves for their fungal gardens and consequently are commonly called leaf-cutting ants. Leaf-cutting ant colonies can grow to include many thousand to several million highly-polymorphic workers. Many leaf-cutters, particularly *Atta* species, are major agricultural pests.

Earlier studies have found striking differences in the foraging and nesting ecology of *Acromyrmex octospinosus* (Reich), *Acromyrmex volcanus* (Wheeler), *Acromyrmex coronatus* (Fabricius), and *Atta cephalotes* (L.), the four species of leaf-cutting ants found on the Atlantic slope of Costa Rica (Wetterer, 1991, 1993, 1994a, b, 1995). *Acromyrmex octospinosus* and *A. volcanus* colonies forage primarily on small herbs and fallen leaves, fruits, and flowers (Wetterer 1991, 1993). These colonies produce two distinct size castes of workers (Wetterer, unpublished). The minima workers stay inside the nest, tending the fungus garden and brood, while the relatively monomorphic maxima workers leave the nest to forage. In *A. coronatus* colonies and small *A. cephalotes* colonies, workers primarily cut the soft leaves of herbaceous plants (Wetterer 1994a, 1995). These colonies produce a narrow range of small workers, the largest of which are just big enough to cut soft vegetation efficiently (Wilson 1983, Wetterer, unpublished). In large *A. cephalotes* colonies, workers primarily attack the leaves and flowers of trees (Cherrett 1968, 1972; Rockwood & Hubbell 1987; Vasconcelos 1990; Wetterer 1994b). These colonies produce an extremely broad continuous size-range of workers (Stradling 1978; Wilson 1983). A wide range of medium-size workers forage, with the larger of these cutting thicker and tougher vegetation (Nichols-Orians & Schultz 1989; Wetterer 1994b).

Recent taxonomic research, based on morphological characters and allozyme polymorphisms, has raised questions as to whether the *A. octospinosus* on the Pacific and Atlantic slopes of Costa Rica are a single species (J. Longino, T. Schultz, & K. Boomsma, personal communication). Because earlier studies indicated marked interspecific ecological differences among leaf-cutting ants, we compared the foraging and nesting ecology of Pacific and Atlantic *A. octospinosus*. We also examined the question as to why *A. octospinosus* was the only leaf-cutting ant species present at our study site in Palo Verde National Park.

METHODS

We studied foraging selectivity and nesting habits of *Acromyrmex octospinosus* colonies at the start of the wet season (June 1996) in tropical dry forest of Palo Verde National Park, Guanacaste Province, Costa Rica. We worked in the area around Palo Verde Biological Station (10°19'N, 85°21'W; elevation 10 m), operated by the Organization for Tropical Studies (see Janzen 1983 for a site description). We conducted our study during daylight hours, when most *A. octospinosus* colonies were actively foraging. On an earlier visit to Palo Verde in the dry season (January 1996), there was no diurnal foraging by *A. octospinosus* (J. Wetterer, personal observation).

Through extensive searches along hiking trails and roads around Palo Verde, we located seventeen *A. octospinosus* colonies. At a nearby open pasture site, Sitio Mojal, we collected data on one additional *A. octospinosus* colony (colony 12), making a total of eighteen colonies. We found no other leaf-cutting ant colonies at the site, although we did find a single live alate *Atta cephalotes* queen. We explored the area for several kilometers in different directions, but never located any *A. cephalotes* colonies.

At each *A. octospinosus* colony, we collected laden foragers from along their foraging trails. To help ensure a representative sample, we collected laden foragers at ten second intervals as they passed a designated point on their trail, or if there were few foragers, we collected consecutive foragers. We used data from twelve colonies in our

foraging selectivity analysis. At four large *A. octospinosus* colonies, we collected 25 foragers from each of the two main trails. From six smaller colonies, we collected 25 foragers for each colony. At two very small colonies, we collected only fourteen workers from one colony and eleven from the other, because no more foragers came in a period of several hours. At six other small colonies we collected none or only one forager due to lulls in foraging activity that seemed to be associated with hot sunny weather. We did not include these collections in our foraging selectivity analysis.

We classified each load as fresh (soft, pliant, and green) or fallen (dry or yellowed) leaf material (fragment or whole leaf), herb section (stem or stem with leaves, leaf buds, or flowers), flower (part or whole), fruit (part or whole berry), insect frass, or "other." Whenever possible, we located and identified the original source of each load.

At each colony we followed laden foragers in order to locate their nests. We partially excavated nests to confirm the location of their fungus garden. In addition, we collected one complete colony.

Voucher specimens from this study have been deposited at the National Museum of Natural History, Washington D.C.

RESULTS

Foraging selectivity

Acromyrmex octospinosus foragers carried a wide variety of vegetable matter (Table 1). There were great differences among the twelve colonies and even between trails of the same colony (Table 1). The fresh leaf material that the ants cut came primarily from leaves of herbs or from tree seedlings. For example, in the colony with the highest proportion of fresh leaf fragments (colony 8), all leaf material came from small *Acacia* seedlings growing in the area. Foragers also commonly cut pieces of fallen leaves, sections of herbs (herb stems and stems with leaves, leaf buds, or flowers), fruits, petals, and flower buds, plus variable amounts of other types of plant material (petioles, seeds, bark, sticks, and wood slivers). At several colonies, foragers carried insect frass, apparently from caterpillars. Although we once found *A. octospinosus* foragers with fruit fragments descending a small tree, we never found foragers cutting the leaves of large trees.

The general types of material gathered by the Pacific *A. octospinosus* foragers was very similar to those gathered by the Atlantic *A. octospinosus* foragers, except that the Pacific *A. octospinosus* foragers harvested less fruit and more insect frass (Table 2).

Nesting Habits

We located the nests of all eighteen *A. octospinosus* colonies. All nests were very shallow and required little excavation. Twelve nests were directly in contact with a tree or woody shrub: eight under organic debris at the base of trees or woody shrubs, two under organic debris on top of tree buttress roots, and two in tree crevasses (one and two meters above the ground). Three nests were associated with artificial substrates: one under roofing slates piled in a gully, one between two pieces of sheet metal on the forest floor, and one in the cracked cement foundation of a building. Finally, two nests were under organic debris in open soil areas and one was in a crevice of a rock outcrop.

Within the *A. octospinosus* nests there was a noticeable bimodal worker size-distribution with two distinct size castes of workers. Only the large workers left the nest to forage.

TABLE 1. FORAGING SELECTIVITY BY TWELVE COLONIES OF *ACROMYRMEX OCTOSPINOSUS* IN PALO VERDE NATIONAL PARK ("A" AND "B" REFER TO TWO TRAILS FROM THE SAME COLONY).

Colony		(n)	fresh leaf	fallen leaf	herb part	fruit	flower	frass	other
1	A	(25)	8	7	0	8	2	0	0
	B	(25)	3	1	0	18	2	0	1 (bark)
2	A	(25)	4	8	8	0	3	2	0
	B	(25)	0	0	0	9	0	16	0
3	A	(25)	6	0	0	0	1	14	4 (seeds)
	B	(25)	6	12	4	0	0	1	2 (leaf stipules)
4		(25)	5	4	3	6	7	0	0
5		(25)	10	5	1	1	3	2	3 (soil)
6		(25)	4	0	0	17	0	4	0
7		(25)	2	21	0	0	1	1	0
8		(25)	22	1	1	0	1	0	0
9		(25)	1	0	0	0	23	0	1 (leaf stipule)
10		(14)	0	4	0	0	9	0	1 (leaf stipule)
11		(11)	3	2	0	0	5	0	1 (wood sliver)
12	A	(25)	14	4	4	0	0	0	3 (2 sticks, 1 seed)
	B	(25)	18	1	3	1	0	2	0
Total		(375)	106	70	24	60	57	42	16

DISCUSSION

The foraging ecology of the Pacific *Acromyrmex octospinosus* appears to be very similar to that of the Atlantic *Acromyrmex octospinosus* (Table 2; Wetterer 1991). The colonies from both areas produce two distinct size castes of workers. The smaller workers stay inside the nest, tending the fungus garden and brood, while the large workers forage. Both Pacific and Atlantic *Acromyrmex octospinosus* show seasonal variation in foraging activity, with primarily diurnal foraging in the wet season and primarily nocturnal foraging in the dry season (Wetterer 1991). Both also primarily cut the leaves and other parts of small herbs and scavenge on fallen leaves, fruits, and flowers (Wetterer 1991). The Pacific ants, however, harvested less fruit and more insect frass than was recorded for the Atlantic ants (Table 2). The great variability in selectivity both among colonies and between trails of the same colony suggests that *A. octospinosus* foragers are opportunists and shift their selectivity based on resource availability (Table 2, see also Lewis 1975, Wetterer 1991). Rather than a strict "leaf-cutting" ant, *A. octospinosus* seems to be a scavenger of small herbs, fallen vegetation, and other organic material.

Many genera of "lesser" fungus-growing ants commonly collect insect frass as a substrate for growing fungus (Weber 1972, Hölldobler & Wilson 1990), though this is rarely observed in leaf-cutting ants (generally << 1% of loads, personal observation). Frass would appear to be well suited for fungal growth, but probably rarely occurs in great enough quantities to support large colonies of leaf-cutting ants. At the time of

TABLE 2. FORAGING SELECTIVITY BY COLONIES OF THE PACIFIC *ACROMYRMEX OCTOSPINOSUS* COMPARED WITH THAT OF COLONIES OF THE ATLANTIC *ACROMYRMEX OCTOSPINOSUS* (WETTERER 1991), *ACROMYRMEX VOLCANUS* (WETTERER 1993), AND *ACROMYRMEX CORONATUS* (WETTERER 1995), AND SMALL COLONIES OF *ATTA CEPHALOTES* (WETTERER 1994A).

Species	(n)	% fresh leaf	% fallen leaf	% herb part	% flower	% fruit	% other
A. octospinosus							
Pacific	(375)	28	19	6	16	15	15
Atlantic	(275)	23	17	9	19	27	5
A. volcanus	(239)	33	8	15	33	6	7
A. coronatus	(380)	82	11	2	3	1	2
A. cephalotes	(200)	97	0	0	1	1	1

our study, the start of the wet season, there was a population explosion of caterpillars at Palo Verde, resulting in a hyperabundance of caterpillar frass.

The nesting habits of the Pacific *A. octospinosus* also appears to be very similar to that the Atlantic *A. octospinosus*, as well as those of other *Acromyrmex* species (Weber 1945; Wetterer 1991, 1993). At La Selva Biological Station, on the Atlantic slope, *A. octospinosus* most commonly nests under organic matter at the base of trees (Wetterer 1993). A similar pattern of nesting for *A. octospinosus* has also been reported by Weber (1945). In contrast, *A. cephalotes* colonies excavate nests deep underground (Weber 1972).

The question arises as to why the two major pest species of leaf-cutting ants in Costa Rica, *Atta cephalotes* and *Atta colombica* Guérin, are absent at Palo Verde, but are common in other dry forest areas of similar climate and vegetation in western Costa Rica, e.g., Santa Rosa National Park, where they co-occur with *A. octospinosus* (Rockwood 1973; J. Wetterer, personal observation). The presence of an alate Atta queen indicates they are not excluded due to limitations of dispersal. Instead, a possible explanation may lay in the soil of Palo Verde, a vertisol with a high proportion of montmorillonite clay (E. Olson, personal communication). This soil absorbs water into its lattice when wet, increasing its volume dramatically (Fanning and Fanning 1989). When the wet soil swells, pore spaces are squeezed out, resulting in very poor drainage and aeration. When the soil dries, it contracts and meter deep cracks form. Surface material fills these cracks causing soil "inversion," hence the name vertisol. Vertisol soil may not be suitable for deeply excavated nests such as those of most *Atta* species, due to insufficient aeration in the wet season and excessive exposure in the dry season (E. Olson, personal communication). The superficial nests of *A. octospinosus* may not suffer from these problems. The soil type may also indirectly explain the insect frass collected by *A. octospinosus*, because many of the lesser fungus-growing ants that collect insect frass also have deep nests (Wetterer, personal observation), and thus may be absent at Palo Verde. Surveys for leaf-cutting ants and other fungus-growing ants in areas of different soil types are needed to test these hypotheses.

In conclusion, although taxonomic studies may distinguish differences between the Pacific and Atlantic *A. octospinosus*, we could find no notable ecological differences in foraging or nesting ecology between sites. This result is particularly surprising considering the distinct differences in vegetation between the Pacific dry forest and the Atlantic rain forest of Costa Rica (see Janzen 1983).

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TWO NEW SPECIES OF *LEPTOHYPHES* (EPHEMEROPTERA:LEPTOHYPHIDAE) FROM ECUADOR

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ABSTRACT

Leptohyphes liniti New Species and *Leptohyphes nicholsae* New Species are described from larvae taken in Ecuador. *Leptohyphes liniti* has a highly developed ridge on the hind femora and otherwise is most similar to *Leptohyphes tacajalo* Mayo, also from Ecuador. *Leptohyphes nicholsae* is closely related to *L. curiosus* Lugo-Ortiz and McCafferty, described from Costa Rica, but differs in the presence of abdominal tubercles and color pattern.

Key Words: Ephemeroptera, Leptohyphidae, *Leptohyphes liniti*, *Leptohyphes nicholsae*, New Species

RESUMEN

Leptohyphes liniti Nueva Especie y *Leptohyphes nicholsae* Nueva Especie son descritas a través de larvas colectadas en Ecuador. *Leptohyphes liniti* tiene una cresta muy desarrollada en los fémures posteriores, pero es muy similar a *Leptohyphes tacajalo* Mayo, también de Ecuador. *Leptohyphes nicholsae* está cercanamente relacionada a *Leptohyphes curiosus* Lugo-Ortiz & McCafferty, descrita de Costa Rica, pero difiere en la presencia de proyecciones abdominales y en el color del abdomen.

Leptohyphes Eaton is a New World mayfly genus with 73 currently recognized species and has been treated by Eaton (1882, 1892), Navás (1920, 1931), Ulmer (1920), Needham and Murphy (1924), Traver (1943, 1958), Allen (1967, 1973, 1978), Mayo (1968), Brusca (1971), Allen and Roback (1969), Allen and Brusca (1973), Kilgore and Allen (1973), Allen and Murvosh (1987), and Lugo-Ortiz and McCafferty (1995). Most species of *Leptohyphes* are known from only larvae or only adults, and thus the taxonomy of the genus will remain difficult until stage associations are established (Lugo-Ortiz and McCafferty 1995). The various and sometimes unreliable characters (e.g., apical spine on abdominal gill 2, which actually originates from underlying gill filament of gill 2) used to describe species of *Leptohyphes* in the past suggest that the status of several species requires further review.

Recently, one of us (RWS) collected mayflies from northern Ecuador, including two distinctive new species of *Leptohyphes*. These species are named after M. L. Linit and B. J. Nichols, who helped to collect the material upon which the descriptions herein are based. Except where noted, the materials examined are deposited in the Wilbur R. Enns Entomology Museum at the University of Missouri-Columbia, USA. All materials examined were collected by the three collectors indicated above.

Leptohyphes liniti Wang, Sites and McCafferty, New Species
(Figs. 1-8)

Larva: Body length 4.5-6.0 mm; caudal filaments ca 3.0-4.0 mm. General color reddish brown to light brown. Head patterned and setae as in Fig. 1. Body with scattered minute spicules and without tubercles. Labrum dorsally with scattered, simple setae and two to three rows of branched setae along the anterior margin (Fig. 2); mandible with partially fused incisors (Figs. 3-4); hypopharynx with poorly developed superlinguae, superlinguae with simple and branched setae (Fig. 5); maxillary palpi three-segmented (Fig. 6); labium with well-developed postmentum, labial palpi with long setae, glossae reduced and with several branched setae (Fig. 7). Pronotum with lateral margins rounded and produced in anterior half (Fig. 1). Fore femora with well-developed median transverse ridge with spines (Fig. 1); mid- and hind femora with elevated longitudinal ridge (highly developed in hind femora) extending from near base to apex of femur, dorsal margins with prominent flat, long, blunt spurs (socketed) and minute setae (Fig. 1); hind femora about 40% longer than fore femora, with ridge width more than one-half length; hind tibiae with row of hairlike setae on ventral and dorsal margins; hind tarsi about one-third length of hind tibiae; tarsal claws with single row of four to six denticles. Abdomen with scattered spicules; lateral flanges developed on segments 2-7 (anterior margins of hind femora fitting on lateral flanges); segments 6-9 with posterolateral projections; sterna reddish brown except hyaline laterally on sterna 2-7. Abdominal gills 2 with basal spine (or projection) (Fig. 8). Caudal filaments with narrow dark brown bands near base in female (Fig. 1), and with broad dark brown area near middle in male.

Adult: Unknown.

Holotype: Female larva, Ecuador, Carchi Prov., Rio San Juan, 1.8 km E Maldonado, 2198 m, 16 July 1993. Paratypes: Nine larvae, same data as holotype; nine larvae, Napo Prov., 6.2 km S Baeza (old town), 1865 m, 21 July 1993 (two housed in the Purdue Entomological Research Collection, West Lafayette, Indiana; two housed in the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; and two housed in Universidad Católica, Quito, Ecuador).

Other material examined: 14 larvae, same data as holotype; 20 larvae, Napo Prov., 6.2 km S Baeza (old town), 1865 m, 21 July 1993; three larvae, Pichincha Prov. Rio Toachi nr footbridge, 0.3 km E Tinalandia, 741 m, 19 July 1993; one larva, Pichincha Prov., tributary of Rio Toachi, 2.6 km S La Union del Toachi at dirt rd S from new Quito Rd, 975 m, 19 July 1993; two larvae, Pichincha Prov., Rio Dos Rios at Dos Rios, 7.0 km NE on old Quito Rd, 1292 m, 19 July 1993; 42 larvae, Napo Prov., Rio Quebrada Juve, 1996 m, 20 July 1993.

Discussion: *Leptohyphes liniti* appears similar to *Leptohyphes tacajalo* Mayo from Ecuador, but differs in the highly developed hind femora with marginal spurs and the well-developed marginal rows of hairlike setae on the hind tibiae.

Larvae were taken in small to large streams with substrates consisting of stones, stones in sand, and stones in vegetation. Elevations of the collection sites ranged from 741 to 2195 m and water temperatures ranged from 15-22°C.

Leptohyphes nicholsae Wang, Sites and McCafferty, New Species
(Figs. 9-16)

Larva: Body length 3.0 mm; caudal filaments ca 1.0 mm. Color pattern as in Fig. 9. Head pale brown, fringed with numerous long, fine, simple setae; ocelli raised slightly on rudimentary tubercles; antennae pale yellow, nearly as long as head width.

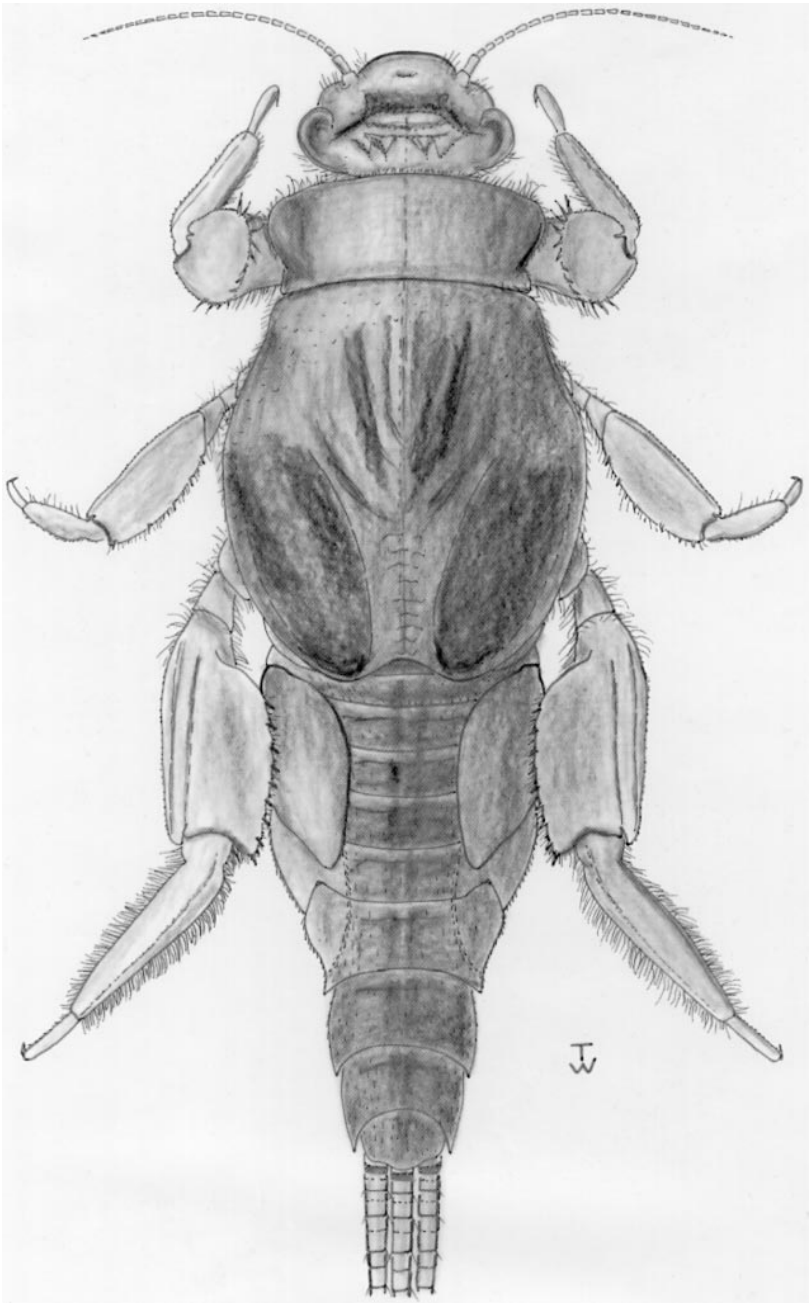
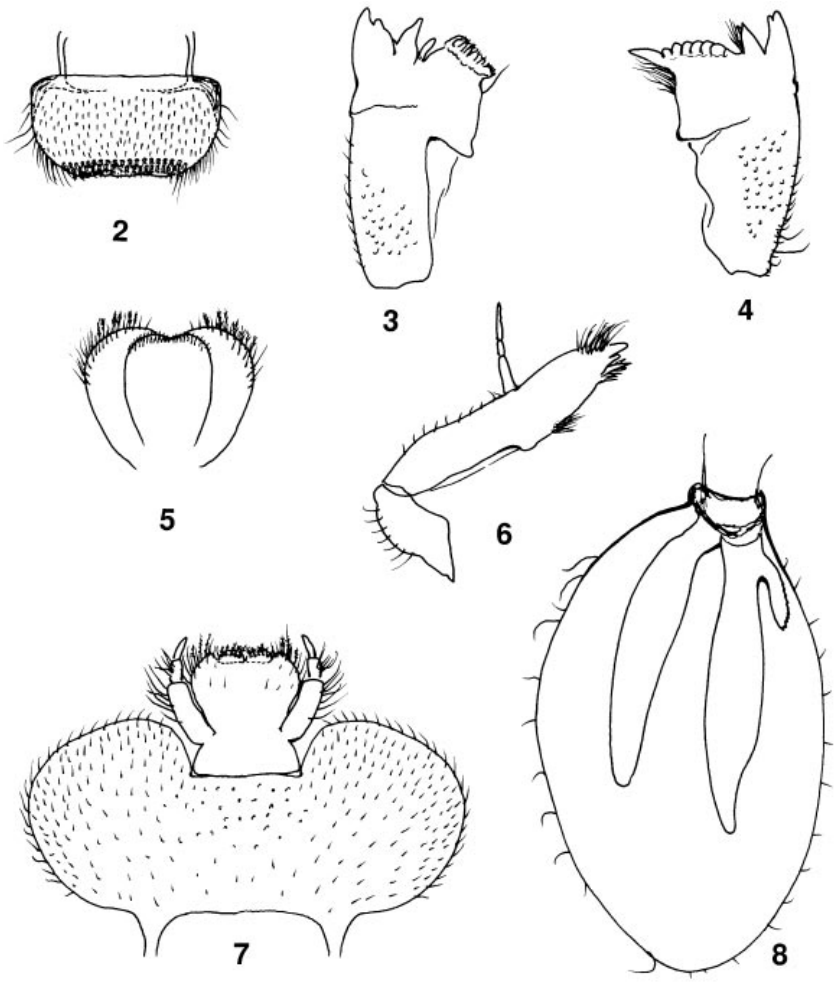


Fig. 1. *Leptohyphes liniti* Wang, Sites and McCafferty, New Species, larva, dorsal view.



Figs. 2-8. *Leptohyphes liniti* Wang, Sites and McCafferty, New Species, larva. 2. Labrum; 3. Left mandible; 4. Right mandible; 5. Hypopharynx; 6. Maxilla; 7. Labium; 8. Gill 2, ventral.

Labrum mostly with branched setae (Fig. 10); mandible with partially fused incisors (Figs. 11-12); hypopharynx with well-developed superlinguae and marginal setae (Fig. 13); maxillary palpi absent (Fig. 14); labium with regularly developed postmentum, labial palpi with sparse setae, glossae small and with apical branched setae (Fig. 15). Lateral margins of pronotum nearly parallel, fringed with fine, simple setae; fore femora with well-developed, curved, setose transverse ridge in basal half of anterior surface (Fig. 9); mid- and hind legs with color pattern as shown in Fig. 9; mid- and hind femora and tibiae with long, fine, simple setae on ventral and dorsal margins; hind femora subequal in length to fore femora; hind tibiae and hind tarsi subequal in length; tarsal claws about half as long as tibiae, and with single row of four to six den-

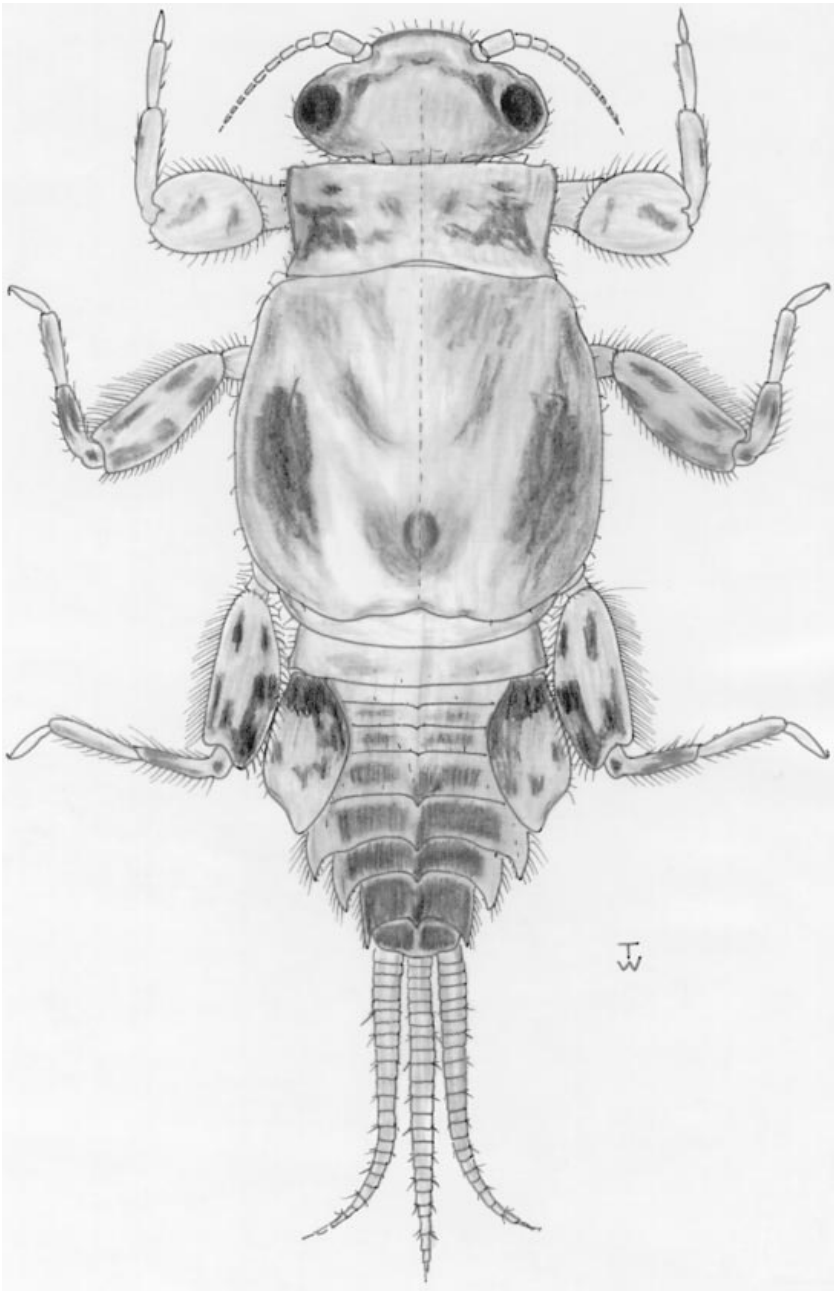
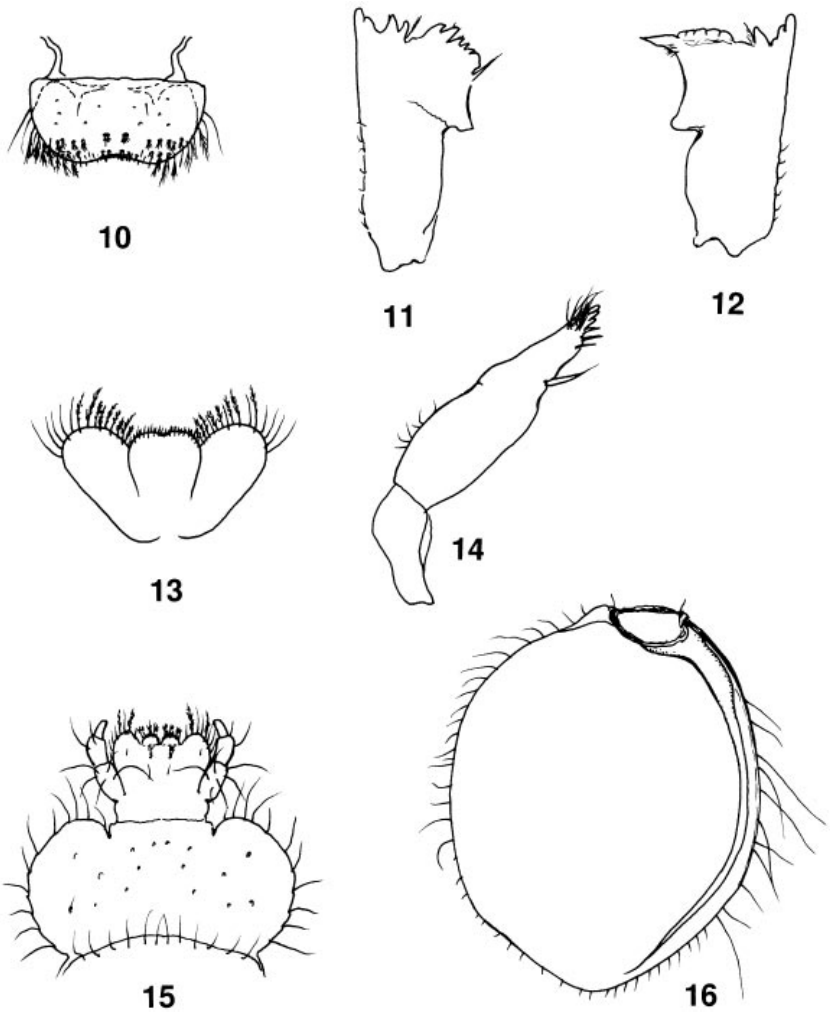


Fig. 9. *Leptohyphes nicholsae* Wang, Sites and McCafferty, New Species, larva, dorsal view.



Figs. 10-16. *Leptohyphes nicholsae* Wang, Sites and McCafferty, New Species, larva. 10. Labrum; 11. Left mandible; 12. Right mandible; 13. Hypopharynx; 14. Maxilla; 15. Labium; 16. Gill 2, ventral.

ticles. Abdominal terga 3-9 each with midposterior tubercle (strongly developed on terga 6-9); abdominal segments 3-9 with well developed posterolateral projections, and 3-8 with moderately developed lateral flanges (Fig. 9); sterna pale yellow. Operculate gills with underlying gill filament longer than operculate gill (Fig. 16), without basal spine, pale yellow, ovate, weakly pointed distally, with distinct basal and median blackish markings (Fig. 9). Caudal filaments without dark brown banded segments, with whorls of short, simple setae at alternating articulations (Fig. 9).

Adult: Unknown.

Holotype: Male larva, Ecuador, Pichincha Prov., Rio Peripa at Puerto Limon, 314 m, 18 July 1993. Paratype: Female larva, same data as holotype.

DISCUSSION

Leptohyphes nicholsae appears to be closely related to *Leptohyphes curiosus* Lugo-Ortiz and McCafferty from Costa Rica because both species possess the following attributes: small size, similar operculate gill shape, ridge and setal arrangements on the legs, and the well-developed posterolateral projections on abdominal segments 7 and 8 (see Lugo-Ortiz and McCafferty 1995). It differs from *L. curiosus* by possessing tergal tubercles and a different color pattern on the legs and operculate gills. Lugo-Ortiz and McCafferty (1995) noted the unique characteristics of *L. curiosus* and commented that it did not exactly fit the traditional definitions of either *Tricorythodes* Ulmer or *Leptohyphes*. They further suggested that it was representative of a distinct Neotropical lineage within *Leptohyphes*. The discovery of *L. nicholsae* shows indeed that the lineage consists of more than one species.

The new species is known from only one collecting site. The Rio Peripa, where it was taken, was at low elevation (314 m) at Puerto Limon. The collecting site was approximately 30 m wide, had a stony substrate, and a water temperature of 24°C.

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THE LYGAEIDAE OF THE CAYMAN ISLANDS WITH THE DESCRIPTION OF A NEW SPECIES OF *OCHRIMNUS* (HEMIPTERA)

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ABSTRACT

A key to the 50 species known from the Cayman Islands is provided, brief descriptions are given and the origin and relationships of the lygaeid fauna are discussed. A new species is described and new synonymy is presented.

Key Words: Cayman Islands, Lygaeidae, new species

RESUMEN

Se introduce una clave para las 50 especies que se conocen de las islas Caimán, se presentan descripciones breves, y se discuten el origen y las relaciones de la fauna Lygaeidae. Se describe una especie nueva y se introduce nueva sinonimia.

The insect fauna of the Cayman Islands has received considerable attention in recent years. Our own interest in these islands has been stimulated by this work since we have for a number of years been concentrating a considerable part of our research and field work on the lygaeid fauna of the West Indies. It thus seems appropriate to

bring together our information on these interesting islands, discuss the faunal relationships, and present a faunal list that is more in keeping with the actual species composition than that currently reflected in the literature.

The natural history and biogeography of the Caymans have been treated in detail by Brunt & Davies (1994) and will not be repeated here except to note that the islands are all low lying and are closer geographically to such islands of the Greater Antilles as Cuba and Jamaica than they are to any of the small island groups of the Caribbean.

One of the interesting aspects of the Cayman lygaeid fauna is that, in contrast to the butterfly fauna (Askew 1994) in which endemism occurs only at the subspecific level, at least 5 species are endemic. It must be admitted, however, that the Lygaeidae have not been collected as intensively as the butterflies of the Caribbean. Thus some of the apparent Cayman endemics may be the result of limited collecting on other islands. Nevertheless, the Cuban lygaeid fauna have been more carefully studied in the past than has that of any of the other islands, and we have collected extensively on Jamaica without taking any of these endemic species.

Our prior knowledge of the Cayman fauna comes from the 1938 Oxford University Expedition material that was studied by Scudder (1958). He reported 17 species present of which four were described as new. Askew (1994) noted that thirteen species were collected on Grand Cayman, eight on Cayman Brac, and three on Little Cayman. Slater (1964) listed the same species. Froeschner (1983) listed two species from Grand Cayman Island, one of which represented an additional species. Based on our collecting over the past 10 years, we can list a total of 50 species, a number surprisingly close to the known butterfly fauna. With this number of species we feel confident that we have a reasonably complete inventory of the fauna of the Caymans.

From the outset we have been interested in the possible vicariant nature of the fauna relative to overwater dispersal. We feel that it is not yet possible to analyze statistically the number of species relative to island size, particularly because Little Cayman seems relatively poorly collected. Nor can we make meaningful contributions to the degree of faunal "turnover" due to arrival of new immigrants and extinction of elements of the known fauna. We do believe that our present knowledge of the lygaeid fauna provides a base line from which future studies can be profitably pursued. All species described as endemic by Scudder (1958), with the exception of *Ozophora minuscula* Scudder, have been taken on the Cayman Islands and none have been taken on any other island of the Caribbean. We also recognize one additional new species as endemic so that at least 5 species are considered endemic, or 10% of the fauna. Askew (1994) commented upon the dominance of Lygaeidae in the Hemiptera fauna, at least on Grand Cayman, and while he noted that this figure represented only a small fraction of the fauna, he believed that the figures probably accurated reflected the balance of family representatives. We see no reason to doubt the validity of this conclusion.

Of the species that are not endemic on the Caymans, the great majority are widespread in the West Indies. Many of these are "weed species" that live in disturbed habitats and frequently reproduce on a number of host plants, or that live on or below host plants that thrive in ruderal environments.

Dieuches armatipes (Walker) and *Oxycarenus hyalinipennis* Costa are Old World species that have only recently been reported from the Western Hemisphere.

Excluding these recently introduced species what can we conclude about the origin and relationships of the Caymans lygaeid fauna? To attempt to answer this question, we compared the fauna of the Caymans with that of Cuba and Jamaica, the two large islands most likely to have served as source areas. Askew (1994) found that the butterfly fauna of the Caymans was derived predominantly from Cuba. He found that 42 of the 48 butterfly taxa were also in Cuba but only 29 were shared with Jamaica and progressively fewer with Hispaniola, Puerto Rico, and the Bahamas.

The lygaeid fauna, while not contradicting this relationship, does not support it to any extent. Of the total of 50 lygaeid species now known from the Caymans, 39 also occur on Cuba, but 34 occur on Jamaica. Even this difference appears more likely to represent lack of collecting than actual absence of species on one or the other of the islands. For example, *Nysius raphanus* Howard and *Cymodema breviceps* Stål have been reported from Cuba but not Jamaica, but both are widespread almost throughout the Caribbean. Conversely, *Oedancala cladiumicola* Baranowski and Slater is a relatively recently recognized species that is known from southern Florida as well as the Bahamas, Caicos, and Jamaica. It is host specific and is almost certain to be found on Cuba.

We conclude that most, if not all, of the Caymans fauna has reached the islands by overwater dispersal rather than as a result of vicariance. Slater's (1988) paper detailing his disagreement with Rosen's (1985) depreciation of dispersalist concepts, should be consulted to understand our position on this matter.

Although we believe the present evidence strongly supports the probability of overwater dispersal as the primary reason for the present Caymans lygaeid fauna (in agreement with Askew's (1994) conclusions on the butterfly fauna), we feel that while Cuba may well be the source area from which much of the fauna is derived, the majority of species are so widespread in the Caribbean that it is impossible to demonstrate this.

In support of our hypothesis that the origin of the Cayman fauna is primarily the result of overwater dispersal, several points should be considered. Most important is to consider what is not there, as Rosen (1985) and some other biogeographers seem reluctant to do. None of the higher taxa that have restricted distributions in the Greater Antilles are present. Particularly striking is the absence of the Pamphantinae. Slater (1988) indicated that the distribution on the islands suggests vicariance between Cuba and Hispaniola (and possibly Puerto Rico) since a number of sister taxa occur on the two islands and the subfamily is not otherwise represented in the West Indies, including its absence from Jamaica. This still seems essentially true for the islands, although extensive collecting in South America has revealed a considerable pamphantine fauna. Concepts of the taxon as an island-mainland vicariance example, however, will require cladistic reexamination once the mainland fauna is better understood.

None of the endemic antillocorine West Indian genera, such as *Bathydema* and *Antillodema*, are present on the Caymans, nor are representatives of the geocorine *Ninyas* that occurs in less disturbed habitats in both Jamaica and Cuba.

Several widespread Caribbean species are absent, indicating a rather random dispersal pattern. Examples are *Pachygrontha compacta* Distant and *Oedancala bimaculata* (Distant), both of which are sedge feeders and might be expected on the islands. The absence of *Ozophora rubrolinea*, an abundant species on the north coast of Jamaica, and common on the mainland of Central and northern South America is unexpected. Its absence appears to be real, for members of the genus come to lights abundantly, and a number of widespread species of *Ozophora* are common on the Caymans.

Thus we see a general pattern of a fauna composed primarily of species very widespread on the islands. This distribution suggests the importance of overwater colonization in producing this pattern, even relative to the two species apparently recently introduced from the Eastern Hemisphere. Superimposed on this basic pattern is the presence of several endemic species and the absence of some widespread and common species, as well as the absence of taxa that tend to be restricted to islands of the Greater Antilles.

All measurements are given in millimeters. The following abbreviations are used; RMB - Richard M. Baranowski collection, JAS - James A. Slater collection, USNM - United States National Museum, BMNH - British Museum of Natural History. Orig-

inal references are not given as they can be found in Slater (1964) or Slater and O'Donnell (1996). We are aware of the higher classification proposed by Henry (1997), but prefer to retain the traditional classification for a faunal paper of this type.

KEY TO THE CAYMAN ISLANDS SPECIES OF LYGAEIDAE

1. Suture between abdominal sterna 4 and 5 curving forward laterally and not attaining lateral margin of abdomen (Rhyparochrominae) 2
1'. Suture between abdominal sterna 4 and 5 straight or nearly so and attaining lateral margin of abdomen 32
2. With at least spiracles of abdominal segments 3 and 4 located dorsally 3
2'. All abdominal spiracles located ventrally 4
3. Lateral margins of anterior pronotal lobe carinate or explanate; only spiracle of abdominal segments 3 and 4 located dorsally (Rhyparochromini) . . . . . *Dieuches armatipes*
3' Lateral margins of anterior pronotal lobe rounded; abdominal spiracles on segments 2, 3, and 4 located dorsally (Myodochini) 16
4. Apical corial margins deeply concave on inner half (Antillocorini) 5
4'. Apical corial margin straight or nearly so 6
5. Posterior pronotal lobe uniformly brown . . . . . *Botocudo* species
5'. Posterior pronotal lobe brown with pale markings . . . . . *Cligenes distinctus*
6. Trichobothria on abdominal sterna 4-5 arranged in a longitudinal linear row with posterior trichobothrium located caudad of spiracle 5; head dorsally with an iridescent area at base; usually with a trichobothrium present at each antero-lateral pronotal area (Lethaeini) . . . . . *Paragonatas divergens*
6'. Two posterior trichobothria on segments 4 and 5 located dorso-ventrad of one another; head above lacking iridescent areas; never with antero-lateral pronotal trichobothria (Ozophorini) 7
7. Forewings coleopteroid, meeting along midline; membrane absent or greatly reduced . . . . . *Ozophora coleoptrata*
7'. Forewings macropterous, fully developed 8
8. Dorsal surface of body with short, but distinct upstanding hairs (viewed laterally) 9
8'. Dorsal surface glabrous or with scattered decumbent hairs, or at most an isolated upstanding hair 10
9. Small species, 5 mm or less in length . . . . . *Ozophora coleoptrata*
9'. Larger species, more than 5 mm in length . . . . . *Ozophora burmeisteri*
10. Bucculae U-shaped; head anteriorly declivent, almost at a right angle to body length . . . . . *Ozophora laticephala*
10'. Bucculae V-shaped; head somewhat declivent, but never downward curved at almost a right angle to body length 11
11. Small species, less than 4.75 mm in length . . . . . *Ozophora minuscula*
11'. Larger species, well over 5 mm in length 12
12. Femora dark brown . . . . . *Ozophora pallidifemur fuscifemur*
12'. Femora stramineous, with or without a brown annulus, never completely dark brown 13
13. Humeral pronotal angles weakly, but distinctly notched . . . . . *Ozophora pallidifemur pallidifemur*
13'. Humeral pronotal angles evenly rounded 14
14. Membrane completely dark, lacking a conspicuous white apical macula or stripe . . . . . *Ozophora umbrosa*

14'. Apex of membrane with a conspicuous pale macula or stripe 15
15. Hemelytra anterior to transverse dark fascia variegated with brown and yellow areas (sometimes colors obscured in very pale faded specimens) . . . . . *Ozophora quinquemaculata*
15'. Hemelytra anterior to transverse dark fascia either completely pale and strongly contrasting or at most with oblique dark dash on corium laterally at level of distal ½ of scutellum . . . . . *Ozophora caroli*
16. Interocular distance less than postocular distance . . . . *Myodocha unispinosa*
16'. Interocular distance greater than postocular distance 17
17. A crescent-shaped striated area present ventro-laterally on anterior portion of abdominal sternum 18
17'. Striated area lacking on anterior portion of abdominal sternum 19
18. Pronotum markedly bilobed with transverse impression deeply incised; forefemur with spines present on both inner and outer edges of ventral surface . . . . . *Froeschneria piligera*
18'. Pronotum with transverse impression not deeply incised; forefemur with spines present only along inner edge of ventral surface. . . . . *Ligyrocoris litigiosus*
19. Evaporative area covering a considerable portion of metapleuron; more than 3 rows of claval punctures; 3rd antennal segment usually longer than interocular distance 22
19'. Evaporative area around metathoracic scent gland auricle reduced to a narrow band around auricle; claval punctures usually in 3 rows; length of 3rd antennal segment usually less than interocular distance (*Prytanes*) 20
20. First antennal segment with distal end dark . . . . . *Prytanes confusa*
20'. First antennal segment unicolorous throughout 21
21. Forefemora light yellow . . . . . *Prytanes minima*
21'. Forefemora chiefly dark brown . . . . . *Prytanes dissimilis*
22. Mesoacetabulum with mesepimeron emergent from between meso- and metepisternum 23
22'. Mesepimeron enclosed by metepisternum touching mesepisternum 29
23. Head relatively elongate with a distinct "neck" present; postocular distance equal to or greater than distance between ocelli (*Heraeus*) 24
23'. Head less elongate, lacking a distinct "neck"; postocular distance less than distance between ocelli (*Neopamera*) 25
24. Smaller species (less than 6 mm), apical area of corium and apex of membrane without white areas . . . . . *Heraeus pulchellus*
24'. Larger species (7-8 mm), apical area of corium with large irregular white macula; apex of membrane with median white area . . . . . *Heraeus triguttatus*
25. Fourth antennal segment with a conspicuous white or light yellow subbasal annulus 26
25'. Fourth antennal segment unicolorous throughout 27
26. Relatively large species (7-10 mm) with eyes strongly produced . . . . . *Neopamera neotropicalis*
26'. Relatively small species (less than 6 mm), eyes not large, not prominently produced . . . . . *Neopamera albocincta*
27. Anterior pronotal lobe impunctate, corium with a distinct dark transverse fascia . . . . . *Neopamera bilobata*
27'. Anterior pronotal lobe punctate, corium nearly uniformly testaceous, lacking a transverse dark fascia 28
28. Third antennal segment only two-thirds length of segment two; smaller species (not over 4.5 mm) . . . . . *Neopamera intermedia*

28'. Third antennal segment much more than two thirds length of segment two; larger species (5 mm) . . . . . *Neopamera vicarius*
29. Elongate (6-9 mm in length); anterior pronotal lobe flattened, slightly convex, in lateral view lower than posterior lobe; pronotal collar with a median "dip" to posterior margin (*Paromius*) 30
29'. Small (not over 5-6 mm); anterior pronotal lobe strongly convex, not lower than posterior lobe in lateral view; pronotal collar essentially straight across midline (*Pseudopachybrachius*) 31
30. Length of anterior pronotal lobe at least 1.8 times length of posterior pronotal lobe; anterior pronotal lobe usually reddish brown . . . . . *Paromius dohrnii*
30'. Length of anterior pronotal lobe less than 1.6 times length of posterior pronotal lobe; anterior pronotal lobe usually black . . . . . *Paromius longulus*
31. Posterior (apical) margin of corium black, posterior femora pale . . . . . *Pseudopachybrachius vinctus*
31'. Posterior margin of corium pale or light brown; posterior femora with dark markings . . . . . *Pseudopachybrachius basalis*
32. Abdominal spiracles on segments 2 through 7 all placed dorsally 33
32'. At least one pair of spiracles on segments 2 through 7 located ventrally . . . 44
33. Clavus punctate; posterior pronotal margin not depressed laterad of base of scutellum . . . . . *Kleidocerys virescens*
33'. Clavus impunctate; posterior pronotal margin depressed laterad of base of scutellum 34
34. General coloration dull yellowish brown, never with bright red or orange markings, apical corial margin sinuate on mesal half; hind wing lacking a subcosta and possessing intervanals (Orsillinae) 35
34'. Generally with red or orange coloration; apical corial margin straight, hind wing possessing a subcosta and lacking intervanals (Lygaeinae) 40
35. Costal margin of corium straight for greater part of length, at least to level of distal end of claval commissure; connexivum often exposed laterad of corium . . . . . *Neortholomus jamaicensis*
35'. Costal margin of corium expanded from base, never straight for distance beyond level of posterior end of scutellum; connexivum not exposed laterad of corium 36
36. Stridulatory structure consisting of a row of fine grooves and ridges present on lateral corial margin (*Xyonysius*) 37
36'. Lateral margins of corium lacking a stridulatory structure (*Nysius*) 38
37. Corium not or scarcely constricted at base; pronotum distinctly longitudinally calloused on each side of midline; veins of corium unspotted or at most very faintly spotted . . . . . *Xyonysius basalis*
37'. Corium conspicuously constricted at base; pronotum not distinctly longitudinally calloused on either side of midline; veins of corium more or less heavily spotted with fuscous . . . . . *Xyonysius californicus*
38. Bucculae low, gradually tapering posteriorly, fading out gradually near base of head . . . . . *Nysius raphanus*
38'. Bucculae high anteriorly, slightly narrowing posteriorly, ending abruptly at or near base of head 39
39. Basal portion of lateral corial margins with prominent hairs . . . . . *Nysius scutellatus*
39'. Basal portion of lateral corial margins devoid of hairs, or at most with minute, extremely small hairs present . . . . . *Nysius tenellus*

40. Scutellum tumid and swollen with a weak median longitudinal carina, but never with lateral areas excavated; lacking a subbasal transverse carina (*Oncopeltus*) 41
40'. Scutellum not tumid and swollen with a median carina and adjacent areas flat or excavated; a subbasal transverse carina usually present 42
41. Hemelytral membrane with a white mark just basad of center . . . . . *Oncopeltus aulicus*
41'. Hemelytral membrane without white markings . . . . . *Oncopeltus fasciatus*
42. Pronotum with 4 short deep transverse impressions present behind calli (*Ochrimnus*) 43
42'. Pronotum often punctate behind calli, but without 4 transverse impressions . . . . . *Ochrostomus pulchellus*
43. Dorsum black except for indistinct ocher pronotal and corial margins . . . . . *Ochrimnus nigriceps*
43'. Dorsum black except posterior pronotal lobe largely orange . . . . . *Ochrimnus bracensis* n. sp.
44. Abdominal spiracles on segments 2 to 5 located dorsally, spiracles of segment 7 located ventrally 45
44'. Abdominal spiracles on at least segments 6 and 7 located dorsally, or all spiracles ventral 48
45. Hemelytra coarsely punctate (Cyminae) 46
45'. Hemelytra impunctate, or at most with a few scattered punctures (Blissinae) 47
46. Head strongly deflexed in front; eyes somewhat stalked and produced away from antero-lateral margins of pronotum; corium chiefly hyaline with only a few mesally located punctures . . . . . *Cymoninus notabilis*
46'. Head not strongly declivent anteriorly; eyes usually in contact with or nearly in contact with antero-lateral pronotal angles; corium not hyaline, densely punctate over almost entire surface . . . . . *Cymodema breviceps*
47. Body relatively short (less than 4 mm); black with white markings; forecoxal cavities open posteriorly . . . . . *Blissus antillus*
47'. Body elongate and slender; gray brown; forecoxal cavities closed posteriorly . . . . . *Ischnodemus praecultus*
48. Abdominal spiracles on segments 3 and 4 located dorsally; eyes protruding and reniform; forefemora not greatly incrassate and not armed below with numerous spines (Geocorinae) 49
48'. All abdominal spiracles located ventrally; eyes not unusually large and reniform; forefemora incrassate and armed below with numerous spines 50
49. Head and pronotum yellow-brown; vertex smooth and shining . . . . . *Geocoris punctipes*
49'. Head and pronotum black, at least pronotum with a strongly contrasting white stripe running longitudinally through meson . . . . . *Geocoris lividipennis*
50. Forefemora only moderately swollen; corium expanded, extending beyond lateral margins of abdomen; bucculae extending to base of head; hind coxae widely separated (Oxycareninae) . . . . . *Oxycarenus hyalinipennis*
50'. Forefemora strongly swollen; corium not extending beyond lateral margins of abdomen; bucculae short, confined to front of head; hind coxae not widely separated (Pachygronthinae) 51
51. Apical corial margin with a distinct dark spot (may be faint) along margin . . . . . *Oedancala crassimana*
51'. Apical corial margin lacking a distinct dark spot . . . *Oedancala cladiumicola*

LYGAEINAE

Ochrimnus bracensis Baranowski & Slater, **NEW SPECIES**

Black, posterior portion of pronotum orange, fourth antennal segment, labium and tarsi brown. Line between black and orange portions of pronotum forming a "W." Head, black areas of pronotum, scutellum, clavus, corium, pleural areas of thorax, and abdominal segments 2-5 densely clothed with decumbent black hairs tipped with gold. Hairs on orange part of pronotum light with gold tips. Lateral margin of membrane narrowly white. Abdominal segment 6 and sternal areas of segments 2-5 and legs with long golden hairs.

Length head 1.0, width 1.20, interocular space 0.75. Pronotum trapezoidal, anterior margin concave, lateral margins straight, posterior margin slightly convex. Length pronotum 1.33, width 2.08. Scutellum with prominent median carina stem and arms. Length scutellum 0.88, width 1.15. Length claval commissure 0.65. Midline distance apex clavus to apex corium 2.10. Midline distance apex corium to apex membrane 2.65. Labium short, extending posteriorly between meso- and metacoxae. Length labial segments I 0.62, II 0.65, III 0.68, IV 0.58. Antennal segments I-III densely clothed with short, decumbent black, gold tipped hairs sparsely interspersed with long upright dark hairs. Segment IV densely clothed with short decumbent gold hairs and long upright gold hairs. Length antennal segments I 0.44, II 1.02, III 0.90, IV 1.06. Total body length 5.50.

Types. Holotype. ♂ CAYMAN BRAC: The Creek, 17-X-1995, H. V. & R. M. Baranowski (blacklight trap). In United States National Museum (USNM). Paratypes. 4♂, 4♀, same data as holotype; 1♂, 2♀, same except 20-X-95; 1♀, same except 6-9-VII-97; 2♂, 3♀ same except 7-XI-95, E. A. Dilbert; 2♀, same except 8-XI-95; 1♀, same except 26-V-96; 1♀, same except 28-V-96; 1♀ 13-VI-96; 2♀, same except 26-VI-96; 1♀, same except 22-VII-96. In R. M. Baranowski, J. A. Slater, United States National Museum, Florida State Collection of Arthropods, American Museum of Natural History collections.

Etymology: Named for the island, Cayman Brac, on which it appears to be endemic.

This striking species very similar to *O. nigriceps*, is readily distinguished by the unique black coloration with only the posterior pronotal lobe a strongly contrasting orange and by the uniquely colored hairs.

Ochrimnus nigriceps Scudder

Moderate sized (5.8-6.8), almost completely black-brown, covered with a dense, decumbent dark pubescence. Apical four-fifths of fourth antennal segment and margin of membrane very narrowly pale.

Grand Cayman (Scudder 1958, RMB,JAS).

Ochrostomus pulchellus (Fabricius)

Head dark brown with pale basal spot. Pronotal calli and 2 broad rays on posterior pronotal lobe dark brown. Area anterior to calli white, lateral areas red. Inner one-half of clavus white, outer one-half dark brown. Corium dark brown with lateral and apical margins broadly white, banded with red stripe just within pale margin. Membrane black with white margin.

Grand Cayman (Scudder 1958, Froeschner 1983, RMB), Cayman Brac (RMB), Little Cayman (RMB).

Oncopeltus aulicus (Fabricius)

Red and black, easily recognizable by the large black macula covering most of posterior pronotal lobe. Usually a conspicuous white bar on forewing membrane.

Grand Cayman (RMB).

Oncopeltus fasciatus Dallas

One of the larger members of the genus (10-12). Orange-red and black. Central area of pronotum with a transverse fascia, most of membrane and appendages black.

Grand Cayman (Froeschner 1983, RMB, NMNH).

ORSILLINAE

Neortholomus jamaicensis (Dallas)

Small (4-5), narrow, elongate. Dull yellowish gray with numerous brown spots on head, pronotum, and hemelytra. Scutellum dark anteriorly with a broad pale Y-shaped callosity.

Grand Cayman (RMB).

Nysius raphanus Howard

Very small (3-4), yellowish brown. Scutellum black, except at extreme distal end. Pronotum short, nearly twice as wide as long. Bucculae very low and tapered to posterior end.

Grand Cayman (RMB).

Nysius scutellatus Dallas

Small (3-3.5), bucculae high anteriorly, ending abruptly at or near base of head. Basal portion of corial margins with prominent hairs.

Grand Cayman (Scudder 1958), Cayman Brac (RMB).

Nysius tenellus Barber

Small (3.6-4), pale yellowish testaceous, bucculae strongly elevated throughout. Pronotum only one-third wider than long. Corial veins usually unspotted. Scutellum bicolored or black.

Grand Cayman (RMB).

Xyonysius basalis (Dallas)

Subequal in size to *X. californicus* and paler in color, yellowish testaceous rather than cinereus. Lateral corial margin scarcely contracted basally, entire lateral corial margin slightly convex rather than straight. Male genital capsule either completely pale yellow or slightly fuscous basally.

Cayman Brac (Scudder 1958).

Xyonysius californicus (Stål)

Moderate sized (4.7-7), dull yellowish to brownish gray. Bucculae very short, scarcely extending midway to base of head, head and pronotum subequal in length. Male genital capsule black with broad pale yellow margin.

Grand Cayman (RMB), Cayman Brac (RMB), Little Cayman (RMB).

ISCHNORHYNCHINAE

Kleidocerys virescens (Fabricius)

Relatively small (3-3.5), with head, pronotum, and scutellum ochraceous with fuscous punctures. Scutellum usually dark anteriorly with distal end pale.

Grand Cayman (RMB).

CYMINAE

Cymoninus notabilis (Distant)

Small (3-3.3), elongate, slender. Head, pronotum, and scutellum somewhat pubescent, dark reddish brown. Corium yellowish with extreme apex darkened. Legs dull yellow. Abdomen usually brownish or yellowish, sometimes, particularly in females, green. Apex of labium and distal tarsal segment fuscous. Second antennal segment 1.5 times length of segment 3.

Grand Cayman (RMB), Cayman Brac (RMB), Little Cayman (RMB).

Cymodema breviceps (Stål)

Moderate sized (3.4-3.7), light yellow-brown with first 3 antennal segments concolorous, head and 4th antennal segment darker. Pronotum with yellow line mesally on anterior half. Scutellum also with median yellow line. Apical margin of corium darker.

Grand Cayman (RMB).

BLISSINAE

Blissus antillus Leonard

Blissus planus Leonard 1968: 151-152. **NEW SYNONYMY**.
Blissus slateri Leonard 1968: 150-151. **NEW SYNONYMY**.

Moderately small (2.5-3.5), posterior pronotal lobe black, strongly contrasting with gray anterior lobe. Labium frequently extending posteriorly beyond middle of mesosternum. Hemelytra white with black-brown markings; membrane white. Both macropterous and brachypterous forms known.

Grand Cayman (RMB), Cayman Brac (RMB), Little Cayman (RMB).

Leonard (1968) described three species of Blissus from the Caribbean: *B. slateri* and *B. antillus* from Puerto Rico, and *B. planus* from Grenada. His descriptions are based largely on color, pruinosity, size, and the shape of the metathoracic scent gland peritreme. In some instances he described a feature for one species, but did not discuss or compare the condition of the same feature in the other species. For example, he stated that the scutellum of *B. slateri* is distinctly punctate, but did not indicate the condition of the punctation in the other two species. In fact, the scutellum is punctate in all three species. We have examined considerable material from Jamaica, Dominican Republic, Trinidad, St. Barthelemy, Dominica, Tortola, Virgin Gorda, and St. Lucia and find the scutellum punctate in all specimens examined. Leonard stated *B. slateri* possesses light straw-yellow setae on the pronotum but that *B. antillus* has silvery setae on the pronotum. We cannot see these differences even in the paratypes examined. Because the scent gland peritreme varies in the island populations we examined, we believe that it is not a reliable differentiating character. We dissected male genital capsules and parameres of several paratypes, representing all three species, as well as from

specimens from other islands and do not find significant differences. In our opinion *Blissus* is represented by a single species in the West Indies. We elect to use the name *antillus* for this species and reduce *B. slateri* and *B. planus* to synonymy.

In addition to our inability to find differentiating features, the West Indian populations occur exclusively in ruderal habitats, suggesting that this is another example of a "weed" species found in disturbed habitats throughout the Caribbean.

The relationship of *B. antillus* to the ubiquitous Florida chinch bug, *B. insularis* Barber, is important. We have not found differences in the genital capsule or in the parameres between West Indian specimens and specimens from Florida. However, this is the case with a number of apparently distinct species of *Blissus*.

B. insularis can be separated from *B. antillus* by a combination of characters. *B. insularis* always has uniformly straw-colored legs whereas *B. antillus* varies from having dark brown legs to light brown with a dark brown annulus on one or more femora. The most constant differentiating feature is the anterior portion of the pronotum, which in *B. insularis*, is covered by a uniform, undivided pubescent band that reached the anterior margin. The pubescent band of *B. antillus* does not reach the anterior margin and is completely, or partially, divided along the midline.

B. insularis does occur in the West Indies, as we have examined specimens from the Bahamas.

Ischnodemus praecultus Distant

Ischnodemus slateri Alayo & Grillo 1982: 58-62 **NEW SYNONYMY**.

Moderate sized (5-5.5). Hemelytra smoky colored with pale white to dull testaceous membrane. Surface of head, pronotum, and scutellum predominantly or entirely dull grayish or reddish brown pruinose. Lateral corial margins grayish brown with shining areas of posterior portion of pronotum separated into three distinct maculae.

Grand Cayman (RMB).

We have examined the holotype of *I. slateri* from Cuba and believe it to be conspecific with the widespread and somewhat variable *I. praecultus*.

GEOCORINAE

Geocoris lividipennis Stål

Small (2.5-3), strikingly colored, with head, pronotum, and scutellum chiefly black contrasting with the pale yellow wings. Pronotum with a complete median longitudinal pale stripe and lateral areas of pronotum often yellow-brown. Vertex granulose.

Grand Cayman (RMB), Cayman Brac (RMB), Little Cayman (RMB).

Geocoris punctipes (Say)

A moderate sized (3-3.5) big-eyed bug; pale straw-yellow, usually with a dark median scutellar stripe. Vertex of head smooth and polished with a median sulcus extending to base of head.

Grand Cayman (RMB).

OXYCARENINAE

Oxycarenus hyalinipennis Costa

Small (3-4), elongate, pronotum and head tapering anteriorly. Head and pronotum uniformly brown with dense, upright hairs, entire hemelytra hyaline. Abdomen and

femora shining dark brown, meso- and metatibiae with a striking median, broad, white annulus.

This insect, known as the cotton seed bug, is a common and widespread species in the Old World tropics. It is an introduced species in the Western Hemisphere and has been established for many years in South America.

Slater & Baranowski (1994) reported it for the first time from the West Indies from Long Island, Bahamas.

PACHYGRONTHINAE

Oedancala crassimana (Fabricius)

A relatively robust yellowish brown species with relatively thick antennal segments. Usually less than 7.5 mm in length. Often with a dark spot present midway along apical corial margin. This is often absent in West Indian specimens, in which case it can be distinguished from *O. acuminata* by the shorter labium; from *O. cladiumicola* by the lack of reddish coloration and from *O. cubana* by the more robust nonlinear body and by not having the scutellum black adjacent to the pale median vitta.

Grand Cayman (Scudder 1958, RMB).

Oedancala cladiumicola Baranowski & Slater

Similar to crassimana, but lacking black spot along apical corial margins. Reddish. Found only on sawgrass.

Grand Cayman (RMB).

RHYPAROCHROMINAE

ANTILLOCORINI

Cligenes distinctus Distant

Small (2.5-3.0), robust with generally dark appearance. Head blackish, anterior pronotal lobe, scutellum, and ventral surface dark brown, strongly contrasting with testaceous hemelytra and legs. Corium with two spots along lateral margins, one at apex of corium, one midway between base and apex. Entire pronotal surface densely punctate with a very coarse row anteriorly, giving impression of a weak pronotal collar.

Grand Cayman (RMB), Cayman Brac (RMB).

Botocudo species

We have collected an apparently undescribed species of the *Botocudo* complex on Cayman Brac. The relationships of species currently placed in *Botocudo* are very unsatisfactory. Therefore, we feel it best to wait until the generic limits of this tribe are studied and redefined before attempting to place this species.

LETHAEINI

Paragonatas divergens (Distant)

Moderate sized (4-5); dark brown with humeral angles of pronotum, an elongate vitta on clavus, and irregular spots on corium yellow. Dorsal surface with sparse upright hairs. Femora dark brown with distal tips pale; tibiae and tarsi light brown.

Grand Cayman (Scudder, 1958, RMB), Cayman Brac (Scudder 1958, RMB).

MYODOCHINI

Heraeus pulchellus Barber

One of the smallest West Indian *Heraeus* species, barely exceeding 4 mm in length; testaceous, lacking an annulus on fourth antennal segment; possesses complete dark brown fascia across hemelytra.

Grand Cayman (RMB), Cayman Brac (RMB).

Heraeus triguttatus (Guerin)

Larger (7-8) than *pulchellus*. Typically bright reddish brown with apex of corium and most of membrane black. Apical area of corium possessing a large irregular white macula. Apex of membrane with conspicuous subquadrate median white area.

We have specimens from Grand Cayman and Cayman Brac that are dark brown rather than bright reddish brown; however, we can find no morphological differences other than the color.

Grand Cayman (Scudder 1958, RMB), Cayman Brac (RMB).

Neopamera albocincta (Barber)

Elongate (5-5.5), pale reddish to reddish brown, postmedian corial fascia generally broken into series of spots. Fourth antennal segment with proximal white annulus. Elongate head relatively more attenuated than *N. bilobata*.

Grand Cayman (RMB), Cayman Brac (Scudder 1958, RMB).

Neopamera intermedia (Barber)

Moderate sized (4-4.5), brownish with pale markings; legs yellowish with a narrow band near distal end of posterior femora; antennae light brown with distal third of segment III and all of segment IV darker.

Grand Cayman (RMB), Cayman Brac (Scudder 1958, RMB).

Neopamera bilobata (Say)

Rhyparochromus scutellatus Dallas 1852: 575-576 **NEW SYNONYMY**.

Resembles *N. albocincta* closely in form and color, but tends to run somewhat darker (although the color is variable), and is slightly larger and more robust and lacks a pale proximal area on the 4th antennal segment.

Dallas' species *N. scutellatus* has been treated as a subspecies of *N. bilobata* since its status was reduced by Van Duzee (1909). Barber (1953) discussed the status, noting the darker femora, relatively shorter anterior pronotal lobe, and shorter second antennal segment. However, such specimens apparently have no geographic significance and occur in many populations. There seems no reason to treat this as a trinomen in the modern concept of the subspecies, and it is here synonymized.

Grand Cayman (Scudder 1958), Cayman Brac (RMB).

Paromius longulus (Dallas)

Elongate, moderate sized (5.5-7), head, anterior pronotal lobe, scutellum and under surface frequently dull black, often thickly clothed with grayish pubescence. Pos-

terior pronotal lobe reddish brown with darker punctures. Corium and clavus dull testaceous. Antennae reddish brown with distal end of third and usually all of fourth segment fuscous.

Grand Cayman (RMB).

Paromius dohrnii Guerin

Light tan, elongate, with anterior pronotal lobe reddish brown and almost twice the length of posterior lobe, with transverse impression shallow and usually obsolete mesally.

Grand Cayman (RMB).

Pseudopachybrachius basalis (Dallas)

Small (3.5-5), robust; lateral corium lacking a distinct postmedian transverse fascia, margins completely pale. Oval pale spot present near inner apical corial angle. Head, pronotum, and scutellum dull black, corium dull yellow with dark brown punctures. Antennae reddish brown.

Grand Cayman (RMB), Cayman Brac (RMB).

Pseudopachybrachius vinctus (Say)

Small (2.8-3.0), head dark, pronotum contrasting with pale hemelytra having a conspicuous black spot on apical corial margin. Fourth antennal segment dark brown, contrasting with 3 pale proximal segments. Legs pale.

Grand Cayman (Scudder 1958, RMB), Cayman Brac (Scudder 1958, RMB), Little Cayman (RMB).

Prytanes minima (Guerin)

Small (2.5-3), reddish brown. Third antennal segment (males in particular) somewhat thickened. Hemelytra variegated. Legs uniformly pale yellow.

Grand Cayman and Cayman Brac (Scudder 1958, RMB).

Prytanes formosa (Distant)

Body relatively elongate, head acuminate, clothed with decumbent sericeous hairs. Anterior pronotal lobe convex, not higher than posterior lobe and considerably narrower. Antennnae prominent, first, third, and fourth segments uniformly dark brown, second segment paler.

Grand Cayman (RMB).

Prytanes dissimilis (Barber)

A relatively robust, moderately large species for the genus (3.5 mm or greater). Scutellum frequently bicolored. Posterior pronotal lobe usually with a median dark stripe. Subdistal ends of middle and hind femora in part dark red-brown.

Cayman Brac (RMB).

Froeschneria piligera (Stål)

Large, robust (7-8) with a deep transverse pronotal impression. Abdominal stridulitrum well developed. Body surface with numerous elongate upstanding hairs.

Head, anterior pronotal lobe, scutellum, and ventral surface black, hemelytra black and dull brown with a transverse macula.

Cayman Brac (RMB).

Ligyrocoris litigiosus (Stål)

Medium sized with a distinct lunate abdominal stridulitrum. First antennal segment pale, fourth antennal segment completely dark. Legs and antennae dull yellow. Femora spotted distally.

Grand Cayman (RMB).

Myodocha unispinosa Stål

Relatively large (8) with very elongate "neck." Head and neck, shining black. Forefemur slender with a single large spine present. Antennae brightly colored, first segment red-brown, strongly shining, contrasting with pale yellow second segment.

Grand Cayman (RMB).

OZOPHORINI

Ozophora umbrosa Slater

Moderately large (5.5-6.5), generally dark chocolate brown with pale spots on corium; membrane lacking pale apical macula. Dorsal surface glabrous. Fourth antennal segment with a conspicuous white annulus.

Scudder (1958) reported *Ozophora atropicta* Barber from the Caymans. Despite our rather extensive collection of *Ozophora* species, we have been unable to collect this species on the Caymans. We have recently examined part of the Scudder material, which is deposited in the Natural History Museum (London—not Oxford as the Scudder paper states). These specimens are *O. umbrosa* Slater, a species not described at the time of Scudder's paper. We are thus referring the Caymans records of *O. atropicta* here.

Little Cayman (Scudder 1958, RMB) Cayman Brac (RMB).

Ozophora burmeisteri (Guerin)

Pronotum nearly uniformly black or dark chocolate brown. Posterior pronotal lobe with yellow streak midway between meson and margin or a pair of yellow spots in same area. Fourth antennal segment with conspicuous white annulus, 3rd segment slightly swollen distally and dark chocolate brown on distal ⅓. Readily distinguishable by the combination of its very dark pronotum and erect dorsal hairs.

Grand Cayman (Scudder 1958, RMB), Cayman Brac (Scudder 1958, RMB).

Ozophora caroli Slater & Baranowski

Body elongate, relatively stout; head, anterior pronotal lobe and broad rays extending through posterior pronotal lobe dark red brown. Anterior pronotal color broadly pale yellow on either side of median red brown spot. Scutellum chiefly dark red brown, but with raised elliptical calloused area yellow, shading anteriorly to reddish brown. Antennal segments I, II, and III pale yellow with distal end of III, proximal end and distal ¾ of IV contrastingly dark chocolate brown. Body nearly glabrous above, lacking conspicuous upstanding hairs.

Grand Cayman (RMB).

Ozophora coleoptrata Slater

Small (3-4.5), chiefly dark chocolate brown with contrasting pale yellow bands on the posterior pronotal lobe, and on the cubital vein of the clavus. Legs and antennae uniformly pale yellow. Dorsal surface possesses numerous upright hairs. Color varies considerably with some specimens pale yellow laterally on the corium.

Slater (1990) described this species from a series consisting only of coleopteroid individuals with the clavus and corium fused and the membrane reduced to a small flap. We have collected immatures on Grand Cayman that molted to macropterous adults. The macropterous form differs from other small (3-4.5) *Ozophora* in having sparse upright hairs on the dorsum.

Grand Cayman (RMB), Cayman Brac (RMB), Little Cayman (RMB).

Ozophora laticephala Slater & O'Donnell

Small (2.8-3.3), short, stout. Generally pale yellow with the posterior pronotal lobe and most of the hemelytra contrasting with the dark anterior pronotal lobe, the latter having pale white or yellow lateral margins. Bucculae U-shaped, rather than V-shaped as in other Caribbean species of *Ozophora*.

Grand Cayman (RMB) and Cayman Brac (RMB).

Ozophora minuscula Scudder

Moderate sized (4.3), markings somewhat similar to *O. pallidifemur*, but much smaller. Known only from the type series consisting of two males collected in a light trap near Georgetown. Dr. Peter Fitzgerald operated a blacklight trap for us for several years but never collected this species.

Originally described and known only from Grand Cayman (Scudder 1958, BMNH).

Ozophora pallidifemur pallidifemur Scudder

Moderate sized (5-5.5), predominantly dark brown with uniformly pale yellow legs. Antennal segments I, II, and III pale with distal ends of II and III darkened. Fourth antennal segment brown with white subbasal annulus. Membrane uniformly dark.

Originally described and known only from Grand Cayman (Scudder 1958, BMNH, JAS, NMNH, RMB).

Ozophora pallidifemur fuscifemur Scudder

Similar to nominal *O. pallidifemur*, but can be separated by the dark brown legs.

Originally described as a distinct species. Slater (1987) reduced this taxon to a subspecies of *O. pallidifemur* on the basis of each being endemic on separate islands.

Cayman Brac (Scudder 1958, RMB), Little Cayman (Scudder 1958, RMB).

Ozophora quinquemaculata Barber

Moderate (5-6) sized, relatively stout with strongly variegated light and dark markings on pronotum and hemelytra. Posterior pronotal lobe with three dark longi-

tudinal stripes, the median one occurring as a broad lobe along the meson, lacking a pale streak. Apical corial margins dark distally from inward extension of dark apical corial macula completely over raised corial margin apex.

Grand Cayman (RMB).

RHYPAROCHROMINI

Dieuches armatipes (Walker)

Large, robust (9-10), variegated with chocolate brown to black and light yellow to almost white. Pronotum with broadly explanate pale lateral margins contrasting strongly with the predominantly dark remainder of pronotum. Scutellum with a pair of small yellow spots. Hemelytra variegated, with a complete transverse dark fascia and large oval elliptical white subapical corial macula.

This African species apparently has recently become established in the Western Hemisphere. It was first reported from Grand Cayman and St. Kitts and from intercepted specimens from the Dominican Republic and Jamaica by Henry and Froeschner (1993). It is also now known from the Florida mainland.

Grand Cayman (Henry and Froeschner 1993, RMB) and Cayman Brac (RMB).

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ORGANIC MULCH AS A FACTOR IN THE NYMPHAL HABITAT OF *MYNDUS CRUDUS* (HEMIPTERA: AUCHENORRHYNCHA: CIXIIDAE)

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ABSTRACT

Certain types of organic mulches spread on the ground in a palm planting with St. Augustine grass, *Stenotaphrum secundatum*, ground cover enhanced the habitat for the nymphal development of *Myndus crudus* Van Duzee, as measured by the greater numbers of adults emerging from mulched areas compared with controls. Plots mulched with chopped and shredded coconut fronds had greater numbers of *M. crudus* than controls. Higher numbers of *M. crudus* emerged from plots with pine bark mulch than from control plots. There were no significant differences in mean numbers of adults captured in plots with eucalyptus and pine bark mulch. The least numbers of adults emerged from plots mulched with pine bark nuggets. *Myndus crudus* nymphs were never in the open but always beneath pieces of mulch. The benefit of mulches to the insects appears to be that of providing shelter.

Key Words: *Myndus*, Cixiidae, Fulgoroidea, palm, lethal yellowing, cultural control

RESUMEN

Ciertas clases de cobertura orgánica dispersada sobre el suelo en un plantío de palmeras con pasto de San Agustín, *Stenotaphrum secundatum*, mejoraron el habitat para el desarrollo de las ninfas de *Myndus crudus Van Duzee*, como fue estimado por el mayor número de adultos emergidos de estas áreas en comparación con testigos. Parcelas con frondas de cocotero picadas y ralladas tenían números mayores de estos insectos que los testigos. Un mayor número de *M. crudus* emergió de parcelas con cáscara de pino picada en comparación con los testigos. El promedio de adultos capturados en parcelas con cobertura de eucalipto y de cáscara de pino no difirió significativamente. Las ninfas de *M. crudus* nunca estuvieron al descubierto, sino siempre debajo de los fragmentos de cobertura. El beneficio de las coberturas orgánicas para *M. crudus* parece ser el de proveer abrigo.

Myndus crudus Van Duzee (Hemiptera: Auchenorrhyncha: Cixiidae), a widely distributed planthopper in the American tropics (Howard et al. 1984, Kramer 1979, Villanueva Barradas 1991), is a vector of lethal yellowing of palms (Howard 1987, Howard et al. 1983). Lethal yellowing is a fast-spreading, destructive disease associated with a phytoplasma to which at least 35 species of Palmae are susceptible, including the economically important coconut palm, *Cocos nucifera* L., and date palm, *Phoenix dactylifera* L. The disease has long been known in western islands of the West Indies, from where it apparently invaded Florida (U.S.A.) and Mexico (Howard 1983, Howard et al. 1984, Villanueva Barradas 1991). It has recently spread to Belize and Honduras (Ashburner et al. 1996). Thus far, there is no evidence implicating any insect species other than *M. crudus* as a potential vector of lethal yellowing.

The nymphs of *M. crudus* develop at or just under soil level on grasses or sedges, and the adults feed on palms (Howard & Villanueva-Barradas 1994, Eden-Green 1978). At least 37 species of grasses (Graminae) and 4 species of sedges (Cyperaceae) have been reported as nymphal hosts of *M. crudus* (Carrillo Ramirez & Piña Razo 1990, Howard 1989, Howard 1990a, Howard 1990b, Piña Quijano 1993, Tsai & Kirsch 1978, Villanueva B. et al. 1987, Zenner de Polania & Lopez A. 1977). When rearing *M. crudus*, Eden-Green (1978) observed that the nymphs were often hidden beneath pieces of coconut fiber. Therefore, we decided to determine whether coconut fiber and similar materials spread on soil among nymphal hosts would improve the habitat for *M. crudus* nymphs, as estimated by the numbers of emerging adults.

MATERIALS AND METHODS

The study was conducted at the Fort Lauderdale Research & Education Center in a 0.6 ha grove of 100 coconut palms and other susceptible species of palms. St. Augustine grass, *Stenotaphrum secundatum* (Walt.) Kuntze, a preferred host of *M. crudus* (Howard 1990b), was the predominant ground cover. Plots (2×2 m) selected at random were not mowed or otherwise disturbed during each experiment.

In the first experiment, which was initiated February 1994, a mulch was obtained by passing coconut palm fronds through a mechanical brush chipper. This material consisted of fine shredded fragments and larger pieces of variable size between 2-5 cm in width and 5-10 cm in length. The material was spread on each of 6 plots (0.05 m^3/plot) and raked lightly so that it settled on soil and allowed the grass blades to emerge. Six similar plots where fiber was not spread were selected as controls.

In May 1994, traps were used to sample adults emerging from the plots. Traps consisted of 60 × 60 × 50 cm plywood boxes. Polypropylene funnels of 5 cm dia and 0.5 cm mouth were fitted over an opening at the center of the top of each box. Transparent plastic test tubes (2.1 × 10 cm) were placed over the funnel mouths. Adults that emerged from the plants attempted to exit through the funnel opening and thus were captured in the tubes and counted.

Emergence traps were placed simultaneously in the center of each of 6 plots with coconut fiber and 6 control plots. Just prior to placing a trap, the grass was agitated vigorously for several minutes to repel any adult Auchenorrhynchous insects from the sample area. Additionally, any adults captured in traps during the first 24 hours were removed and not counted in samples. The traps then remained in place for 1 week, after which the numbers of male and female *M. crudus* captured in emergence vials were determined.

In the second experiment, initiated February 1995, the effect of the following materials on the nymphal habitat for *M. crudus* were tested: (1) pine nuggets, (2) pine bark mulch (Hyponex Corporation, Marysville, Ohio), (3) cypress mulch (Greenleaf Products, Inc., Haines City, Florida) and (4) eucalyptus mulch (AACTION Nursery Products, Inc., Fort Myers, Florida). The length and width of 10 of the larger fragments were determined for each type of material. The materials were spread as in the first experiment in 6 plots per material, with 6 control plots.

Adult *M. crudus* emerging from plots were sampled during June - July, 1995. In each plot, an emergence trap was placed successively for 4 days each in the NE, NW, SW, and SE quadrants, and *M. crudus* female and male adults captured were counted.

Plots were closely examined for *M. crudus* nymphs for 2 hours on the afternoon of October 12, 1995. Grass stolons were carefully parted to examine soil surfaces of about 400 cm^2 at a time, and mulch fragments were lifted to examine the soil surface beneath them.

Data of the experiment with coconut fiber were analyzed by Student's *t*-test and of the experiment with several types of mulch with Analysis of Variance and the Waller-Duncan Bayesian *k*-ratio *t*-test (SAS Institute 1985).

RESULTS

A mean of 4.16 (SEM = 1.74) adults were captured in emergence traps from plots mulched with coconut fiber, compared to 0.17 (SEM = 0.17) adults from control plots ($P \leq 0.05$, t = 2.29). The total of 25 adults captured from mulched plots included 18 males and 7 females.

In the second experiment, the numbers of *M. crudus* adults captured varied among mulch types ($F = 4.08$, df 4, 115, $P < 0.05$)(Table 1). More adults were captured in plots with pine bark mulch than from plots with cypress mulch, pine bark nuggets or the control plots. The highest numbers of *M. crudus* resulted from plots with pine bark mulch and eucalyptus mulch. Similar numbers of *M. crudus* resulted in plots with cypress mulch, pine bark nuggets and the control plots.

There were differences between mulch types in lengths of pieces (F = 13.5, df 3, 36, $P < 0.0001$). Based on the length and width of the largest pieces, pine bark nuggets was the coarsest of the materials in the second experiment, followed by pine bark mulch, eucalyptus mulch, and cypress mulch (Table 2). Pine bark nuggets consisted of large pieces of bark with almost no fine material. All the other materials consisted of about equal volumes of large pieces and fine fibrous material.

During the 2-hour examination of plots on October 12, a total of only 10 *M. crudus* nymphs were observed. All were beneath fragments of mulch. Nymphs occurred singly or in groups of up to three.

TABLE 1. MEAN NUMBERS OF *M. CRUDUS* ADULTS CAPTURED IN EMERGENCE TRAPS IN PLOTS WITH DIFFERENT TYPES OF MULCH.

Mulch material	Mean[1] number of *M. crudus* adults captured ± Standard Deviation
Pine bark mulch	3.04 ± 3.20 a
Eucalyptus mulch	2.00 ± 2.48 ab
Cypress mulch	1.71 ± 1.97 b
Control	1.08 ± 1.41 b
Pine bark nuggets	0.75 ± 1.03 b

[1]Means within a column followed by the same letter are not significantly different (P < 0.05, least significant difference.)

DISCUSSION

The higher numbers of adult *M. crudus* emerging in plots with certain types of organic mulches probably reflects higher numbers of nymphs in these plots. It is not known whether this was due to (1) preference of these microhabitats by ovipositing females, (2) movement of nymphs into plots from adjacent areas, or (3) a greater rate of survival in plots. In any case, the fragments benefit the nymphs of this species by providing shelter.

Possibly, organic mulches may also benefit nymphs indirectly by improving the soil, thus the quality of host plants. The principal benefit to plants of wood mulches is in improving water retention of the soil, thus increasing the availability of water and reducing the rate of leaching of nutrients. The nitrogen content of wood mulch is generally about 0.09% and release of nutrients due to decomposition is extremely slow (Anon. 1994). Release of nutrients from decomposing organic mulch may be important to plants over long periods, but probably would have been insignificant during the period of this experiment.

Based on evidence from the first experiment, that coconut frond mulch enhanced the ground habitat for *M. crudus* development, we expected that any organic mulch would have similar effects. However, other materials differed in this respect. Fewer *M. crudus* adults developed to adult in the coarsest (pine bark nuggets) and finest (cypress mulch) materials than in the materials of intermediate sizes. Whether these dif-

TABLE 2. MEAN WIDTHS AND LENGTHS OF FRAGMENTS (EXCLUDING FINE FIBER) OF DIFFERENT MULCH TYPES TESTED FOR ENHANCEMENT OF *M. CRUDUS* NYMPHAL HABITAT.

Mulch type	Mean width ± SD[1]	Mean length ± SD
Pine nuggets	3.190 ± 1.15 a	6.1 ± 2.22 a
Pine bark mulch	1.620 ± 0.69 b	5.5 ± 1.28 a
Eucalyptus mulch	0.950 ± 0.62 c	3.4 ± 1.07 b
Cypress mulch	0.840 ± 0.31 c	2.4 ± 1.02 b

[1]Means within a column followed by the same letter are not significantly different (P < 0.05, least significant difference.)

ferences in production of the insects were related to the obvious differences in mulch texture, or to volatile substances in the materials, decomposition rates, or other factors is not known. Of the materials tested in the second experiment, pine bark nuggets were ranked lowest in productivity of *M. crudus*. Fine fibrous material, which pine bark nuggets lacked, may be important in enhancing the ground habitat for *M. crudus* nymphs.

The results of this study are applicable to enhancing *M. crudus* populations in lethal yellowing research areas including field trial areas for testing palms for lethal yellowing-resistance. In attempting to subject palms to adequate testing, efforts are made to enhance disease pressure, which is presumably partly dependent on the levels of vector populations (Howard & Harrison 1997). Populations of *M. crudus* may be increased by spreading organic debris among their nymphal host plants to provide shelter. Coconut palm fiber was found to be suitable for this and can be derived from palms on and near the testing site. This technique could be combined with that of maintaining a ground cover of preferred nymphal host plants of this insect (Carrillo Ramirez & Piña Razo 1990, Howard 1989, Howard 1990a, Howard 1990b, Piña Quijano 1993, Tsai & Kirsch 1978, Villanueva B. et al. 1987, Zenner de Polania & Lopez 1977).

On the other hand, elimination of organic debris in palm plantings to reduce the suitability of the habitat for development of *M. crudus* would probably not be a practical management method for lethal yellowing. Continual removal of organic debris from coconut plantations would be prohibitively costly. Additionally, the role of organic debris in improving the water-holding capacity of soil and in slowly releasing nutrients is regarded as beneficial to palms.

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STIMULATION OF SEX PHEROMONE PRODUCTION IN CORN EARWORM MOTHS BY INJECTION OF EXTRACTS OF HEADS OF MALES OF THE CARIBBEAN FRUIT FLY

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ABSTRACT

Females of the Corn earworm moth, *Helicoverpa zea* Boddie, were induced to produce sex pheromone during the photophase, when no pheromone is normally produced, by injection of aqueous extracts obtained from the heads of sexually mature males of the Caribbean fruit fly, *Anastrepha suspensa* (Loew). The amounts of sex pheromone present in extracts of pheromone glands from moths, obtained 1 h after injection of between 0.25-10 head equivalents of extracts, were greater than that present in extracts from females injected with only saline. Moths injected with 1 head equivalent of fly extract produced as much pheromone as was produced by moths injected with 5 pmol of synthetic pheromone biosynthesis activating neuropeptide (PBAN). However, the amount of pheromone was lower in extracts obtained from females injected with 10 head equivalents than in extracts from females injected with 1 head equivalent. ELISA studies, conducted using antisera which binds with PBAN, and the biologically active C-terminal decapeptide fragment of PBAN, indicated that material present in extracts from fly heads bound with the antibody in a dose dependent fashion.

Key Words: Sex pheromone biosynthesis, neuropeptide, Caribbean Fruit fly, Corn Earworm moth

RESUMEN

Palomillas hembra del gusano del maíz, *Helicoverpa zea* Boddie, fueron inducidas para producir feromona sexual durante la fotofase, cuando normalmente no producen feromona, con una inyección de extractos acuosos obtenidos de la cabeza de machos sexualmente maduros de moscas fruteras del Caribe, *Anastrepha suspensa* (Loew). Las cantidades de feromona sexual en los extractos de la glándula feromonal de las palomillas, extraída una hora después de inyectarlas con el equivalente del extracto de 0.25 a 10 cabezas de la mosca del Caribe, fueron mayores que las cantidades presentes en extractos de hembras inyectadas solamente con solución salina. Las palomillas inyectadas con 1 unidad del extracto produjeron una cantidad de feromona igual a la que produjeron palomillas inyectadas con 5 pmol del neuropéptido sintético que activa la biosíntesis de feromona (PBAN, "pheromone biosynthesis activating neuropeptide"). Sin embargo, la cantidad de feromona obtenida de palomillas hembra inyectadas con 10 unidades del extracto de la mosca fué menor que la cantidad obtenida de hembras inyectadas con 1 unidad. Las pruebas de ELISA, las que se realizaron usando antisueros que se enlazan al PBAN, al carbón terminal del fragmento decapéptido del PBAN biológicamente activo, indicaron que el material presente en los extractos de las cabezas de la mosca del Caribe se unió al anticuerpo de una manera dependiente del nivel de la dosis.

Adult females of Heliothine moths including *Helicoverpa* and *Heliothis* species exhibit a diel periodicity of sex pheromone production during which pheromone is produced only during discrete periods of the scotophase (Pope et al. 1982, 1984; Teal et al. 1993). However, females of these moths can be induced to produce pheromone during the photophase, when little or no pheromone is present in the sex pheromone gland, by injection with aqueous extracts of their cephalic ganglia or synthetic pheromone biosynthesis activating neuropeptide (PBAN) (Abernathy et al. 1995; Teal & Tumlinson 1989; Teal et al. 1993).

Decapitation of females of the Hessian fly, *Mayetiola destructor* (Say), inhibits pheromone production and injection of extracts of the heads into decapitated females restores the capacity to produce pheromone (Foster et al. 1991). Injection of PBAN from moths also induces production of pheromone in this fly (Foster et al. 1991). These results indicate that pheromonotropic peptides are used by insects other than Lepidoptera to regulate the diel periodic production of sex pheromone. Males of tephritid fruit flies, like the Caribbean fruit fly (*Anastrepha suspensa* (Loew)), produce and release sex pheromones in a diel periodic fashion (Nation 1990; Epsky & Heath 1993). In this regard, males of *A. suspensa* are similar to other insects, like moths and the Hessian fly, which regulate the diel periodic production of pheromones using pheromonotropic neuropeptides. However, studies on the endogenous regulation of production of pheromones by males of *A. suspensa* have not been conducted. I report here the results of studies conducted to determine if the heads of sexually mature males of *A. suspensa* contained factors that would induce pheromone production when injected into females of the Corn earworm moth, *Helicoverpa zea* (Boddie), and whether these factors had structural similarities with PBAN as indicated by ELISA studies.

Materials and Methods

Insect Cultures:

Females of *H. zea* were obtained as pupae from a colony maintained at our facility and were allowed to eclose in 4-L paper cartons with screen tops under a 14L:10D photoperiod at 26 ± 2°C and 60 ± 5% relative humidity. Newly eclosed females were transferred to different cages daily and were supplied with a 5% aqueous sugar solution soaked onto commercial cotton balls. All experiments with moths were conducted using 2-3 day old females during the 6th-8th h of the photophase, when pheromone is not normally produced (Teal & Tumlinson 1989). Pupae of *A. suspensa* were obtained from cultures maintained at the Division of Plant Industry, State of Florida in Gainesville Florida. Flies were housed in 30 cm^3 screen cages in environmental chambers maintained under the above conditions. Newly eclosed adult males were transferred to new cages daily and provided with a 3:1 mixture of torula yeast hydrolysate and sucrose as food and with water. Males were aged for 10 days prior to use to insure that they were reproductively mature (see Nation 1990). Only male flies were used because this sex produces the attractant sex pheromone.

Pheromonotropic Assays:

Heads of male flies were excised during mid scotophase, when no pheromone is produced (Nation 1990), and homogenized in cold (4°C) H_2O containing 0.1% trifluroacetic acid. The supernatant recovered after two separate homogenizations and centrifugations (18000 × g) was concentrated to dryness using a Speed Vac concentrator and reconstituted in physiological saline (Christensen et al. 1991) at doses of 0.1,

0.25, 0.5, 1.0, 5.0 or 10 head equivalents per 20 µl of saline. Pheromonotropic assays were conducted by injecting female moths with 20 µl of either saline or saline containing various doses of extracts of the heads of *A. suspensa* or 5 pmol of synthetic PBAN during the mid photophase (Teal & Tumlinson 1989). After a 1 h incubation the pheromone glands were excised and extracted in 10 µl of hexane containing 1 ng/µl each of heptadecane and nonadecane as internal standards. The extracts were analyzed by capillary gas chromatography to determine the amount of pheromone, indicated by (Z)-11-hexadecenal (Z11-16:AL), the component of the sex pheromone present in greatest amount (Teal & Tumlinson 1989). Data were analyzed using a Fisher's least significant difference test ($p = 0.05$) performed after an analysis of variance indicated differences among treatments.

ELISA Assays:

For these tests antisera formed against a synthetic PBAN-Keyhole limpet hemocyanin (KLH) complex were used. Five mg of peptide (L-S-D-D-M-P-A-T-P-A-D-E-M-Y-R-Q-D-P-E-Q-I-N-S-R-T-K-Y-F-S-P-R-L-NH_2) was mixed with 30 mg of KLH in 2 ml of 0.1 M sodium phosphate buffer (pH 7.25) in a 20 ml conical vial containing a teflon® coated vane magnetic stir bar. Linkage was accomplished by addition of 50µl of 25% glutaraldehyde in 5 µl aliquots while constantly stirring. One h later the sample was diluted by addition of 12 ml of 10 mM sodium phosphate buffer containing 150 mM NaCl (pH 7.25). The sample was concentrated using an Amicon Centriprep® 30 concentrator, diluted to 5 ml with HPLC grade distilled H_2O and provided frozen to Kel Farms (Alachua, Fl.) for the production of antisera. Inoculation of each of 2 rabbits followed the protocol of Davis et al. (1989), except that booster inoculations were made at 3-week intervals and the final bleeds were obtained 12-weeks after the initial inoculation.

The immunoreactivity of the antisera to PBAN was determined by ELISA as described by Gazit et al. (1992) with minor modifications. Briefly, wells of Corning ELISA plates were coated with 200 µl of 0.1M Na_2CO_3 buffer (pH 9.6) containing amounts of PBAN ranging in concentration from 0.075-1.00 pmol/well and incubated at 4°C overnight. Wells were washed 3 times with PBS-Tween (0.15M NaCl in 50 mM Na_2HPO_4, pH 7.25, containing 0.05% Tween-20), filled with 200 µl of blocking solution (1% gelatin in PBS) and incubated at 35°C for 1.5 h. After blocking, the plates were washed with PBS-Tween and 200 µl of either preimmune sera or the antisera, diluted to 1:1500 in PBS, were added to each well and the plates incubated overnight at 4°C. After the final incubation all plates were washed as above and 200 µl of alkaline phosphatase conjugated goat anti-rabbit IgGs (Bio-Rad Laboratories) diluted 1:2000 in PBS were added to each well. The plates were incubated at 35°C for 1.5 h and washed. One hundred fifty µl of 1.0 mg/ml p-nitrophenyl-phosphate in diethanolamine buffer (Bio-Rad Laboratories) were added to each well, and incubated 1 h at room temperature. Enzymatic activity was stopped by adding 100 µl of 0.4M NaOH to each well. Plates were read at 405 nm using a Model 450 Bio-Rad Microplate Reader. Specificity of the antibody for other peptides was determined as above using up to 1 nmol of the peptides. Each plate included blank lanes, lanes containing different dilutions of the test peptides and lanes containing 0.75 pmol of PBAN as a positive control. After subtraction of blank values, binding of the antisera with test peptides was expressed as a percentage of binding of the antisera with 0.75 pmol of PBAN. All synthetic peptides were custom synthesized and purified by reversed phase liquid chromatography prior to use (see Abernathy et al. 1995).

For studies to determine if the extracts of the heads of males of *A. suspensa* reacted with the antibody five lanes of the plate were initially incubated with amounts of PBAN from between 0.05-0.75 pmol as above and six lanes were filled with 200 µl of

buffer containing 0.05-2.5 head equivalents of extract overnight at 4°C. Lane 12 contained only buffer and served as a blank control. After incubation the plates were treated with antibody and developed as above. ELISA results were calculated as a percentage of maximum binding to PBAN (0.75 pmol) after subtraction of the blank.

Results and Discussion

To determine if the heads of sexually mature males of *A. suspensa* contained compounds that were potentially pheromonotropic, extracts of heads were injected into females of *H. zea*. *H. zea* was chosen as a recipient for treatments because our laboratory has conducted a number of studies on the actions of pheromonotropic neuropeptides from different sources using this moth (Abernathy et al. 1995). Moths injected with 0.25-10.0 head equivalents of the head extract from male flies were induced to produce significantly more pheromone than that obtained from pheromone glands of females injected with only saline. In fact, females injected with 1.0 head equivalent produced as much pheromone as was present in extracts obtained from females injected with 5 pmol of synthetic PBAN, the optimal dose for stimulation of pheromone production in this moth (Abernathy et al. 1995). Although extracts obtained from moths injected with 10 head equivalents contained more pheromone than was present in extracts from females injected with only saline, the amount was lower than that present in extracts obtained when 5 head equivalents were injected. This appears to reflect the fact that moths injected with 10 head equivalents were immobile and were apparently suffering from a toxic reaction in response to injection of the crude extracts from the heads of the flies.

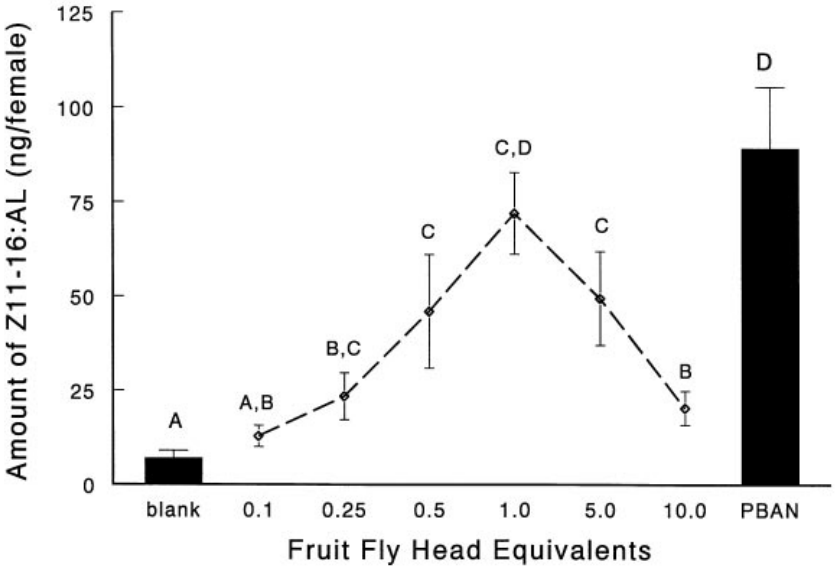

Fig. 1. Comparison of amounts of pheromone present in extracts obtained from females of *H. zea* 1 h after injection with different amounts of extracts of heads of male *A. suspensa* or 5 pmol of synthetic PBAN or only saline. Means (± SE, n = 5/treatment) superscribed with the same letter were not significantly different when compared in a Fisher's least significant difference test at p = 0.05.

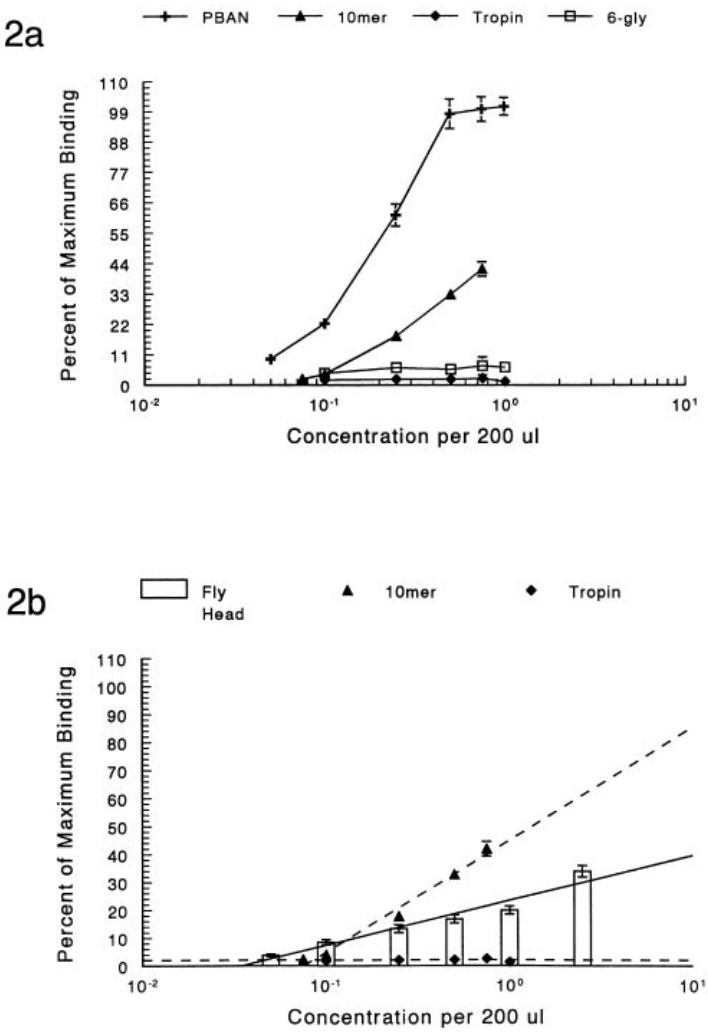

Fig. 2. Binding of antiserum to PBAN, the C-terminal 10 amino acid fragment of PBAN (10mer), allatotropin (Tropin), the pyroglutamated octapeptide (6-gly), and extracts of the heads of males of *A. suspensa* as indicated in ELISA studies. Data are presented as mean percentages of maximal binding (0.75 pmol PBAN) (± SEM, 8 replicates) after subtraction of the buffer blank. 2a. Relative binding of antiserum with synthetic peptides. T-tests and regression analysis indicated that significant binding occurred only when PBAN or the C-terminal 10 amino acid fragment of PBAN were used. 2b: Relative binding of fly head extracts compared with relative binding of the C-terminal 10 amino acid fragment and allatotropin (data from 2a). Regression analysis indicated that binding of from head extracts increased in a linear fashion with increasing dose ($R^2 = 0.886$). Mean absorption values for head extracts, calculated prior to subtraction of the blank, were significantly greater than that of the buffer blank lane for all concentrations (at 0.05 head equivalents T = 23.43, 14 df).

To determine if substances present in the head extracts from male *A. suspensa* had any structural similarity to PBAN we conducted ELISA studies. Studies on the specificity of the antiserum for PBAN and other neuropeptides including: allatotropin (A-K-S-Y-N-F-G-L-NH_2), a pyroglutamated octapeptide (pE-T-S-F-T-G-R-L-NH_2), the C-terminal 10 amino acid fragment of PBAN (S-R-T-K-Y-F-S-P-R-L-NH_2) and PBAN (L-S-D-D-M-P-A-T-P-A-D-Q-E-M-Y-R-Q-D-P-E-Q-I-D-S-R-T-K-Y-F-S-P-R-L-NH_2) indicated that significant binding occurred only when PBAN or the C-terminal decapeptide fragment of PBAN were used as substrates in the ELISA (Fig. 2). Additionally, immunochemical studies conducted by Davis et al. (1996) have shown that the antiserum complexes with PBAN and the pentapeptide F-T-P-R-L-NH_2, but not with other insect neuropeptides like FMRFamide and proctolin. Thus, the antiserum has reactivity for PBAN-like molecules and has antibodies directed against the C-terminal portion of the molecule. This C-terminal fragment is the active core of PBAN, which is necessary and sufficient for pheromonotropic activity (see Abernathy et al. 1996).

ELISA studies comparing the reactivity of head extracts of flies showed that the extracts bind the antiserum (Fig. 2). The binding increased in a linear fashion (percent maximum binding = $6.567 + 11.70 \times$ concentration of head extract, $r^2 = 0.886$) over the range of doses tested. Therefore, the extracts from sexually mature males of *A. suspensa* contained substances that had some structural similarity with PBAN.

I conclude from the results of pheromonotropic and ELISA studies, that pheromonotropic neuropeptides with structural similarity to moth PBAN are present in the heads of sexually mature males of *A. suspensa*. It is not known if these same peptides are present in the cephalic ganglia of females of *A. suspensa*, but it is likely that they are because PBAN is produced by males of the corn earworm moth (Raina & Klun 1984). Although males of *A. suspensa* exhibit a diel periodicity of pheromone production, which in insects like the Hessian fly is regulated by neuropeptides (Foster et al. 1991), studies to determine if these factors are responsible for induction of pheromone production by males of *A. suspensa* have not been conducted. It is possible that the peptides in question are responsible for regulation of other physiological functions, for example myotropic stimulation of the gut, because myotropic neuropeptides from roaches and the migratory locust will stimulate pheromone production when injected into females of H. zea (Abernathy et al. 1995). However, no myotropic neuropeptides having homology with the active core of PBAN have been identified from Diptera. Further research will be required to determine if males of *A. suspensa* regulate the induction of pheromone production with these or other neuropeptides.

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ST. LOUIS ENCEPHALITIS VIRUS TRANSMISSION TO EMUS (*DROMAIUS NOVAEHOLLANDIAE*) IN PALM BEACH COUNTY, FLORIDA WITH EVIDENCE OF WESTERN EQUINE ENCEPHALITIS VIRUS ANTIBODY TRANSPORT TO FLORIDA BY EMUS INFECTED IN OTHER STATES

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ABSTRACT

From November 1993 through January 1995, sera were collected from 59 domestic emus (*Dromaius novaehollandiae*) at a ranch in Palm Beach County, FL and tested for antibody evidence of arboviral infection. Hemagglutination inhibition (HI) and neutralizing (NT) antibodies to St. Louis encephalitis (SLE) virus were identified in sera collected each year. In addition, HI and NT antibodies to eastern equine encephalitis (EEE) virus and NT antibodies to western equine encephalitis (WEE) virus were detected in emus imported to and then maintained at the ranch. Neither of the equine

encephalitis viruses are common in Palm Beach County and many of the EEE and WEE antibody-positive emus were imported from other states prior to vaccination. Emus imported from California, Louisiana and Texas had evidence of naturally acquired antibodies to EEE and WEE viruses. This observation underscores the potential threat of arboviral introduction by infected vertebrates and emphasizes the importance of instituting quarantine procedures to regulate the transport of hosts that may be infected with arboviral agents.

Key Words: Encephalitis virus, SLE, EEE, WEE, emu

RESUMEN

Desde noviembre 1993 hasta enero 1995 se colectaron sueros de 59 emúes domésticos (*Dromaius novaehollandiae*) ubicados en una finca en el condado de Palm Beach, Florida, y se examinaron para determinar la presencia de anticuerpos contra infección arboviral. La inhibición de la hemoaglutinación (HI) y los anticuerpos neutralizadores (NT) del virus de la encefalitis de St. Louis (SLE) fueron identificados en los sueros colectados anualmente. Además, la HI y el NT del virus de la encefalitis equina oriental (EEE) y el NT del virus de la encefalitis equina occidental (WEE) fueron detectados en emúes importados a la finca y luego mantenidos allí. Ninguno de los dos viruses de encefalitis equina son comunes en el condado de Palm Beach y muchos de los emús que resultaron tener anticuerpos contra EEE y WEE habían sido importados de otros estados antes de recibir vacunaciones. Los emús importados de California, Louisiana, y Texas tenían evidencia de anticuerpos para EEE y WEE adquiridos naturalmente. Esta observación enfatiza la amenaza potencial de la introducción de arboviruses en vertebrados infectados y subraya la importancia de establecer procedimientos de cuarentena para reglamentar el transporte de hospederos infectados con arboviruses.

Naturally occurring mosquito-borne arboviruses infect and cause mortality in domestic emus (*Dromaius novaehollandiae* Linn.). In Texas, emus from 8 flocks were infected with western equine encephalitis (WEE) virus in 1992 and suffered 15-50% morbidity and 8.8% mortality (Ayers et al. 1994). In 1991, emus were infected with eastern equine encephalitis (EEE) virus in Louisiana, where an 87% mortality rate was reported (Tully et al. 1992). Two emus died of EEE virus infection in Georgia during the summer of 1992 (Brown et al. 1993). In Volusia County, FL during the spring of 1992, EEE-related morbidity and mortality rates in an emu flock were 40.5% and 14.1%, respectively. This outbreak resulted in a one year financial loss of an estimated $192,000 (Day and Stark 1996a).

In southern Florida and many parts of the central USA, St. Louis encephalitis (SLE) virus is the most commonly transmitted mosquito-borne arbovirus (Chamberlain 1980, Day & Stark 1996b). However, SLE infection in emus maintained in Florida, and in other areas of North America where SLE is endemic, has been reported only once (Day & Stark 1996b).

Eastern equine encephalitis virus, as well as antibody evidence of its transmission, is reported frequently in the northern half of Florida, but is rarely found in the 10 counties comprising the southern tip of the state (Day & Stark 1996b). The WEE virus is found west of the Mississippi drainage basin (Reisen & Monath 1989). However, WEE virus comprises a complex of at least six serologically related but distinct viruses. One of these, Highlands J (HJ) virus, is present in central and north Florida, but is absent from the southern tip of the state (Trent & Grant 1980).

The purpose of our study was to monitor natural arboviral transmission to emus in Palm Beach County, FL. Additionally, we present evidence that emus imported into Florida were initially infected with EEE and WEE viruses in the central and western USA.

Materials and Methods

Study Site

Emus were maintained at a 4 ha ranch in Palm Beach County (26°40'N, 80°15'W), FL. The ranch was located within a slash pine (*Pinus elliottii* Engelm.)/saw palmetto [*Serenoa repens* (Bartr.) Small] habitat in the western part of the county.

During the spring of 1993, approximately 150 juvenile emus were imported to the ranch from locations in Florida, California, Louisiana, Pennsylvania and Texas. Our study began in November 1993 in response to emu morbidity that was suspected of being caused by an arboviral agent. The study continued through January 1995.

When the first blood sample was taken, emus were sexed and placed into one of 3 age groups: hatching year (HY) = 1-120 days old, juvenile (J) = 121-365 days old, and adult (A) = ≥366 days old.

Serum Collection and Analysis

Blood was drawn from the jugular veins of restrained emus. A 3.0 ml sample was collected from HY emus, and a 5.0 ml sample from J and A birds. Blood samples were allowed to clot overnight at room temperature, were centrifuged at 3,400 × g for 30 min, and the resulting sera used for SLE and EEE virus hemagglutination inhibition (HI) and neutralizing (NT) antibody assays. All sera were analyzed for HI antibody to SLE and EEE viruses and for NT antibody to SLE virus. Selected sera were also analyzed for NT antibody to EEE and WEE viruses.

A micro-adaption of the HI antibody test of Beaty et al. (1989) was used with a hemagglutinin (HA) prepared from a Florida human SLE isolate (TBH-28, Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory). Additionally, all sera were examined in the same manner for HI antibody against EEE virus using an HA prepared from a Florida human isolate (NJ-60, Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory). The methodology used for HI antibody testing is described in detail by Day et al. (1996).

Aliquots of all sera were examined for NT antibody to SLE virus by serial virus dilution with undiluted serum (Beaty et al. 1989). The challenge virus was a Florida isolate (SLE-P15, Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory) obtained from a pool of *Culex nigripalpus* Theobald mosquitoes. Two NT tests for EEE antibody were performed on selected serum aliquots. The challenge viruses for these tests were a 1964 Florida human isolate (D64-837, Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory) and an isolate (VO-73, Florida Department of Health and Rehabilitative Services, Tampa Branch Laboratory) from a pool of 7 *Cx. erraticus* (Dyar and Knab) collected in August 1992 in Volusia County, FL (Day & Stark 1996a). A single NT test for WEE antibody was performed on selected serum aliquots. The challenge virus for these tests was WEE Fleming strain (VR-1251, American Type Culture Collection, Rockville, MD). We tested for cross reactivity of the VR-1251 strain with Florida EEE and HJ viral strains and found none.

The LD_{50} virus dilutions for each series of serum-virus mixtures, along with that of the control, were determined to a single decimal point. A logarithmic LD_{50} was ex-

pressed as the exponent of the reciprocal of the endpoint dilution. The log neutralization index of each serum was obtained by subtracting its LD_{50} from that of the control. Indices of <1.0 were considered negative, 1.0 to 1.6 were equivocal and those ≥1.7 were positive. The methodology used for NT antibody testing is described in detail by Day et al. (1996).

Viral Isolation Attempts

Blood from 10 emus and tissue (brain, heart, liver and spleen) from 2 emus that died of encephalitis-like symptoms were assayed for arboviral agents as described below. One drop of blood was mixed in 0.7 ml of laboratory-prepared biological field diluent (BFD) (90% Minimum Essential Medium with Hank's salts (Sigma Chemical Co., St. Louis, MO), 10% fetal bovine serum (Intergen Co., Purchase, NY), 200 U/ml penicillin (Sigma Chemical), 200 ug/ml streptomycin (Sigma Chemical), 2.5 ug/ml amphotericin B (Sigma Chemical), and 50 ug/ml kanamycin (Sigma Chemical). Blood samples were placed immediately on wet ice in the field and transported to the laboratory where they were stored at -70°C until analysis.

Approximately 0.5 g of tissue was pulverized in 0.7 ml BFD with a chilled 1.0 ml Potter-Elvehjem tissue grinder (Fisher Scientific, Orlando, FL) in a laminar flow biosafety cabinet. The suspension was clarified by centrifugation at 800 × g and rendered free of bacteria either by centrifugation at 4,300 × g or filtration with a 0.2 um syringe filter. The supernatant was aliquoted into sterile 1 ml polypropylene cryopreservation vials (Fisher Scientific, Orlando, FL) and stored at -70°C until analysis as described by Day et al. (1996).

Vaccination and Maternal Antibody Transfer

During April and May 1994, selected emus were vaccinated with 1.0 ml of Encephaloid IM^{R}, an inactivated EEE/WEE vaccine (Ft. Dodge Laboratories, Ft. Dodge, IA). Emus were bled before vaccination to establish baseline titers and periodically following vaccination to track resulting antibody titers. Chicks from hens with natural SLE infections were bled within 24 days of hatching to determine the presence or absence of maternally acquired SLE antibody.

Statistical Tests

Statistical differences in EEE antibody titers (HI and NT) before and after vaccination were tested by using unplanned tests of the homogeneity of replicates tested for goodness of fit (G-statistic) (Sokal and Rohlf 1981).

Results

Sera from 59 emus maintained at the Palm Beach County ranch were tested between November 1993 and January 1995 for evidence of arboviral transmission. Twenty-six of the emus originated in California, 13 in Florida, 11 in Louisiana, 8 in Texas and one in Pennsylvania. Twenty-four of the emus were bled more than once. Five were HY, 34 were J and 20 were A age group when first bled.

Most of the emus had HI (43 of 59, 73%) and NT (44 of 59, 75%) antibody to SLE virus. Antibody titers for individual emus were as follows. SLE HI antibody titers: 1:10 = 2 emus, 1:20 = 5, 1:40 = 2, 1:80 = 6, 1:160 = 15, 1:320 = 11 and ≥640 = 2. SLE NT antibody titers: ≥1.8 = 6 emus, ≥2.0 = 3, ≥2.1 = 4, ≥2.3 = 5, ≥2.4 = 1, ≥2.6 = 1, ≥2.7

= 5, ≥2.8 = 1, ≥2.9 = 3, ≥3.1 = 4, ≥3.2 = 3, ≥3.3 = 2, ≥3.4 = 1, ≥3.6 = 2, ≥3.7 = 2 and ≥ 3.9 = 1. Twenty-five percent (15 of 59) had HI antibody to EEE virus, 32% (16/50) had NT antibody to EEE virus, and 57% (8 of 14) had NT antibody to WEE virus (Fig. 1). Antibody titers (HI and NT for EEE and WEE viruses) for individual emus appear in Table 1.

No virus isolations were made from the blood of 10 emus that displayed encephalitis-like symptoms nor from the tissues of 2 emus that died of encephalitis-like symptoms in 1993.

Sera from 5 emus were tested for antibody titers prior to EEE\WEE vaccination. Four of 5 had detectable HI and NT titers to SLE virus resulting from natural infections. None of the birds had detectable HI titers, but one had positive NT titers to EEE virus. Eight emus (the 5 described above plus 3 additional birds) were tested for antibody titers following vaccination. Six of 8 had HI and NT antibody titers to naturally acquired SLE virus. The mean age of vaccinated birds was 408 ± 37 (SD) days (range = 362-464 days). The mean number of days between vaccination and the first serum sample was 27 ± 14 days (range = 22-52 days). There was a significant increase in the proportion of emus with HI antibody titers ($P < 0.05$, G = 8.95, df = 1) and NT antibody titers ($P < 0.05$, G = 8.55, df = 1) to EEE virus following vaccination.

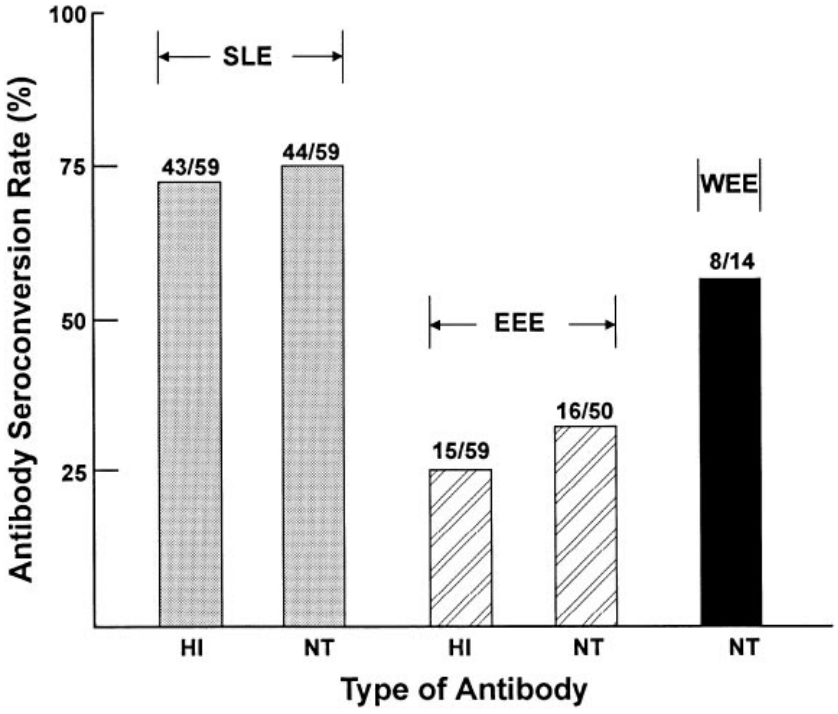

Fig. 1. Arboviral antibody seropositive rates for emus maintained at the West Palm Beach ranch during 1993 and 1994. Abbreviations are as follows: SLE = St. Louis encephalitis, EEE = eastern equine encephalitis, WEE = western equine encephalitis, HI = hemagglutination inhibition antibody and NT = neutralizing antibody.

TABLE 1. PROBABLE SOURCE OF HI AND NT ANTIBODY TO EEE AND WEE VIRUSES IN EMUS MAINTAINED AT A RANCH IN PALM BEACH COUNTY, FLORIDA: 1993-94.

Point of emu origin	Number imported to Florida	Number tested for HI antibody	Number tested for NT antibody	Source of antibody[1]	No. EEE-positive/no. tested				No. WEE-positive/no. tested	
					HI antibody	HI titers for each emu	NT antibody	NT titers for each emu	NT antibody	NT titers for each emu
California	26	26	23	Nat.	0/26		0/23		4/8	1 = >4.5
										2 = 3.3
										1 = 2.5
				Mat./Vac.	7/26	5 = 1:10	5/23	3 = >1.7	0/8	
						2 = 1:20		2 = 1.9		
				Vac.	3/26	3 = >1:40	5/23	2 = 1.9	1/8	= 1.9
								3 = 2.0		
Louisiana	11	11	8	Nat.	1/11	= >1:40	2/8	1 = 2.6	2/4	both = 2.5
								1 = >2.7		
				Vac.	0/11		0/8	both = 2.6	0/4	
Texas	8	8	8	Nat.	0/8		2/8		1/2	= 2.7
				Vac.	0/8		0/8		0/2	
Totals:	45	45	39	Mat./Vac.	7/45		5/39		0/14	
				Vac.	3/45		5/39		1/14	
				Nat.	1/45		4/39		7/14	

[1]Mat./Vac. = maternal antibody transfer by a naturally infected or vaccinated hen, Nat. = natural infection, Vac. = vaccinated emu.

Natural EEE transmission is rare in Palm Beach County (Day & Stark 1996b). Because many of the emus in our study were HI and NT antibody-positive for EEE virus and because many of the birds originated west of the Mississippi River, selected sera were tested for NT antibody to WEE virus. Most of the sera were collected before the emus were treated with an EEE/WEE vaccine. Therefore, positive findings in these birds indicated the possibility of natural infection or maternal antibody transfer (Day & Stark 1996a). In Volusia County, Florida, we observed that emus naturally infected with EEE virus usually had NT antibody titers >2.0. Newly hatched emus with maternally derived antibody titers (through natural infection or vaccination of the hens) usually displayed NT antibody titers <2.0. Eight of 14 emus tested for NT antibody to WEE virus were positive, all but one with NT antibody titers >2.0, indicating possible natural infection at their hatching site. One of 45 (2%) HI tests and 4 of 39 (10%) NT tests indicated EEE antibody titers that most likely resulted from natural infection (Table 1).

Four of 5 newly hatched chicks from hens with a natural SLE infection had HI and NT antibody titers to SLE virus. The mean age of the chicks was 11.2 ± 8.1 days (range = 6-24 days) when they were first tested for antibody. All had negative EEE antibody titers.

Discussion

The introduction of exotic hosts into habitats that have active arbovirus transmission provides a potential vehicle by which transfer of virus from one location to another may be facilitated. Emus are susceptible to infection by EEE virus (Tully et al. 1992, Brown et al. 1993, Day & Stark 1996a), WEE virus (Ayers et al. 1994) and SLE virus. An important, and yet unanswered question is whether and for how long infected emus circulate virus titers sufficient to infect mosquitoes or other potential vectors. Emus are sold and transported throughout North America and can potentially transport an arbovirus from an active focus to an area where the virus is not extant but vectors suitable to establish an active viral focus are present.

The consistently high SLE antibody levels in emus from Palm Beach County indicate that these birds were most likely infected naturally with SLE virus during the autumn of 1993 when an unusually high level of SLE transmission was reported in sentinel chickens along the east-central coast of Florida (Stark, unpublished data). The emu ranch was located in a habitat favored by the major vector of SLE virus in Florida, *Cx. nigripalpus*, and it is likely that an SLE transmission focus involving mosquitoes, emus and wild birds was established around the emu ranch during 1993. It is also possible that some of the emus were infected with SLE virus in California, Louisiana or Texas prior to their import into Florida. However, the facts that the majority of emus in the flock were HI and NT antibody positive (73% and 75% respectively) for SLE virus and that the titers for both types of antibody were high, indicates that SLE transmission was not sporadic and, regardless of the state of origin of the emus, virtually all of them ended up SLE positive at the West Palm ranch.

No viral isolates were made from sick or dead emus in 1993. Judging from the high SLE antibody rates and the low morbidity and mortality rates among infected birds, it does not appear that SLE virus causes as severe an infection nor as high a mortality rate as do EEE and WEE viruses.

Natural transmission of EEE and HJ viruses is uncommon in Palm Beach County (Day & Stark 1996b). However, 15 of 59 (25%) of the emus in our study had HI antibody titers and 16 of 50 (32%) had NT antibody titers to EEE virus. Additionally, 8 of 14 (57%) had NT antibody titers to WEE virus. Forty-six (78%) of the emus in our

study originated outside of Florida (one emu, not shown in Table 1, originated in Pennsylvania). Five of the 13 emus that originated in Florida hatched at the Palm Beach facility, whereas 8 were imported from a ranch in Volusia County where EEE virus is endemic (Day & Stark 1996a). Some of the antibody-positive emus reacted to EEE or WEE tests because of vaccination or maternally-derived antibody. However, judging from the high antibody titers, at least some of the emus had antibody acquired as the result of natural infection at their hatching location (Table 1). Emus and other exotic avian hosts may potentially transport live virus across state lines. It is important to determine the extent and duration of viremias in infected emus to evaluate the risk of viral introduction by emus infected at one site and then transported to a secondary or even a tertiary location supporting suitable vector populations.

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A NEW GENUS AND SPECIES OF SPIDER BEETLE FROM THE VIRGIN ISLANDS: *LACHNONIPTUS LINDAE* (COLEOPTERA: ANOBIIDAE: PTININAE)

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ABSTRACT

Lachnoniptus lindae, a **new genus** and **new species** from the Virgin Islands, is described. It appears most similar to *Trigonogenius*, and characters differentiating the two genera are given. The habitat and probable biology are discussed.

Key Words: Ptininae, Ptinidae, spider beetles, Virgin Islands, West Indies

RESUMEN

Lachnoniptus lindae, un nuevo género y especie de las Islas Vírgenes, es descrito. Es parecido a *Trigonogenius*, y los caracteres que diferencian a ambos géneros son provistos. El hábitat y probable biología de esta nueva especie son discutidos.

The ptinine fauna of the Virgin Islands includes one recorded species, *Pitnus antillanus* Bellés (Bellés 1992). In the more inclusive West Indies, another species of *Pitnus* Gorham, four species of *Ptinus* Linnaeus, three *Gibbium* Scopoli, and one *Fabrasia* Martinez and Viana (= *Cubaptinus* Zayas, Philips 1997) have been recorded (Boieldieu 1856, Gorham 1898, Pic 1906, Lepesme 1947, Wolcott 1948, Bellés and Halstead 1985, Zayas 1988, Bellés 1992). Recent investigations on the beetle fauna of the Virgin Islands have resulted in the discovery of two undescribed ptinine species. One of these belongs in the genus *Ptinus*, but the unique morphology and phylogenetic position of the other requires the creation of a new genus. I take this opportunity to make a name available for the latter.

Lachnoniptus Philips **New Genus**

Type Species. *Lachnoniptus lindae* **New Species**.

Diagnosis. This genus is easily recognized by the transverse pronotum and the very convex globose shape of the elytra. The dense pubescence dorsally results in a woolly, fluffy appearance. Also, the apical antennomere is slightly but distinctly wider than the penultimate one. *Trigonogenius* is the only genus that approaches this elytral and pronotal shape, but *Trigonogenius* has dense, appressed setae on the elytra, unlike the fluffy elytral setae of *Lachnoniptus*. Further, *Trigonogenius* does not have the laterally enlarged and distally rounded apical antennomere of *Lachnoniptus*. In contrast, *Trigonogenius* is characterized by the apical and penultimate antennomeres subequal in diameter and the apex acuminate. Other differences include the following: *Lachnoniptus* with a mesosternal process $^{2}/_{3}$ the width of the mesocoxa ($^{1}/_{3}$ the width for *Trigonogenius*); the absence of the mesosternal-mesepisternal suture (present in *Trigonogenius*); metepisternum not visible due to fusion with metaster-

num (distinctly visible in *Trigonogenius*); metacoxae approximately round *(rectangular* in Trigonogenius); the metacoxae laterally contacting the first ventrite (laterally adjacent to the metepisternum in *Trigonogenius*); the fourth ventrite compared to third about equal in length (a ratio of about 1.15:1) (greatly reduced in *Trigonogenius* (a ratio of about 3:1)); and the anterior margin of the first ventrite narrowly pointed laterally (sharply pointed in *Trigonogenius*). Two more subtle characters also differentiate these two genera. The scutellum is narrowly rounded in *Lachnoniptus* but is broadly rounded in *Trigonogenius.* In some specimens of *Lachnoniptus* there is a faint row of transverse setal tufts on the pronotum. Pronotal tufts are always absent in *Trigonogenius*. While *Lachnoniptus* is known from the West Indies, *Trigonogenius* is found in the western part of North and South America.

Description. Body robust and globular, densely covered with erect fluffy setae that obscure cuticular surface.

Head. Very robust, not visible from above, partially hidden within the pronotum up to the posterior dorsal margin of the eye, eye nearly semicircular, slightly rounded on dorsal side; longitudinal groove on the frons between antennal insertions, clypeus equilaterally triangular, labrum narrow, no wider than proximal edges of antennal insertions, anterior margin approximately truncate, anterio-lateral edges broadly rounded; antennae 11 segmented, second segment attached on side of scape near apex, apical antennomere distinctly widest at anterior $^1/_3$, tapering to rounded tip; mentum slightly longer than wide, triangular, not truncate but narrowly rounded at anterior margin, with a small round depression medially at basal $^1/_3$, a patch of 4-8 moderately long setae anterio-medially; hypopharygeal setal rows closely spaced and nearly overlapping; maxillary and labial palpi with apical segment tapered to a point; galea and lacinia with stout spines, spines obscured with fine setae.

Thorax. Pronotum globose and convex, transverse, 1.35 times wider than long, widest at middle; scutellum small, hidden, slightly tranversely ovoid, distinctly below level of elytra; procoxae cylindrical, projecting, prosternal process with apex expanded and rounded, extending ventrally about as far as coxae, at narrowest width about $^1/_3$ the width of coxa; mesosternum smoothly concave, slightly narrower posteriorly, process about $^2/_5$ width of mesocoxa; mesepimeron visible but narrow, mesosternal-mesepisternal suture absent; metasternum about half the length of the mesosternum, sharply, obtusely emarginate at posterior margin; metacoxae transversely triangular, laterally in contact with first ventrite.

Elytra. Globose and convex, fused, nearly as wide as long, length 1.10 times width; large strial punctures easily discernible and in longitudinal rows, puncture edges broadly rounded, intervals convex, surface usually hidden beneath dense pubescence.

Ventrites. All sternal sutures clearly defined, second ventrite widest at middle and at lateral edge, third ventrite distinctly narrowest at middle, third ventrite only slightly longer than fourth, about 1.1-1.2 times length of fourth.

Legs. Femora gradually increasing in size towards apex, pro- and mesotibiae about $^2/_3$ as long as metatibiae, all tarsomeres about equal in length, except first metatarsomere about $^1/_3$ longer than second.

Etymology. Derived from the Boieldieu genus *Niptus* combined with the greek *lachno*. The name translates as “woolly haired” *Niptus*.

Discussion. Putative synapomorphies for *Lachnoniptus* are as follows: 1) the first ventrite narrowly pointed laterally; 2) the ultimate antennomere enlarged; 3) the scutellum vertical and narrowly rounded posteriorly; and 4) the fourth ventrite approximately equal in length to the third. The first character state appears to be uniquely derived while the second and third have similar states or convergences in other ptinine taxa. The fourth character state is hypothesized to be a reversal to the pleisiomorphic state. While most ptinines have the fourth ventrite reduced to various

degrees relative to the third, *Lachnoniptus* and the Gibbiinae (sensu Bellés 1985) have the fourth and third ventrites approximately equal, similar to the non-ptinine Bostrichoidea.

Lachnoniptus lindae **New Species**

Figs. 1-6

Diagnosis. This species is easily recognized by the variegated pattern of brown and tan pubescence on the elytra. It can also be recognized by the laterally (but not posteriorly) carinate antennal fossae that are separated by a ridge as broad as the second antennomere length. Pronotal tufts are usually absent or, at most, very loose and indistinct.

Description. Length: 2.25-3.04 mm (n = 23). Body very robust and globular, covered with dense fine short brown and tan pubescense, on pronotum and elytra relatively longer and more erect than the rest of the body, also much longer scattered erect or suberect setae arising above short setae that usually have the tips curved towards the posterior.

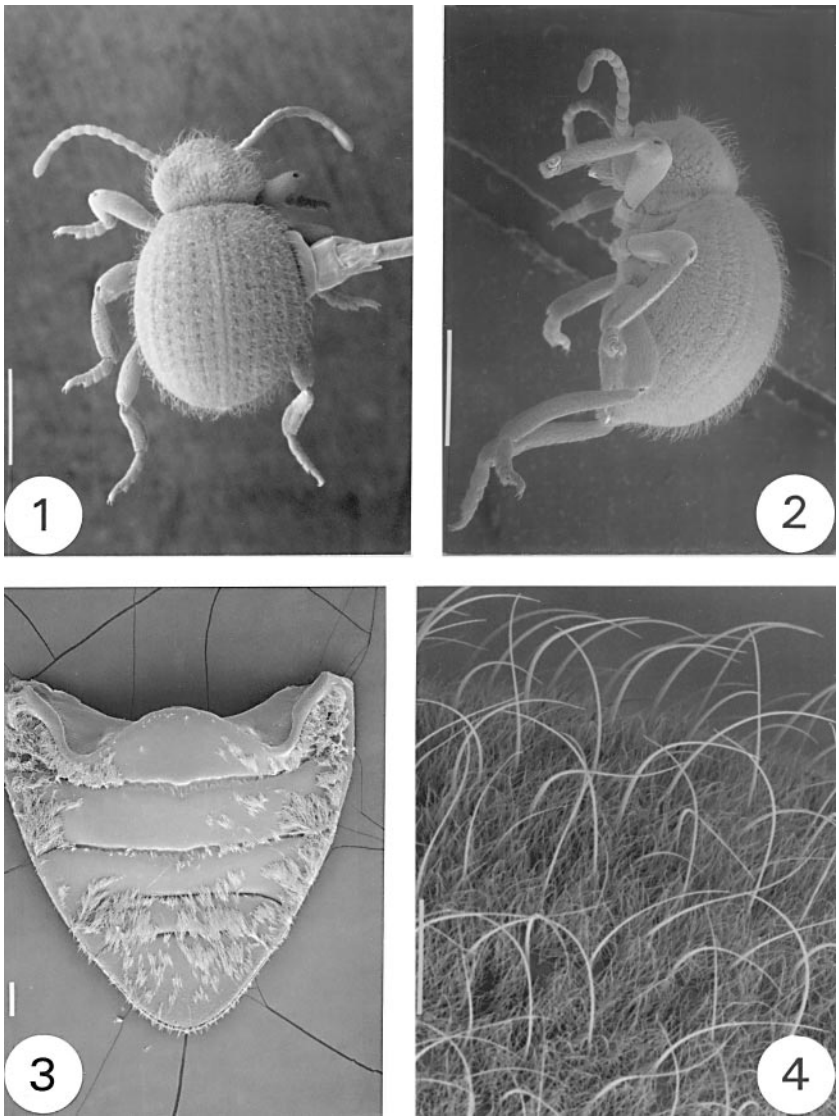
Head. Covered with appressed very dense tan setae, slightly darker towards vertex and on the fronto-clypeal area, longer, slender, suberect brown setae scattered on front of head; antennal fossae separated by a ridge as broad as second antennomere, laterally with carinate borders that become obsolete posterior to antennal insertions; relatively deep narrow longitudinal groove between fossae, deepest at a point about equal to posterior margin of fossae; eyes moderate in size, maximum length about as long as second antennomere, usually eight ommatidia at minimum width, 9-10 ommatidia at maximum.

Thorax. Pronotum covered with dense brown pubescence except pale orange or tan in a longitudinal median band at middle on anterior $^{3}/_{5}$, expanding on posterior $^{2}/_{5}$ to form a triangular patch adjacent to base about 3 times as wide as scutellum; this same color of setae laterally at posterior edge expanding slightly from a point near coxae up to dorsal-lateral border and forming an elongate triangle on each side, another less distinct lateral band near anterior margin; shallowly, moderately rugose-reticulate surface visible beneath setae; erect, elongate curved setae occasionally forming very loose, indistinct tufts on dorsal surface, two inner tufts at posterior $^{1}/_{3}$ on either side of midline, two outer tufts at middle but laterad inner tufts; scutellum covered with pale tan pubescence.

Elytra. Dense tan and brown pubescence in a mottled or variegated pattern, slightly darker brown surrounding scutellum and along first elytral interval at basal $^{1}/_{5}$; moderately large, well-separated, somewhat square-shaped strial punctures slightly visible beneath pubescence, edges smoothly rounded, middle punctures separated longitudinally by about 3 times their length, puncture rows separated by about 4 times puncture width; long erect setae rising above dense pubescence, about 1.5 times as long as one elytral interval at middle, decreasing in length laterally and posteriorly; dense pubescence slightly more orange adjacent to apical margin.

Ventral surface. With dense yellowish-tan pubescence, slightly darker patches near margins of second through fourth ventrites, and evenly scattered suberect dark brown setae; posterior margin of mesepisternum with orange pubescence; first and second sutures between ventrites becoming more obscure laterally; ventrite ratios (first to fifth): 20: 21: 15: 13: 30.

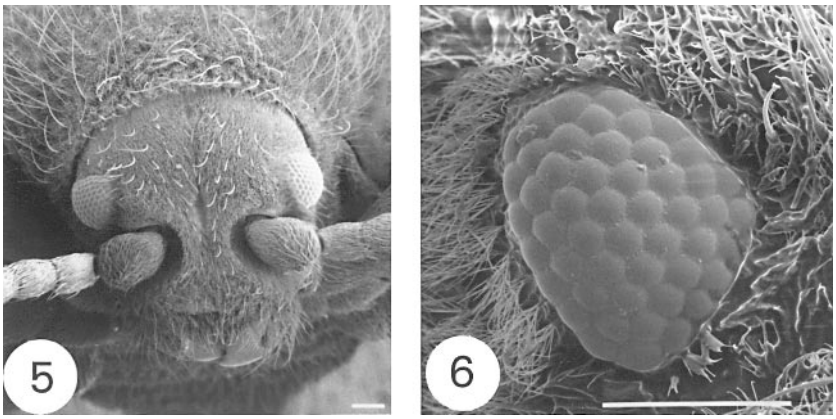
Legs. Covered with dense recumbent tan pubescence and longer darker scattered appressed setae; trochanters and apices of femora and tibia orange-tan, longer, coarser setae at tibial apex and ventral margin distinctly orange; margins at apical 2/5 of pro- and mesotibiae and apical $^{1}/_{3}$ of metatibiae covered with longer, coarser more erect setae.



Figs. 1-4. External morphology of *Lachnoniptus lindae*: 1) dorsal habitus; 2)lateral view; 3) ventrites (most of the setae abraded); 4) elytral setae. Scale line = 1.0 mm for figs. 1-2, 100 um for 3-4.

Sexual dimorphism. None.

TYPES. Holotype: **Virgin Islands**: Guana Island, Quail Dove Ghut, 600 ft., 12.VII-09.X.1994, flight intercept #13, M. A. & L. L. Ivie colr [600, 18°28.49'N, 64°34.21'W] (NMNH); Paratypes, same data as holotype (10), same data except 12-24.VII.1994, S. A. Bucklin colr (1), 25.I-25.II.1993, Lio Wei Peng colr (1), 25.II.-



Figs. 5-6. Head of *Lachnoniptus lindae*: 5) frontal view; 6) lateral view of eye. Scale line = 100 um.

25.III.1993, Lio Wei Peng colr, flight intercept trap #5 [400', 18°28.64'N, 64°34.20'W] (5), Monkey Point Trail, 5-10.X.1997, T. K. Philips, dung pitfalls (26), St John, Estate Carolina, NW Coral Bay, 250 ft., 09.V.1994, litter among rocks, Muchmore (1), St John, Lameshur Bay, V.I.E.R.S., 10.III.1984, leaf litter, W. B. Muchmore (1), St John, Maho Bay, 12.III.1984, in hollow tree, W. B. Muchmore colr (1), Guana Island, VII-X.1993, "beetle-trap," collected by C. Bartlett & J. Cryan (1), Tortola, Windy Hill, 25-28.XII.1993, 350', thorn-scrub for., T. K. Philips, colr., dung pitfall (1) (Paratypes in the collections of the author, the Virgin Islands Beetle Project Collection [Montana State University, Bozeman, Montana], Xavier Bellés, Fred Andrews, The Natural History Museum [BMNH], Canadian Museum of Nature [CMNC], Muséum National d'Histoire Naturelle de Paris [MHNP], United States National Museum [USNM]).

Distribution. This species is known from three of the northern Virgin Islands (Guana Island, St John, and Tortola). It seems likely that it will be found on other Virgin Islands and Puerto Rico, of the Puerto Rican Bank, which were connected as a single land mass during periods of low eustatic water levels during the Pleistocene (Heatwole and MacKenzie 1966).

Etymology. Named after my wife Linda, in recognition of her support and encouragement of my career.

DISCUSSION

Lachnoniptus lindae is one of the more highly derived ptinines as characterized by fused elytra, winglessness, and a very globular body form. The majority of species in this group use dung or other accumulated organic material of animal or plant origin as a food source. Most specimens have been captured with dung baited pitfall traps. Dung from numerous reptiles and introduced mammals, such as sheep and goats, are likely sources of food for both adults and larvae. Larvae have been easily reared on cat dung in the laboratory.

All sites where this species was collected are tropical dry forest, characterized by rocky, thin red soils. Evapotranspiration is considerably higher than rainfall for much of the year, especially during droughts, such as those occurring in 1993-1994. The absence of scarabaeine competition in these areas might be critical for successful reproduction of this ptinine.

ACKNOWLEDGMENTS

My gratitude to James Lazell and The Conservation Agency for logistic and financial support on Guana Island and to Molly and Wilfred Gerofsky for their support of field work on Tortola, British Virgin Islands. My appreciation to Michael Ivie for lending specimens of this species and for his review of the manuscript. Also thanks to Joseph McHugh and one anonymous individual for their careful reviews. Miguel Archangelsky helped with the Spanish version of the abstract and John Mitchell with the scanning electron microscope pictures.

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ANTS ON *CECROPIA* TREES IN URBAN SAN JOSÉ, COSTA RICA

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The symbiosis between ants and Cecropia trees is among the best-studied ant-plant relationships (Belt 1874, Müller 1874, Janzen 1969, Longino 1989). Resident *Azteca* ants, the commonest *Cecropia* symbionts, typically defend their host trees against herbivory and overgrowth by vines (Janzen 1969, Schupp 1986, Rocha and Bergallo 1992). *Cecropia* trees, in turn, provide resident ants with shelter within their trunks and with food in the form of nutrient-rich Müllerian bodies on the base of the petioles and pearl bodies on the undersides of the leaves (Rickson 1971). Resident ants also often gain additional nutrition through feeding on honeydew produced by homopterans which the ants tend within the *Cecropia* trunk (Belt 1874, Wheeler 1942).

In the forests of Costa Rica, the majority of *Cecropia* trees, including *Cecropia obtusifolia* Bertol., are occupied by mutualistic *Azteca* ants (Longino 1989). In the present study, I surveyed ants on *C. obtusifolia* trees planted as ornamentals in the capital city of San José, Costa Rica, to determine whether these trees, isolated from native forest by several kilometers of urban areas, were occupied and protected by *Azteca* ants.

In June 1996, I surveyed ants on all 27 *C. obtusifolia* trees planted in the plaza in front of the Costa Rican National Museum near the center of San José, Costa Rica. Trees ranged from 0.5 to 7 m in height. For trees five meters or more in height (estimated to the nearest 1 m), I collected from the trunk all ants I could reach (up to ~2.5 m). For trees three meters or less in height (estimated to the nearest 0.5 m), I examined every leaf for ants, and searched the entire trunk for any ant nest entrance holes. When surveying, I shook all trees to stimulate ant activity. Voucher ant specimens from this study are in the Museum of Comparative Zoology, Harvard University and the Smithsonian Institution.

Ants were on twelve of the 27 *C. obtusifolia* trees. Ants were more common on larger trees: on nine of twelve large trees (> 2 m height), and three of fifteen small trees (< 2 m height) ($X^2 = 8.3$, $P < 0.05$). There were only three species of ants on the trees: *Paratrechina longicornis* (Latreille), *Acromyrmex octospinosus* (Reich), and *Azteca* sp. (Table 1). *P. longicornis* was by far the most common and widespread ant, occurring on ten of the twelve trees with ants (Table 1). *A. octospinosus*, a leaf-cutting ant, was also common, with foragers carrying leaf fragments and pieces of other vegetable matter coming down six trees. There was leaf-cutting ant damage on the leaves of at least three additional trees without leaf-cutters present. One of these damaged trees had *P. longicornis* and two were without any ants on them. *Azteca* ants were on only two *Cecropia* trees, both five meters in height. On these two trees, large numbers of *Azteca* poured out of their nests within the trunk when I shook the tree. The *Azteca* workers could not be identified to species because queens are needed for such identification and I could not cut down and dissect these ornamental *Cecropia* trees to obtain the queens. Dense setae on the workers' scapes and tibiae indicated they did not belong to the "alfari" group (Longino 1991a, b.) *Paratrechina longicornis* occurred in both trees occupied by *Azteca*, but *A. octospinosus* occurred in neither. The *P. longicornis* and *A. octospinosus* nested in the ground in the plaza, whereas the *Azteca* sp. nested within the trunks of the *Cecropia* trees. I noted tens to hundreds of unharvested Müllerian bodies on the leaf petioles of the small *Cecropia* trees.

TABLE 1. ANTS ON TWELVE *CECROPIA OBTUSIFOLIA* TREES IN THE PLAZA IN FRONT OF THE COSTA RICAN NATIONAL MUSEUM, SAN JOSÉ, COSTA RICA. IN ADDITION, FIFTEEN *C. OBTUSIFOLIA* TREES HAD NO ANTS (ONE 6 M, TWO 5 M, THREE 1.5 M, SEVEN 1 M, AND TWO 0.5 M TALL). CRAZY ANT = *PARATRECHINA LONGICORNIS*; LEAF-CUTTER = *ACROMYRMEX OCTOSPINOSUS*, AND AZTECA = *AZTECA* SP.; X = ANTS PRESENT; D = LEAF-CUTTING ANT DAMAGE OBSERVED.

Tree	height (m)	Crazy ant	Leaf-cutter	*Azteca*
1	7	X	X	
2	6	X	X	
3	6	X		
4	6		X	
5	5	X	X	
6	5	X		X
7	5	X		X
8	3		X	
9	2	X	D	
10	1.5	X	X	
11	1.5	X		
12	1.5	X		

The most numerous ants on the *C. obtusifolia* trees in urban San José were *P. longicornis*. *P. longicornis* is called the "crazy" ant because of the fast, jerky movements of the workers. This species is of Old World origin, but is now one of the most common tramp ants throughout the tropics and subtropics, usually associated with disturbance, e.g., in disturbed natural environments, in urban environments, and even on ships (Weber 1940, Smith 1965, Miller 1994, Ferster and Prusak 1994, Klotz et al. 1995; Delabie et al. 1995). *P. longicornis* dominates a variety of disturbed habitats, including the Dry Tortugas, the highly-exposed, outermost islands of the Florida Keys (Hölldobler and Wilson 1990) and the disturbed artificial ecosystems of Biosphere 2, a 1.28-hectare greenhouse structure outside Tucson, Arizona (Wetterer et al. 1997). In Biosphere 2, the main source of carbohydrates for *P. longicornis* was honeydew produced by homopterans (Wetterer et al. 1997). This also appeared to be the major food source of tramp ants on *Cecropia* trees in Hawaii (Wetterer 1997), and probably in the present study as well.

A. octospinosus foragers were also common on the San José *Cecropia* trees. These leaf-cutting ants are native to Central America, South America, and the Caribbean (Weber 1972). They seem to do well in disturbed urban habitats and are also common in Panama City, Panama (personal observation). In the both the wet and dry forests of Costa Rica, *A. octospinosus* foragers typically cut the leaves of small herbaceous plants, fallen flowers, and fallen fruit parts (Wetterer 1991, Wetterer et al. 1998). They appear to be opportunists, however, and will cut the leaves and flowers of plantation trees (Lewis 1975) and even collect insect frass (Wetterer et al. 1998).

Azteca ants occupied only two 5-m *Cecropia* trees in the museum plaza, 7% of the trees studied. This is a much lower occupancy rate than in natural habitats in Costa Rica. For example, Longino (1989) found that on transects through the Arenal and Monteverde areas (400-1500 m elevation), obligate *Azteca* mutualists occupied 86% of

all *Cecropia* trees. The majority of the trees without *Azteca* were saplings. Questions arise as to how the *Azteca* ants came to occupy two *Cecropia* trees in San José, so far away from native forest. It seems likely that the *Azteca* ants had already colonized these trees before they were transplanted to San José. Longino (1989) found that most unoccupied *Cecropia* trees showed evidence within their trunks of *Azteca* colonies that had died. It is unknown whether any of the unoccupied trees in San José once housed *Azteca* colonies.

The *Azteca* ants showed no evidence of excluding crazy ants from their host *Cecropia* trees. It may be that the *Azteca* ants do not recognize this non-indigenous ant as a threat. Alternatively, the *Azteca* colonies may not be capable of fending off the large numbers of crazy ants. On the other hand, the *Azteca* ants in San José appeared to be excluding the native leaf-cutting ants. *A. octospinosus* foragers were not attacking either of trees occupied by *Azteca*, but were attacking or had attacked at least nine of the 25 *Cecropia* trees without *Azteca*.

It would be interesting to census these *Cecropia* trees at a later date to determine whether the *Azteca* ants persist in the trees and spread to others, or whether crazy ants exterminate them as they appear to have done with ant species in other disturbed environments (Hölldobler and Wilson 1990, Wetterer et al. 1997, see also Zenner Polania 1994).

Earlier studies have indicated that *C. obtusifolia* trees are not obligately dependent on ants (see Wetterer 1997). *C. obtusifolia* has been introduced to Hawaii, apparently as an ornamental (Wagner et al. 1990). *Azteca* ants have not been recorded in Hawaii. Either they did not accompany the *Cecropia* trees to Hawaii or did not survive there. Still, the *Cecropia* trees are thriving in disturbed lowland forests of Hawaii in the complete absence of mutualist *Azteca* ants (Wetterer 1997). In part, this success may be because most of *C. obtusifolia*'s Neotropical herbivores and competitors are absent in Hawaii. A similar absence may explain their survival in urban San José.

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Summary

Three species of ants inhabited 12 of 27 *Cecropia* trees in urban San José, Costa Rica: crazy ants (*Paratrechina longicornis*) in ten, leaf-cutting ants (*Acromyrmex octospinosus*) in six, and "*Cecropia*" ants (*Azteca* spp.) in only two. Occupancy rate by *Azteca* was much lower than in local forest *Cecropia*. *P. longicornis* inhabited both *Azteca*-occupied trees, but *A. octospinosus* occurred in neither.

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FIRST RECORDS OF *LEPTOTHORAX RUGATULUS* (HYMENOPTERA: FORMICIDAE) WITH CYSTICERCOIDS OF TAPEWORMS (CESTODA: DILEPIDIDAE) FROM THE SOUTHWESTERN UNITED STATES

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Ants of the myrmicine tribe Formicoxenini may serve as intermediate hosts of immature stages (cysticercoids) of two genera of dilepidid cestodes. The parasites are thought to enhance the transmission to their final hosts, piciform, galliform or passeriform birds (Gabrion et al. 1976, Péru et al. 1988, 1990) and also shrews (Sawada & Harada 1995), by modifying the behavior and the pigmentation of their hosts. Infected *Leptothorax* are yellowish rather than brown or black as are their unparasitized nestmates, and they also do not flee when the nest is disturbed (Plateaux 1972, Buschinger 1973, reviewed in Moore 1995), thus increasing the probability that they are eaten. The tapeworms mature and reproduce in the intestine of the final host (Péru et al. 1990), and the eggs are still contained in parts of the tapeworm's uterus or in complete proglottids when released with the bird's feces. Ants collect the protein-rich pieces and feed them to their larvae (Gabrion et al. 1976, Péru et al. 1988).

Ants of the subgenus *Leptothorax* (s.str.) infested with *Choanotaenia* cysticercoids and *Leptothorax* (*Myrafant*) infested with *Anomotaenia* cysticercoids have been reported from various parts of Europe and Northern Africa (Germany, Hungary, Italy, France, Spain, Algeria, Morocco, Ukraine (Crimea); Plateaux 1972, Buschinger 1973, Espadaler Gelabert & Riasol Boixart 1983, A. Buschinger, unpublished data) and eastern North America (Illinois, Michigan, Ohio, Quebec; Stuart & Alloway 1988). Here we report on the occurrence of cysticercoids in several populations of *Leptothorax* (*Myrafant*) *rugatulus* in the Chiricahua, Huachuca, and Mimbres Mts. in southern Arizona and New Mexico.

Infested ants were easily recognized by their yellowish coloration, whereas typical *L. rugatulus* workers are reddish brown. Dissection of 24 yellowish workers revealed the presence of one to 28 cysticercoids (mean 7.8, median 6), closely associated with the midgut of the ants (Fig. 1a). A single cysticercoid was found in a worker with normal, reddish brown coloration. Eleven "normally" colored workers from the same colony, 5 "normally" colored workers from five other colonies with yellowish ants, and 18 from colonies without yellowish ants were not infected.

Whereas *Leptothorax* infested with tapeworms occasionally show morphological aberrations, such as a broadened postpetiole, a stronger petiolar spine etc. (Plateaux 1972, Buschinger 1973, Stuart & Alloway 1988), yellowish *L. rugatulus* were not conspicuously different in morphology from their uninfested nestmates.

By gently squeezing cysticercoids under a microscope, the rostrum evaginated and the number of mouth hooks could be counted (Fig. 1b). Cysticercoids found in *L. rugatulus* had between 18 and 21 hooks in two circles (28 cysticercoids, mean 19.9, me-

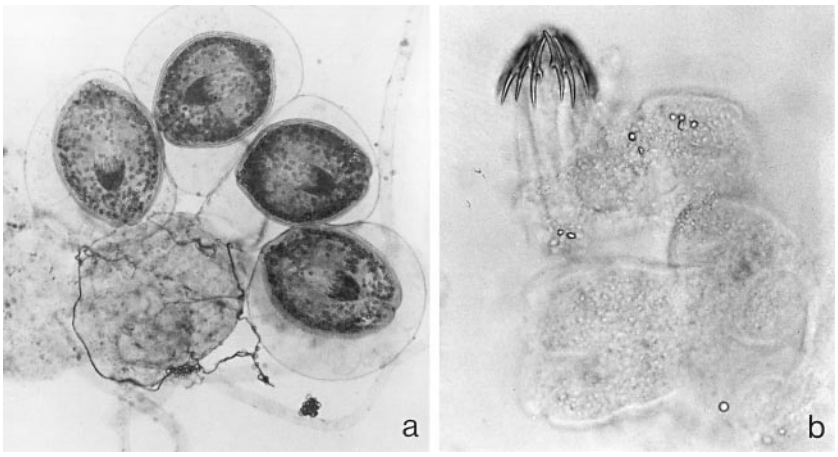

Fig. 1. a) Four cysticercoids of a dilepidid cestode associated with the midgut of a worker of the ant *Leptothorax rugatulus*. b) Cysticercoid after devagination of the rostrum. The hooks are clearly visible.

dian 20; compared to *Anomotaenia brevis* with 17 to 22, rarely 26 hooks, and *Choanotaenia* with 18 to 27 hooks, Buschinger 1973, Gabrion et al. 1976). One exceptional cysticercoid from *L. rugatulus* had one circle consisting of 18 large hooks and a second circle of 13 small hooks. Cysticercoids from *L. rugatulus* were similar in size to those from Europe (48 cysticercoids in *L. rugatulus*: mean 224 µm, median 216 µm, range 180-290 µm; compared to A. brevis 220-250 µm and *Choanotaenia* 170-210 µm, Buschinger 1973, Gabrion et al. 1976), but the average length of the hooks by far exceeded that of European specimens (in *L. rugatulus*: 60 µm; compared to A. brevis 23.5-28.5 µm and *Choanotania* 40-45 µm). Overall, cysticercoids from *L. rugatulus* appear to belong to a taxon different from both European species, but closer related to *Anomotaenia* than to *Choanotaenia*. The final host of the tapeworm is unknown.

In addition to yellowish workers, several colonies also contained yellowish dealate queens (Table 1). None of 12 dissected yellowish queens was found to be inseminated, and none of approximately 90 dissected, inseminated queens was infected, suggesting that infestation somehow interferes with the queens' sexual behavior. The ovaries of five yellowish virgin queens contained 1 to 3 developing eggs, but according to the absence of corpora lutea, they had only recently become fertile.

In the Chiricahua, Huachuca, and Mimbres Mts., between 5% and 20% of the inspected colonies contained yellowish workers (Table 1), and in single colonies, up to 50% of the workers were infected (mean appr. 10%). Infestation by tapeworm cysticercoids thus appears to be a rather common phenomenon in the mountain ranges of Southern Arizona and New Mexico. No cysticercoids, however, were found in *L. rugatulus* from several other populations in Arizona, New Mexico, and Colorado. Similarly, a species of *Leptothorax* (s.str.), regularly co-occurring with *L. rugatulus* in Southern Arizona and New Mexico (an as yet undescribed member of the *L.* (s.str.) *muscorum* complex referred to as *Leptothorax* (s.str.) F, Heinze 1989), was never found infested with cysticercoids. The apparent restriction of the *Anomotaenia*-like cysticercoids to *L. rugatulus* is consistent with the hypothesis that cysticercoids of dilepidid tapeworms are limited to host species from a single *Leptothorax* subgenus (Buschinger 1973, Péru et al. 1990).

TABLE 1. OCCURRENCE OF *LEPTOTHORAX RUGATULUS* ANTS INFECTED WITH CYSTICERCOIDS OF A DILEPIDID TAPEWORM. THE TABLE GIVES THE RATIOS OF YELLOWISH DEALATE QUEENS AND WORKERS PER COLONY TO THE TOTAL NUMBER OF DEALATE QUEENS AND WORKERS, AND OF COLONIES CONTAINING INFECTED INDIVIDUALS TO THE TOTAL NUMBER OF COLONIES COLLECTED PER POPULATION.

Mountain Range, County, State	Collecting Site, Elevation	yellowish individuals per colony: queens	yellowish individuals per colony: workers	colonies with yellowish individuals
Chiricahua Mts., Cochise Co., AZ	Barefoot Lookout, 2630m	0/2	4/18	
		0/16	14/174	4/30
		3/25	16/137	
		0/3	6/62	
	FSR 40, 0.8km W of Onion Saddle, 2200m	17/19	0/51	1/13
	FSR 40, 1.5km W of Onion Saddle, 2100m	0/1	3/139	2/25
		0/18	3/115	
	Pinery Campground, 2100m	42/43	49/156	1/5
	Onion Saddle, 2280m	0/5	8/104	
		0/1	4/33	
		0/1	3/21	4/84
		0/0	1/31	
	Rustler Park, 2580m	0/7	1/46	1/5
	Morse Canyon Trailhead, 1980m	1/4	10/342	1/11
Huachuca Mts., Cochise Co., AZ	Carr Canyon Road, 2400m	0/2	1/79	1/20
Mimbres Mts., Grant Co., NM	4.8km west of Emory Passm 2200	0/1	2/30	
		0/1	6/17	3/12
		5/6	1/17	
total number, including additional populations of *L. rugatulus* in New Mexico, Arizona, and Colorado				18/523

Field work in the USA was supported by the Deutsche Forschungsgemeinschaft (Heisenberg-grant He 1623/6-1 and Graduiertenkolleg "Arthropodenverhalten"). The studies were performed in part in the Southwestern Research Station of the American Museum of Natural History, Portal, AZ.

SUMMARY

Cysticercoids of a dilepidid cestode were found by dissection of aberrant yellowish workers and virgin queens of the ant *Leptothorax rugatulus* from several mountain ranges in the southwestern United States. The cestode was not positively identified, but cysticercoids are similar to those of the genus *Anomotaenia* previously found in related ants.

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BOOK REVIEWS

KUZNETSOV, V. N. 1997. Ladybeetles of the Russian Far East. Center for Systematic Entomology; Gainesville, Florida. Memoir 1, 248 p. ISBN 1-877743-25-5. Hardback. Price per copy $58 ($29 to members of CSE) plus $1.65 postage and handling to USA addresses, from The Treasurer, Center for Systematic Entomology, P.O. Box 147100, Gainesville, FL 32614-7100.

This is the first volume of the Memoir Series of the Center for Systematic Entomology (CSE), an organization which is a direct support group for the Florida State Collection of Arthropods, the 6th largest public insect collection in the USA, with 7.5 million specimens housed. The reduced price to members is intended to attract new members to CSE for an annual subscription of US$35.00 (for which members receive issues of **Insecta Mundi**, a quarterly journal of insect systematics, and a quarterly newsletter). Prospective new members should write to Dr. Avas Hamon, Treasurer, Center for Systematic Entomology [address above]. CSE supports insect systematics not only in Florida, but throughout the world. There is no better bargain in insect systematics in the USA: where else can systematists publish their works in a reputable peer-reviewed journal without page charges?

This book was published in English thanks to a facilitation grant from the National Biological Control Institute, USDA-APHIS. Translation from Russian was made by S. S. Ishevsky and M. S. Ishevskaya. It provides keys, species descriptions, illustrations (drawings), and some information on food and behavior of the coccinellid species of the Russian Far East. It draws its information from numerous publications in Russian (and some in other languages) as well as the decades of experience of its author Victor Kuznetsov, including a book that he published in Russian in 1993. Thus, it is indispensable to all serious students of Coccinellidae. It does not fail to point out, that members of the genera *Halyzia*, *Vidibia* and *Psyllobora* (tribe Psylloborini) feed on mildew, and that *Henosepilachna*, *Epilachna*, *Subcoccinella* and *Cynegetis* (subfamily Epilachninae) are phytophagous, and some of them are important pests. It does not discuss the controversy caused by introduction of *Harmonia axyridis* into the USA as a generalist predator of aphids. It offers essential information to biological control practitioners who would import predatory coccinellid species from the Russian Far East to control pest Homoptera.

Three other publishers in Gainesville specialize in entomological books. One of them is The Sandhill Crane Press, which in 1996 published "The Beetles of northeastern North America" by N. M. Downie and R. H. Arnett, Jr., 2 vols. (for a review see Florida Entomologist 79: 471-473). The second is Associated Publishers, which in 1995 published Memoirs on Entomology, International, vol. 3 "Rove beetles of the subtribe Philonthina of America north of Mexico (Coleoptera: Staphylinidae), classification, phylogeny and taxonomic revision" by A. Smetana (for a review, see Florida Entomologist 79: 81-82). The third is Scientific Publishers, which in 1996 published "Damselflies of North America" by M. J. Westfall, Jr. and M. L. May. The Florida Entomological Society publishes Florida Entomologist but no books. The Center for Systematic Entomology is a new entrant in the Gainesville book-publishing scene.

The introductory materials of the book occupy pages that are numbered in Roman numerals i-xii, but which are also (curiously) considered to be pages 1-12. Pages 13-72 then consist of an historical review of Coccinellidae of the area of interest, methods, many pages on general morphology, including a morphology of larvae, and sections on biology and ecology, on natural enemies, and on employment of Coccinellidae in bio-

logical control of homopterous pests in the former USSR. Then comes the major part of the text, on taxonomy, down to the species level, and including notes on food, habitat, and seasonality. This is extremely useful to anyone concerned with taxonomy of Coccinellidae, including persons concerned with importation of Russian species for biological control purposes.

Literature cited occupies p. 229-244. It translates Russian titles of papers and book chapters and books into English, and transliterates names of Russian journals from Cyrillic into Roman characters. For readers who need to go no further (the vast majority), this is ideal: the work of translating, summarizing, and integrating the Russian literature has been done.

For readers who are taxonomists and bibliophiles and want to go further by obtaining copies of items cited, this bibliography will cause problems because it defies conventions. If you can read the languages of the original references, you will note errors and peculiarities in the bibliography. Your inter-library-loan librarian also will have trouble with it if you try to request copies of the articles cited. For example, it omits all diacritical marks (accents) in French, German, Spanish, Swedish, and Italian. For another example, where the latest C.B.E. style manual recommends that book citations should list the name of the city of publication and name of publisher (in that order, separated by a semi-colon, and using the English name of the place of publication) the reader will not find such a scheme in citations of this bibliography such as "Moscow, Leningrad" or "New York, London" or "Hafniae" or "Lipsiae" or "Wien" (the words "Hafniae" and "Lipsiae" are the genitive case of the Latin names of the cities Copenhagen and Leipzig). It seldom gives the name of the publisher. Where it transliterates Russian into English, it frequently slips into non-standard conventions, for example by writing энтомологическое as "entomologicheskoje" rather than the standard "entomologicheskoe" for no apparent reason. Where it transliterates the Russian word "И" (meaning "and") into the Roman character "i" it uses a capital "I", which looks very strange among a string of words all in lower case. On the other hand, all these foreign-language publications will be useful only to people who can read the languages, and they—potential users—will simply have to explain the correct spellings to their inter-library-loan librarians—to the rest of the world it does not matter.

The final chapter, p. 245-248, is called a taxonomic index but is, in fact, a useful non-alphabetical classification that lists page numbers of the main entries in the chapter on taxonomy. An additional, alphabetical index would have given additional value especially because it could have included information from all chapters.

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WHITE, I. M., AND D. L. HANCOCK. 1997. Indo-Australasian Dacini Fruit Flies. (Computer Aided Biological Identification Key). International Institute of Entomology, London. ISBN 0-85199-171-0. Compact diskette. $320.00 (for single user).

Among the tephritid fruit flies, the Dacini comprise one of the largest and most taxonomically challenging groups. Here Dacini refer largely to the genera *Bactrocera* and *Dacus*, which include many important tropical and subtropical fruit and vegetable pests, such as the Oriental, melon, and Queensland fruit flies. Accurate identification is a problem, especially when keys are written for females, but interceptions and surveys are usually of males taken in pheromone traps.

This CD-ROM conveniently brings together in one place an enormous amount of information on the dacines. It includes four programs: Key to the Dacini of the Indo-Australasian region, which forms the heart of the offering; CABIKEY Help with details on system requirements, general workings and capabilities of the software, and a simulated identification session; Dacini Help with a glossary of about 200 terms covering fruit fly morphology plus a few nomenclatural and ecological terms; and an Uninstall utility. Recommended computer system specifications include Windows 3.1x or Windows 95 operating system, 8 MB of RAM (16 is ideal, 4 is adequate), and display of 256 colors or more. The installation proceeded quickly and seamlessly on my Dell® 486 running Windows 95 and its files consumed 1.32 MB of hard disk space (it may install up to 4.73 MB of files).

The usual advantages of computer aided keys over dichotomous keys apply here; e.g., it is possible to circumvent certain characters in working through the key, and a complete and consistently scored set of character states (a "description") is viewable for each taxon. The key covers 507 taxa and is based on a 66-character matrix including geographic range and host plants. Data are included for all valid species found in the Oriental, Australasian and Pacific areas, and the Mascarene Islands. Special attention was paid to separation of the 68 species in the Oriental fruit fly (*Bactrocera dorsalis*) complex. For this complex several characters are used that are not applied to other species, such as measurements of the male aedeagus and female aculeus. To "complete" the system for worldwide coverage of dacine species of quarantine importance, pest species from the Afrotropical region are also included. This is not a key to Dacini of the world, as about 150 African non-pest species and over 100 other known but undescribed species are excluded. A complete world checklist is included as an appendix.

The user-friendliness of the system is very high. Even upon first use, choice of the "standard" option allows one easily to work through an identification without resorting to help screens. This option automatically chooses the best characters and queries the user with a choice of available character states. The initial screens allow the user to limit the taxa or characters considered based on sex, geographic region, or pest status. For example, choice of only pest species reduces the list to 52 taxa. Each query presents a very clear choice of character states with excellent supporting illustrations, in which character state differences are highlighted by use of color overlays on black and white drawings, and text explanations. At any step in the process, it is possible to review and alter previous character state choices, examine character illustrations, list remaining taxa, preview taxa to be included/excluded by a given character state selection, check the glossary, etc.

For pest taxa, there is significant accompanying text on taxonomy, host plants, identification characteristics, and distribution information that is largely verbatim of that in White & Elson-Harris (1994, Fruit Flies of Economic Significance, CABI, UK, 601 p.) but updated with recent nomenclature, especially from Drew & Hancock (1994, The *Bactrocera dorsalis* complex of fruit flies in Asia, Bull. Ent. Res. Suppl. 2, 68 p.). Good color photographs of actual specimens are provided for almost all pest species. Non-pest species receive only a short catalog entry stating synonymies, distribution, and the specimens examined upon which the character matrix was built. A habitus drawing, distribution map, diagnosis and description (entire character state set) is provided for every species.

Much of the information in the system can be printed out for more convenient usage away from the computer. Especially useful to the working taxonomist is the program's ability to generate a table of character states that vary among as many as five taxa and copy the table to a spreadsheet for printing. This is something that no traditional key or monograph can do and is invaluable for doing a thorough inspection and

comparison of specimens at the microscope. Descriptive text, distribution maps, glossary entries including labeled line drawings of morphological features, and even the color and SEM photos can all be printed out. Complete descriptions and diagnoses of individual species, however, cannot be exported for printing, nor can those screens be printed that illustrate character state choices as one progresses through the key.

Within the Key program is a set of useful appendices. The aforementioned checklist of world Dacini (all described species as of late 1996) is not available elsewhere. Association Data (economically important host plants, arranged alphabetically by genus and by common name with corresponding fruit fly denizens), Methods of Study, Morphology, and other appendices are modified versions of text in White & Elson-Harris (1994).

If the potential user is concerned only with pest species, e.g., a port identifier needing only to recognize pests of quarantine significance, one's library budget is better spent on White & Elson-Harris's 1994 book, which contains nearly all the same information on pest dacines plus a whole lot more on other fruit fly pests and identification of larvae. The book may not be high tech, but it's $250 cheaper and a truly excellent reference. Museum curators, collectors, surveyors, and other taxonomists who are likely to encounter a diverse assemblage of non-pest species will be most likely to fully utilize and appreciate the wealth of character data presented here. This is a wonderful tool that is well-designed for easy use. Yet, using even this good a tool, one may still arrive at an "answer" and nonetheless feel a nagging doubt about its veracity. Then one must resort to even better tools—comprehensive collections and human experts!

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BRODSKY, ANDREI K. 1996. The Evolution of Insect Flight. Oxford University Press, New York. xiv + 229 p. ISBN 0-19-850089-0. Paperback (first paperback edition). $55.00.

In the preface to this translation of the original Russian hardback, the author frankly states that "This book is not for easy reading at idle moments." I like that. Gaining an understanding of the physiology of flight, and indeed of any aspect of insect physiology, is serious business. Brodsky, Professor in the Department of Entomology of St. Petersburg University, St. Petersburg, Russia, has presented an in-depth analysis of the basic principles of flight in part I, and the evolution of flight in Part II. Part I consists of 4 chapters, detailing structure of wings, the way wings work, the aerodynamics of flight, and the role of flight in insect behavior.

In chapters 5, 6, and 7 in Part II, the author describes models and ideas about the origin of flight and wings in insects, with details and examples from mayflies, dragonflies, stoneflies, and cockroaches. In chapter 8 he discusses the differences in flight of four-winged insects and two-winged insects, with examples from Psocoptera, Homoptera, and Heteroptera. Chapter 9 is a discussion of changes in wing structure, thorax, hinging of wings, and musculature as insects evolved into more diverse forms. What, for example, are beetles to do with the hard, inflexible elytra (forewings) during flight? The answer is that all Coleoptera except the rose chafers (*Cetonia* spp.) spread the elytra at some angle to the long axis of the body, and often swing them in small

arcs at the frequency of the hindwings. Tiger beetles, which are fast fliers with rapid take-off from a surface, hold the forewings nearly at right angles to the body axis and support them with the first pair of legs ". . . like the struts of a high-wing monoplane." Especially, but not exclusively, during evolution of Diptera and Hymenoptera changes occurred in wing structure, musculature, and thoracic structure that enabled much faster flight and greater maneuverability, such as hovering and frequent changes in direction. Maneuverability during flight made possible swarming behavior in many small species of Diptera, some of which fly equally well forward, backward, or sideways.

Just as high speed flight is essential to the behavior and biology of flies and bees, so is slow flapping and gliding flight important to some species of Neuroptera, and many species of Lepidoptera. I was surprised to learn that up to 40-50% of flight time in some Lepidoptera is gliding flight. Changes in wing shape in Lepidoptera are traced from the narrowing of the wing plane and development of long fringes on the wings of some small moths, to the large wings of some butterflies and moths. Gliding flight required changes in wing structure and in the articulation of the wings to the thorax. Airflow, vortices, and drag forces are discussed in relationship to wing structure and shape. I found very interesting a physiological explanation for the evolution of the tails of *Papilio* spp. as modifying the drag of air vortices coming off the main surface of the wings, and thus enabling the butterflies "to use greater angles of attack during gliding without significant increase in drag." Other gliding butterflies that do not have tails solved the problem of drag in other ways.

The last chapter is a general summary of the evolution of wing structure, the axillary apparatus that hinges the wing to the thorax, and muscles that power flight. There are 3+ pages of Postscript as a sort of brief summary of principles without technical terms and jargon.

Having to grapple with many technical terms is one of the features of the book that make it, as the author warns, heavy reading. These terms include thoracic anatomy, wing venation, the names of numerous sclerites at the base of the wings, and taxonomic groupings. Many of the anatomical terms are abbreviated, and a list of abbreviations is given at the front of the book. The book is well illustrated with diagrams, and line drawings of thoracic structure, wing structure and venation, and musculature. There are nine pages of references, many of which are in the older literature, and in foreign publications probably less well known to many entomologists. There is a taxonomic index for those who might like to know what the book contains that is relevant to a particular insect or group, and a subject index.

I recommend this book to those teaching introductory entomology, insect anatomy, and insect physiology. It is packed with useful information, and is well worth serious study.

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SMITH, D., G. A. C. BEATTIE, AND R. BROADLEY (eds.). 1997. Citrus Pests and Their Natural Enemies. Integrated Pest Management in Australia. Department of Primary Industries, Brisbane, Queensland, Australia. xvi + 282 p. ISBN 0 7242 6695 X. Paperback. Australian $75.

The high quality of the cover photograph—eggs, nymphs, and adult of a spined citrus bug in beautiful color—immediately caught my eye. As I paged through the book, I realized it was just one of over 400 wonderful color photographs in this book on citrus pests and their natural enemies in Australia! The photographs are of unusually high quality and justify the price of the book. There is much more to admire about this book because it has several features that make it particularly useful, even to pest managers in other countries.

The book includes descriptions of the biology and damage caused by over 100 citrus pests, a taxonomic key to the parasitic wasps of scales and mealybugs in Australian citrus groves, a good index, and a list of relevant references. It begins with a glossary of terms, a brief introduction of the Australian citrus industry, a description of the citrus varieties grown, and the weather conditions in the major citrus growing regions. The book deals with tree diseases, insects, mites, nematodes, snails, and (even) a pest spider! Over 100 pest species are described, and their frequency is categorized as "Major," "Occasionally important," or "Minor" in each of the growing regions using color-coded maps. I decided to focus on one section, describing the mite pests of citrus, to determine whether I could use the manual as intended.

Citrus in Australia has several pest mites, including the brown citrus rust mite, *Tegolophus australis*. Photographs show all the life stages of the mite, with discriminating characters to differentiate it from the citrus rust mite, *Phyllocoptruta oleivora*, also a pest in Australia. The photographs were sufficiently good that I could use them to identify the mites in the field using a hand lens. A map showed the importance and distribution of the brown citrus rust mite in Australia. A diagram of the life cycle is given, and photographs illustrate the type of damage these mites do to lemons and Valencia oranges. A separate box labeled "Damage" summarizes the damage to the fruit, leaves, and twigs.

The natural enemies of the brown citrus rust mite are described and a beautiful photograph of the predatory mite *Euseius victoriensis* is given. This phytoseiid mite is described as an effective predator, particularly in inland citrus areas and in subcoastal Queensland. Other phytoseiid mites are listed as important in other geographic regions, and other natural enemies are mentioned, including predatory stigmaeid mites, cecidomyiid fly larvae, and fungal pathogens.

Cultural practices that are important in managing the brown citrus rust mite are included: grass should be planted between tree rows in order that pollen for the predatory mites is consistently available as a supplementary food source. Pollen also can be provided by eucalyptus trees serving as windbreaks. Monitoring is an integral component of the management program. Guidelines are given on how to monitor pest mite densities, an "Action level" is given, and "Appropriate action" is described if the pest population exceeds the action level. A graph takes the number of predatory mites per 100 leaves into account as well as the number of rust mites, and miticides are recommended that are least toxic to the predatory mites. Under the "Additional management" notes, recommendations are made to encourage growth of pollen-producing plants that will provide food to natural enemies (including predatory mites and parasitoids of red scale), discourage growth of plants (broadleaf weeds and legumes) that are hosts of the lightbrown apple moth, *Epiphyas postvittana* (another citrus pest), avoid overzealous mowing by mowing alternate rows every 2 to 4 weeks, and establish

peripheral windbreaks of predator-harboring plans such as eucalyptus, especially in new citrus plantings.

Another interesting section is on aphids, in part because the "brown citrus aphid" recently invaded Florida's citrus. Brown citrus aphid (but called black citrus aphid in Australia), *Toxoptera citricida*, and *Toxoptera aurantii* are described as "minor" pests in Australia. This is of particular interest to Florida's citrus growers because *T. citricida* is expected to transmit tristeza virus to trees grafted on susceptible rootstocks. In Australia, the "Damage" listing does not mention tree loss due to tristeza. The description of natural enemies includes the statement: "Natural enemies are important in controlling citrus aphids." Diverse predator species are pictured, including the transverse ladybird, *Coccinella transversalis*; the common spotted ladybird, *Harmonia conformis*; *Harmonia testudinaria*; the variable ladybird, *Coelophora inaequalis*; the yellow-shouldered ladybird, *Scymnodes lividigaster*; syrphid flies, including *Simosyrphus grandicornis*; and lacewing larvae. A photograph of aphid mummies shows high levels of parasitism resulting from "a small aphelinid wasp"; and both "*Aphidius* spp. and *Aphelinus* spp." are listed as natural enemies of the aphids. In addition, an *Entomophthora* fungus attacks the aphids. The authors state "It is rarely necessary to spray aphids in mature orchards, as the large numbers of natural enemies usually give satisfactory control." It is likely that these aphids are relatively unimportant in Australia due to the combined effects of natural enemies and because the citrus rootstocks recommended are resistant or tolerant to tristeza.

Unusual facts contained within this book include the description of a **pest** spider. Most of us consider spiders as beneficial, but the brown house spider, *Badumna longinqua*, is a pest in Australian citrus groves because the webbing snares numerous **natural enemies** of pest insects. The webs are also a nuisance to fruit pickers.

A section on IPM provides a template for IPM in citrus. The authors note that several components make up a practical IPM program, including identification of pests and their natural enemies, monitoring of pests and their natural enemies, data recording and reporting, decision making, taking appropriate action to manage pests, and reappraisal and research. Each of these components is addressed in this section, with sample data sheets and monitoring guides provided. The monitoring guides are very well constructed with small color photographs of each pest and a color-coded key to their location (i.e., on shoots, flowers, leaves, young fruit, maturing fruit, or twigs and branches). The recommended frequency of sampling for each pest is provided and action levels are given for each pest (i.e., 25%, 50%, 15% infestation levels). The Monitoring Guides are specific to each geographic region (Queensland and coastal New South Wales; inland New South Wales, Sunraysia and Riverland regions; or Western Australia) and are divided into Early Season, Mid-Season, and Late Season.

The acute toxicity of pesticides (insecticides, miticides, and fungicides) to natural enemies is rated as low, moderate, or high. In addition, the residual toxicity is estimated for each product in weeks so that natural enemies can be released safely into groves after a pesticide application. Petroleum spray oils are recommended as solutions to widespread resistance to synthetic pesticides by the pests and to environmental and health problems associated with pesticide use. Spray oils are recommended because their toxicity to vertebrates is low, they have fewer detrimental effects on beneficial insects and mites, they do not stimulate pest outbreaks, no pests have become resistant to them, and they can be broken down within weeks by microbes, oxidation, and UV light. Guidelines are provided for timing applications of spray oils in the different growing regions to control an array of pests, including armored scales, soft scales, mealybugs, whiteflies, thrips, and mites.

This book is very well presented and organized. It is packed with useful information on citrus pests and their natural enemies that will be helpful to biological control

workers and pest managers everywhere. *Citrus Pests and their Natural Enemies* is an outstanding contribution to the IPM literature because it emphasizes ecologically- and biologically-based pest management tactics and is not simply a manual describing how to apply toxic pesticides more efficiently.

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STERILE INSECT AND PARASITE AUGMENTATION TECHNIQUES: UNEXPLOITED SOLUTIONS FOR MANY INSECT PEST PROBLEMS[1]

E. F. KNIPLING[2]

The Florida Entomological Society is to be commended for selecting The Screwworm Research Team as the recipient of your Pioneer Award. The selection of this team for the award will not only be an honor for this pioneering group of scientists, it will also enhance the prestige of the new awards program. I feel doubly honored to have been invited to deliver the Pioneer Lecture for this special occasion.

It is regretted that several members of the team are no longer with us. I am sure that if they were here today they would be as proud and would feel as honored as those of us who have had the good fortune to survive the years that have gone by.

I wish to pay special tribute to the deceased members of the team. I would like to acknowledge one of my most respected colleagues and a special friend of the family, Dr. Raymond C. Bushland. Dr. Bushland and his assistant D. A. Hopkins, who is also deceased, demonstrated in the laboratory that the sterile insect technique was a viable concept. They participated in the field studies that proved that the sterile flies would perform under natural conditions. Dr. Bushland was a technical advisor to the pest mangers who conducted the suppression programs.

I also wish to pay tribute to another highly respected colleague, an able and dedicated scientist and a special friend of the family, Dr. Arthur W. Lindquist. He had confidence in the sterile insect technique from the beginning. As chief of the section on Insects Affecting Man and Animals, he did all that he could to support the efforts of those who were conducting the laboratory and field investigations.

Another key member of the team who made the technique work in practice was Chet Husman. Mr. Husman was the engineer who designed the machinery for the mass rearing of the flies. He designed and supervised the construction of the first screwworm rearing facility that was located at Sebring, Florida, and the larger facility that was later constructed in Texas. Every aspect of the engineering work required innovation on the part of Chet Husman because never before had insects been reared on the scale of 50 to 100 million per week.

I want also to acknowledge the members of the team who have had the good fortune to survive the many years that have passed. A key member of the team who was directly in charge of the field release experiments was Al Baumhover. He made the first sterile fly releases on the Island of Sanibal which is not far from here. That experiment demonstrated that the sterile males would perform their mission in a natural environment. He was also in charge of the experiment conducted on the island of Curacao, Netherlands Antilles. This classic experiment was of great importance. It demonstrated that the technique could eradicate an isolated screwworm population. In the conduct of this experiment he had the cooperation and support of Dr. B. A. Bitter, the veterinary officer for the island.

I hope that Al will have the opportunity to describe the details of the pioneering experiment. I recall the great satisfaction that Drs. Bushland, Lindquist, and I had in receiving Mr. Baumhover's favorable report each week for the first 9 weeks after the

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[1]This is a more detailed version of the lecture that was presented to the society members August 5, 1997.

[2]Former Director Entomology Research Division, Agricultural Research Service, United States Department of Agriculture.

sterile fly releases began. The proportion of the sterile egg masses deposited by the wild female flies increased each screwworm cycle, while the number of egg masses deposited decreased. The results confirmed the type of suppressive action predicted by the model I had developed. Within a period equal to four generations of the fly no more egg masses, either fertile or sterile, were collected.

There were other key members of the team. They included A. J. Graham, F. H. Dudley, W. D. New and G. W. Eddy. All these individuals played important roles in the research that led to the eradication of the screwworm from Florida and the southeastern states and later in the Southwestern United States and Mexico.

During my long career I observed important research in progress by many able and dedicated scientists. No research team has ever performed more diligently or accomplished as much as did the team you are honoring today.

It would be a serious omission, however, if I did not acknowledge the contributions of the many able and dedicated pest managers and workmen with the United States Department of Agriculture and the cooperating state agencies who put the research findings into practice - first in Florida and the Southeast and later in the Southwest and Mexico. Virtually every aspect of those unique programs required ingenuity, perseverance and innovations by those who conducted them. They involved the production and handling of millions of insects per week and the distribution of the flies by aircraft on several hundred thousand square miles of all types of terrain. They dealt with thousands of livestock producers in the United States and Mexico who were involved in one way or another with the program.

Many people have asked me how I got the idea of controlling the screwworm fly by the sterility technique? The answer to this question involved a number of other developments. The discovery by Cushing and Patton (1933) that the screwworm was a true parasite and differed from the common and very abundant scavenger blow fly, *Cochlomyia macellariia*, was an important factor. This meant that the pest existed in relatively few numbers in the natural population. Also, Melvin and Bushland (1936) had developed an artificial medium for rearing the fly. These two factors suggested that it might be feasible to rear more flies than existed in the natural population.

For years, research effort had been focused on controlling the worms in the animal wounds and on protecting the animals from reattack by the flies. But I kept thinking of possible ways to control the pests before most of the damage had been done to livestock and wild animals. This suggested the possibility of control by rearing and releasing flies that were sterile or that had genetic deficiencies that could be transmitted to the natural population.

It was not possible for any of us to undertake research on the idea of sterility releases for a number of years. During the 1940's we were assigned to other projects, including the research conducted at Orlando, Florida to develop means to control insect pests and disease vectors of military importance. But I kept thinking of ways that screwworm might be controlled before it caused damage to the livestock and wild animals. I discussed the feasibility of the genetic approach with a number of scientists. Most expressed skepticism that this would be successful. It was not until after the war that active research was started on the sterility procedure.

I wish I could say that all aspects of the operational programs that followed went smoothly. But this would not be correct. Those responsible for the control programs encountered and had to resolve many operational problems. There was skepticism by many; there were critics. After the programs in the southwest were initiated some scientists tried to discredit the work. Self-proclaimed authorities on the screwworm and the sterility technique grew in numbers. Some even went so far as to advocate that the program be discontinued.

I am happy to say, however, that all the obstacles were eventually overcome. The rewards by the dedicated people who executed the program have been very great. The savings for the livestock economy in the United States and Mexico have amounted to many billions of dollars during the past 40 years. Those benefits will continue to accrue by a half billion dollars each year so long as measures are taken to prevent the reestablishment of the pest in its former range. One of the greatest satisfactions from the success of the programs is the knowledge that one of nature's most cruel and obnoxious pests can be brought under control. Only those who have witnessed the trauma and suffering that helpless domestic and wild animals experience when they are literally eaten alive by thousands of maggots can fully appreciate the full benefits of this achievement.

It was a privilege for me to be associated in one way or another with various aspects of the research and control programs from the time of their inception until they became a reality. When I see the difficulty today of gaining the support needed to undertake other new approaches to insect pest control and think of the many obstacles that people can throw in the paths, I consider it miraculous that the screwworm programs ever materialized and that they proved to be so successful.

I wish time would permit a more detailed discussion of some of the aspects of the research and operations that became involved in the development and execution of the sterile insect technique for screwworm control. This is not feasible here. However, I would like to call attention to some of the publications that deal with the early research and the control program that followed. They include those by Bushland and Hopkins (1951 and 1953), Baumhover et al. (1955), Lindquist (1955), Knipling (1955 and 1959), O. H. Graham (1985), Scruggs (1975) and Meyer and Simpson (1996).

Merits and Limitations of the Sterile Insect Technique

The sterile insect technique (SIT) represented a new principle of insect population suppression. The type of suppressive action that follows the release of sterile insects is generally well understood. However, I have developed a model to demonstrate how a pest population will respond to the release of sterile insects throughout its ecosystem.

A basic model that depicts the demographics and dynamics of an uncontrolled insect pest is first needed to show how a pest population grows in the absence of control. Such model is shown in Table 1. Authorities on various pests could make appropriate modifications to such a model so that it would be reasonably representative of the demographics and dynamics of a wide range of insect pests. I have developed hypothetical models of this nature for many of our important insect pests (Knipling 1979, 1992). The degree of accuracy of some of the models may be questioned. Nevertheless, they have proved to be very valuable for analyzing the principles and for estimating the influence of various methods of control.

The hypothetical pest is assumed to exist at its normal low density level at the beginning of a season. It will grow to its normal high level as the season advances. Each generation the rate of population growth diminishes as the population increases. It will eventually stabilize due to the action of various density dependent suppression factors. By season's end this hypothetical population has increased by about 20 fold. Then, due to the high mortality that generally occurs during the winter months the population at the beginning of the next year will be similar to the population at the start of the first year. Populations of most insects are extremely variable from habitat to habitat, generation to generation, and from year to year. But they establish a steady density level that when averaged over a period of years tends to remain rather constant. This is a fundamental characteristic of all animal populations.

TABLE 1. THE DEMOGRAPHICS AND DYNAMICS OF A TYPICAL INSECT PEST POPULATION AS IT DEVELOPS DURING A CROP GROWING SEASON.*

Parameters	Generation			
	1	2	3	4
Normal females	1,000	4,000	10,498	19,415
Normal males	1,000	4,000	10,498	19,415
Eggs deposited per female	200	180	162	146
Total eggs deposited	200,000	720,000	1,700,676	2,834,590
Survival of eggs to small established larvae, percent	40	36	32	29
Total small larvae	80,000	259,200	544,216	822,031
Survival of small to large larvae, percent	40	36	32	29
Total large larvae	32,000	93,312	174,149	238,389
Survival large larvae to adults, percent	25	22.5	20	18
Adult progeny, next generation, both sexes	8,000	20,995	38,830	42,910**
Increase rate	4.0	2.6	1.7	1.1

*The density-independent control factors such as weather conditions are assumed to be normal and favorable. The density-dependent control factors such as biological agents are assumed to intensify by 10 percent each generation as the population grows.

**The progeny of the fourth generation are assumed to be the overwintering population. If the probability of winter survival is 5 percent, the population the next spring would again be near 1,000 adults of each sex. The model is considered representative of a steady density population.

The actual number of insects in natural populations and the growth rates of the population are not of much importance when the pests are to be controlled by the application of insecticides or other methods that have suppressive action independent of the pest density. But if the objective is to regulate or eliminate populations by the use of control measures that have pest density dependent suppressive action such as the sterile insect and parasite augmentation techniques, the number of insects in the natural population and their growth rates are key parameters. Obtaining such information has been one of the most neglected aspects of insect population ecology. Therefore, I have used indirect procedures to make realistic estimates for these parameters.

Nearly all insect populations have the potential of increasing by a hundred fold or more during a single generation. However, all of their life stages are subjected to many hazards even when conditions for reproduction are favorable. This restricts the reproductive rate to a low level. The population shown has an increase rate of 4 fold during the first generation. If the species has the potential of producing 1,000 progeny per female, which would be typical of a number of our major pests, then less than 1 percent of the potential progeny will normally survive even under favorable conditions.

This suggests that if a new pest specific hazard is superimposed on existing hazards, it will not require a high degree of control to cause a marked decline in a pest population. But, if in the process of achieving control a high proportion of the natural biological agents are also destroyed, the potential rate of increase of the surviving

pests and coexisting non-targeted pests that are normally held in check by natural biological control agents may increase by 10 fold or more per generation. This in essence is what we have been doing to many insects during the past 50 years because of the use of broad-spectrum insecticides.

The model in table 2 depicts the influence of the release of sterile insects into a pest population of the nature shown in table 1. If enough fully competitive sterile insects are released *throughout* the pest population to achieve a sterile to fertile ratio of 9:1, only 10 percent of the normal females will mate with normal males and the reproductive success of the population will be reduced by 90 percent. If the reproducing females produce an average of 10 adult progeny the population will decrease by 50 percent. The release of the same number of sterile insects will then result in a sterile to fertile ratio of 18:1, and reproduction will be inhibited by about 95 percent. This in turn will cause an even sharper decline in the pest population and the release of the same number of sterile insects during generation 3 will then inhibit reproduction by more than 98 percent. By generation 4 the natural population will be so low that the release of relatively few insects will reduce the probability of a fertile female mating to less than one. The model shown is representative of a classic sterile insect suppression model I first described in 1955 (Knipling 1955). In theory all reproduction will cease by the fourth generation. This is what happened to the screwworm on Curacao.

The success of the sterile insect technique against the screw worm prompted scientists to investigate the feasibility of using the technique for dealing with other insect pests.

The first intensive research effort on other insects involved tropical fruit fly species. As a complex these are the world's most important fruit insect pests. Early research on the technique was led by L. F. Steiner, Director of the Agricultural Research Service Laboratory in Hawaii. He and his associates demonstrated that the technique could be used to suppress and eliminate isolated populations of the melon fly, *Bactrocera cucurbitae*, and the oriental fruit fly, *Bactrocera dorsalis*, (Steiner et al. 1965 and Steiner 1970). Japanese scientists further developed the technique in order to eradicate the melon fly from the Okinawa islands (Kakinohama *et.al*. 1997). This virtually

TABLE 2. THE INFLUENCE OF STERILE INSECT RELEASES ON THE DYNAMICS OF A PEST POPULATION OF THE NATURE SHOWN IN TABLE 1.

	Generations			
Parameters	1	2	3	4
Normal females	1,000	500	132	10
Normal males	1,000	500	132	10
Sterile insects released, both sexes	18,000	18,000	18,000	400
Sterile-to-fertile ratio	9:1	18:1	68:1	20:1
Normal females mated with normal males	100	26.3	2	0
Expected adult progeny per normal mated female	10	10	10	—
Adult progeny, next generation, both sexes	1,000	263	20	—

doubled the vegetable economy of the islands. The technique also played a role in the elimination of the oriental fruit fly from Japan, which was accomplished largely by the use of the male attractant, methyl eugenol (Koyama *et al.* 1984).

The SIT is playing a major role in dealing with the Mediterranean fruit fly, *Ceratitis capitata*, (medfly) in various parts of the world. This is the most important of the tropical fruit fly species. Scientists in several countries have contributed to the development of the technique for controlling or eradicating this pest. Much of the research effort has been sponsored by the International Atomic Energy Agency (IAEA). Scientists with the U.S. Department of Agriculture (USDA) Laboratory in Hawaii in cooperation with the University of Hawaii and the University of California conducted much of the early research that led to use of the technique as a key component in eradication and containment programs for the medfly in the United States, Mexico and other countries.

There have been numerous introductions and establishments of medfly populations in the United States during the past half century. Until the SIT came into use control agencies relied largely on insecticide applications and drastic host removal to eliminate them. However, there is strong public opposition to the use of non-selective insecticides for eradicating insect pests, especially in urban areas where medfly introductions are most likely to become established. Relying on SIT for dealing with such introductions was slow to be accepted. The technique is not very effective when the pest populations are high and its suppressive action is slow compared with the use of insecticides. But limited use of insecticides followed by the release of sterile flies to complete eradication or to prevent the reestablishment of populations is now an accepted practices.

SIT has also had a rather slow history of development for the eradication of tsetse fly populations, *Glossina spp*. Tsetse flies are probably the most important insect pests in the world. The IAEA assumed leadership in developing and promoting the use of SIT for eradicating these disease vectors. Because of the difficulty and high cost of rearing tsetse flies these insects would seem to be poor candidates for eradication by SIT. However, by using insecticides when the pest populations are high and then releasing sterile flies against the reduced populations, this pest management strategy has been used successfully.

Sterile pink boll worm moths have also been used for some years to prevent the establishment of this cotton pest in the San Jauquin Valley of California. This important cotton growing area has been kept free of the pink boll worm for about two decades by the use of the technique (Bartlett and Staten 1996). Canadian scientists are using the technique in efforts to eradicate the codling moth from Western Canada.

Thus the SIT is playing an increasing role in dealing with several important insect pest problems. It is my opinion, however, that the technique has not been developed and put into use to the extent that it should have been. There are a dozen or more major insect pests in the United States and in other parts of the world that would be good candidates for management on a year by year basis by the sterility technique, or for eradication when this is a feasible option. The pests I have in mind would include all of the tropical fruit fly species; European corn borer, *Ostrinia nubilalis*; sugarcane borer, *Diatraea succharalis*; and even the widespread and costly Helicoverpa/Heliothis complex. However, development and use of the technique has lagged for a number of reasons. Technology must be developed and made available to mass produce large numbers of insects. This has not yet been done for a number of candidate species. Some insects are very susceptible to irradiation damage and thus are not sexually competitive with wild rivals. This is the case for the boll weevil, *Anthonomus grandis*.

However, one of the main reasons for the limited use of the technique has been the lack of support from and even opposition by much of the pest management community

to the holistic approach to insect pest management. This makes it difficult to obtain the public and political support for areawide insect pest management programs. As time goes on there will be increasing concern over the use of potentially hazardous insecticides. It will also become increasingly apparent that a defensive reactive pest management procedure based largely on the use of insecticides will not provide satisfactory solutions for many pest problems. SIT has some important limitations, but it also has merits not possessed by other methods of control. With greater recognition of the advantages of the holistic approach to insect pest problems there will be more interest in feasible ways to achieve this objective.

Merits and Limitations of the Use of Insecticides

Control of insects by the use of insecticides has always appealed to agriculturists. The availability of many effective synthetic insecticides has made it possible for farmers to control most insects of agricultural importance. Their intensive use worldwide is one of the reasons that agriculture has been able to meet the food requirements for the expanding world population. Also their availability for the control of arthropod vectors of human diseases has prevented illness or the death by hundreds of millions of people each year during the past 50 years.

Insecticides have a number of advantages over other methods of insect control. They are rapid and positive in action. Insect outbreaks can be controlled in a matter of days and disease transmission can be halted within hours by the application of insecticides. They are readily available to consumers and equipment for their application is also readily available. Society should be mindful of the important contributions that insecticides have made to human welfare. People should also be mindful of the continuing need for these chemical insecticides for the indefinite future.

At the same time, however, the extensive use of the insecticides, most of which have broad-spectrum activity, has created many complex environmental problems. Residues of the chemicals in or on agricultural products pose potential hazards to people and animals. The welfare of fish and wildlife in environments treated for insect pest control can be jeopardized. The balance between destructive and beneficial insects can be so seriously disrupted that natural biological control agents cannot perform their normal function. In my opinion, the ecological disruptions resulting from the use of broad-spectrum insecticides is the most serious of the environmental hazard problems associated with the use of insecticides. I can say without qualification that ecologically sound insect pest management will not be possible so long as the use of broad-spectrum insecticides is a major component in pest management systems.

Pest management scientists are aware of this, and accordingly have devoted much effort to the development of safer ways to control insects. Major efforts have been made to find new and better insect attractants; insect pathologists have discovered a wide range of insect pathogens and microbial agents that offer promise as safe alternatives to chemical insecticides. More emphasis has been placed on classical biological control and the use of entomophagous insects for augmentation purposes. Plant breeders and entomologists have intensified investigations on host plant resistance, including resistance by biotechnology.

Good progress has been made on all of these approaches for insect control. But when viewed from a broad perspective very little of the new technology has been put into practice. Agriculture still depends largely on insecticides for the control of insects (U.S. Congress 1995).

In the efforts to reduce the amount of insecticides used, a supervised system of insect control evolved that is broadly defined as Insect Pest Management (IPM). To minimize the use of environmentally hazardous insecticides and to reduce costs farmers

are urged to rely as much as possible on natural control agents before applying insecticides. They are also encouraged to use supplemental control measures such as cultural procedures and to grow pest resistant crop varieties. As a guide for growers, economic treatment levels have been established by pest managers for various insects on different crops.

IPM has achieved some important objectives. It has virtually eliminated the indiscriminate use of insecticides. It has been profitable for growers because it minimizes expenditures for insecticides yet prevents the heavy losses that can occur if control measures are not applied. However, it has not reduced primary reliance on pesticides to control pests.

After intensive efforts to develop alternative ways to control insects, we must ask ourselves why is agriculture still so dependent on insecticides? The answer involves a number of complex factors. But the basic reasons are clear. Most of the possible alternative methods of control are not as effective or as practical as insecticides after insect pest populations have already reached economic treatment levels. They also lack the fast and positive action that growers desire for protecting their crops when insect pest populations reach such levels. Moreover, the alternative methods of control are usually not available to individual growers. Therefore, agriculture has continued to depend largely on fast-acting insecticides for controlling insect pests for a half century. And when broad-spectrum insecticides are applied it defeats one of the primary objectives of IPM programs: to obtain optimum benefits from natural biological agents.

Despite all that has been said about the benefits of IPM, when we analyze the dynamics of insect pest populations and the kinds of suppressive action that is achieved by the use of insecticides, the defensive reactive method of insect control that has evolved is not a sound insect pest management system. It gives insect pest populations the opportunity to increase virtually unhampered from their normal low to their normal high levels each year. And when they reach the economic treatment levels about the only option that growers have is to apply fast-acting, broad-spectrum insecticides. Then, the reproductive success of the proportion of the target pest population not controlled is higher than normal leading to possible resistance and the serious depletion of the total complex of natural control agents will permit normally minor or secondary pests to become important pests. The method also concedes to insects the losses they cause below the economic threshold levels. For some of our important insect pests such as the corn earworm on corn and the European corn borer, these losses amount to about $500 million per year for either pest. What the total damage is that falls below the economic pest control level is difficult to determine, but it probably amounts to several billion dollars annually. The losses that fall below current economic threshold levels give us a good perspective of the amount that agriculture could afford to spend on alternate ways to deal with specific pest problems that would be less costly and more acceptable from environmental standpoints.

This is the current status of insect pest management. While the methods of control that have evolved are profitable for the growers, they have not reduced the overall threat that insects pose for agriculture. In support of this conclusion, if a list were made of the insect pests that were of major concern to agriculture before the new insecticides came into being and such list were also drawn up today most of the same pests would be on both lists—except that the current list would be longer. Only two important insect pests would not be on the current list: the screwworm and the boll weevil in the southeastern cotton growing region. It is significant that these are the only insect pest problems that have been subjected to organized suppression programs that are designed to eliminate or maintain total populations below damage levels.

The limitations of the largely defensive systems of insect control have prompted me to continue theoretical appraisals of other techniques and strategies for control-

ling insects. My efforts have been focused on the possibility of making use of entomophagous insects to regulate total pest populations as a preventative measure. As the investigations have progressed and with the promising results obtained on several of the major insect pests by research entomologists who are investigating area wide management by the release of biological agents, I have gained more and more confidence in the holistic approach to insect pest control.

The Holistic Approach to Insect Pest Management by the Parasite Augmentation Technique

The possibility of controlling insect pests by the release of reared insect parasitoids or insect predators into pest habitats is not a new concept. Indeed, biologists have devoted as much or more research efforts to this method of control than to any other method besides the use of insecticides. Much of this effort has been on Trichogramma parasitoids. While the use of these parasitoids is reportedly successful in some countries for controlling certain lepidopterous pests (Ridgway and Vinson 1977), it has not been very successful in other countries. The results obtained with other parasitoids or predators have been largely unsatisfactory. This is reflected in the limited use of reared biological agents for controlling insect pests. While a number of such biological agents are being produced and sold by small private industries (Hunter 1994), probably less than one percent of the agricultural insect pests are currently controlled by the release of insect parasitoids or predators into insect pest habitats.

There are several reasons for such limited use of the technique. It is a technique that is not very effective, practical or reliable when used on a farm-by-farm basis and only as the need arises. But when used as a preventative measure to regulate total insect pest populations it has very important advantages over all other methods of control.

Until recent years the possibility of rigidly regulating total insect pest populations as a preventative measure by the release of selected parasitoids or predators throughout pest ecosystems has been given little consideration by biologists. Very few insect pests have been subjected to such releases. The use of natural enemies to control insect pests in greenhouses would be an exception to this generalization. Releases of insect predators or parasitoids are often quite successful because the total pest populations are subjected to the releases.

Notwithstanding the poor record of certain insect parasitoids both in nature or when spot released, I undertook a detailed study of parasitism processes and the influence that parasitoids have on the dynamics of insect pests (Knipling 1992). The study was conducted largely by theoretical means, but I reached the conclusion that the parasite release technique offers almost unlimited possibilities for regulating populations of many of the nation's and world's major insect pests if selected species can be mass produced at reasonable costs and appropriate numbers of the parasitoids are distributed *throughout* pest ecosystems at strategic times during the seasonal or periodic cycles of the pests. I emphasize the term *throughout*. Like sterile insects, parasitoid releases are not effective when releases are made in small, unisolated habitats.

The results of the investigation I conducted have been published in a handbook entitled *Principles of Insect Parasitism Analyzed from New Perspectives: Practical Implications for Regulating Insect Populations by Biological Mean*. U.S. Department of Agriculture, Agricultural Research Service. Handbook No. 693, (1992).

The publication explains how parasitism works in natural environments and how biological actions evolved under nature's natural balancing mechanisms to maintain the relative number of parasites and hosts within safe limits. Simple rationalizations tell us that the numerical relationships between parasites and hosts must be maintained within certain limits for the welfare of the hosts as well as for the parasitoids

that are dependent on specific hosts or host complexes for reproduction and survival. It is nature's objective to maintain a safe balance between associated organisms, and it is very successful in achieving that objective. But this objective can be in conflict with agriculture's needs. It permits too many insect pests to cause excessive damage to crops and livestock. Also, intensive agriculture favors many insect pests. So, the implications are clear. To achieve satisfactory management of insect pest populations by the use of insect parasitoids it will be necessary to increase the ratio of parasitoids to hosts in coexisting populations in all parts of the ecosystem they cohabitate. About the only way this can be done will be to augment the natural populations by artificial means.

To determine if it is feasible to regulate total populations of various insect pests by use of the parasite release technique, it is necessary to have reasonably good information on the actual number of parasitoids that must be produced and maintained in the pest ecosystems to achieve various rates of parasitism. Such information is not now available for any of our parasitoids. However, largely by deductive procedures and by the use of hypothetical models of the nature already described, I feel that I have been very successful in making realistic estimates of the *relative* number of parasitoids and hosts that normally coexist in natural populations for a wide range of our pests. This in turn makes it possible to estimate the *actual* number of parasitoids that will have to be produced and released in pest ecosystems to achieve satisfactory control.

For solitary parasite species, the proportion of the host population that is normally parasitized provides a good clue to the normal parasitoid to host ratio that occurs in natural populations. It is a good clue because the probability of survival of the immature parasitoids in the host to the adult parasitoid stage and the probability of survival of the hosts that are not parasitized to the adult host stage are very closely linked at all host and parasite density levels. Biologists have obtained considerable information on the usual rates of parasitism caused by virtually all of the better known parasitoid species of our major insect pests. While such data are usually variable because of agricultural practices and other factors, including inadequate sampling, they nevertheless give us a good indication of the normal ratio of parasitoids to hosts in natural populations and a good indication of the rate of parasitism to expect from different ratios. Recognition and adoption of this logical theory has made it possible to gain a good understanding of virtually all aspects of insect parasitism. It has shed new light on what we can and cannot expect from insect parasitoids.

If a parasitoid species causes an average of about 10 percent parasitism, which would be typical of some parasite species, the normal ratio of adult parasites to adult hosts will be near 10:90 or 1:9. If the average rate of parasitism is near 20 percent, which would be typical of many other species, the ratio will be near 20:80 or 1:4 and so forth. Those approximate numerical relationships will hold regardless of the biology and behavior of the parasitoid and regardless of the host stage parasitized. Most importantly such numerical relationships and rates of parasitism hold regardless of the density of the host and parasitoid populations. The practical implications of this theory are clear when pest populations exist at low levels.

Another very important conclusion reached from the investigation is that, contrary to popular opinions, differences in the rates of parasitism caused by different parasite species are due to differences in the ratio of parasites to hosts that can coexist because of the constraints imposed by nature's natural balancing mechanisms.

Many biologists assume that differences in the rates of parasitism caused by various parasite species are due to differences in their host-searching and host-finding ability. Parasitoids are often categorized as good or poor host-finders based on the rates of parasitism they achieve. But we can accept with complete assurance that *all parasite species are diligent host-searchers and highly efficient host-finders and at all host density levels*. Otherwise they would not exist.

The way parasitism works has very great practical implications. It means that the usually low rates of parasitism that occur naturally can be overcome by the simple procedure of mass producing and liberating appropriate numbers of key parasitoid species *throughout* pest ecosystems. This may not be easy to accomplish, but there will be few if any barriers to the attainment of the objective if insect rearing experts are given even modest support for conducting research on parasitoid and host rearing procedures. I am confident that scientists and engineers can, by in vivo or in vitro procedures, mass produce any parasitoid species in unlimited numbers and at reasonable costs if given such support.

If the approximate rate of parasitism caused by a given parasitoid to host ratio is known it is possible by extrapolation to calculate the approximate rate of parasitism that will be achieved by increasing the parasitoid to host ratio. If a ratio of 1:4 causes 20 percent parasitism, a ratio of 2:4 will cause 20 + .20 (100-20) or 36 percent parasitism. A ratio of 4:4 or 1:1 will in theory cause 36 + .36 (1000-36) = 59 percent parasitism. This procedure makes allowances for the intraspecific competition factor. It does not, however, make allowances for the probable shorter life span and the lower average host-finding ability of the female parasitoids when the populations exist at abnormally high levels. But adequate allowances can also be made for this factor.

When allowances are made for both factors, I estimate that an adult parasitoid to adult host ratio of 1:1 will cause about 50 percent parasitism; a ratio of 2:1 will cause about 75 percent parasitism; and a ratio of 5:1 will cause about 95 percent parasitism. If these estimates are accepted as realistic, we have a good idea of the influence that various rates of parasitism will have on the dynamics of different insect pests. We have already noted that natural control factors greatly limit the growth rate of insect populations. I believe that most of our major insect pests would be of minor importance if an additional 50 percent control were superimposed on all natural hazards that each pest faces and if this occurred *throughout* the pest ecosystem. Again, I emphasize that such additional mortality must be achieved against the total population.

One might ask how realistic are these assumptions? I believe that most biologists would agree that if a new biological agent were introduced that achieved 50 percent parasitism every cycle, most of our major insect pests would become minor pests. If this is true, there is every reason to assume that 75 percent mortality above normal hazards would assure virtually complete control of nearly all of the major insect pests. It would seem almost certain that 95 percent control superimposed on all natural control factors would within a few cycles result in complete elimination of a pest population—and keep in mind that the lower the pest density the fewer the number of parasitoids that will be required to achieve high parasitoid to host ratios.

If we accept these hypotheses as reasonable expectations—and I firmly believe that they are—the practical question is whether there are any feasible ways to superimpose such levels of control with reasonable consistency and uniformity throughout pest ecosystems each pest cycle. In my opinion, the most feasible way to accomplish this will be by the release of mobile parasitoids that have the instincts and the *capability* of finding the precise location of the hosts.

We have already estimated the rate of parasitism to expect from different parasitoid to host ratios. But, we must consider how pest populations will respond to different rates of parasitism. We will use a hypothetical pest population to estimate the influence as we did for the sterile insect technique.

Influence of Parasitoid Releases on Pest Host Populations

To estimate the influence of the release of parasitoids in pest host ecosystems, we need information on the rates of parasitism to expect from different parasitoids to

host ratios as well as information on the average host-finding efficiency of the parasites to be released. I have indicated the rates of parasitism to expect from different parasitoid to host ratios, but we also need to quantify the actual numerical relationships and rates of parasitism.

The basic host population model shown in table 1 can be used to postulate the relative and actual number of parasitoids and hosts that will normally coexist in natural populations and also estimate the average number of host larvae that the female parasitoids will parasitize during their lifetimes if the normal rate of parasitism is known. The model shown in table 3 depicts the coexistence pattern of a pest an associated parasitoid species. The hypothetical parasitoid is a solitary species that averages between 15 to 20 percent parasitism. For this model an average of 17 percent parasitism is assumed. Therefore, based on the comparable survival theory, the normal ratio of adult parasitoids to adult hosts will be near 17:83 or about 1:5. If the host population numbers 1,000 females, as we have assumed, this would mean that 200 female parasitoids will normally coexist with 1,000 female hosts. It will also mean that if the rate of parasitism averages 17 percent, the female parasitoids will parasitize 13,600 of the 80,000 host larvae presumed to be present. It follows that each female parasitoid will on average parasitize 68 hosts during their lifetime during the first generation. Thus, by indirect procedures we have established approximate values for all the parameters needed to calculate the influence a known number of parasitoids will have on the dynamics of a host population having a known number of hosts.

The model depicted in table 4 shows the theoretical results to expect if enough parasitoids of the nature depicted in table 3 are released during generation 1 to achieve an adult parasitoid to adult host ratio of 3:1. This would require the release of 3,000 female parasitoids (6,000 of both sexes.) It should be kept in mind that a 3:1 ratio would be *15 times* the 1:5 ratio that is estimated to cause 17 percent parasitism of the host larvae. Thus, the pest population would be subjected to a very high parasitoid population. We have estimated that at normal densities each female parasitoid will parasitize 68 host larvae. But because of the high parasitoid density I assume, rather arbitrarily, that the average host finding ability of the female parasitoids will be 25 percent lower or 51 per female. However, this will permit 3,000 females to find and parasitize 153,000 host larvae.

Since only 80,000 host larvae are available to be parasitized, the ratio of hosts encountered to hosts available will be about 1.9:1. According to the formula described for table 1 in the publication by Knipling (1992), approximately 15 percent of the host larvae will escape parasitism by chance and 85 percent will be parasitized one or more times when the ratio of total hosts parasitized to hosts present is 1.9:1. Therefore 12,000 host larvae will escape parasitism by chance and 68,000 will be parasitized one or more times. Being a solitary species only one immature parasitoid can develop successfully in one parasitized host.

According to the basic model, table 3, the survival rate of the unparasitized larvae to the adult host stage and the survival rate of the parasitized host larvae to the adult parasitoid stage will be 12 percent during the first generation. Therefore, in generation 2 the adult host population will number 720 females, and the adult parasitoid population will number 4,088. This would be a 28 percent decrease in the host population but a 32 percent increase in the parasitoid population. Therefore, the ratio of adult parasitoids to adult hosts during generation 2 would increase substantially. There are only slight changes in the average number of host larvae produced per female host and the average number found per female parasitoid so the ratio of hosts encountered to hosts present will increase to 3.3:1. This in theory will cause 96 percent parasitism.

Such high rate of parasitism would cause a marked decline in the pest population for generation 3, but, significantly, the parasitoid population would not decline as

TABLE 3. THE ESTIMATED COEXISTENCE PATTERN OF A LARVAL PARASITOID WITH A HOST POPULATION OF THE NATURE SHOWN IN TABLE 1.

	Generation		
Parameters	1	2	3
Female hosts	1,000	3,984	10,668
Small larvae produced per female	80	72	65
Total small larvae	80,000	286,848	693,420
Coexisting female parasitoids, natural population	200	816	2,240
Adult parasitoid-to-adult host ratio	1:5	1:4.9	1:4.8
Larvae parasitized per female parasitoid	68	61	55
Total host larvae parasitized	13,600	49,776	123,200
Percent parasitism	17	17.3	17.7
Host larvae not parasitized	66,400	237,072	570,220
Survival, unparasitized host larvae to adult hosts, percent	12	9	6.75
Adult hosts, next generation, both sexes	7,968	21,336	38,490
Survival, parasitized host larvae to adult parasitoids percent	12	9	6.75
Adult parasitoids next generation, both sexes	1,632	4,480	8,316
Increase rate of host population	4.0	2.7	1.8
Increase rate of parasitoid population	4.0	2.7	1.8

much. Therefore, the ratio of adult parasitoids to adult hosts during generation 3 would increase dramatically to a ratio of 96;4 or 24:1. This ratio of parasitoids to hosts would be about *120 times* higher than the ratio that is estimated to exist in natural populations which is assumed to cause 17 percent parasitism. While the host population has declined sharply during generation 3, enough hosts should be present for the female parasitoids to find their normal quota of hosts. This will mean that the ratio of hosts found and presumably parasitized to host present will exceed 13:1. Therefore the rate of parasitism during generation 3 should be near 100 percent. Near complete collapse of the host population could be expected for generation 4. In all probability a few adult hosts would still be present during generation 4. Some adult survivors can be expected to overlap into generation 4 and a few adult progeny might be expected from larvae that escaped parasitism during generation 3. But the ratio of parasitoids to hosts would remain very high until the parasitoid population also collapses due to the lack of hosts.

It is possible that certain biological actions of which we are not aware might occur that would not permit the degree of suppressive action that is shown in the model. However, it is difficult to envision how any host population could maintain a damaging level or even survive if subjected to the dramatic changes in the numerical relationships between parasitoid and host populations that would be brought about by the type of release procedures proposed. It is certain that no insects in all of their evolutionary history have ever come close to experiencing such dramatic changes in para-

TABLE 4. INFLUENCE ON THE DYNAMICS OF A HOST POPULATION WHEN ENOUGH LARVAL PARASITOIDS ARE RELEASED IN THE HOST ECOSYSTEM TO ACHIEVE AN ADULT PARASITOID-TO-ADULT HOST RATIO OF 3:1.

	Generation		
Parameters	1	2	3
Female hosts	1,000	720	154
Host larvae produced per female*	80	82	86
Total host larvae	80,000	59,040	13,244
Female parasitoids released generation 1 only	3,000	4,080	3,684
Adult parasitoid-to-adult-host ratio	3:1	5.7:1	24:1
Host larvae parasitized per female**	51	48	49
Host larvae parasitized	153,000	195,840	180,516
Ratio, host parasitized to hosts present***	1.9:1	3.3:1	13.6:1
Percent parasitism	85	96	99+
Host larvae parasitized, number	68,000	56,678	13,112
Host larvae not parasitized, number	12,000	2,362	132-
Survival, unparasitized host larvae to adult hosts, percent*	12	13	14
Adult hosts next generation, both sexes	1,440	307	18-
Survival, parasitized hosts to adult parasitoids, percent*	12	13	14
Adult parasitoids, next generation, both sexes	8,160	7,368	1,836+

*Some changes in parameter values are made because of changes in parasitoid and host densities.

**Females in a natural population as shown in Table 3 are estimated to parasitize an average of 68 larvae. However, because of the high density the average has been reduced by 25 percent to 51 per female.

***The rates of parasitism at different ratios of hosts parasitized to hosts present are based on data in Table 1 of USDA Handbook, Number 693, "Principles of Insect Parasitism Analyzed from New Perspectives; Practical Implications for Regulating Insect Populations by Biological Means" published in 1992.

sitoid-host relationships. And, since no insect pest, to my knowledge, has ever been subjected to the release of such large numbers of reared parasitoids *throughout* its ecosystem we have no direct information on the results to expect. Therefore, until this is done for a number of species, we will not know for certain how much influence parasitoid releases will have on the dynamics of pest host populations. But, in my opinion, the probability is near 100 percent that the suppression model reasonably reflects the results that can be expected from the parasitoid augmentation technique. Keep in mind that all such actions have remained obscured for years because parasitoid releases have never been made *throughout* a pest ecosystem in the manner proposed and the theoretical effect has never before been calculated in the manner I have used.

The release of 6,000 parasitoids during one pest generation would achieve about the same results that can be expected from the release of about 54,000 sterile insects during 4 generations as shown in table 2. This would be a 9 fold difference in numbers of insects required. It should be kept in mind that this assumes that the sterile insects are completely competitive. For many insects some loss in competition is likely to oc-

cur because of radiation damage. Therefore, there could be an even greater difference in the relative efficiency of parasitoids and sterile insects than is indicated by this study. Also, the higher the parasitoid to host ratio the greater will be the advantage of parasitoids over sterile insects.

I have developed and critically analyzed similar models involving known parasitoids of a number of our major pests including the boll weevil, *Anthonomus grandis*; corn earworm, *Heliothis zea*; tobacco budworm, *Heliothis virescens*; European corn borer, *Ostrinia nubilas*; sugarcane borer, *Diatraea saccharalis*; Colorado potato beetle, *Leptinotarsa decimlineata*; Mediterranean fruit fly, *Ceratitis capitata*, tsetse flies, *Glossina spp.* and a dozen other parasitoid-host associations. In every case, the parasitoid population will, in theory, so dominate the host population within a few cycles that the elimination of completely isolated host populations would seem to be inevitable. But until we subject completely isolated populations to parasitoid releases in the manner proposed we will not know for certain to what level augmented parasitoid populations can suppress their host populations. However, the same question confronted researchers on the sterile insect technique. But the question no longer exists for the sterile insect technique. Sterile insects have been shown to be capable of eliminating populations of several different pests on numerous occasions. I feel certain that host specific or primary parasitoids will be much more effective than sterile insects for the management or elimination of pest populations. This assumption is of such great importance from both economic and environmental standpoints that it will be critically analyzed in greater detail.

A Comparison of the Suppression Characteristics of the Parasitoid Augmentation and Sterile Insect Techniques When Used for Regulating Total Populations

We have shown by hypothetical population models how insect pest populations will respond to sterile insect and parasitoid releases. The suppression characteristics of the two techniques have also been discussed to some extent. However, a full understanding of the suppression characteristics of both techniques is vital to the total pest management concept and to the role that the two techniques can be made to play in future insect pest management systems. Therefore a critical comparison will be made of the suppression characteristics of the two techniques with some comments on how they differ from other insect control methods. There is increasing interest in the areawide approach to insect pest management. However, it is very important to have a good understanding of the suppression characteristics of different methods of control because they differ in their effectiveness for areawide management.

Target Pest Specificity

The chief goal of insect pest management scientists for several decades has been to develop ways of controlling insects that will permit natural biological agents to perform their normal functions. We noted previously how important this is and why ecologically sound insect pest management will not be possible so long as the use of broad-spectrum insecticides is a major component in pest management systems. Yet, most agricultural insect pests are now being controlled by the use of broad-spectrum insecticides. Fortunately, most alternative methods of control that scientists are investigating have a high degree of pest specificity. The parasitoid release technique using host specific or primary parasitoids would be about as pest specific as is possible to achieve. The sterile insect technique is also highly pest specific although when the

adult stage causes harm to plants or animals the technique may not be acceptable. For some insects this is not a matter of great importance because when the pest populations are very low the number of sterile insects that will be required will usually cause little damage. But no harm to people, animals or plants will occur when parasitoids are released in pest ecosystems.

Pest Density Dependent Suppressive Action

The suppressive action of all methods of insect control can be placed in two categories: those that achieve about the same degree of control whether the pests are abundant or scarce; and those that have low effectiveness and efficiency when the pest populations are high but which become increasingly effective and efficient against declining pest populations. The sterile insect technique, the parasitoid augmentation technique and the use of sex pheromones have pest density dependent suppressive action. This is a negative characteristic when pest populations are high, but it is a very positive characteristic when the pest populations are low.

The suppressive action of all other methods of control is independent of the pest density. A given chemical or biological insecticide formula will kill about the same proportion of a pest population whether the insect population are high or low. It is a favorable characteristic when the pest populations have reached high levels. However, there may be little or no advantage to the use of insecticides against low pest populations in areawide insect management programs. But, it should be kept in mind that there can be a great advantage to the integration of density independent and density dependent methods of control when the objective is to manage total populations on an areawide basis. This is a principle of insect pest management that has not been adequately exploited.

Mobility Factors

The excessive movement of released parasitoids and their progeny out of small unisolated pest habitats and the excessive movement of the pests into habitats where parasitoids have been released has probably done more to obscure the true efficiency of the parasitoid release technique than any other factor. This can also be said for the sterile insect technique and probably also for the sex pheromone control technique. However, when the objective is to manage insect pests on an areawide basis, the ability of the organisms to disperse and achieve control in all of the pest habitats becomes one of the most favorable characteristics of the parasitoid release and the sterile insect techniques.

One of the major disadvantages of the use of control methods that lack mobile action is that it will require much greater precision in their application than will the release of mobile parasitoids or sterile insects. Treatment intervals of 100 feet or less will probably be required for highly effective control by non-mobile biological organisms, such as insect pathogens and immature insect predators, whereas release intervals ranging between one half to one mile (approximately 2,500 to 5,000 feet) should be adequate for most parasitoid species and sterile insects. Therefore there can be as much as a 25 fold difference in the cost of applying mobile versus non-mobile control procedures when the objective is areawide pest management.

Pest Guidance Factor

When host-specific parasitoids are released in pest ecosystems, the released organisms will tend to disperse into all of the pest habitats in their search for the hosts.

These highly specialized organisms by nature have the ability to find their hosts with a high degree of efficiency (Nordlund et al. 1981) even when the host populations are very low. Their highly developed host-detection mechanisms, plus their mobility and instincts for host-finding give real meaning to the often used phrase: "You can run, but you can't hide." One could characterize insect parasitoids as "biological guided missiles." I am sure that they can find pest targets with much greater precision than can the most sophisticated guided missiles for detecting military targets. Sterile insects also have the mobility factor, but when both sexes are released the sterile males or females are no more likely to search specifically for wild mates than for their sterile siblings. If it is feasible to release males only the pest guidance factor should also apply to the sterile insect technique.

The pest guidance factor is a characteristic of immense practical significance for insect pest management or eradication programs. The parasitoid release procedure and the release of males only in sterile insect programs are the only techniques that possess these characteristics.

Self-Perpetuating Parasite Populations

The frequency that the control procedure must be applied can be a very important factor in selecting the way to deal with insect pest problems. Long residual action of insecticides can be a desirable characteristic in controlling certain pests. However, when an insecticide has broad-spectrum activity long lasting effects can also be very objectionable because of ecological reasons. New plant growth can nullify insecticide residual action under certain circumstances.

The ability of released parasitoids to maintain self-perpetuating populations and achieve control from cycle to cycle throughout a pest ecosystem is without a doubt one of the most important characteristics of the parasitoid release technique. This is an inherent characteristic of both classical and augmentative biological control. However, in natural populations, as we have already noted, there are constraints imposed by nature's natural balancing mechanisms which tends to maintain the relative number and the rate of parasitism within certain limits. This natural barrier can be overcome by augmented populations. If enough parasitoids are released throughout a pest ecosystem to achieve an adult parasitoid to adult host ratio higher than 1:1 this can, in theory, induce a progressive increase in the rate of parasitism from cycle to cycle without the release of additional parasitoids. This theoretically will continue until the host population is eliminated. For some parasitoid-host associations, there seem to be mechanisms that will prevent this progressive increase, as described by Knipling (1992). For others, however, such mechanisms seem not to exist. The self-increasing effect cannot be triggered so long as the rate of parasitism remains below 50 percent. It can occur only when the parasitoid progeny will exceed the host progeny that are produced throughout coexisting populations. If such increasing action can be confirmed for any parasitoid species until the host population is eliminated it would be a biological action new to science.

The self-perpetuating characteristic is one of the most important advantages of the parasitoid release technique over the sterile insect technique and most other control methods. There is some persistent suppressive action when lepidopterous insects that receive substerilizing dosages of irradiation are released in pest ecosystems (Carpenter, et al. 1987), but such action does not persist for more than about one generation. Growing pest resistant host plants, whether developed by genetic selection or by biotechnology, is perhaps the most persistent suppressive action that can be achieved. But host resistance is not applicable for some pests and has limited action for others.

General Discussion

Thus, when the objective is total population management, no method of control has as many desirable characteristics as does the parasitoid augmentation technique. However, the full potential of this technique for dealing with insect pest problems has long remained obscured because the science of insect pest management has not considered or tested its use to manage total pest populations. The effort that have been made in the past to use the technique has generally been patterned after the way insecticides are employed. However, it is my opinion that neither the parasite augmentation or sterile insect techniques will ever play prominent roles in future insect pest management systems if they are intended for use against high pest populations on a farm by farm basis as a substitute for insecticides. Their density dependent suppressive action, the propensity for the organisms to move out of small size habitats, plus their slow action will make these two method of control unacceptable for growers no matter how much they might be encouraged to use such biological control procedures.

However, one or the other of the two techniques has characteristics which are of special importance for regulating total pest populations. They offer almost unlimited potential for dealing with many insect pest populations in an effective, low-cost and environmentally safe manner. The only requirement will be the technology for mass producing the organisms in large numbers and at reasonable costs. Considering the progress that insect rearing experts have achieved in rearing a variety of insects on a large scale (King and Leppla 1984) (Anderson and Leppla 1992) there are reasons to believe that rearing insects for augmentation purposes or for autocidal control will pose no serious problems.

A few examples can be cited. Excellent progress has been made on rearing several parasitoids of tropical fruit fly species, Harris and Okamoto Cyo 1991, (Wong and Ramadan 1992, Burns 1993). A tachinid parasitoid of the corn earworm *Archytas marmoratus* can be readily reared under laboratory conditions, Gross and Johnson 1985 as can be the tachinid *Lixophaga diatraeae*, a parasitoid of the sugarcane borer.

It might be necessary to rear most insect parasitoids on their hosts or a surrogate host, but excellent progress is being made in rearing parasitoid species by in vitro procedures. This has been accomplished for the boll weevil parasitoid *Catolaccus grandis* by Royas et al. (1996). Carpenter and Greany, (1997), report progress in rearing a pupal parasitoid of the corn earworm on artificial media. Also, Cohan (1997) has developed in vitro procedures for rearing two well known insect predators, *Geocoris punctipes* and *Chrysoperla carnea*.

An important obstacle to overcome before making wider use of the parasitoid augmentation technique to manage insect pests on an areawide basis is the need to demonstrate that the techniques will in fact be highly effective and practical. This is the same problem that has handicapped researchers developing the sterile insect technique.

It is not possible to obtain a high degree of suppression or to achieve eradication of insect pest populations by the release of parasitoids unless the releases are made against isolated populations or in large areas. Research scientists have not had the opportunity to conduct such experiments for any parasitoid species. Until this is done we will not know the full potential of the parasitoid release technique for rigidly managing total pest populations or if the technique can be used to eradicate isolated pest host populations.

To demonstrate that mobile biological organisms are capable of suppressing pest populations to very low levels or to achieve eradication of isolated populations will require carefully planned and well executed experiments. Each trial is likely to cost several million dollars. However, this would be a very small investment in research on

methods of insect management that could eventually benefit agriculture by several billion dollars per year and also make a major contribution to reducing the need for ecologically disruptive insecticides.

Synergistic Suppressive Action When Different Insect Control Methods are Integrated

In appraising the influence of the integration of different methods of insect control, I recognized a suppression mechanism that I call *mutual synergistic suppressive action*. The concurrent release of sterile insects and parasitoids produces this type of action.

This previously unrecognized type of suppressive action can add a new dimension to insect pest management methodology. It offers the science of insect pest management the opportunity to achieve extraordinary effectiveness and efficiency when it is feasible to integrate two or more control techniques that have this characteristic.

The model shown in table 5 depicts the theoretical influence of the concurrent release of enough sterile insects and parasitoids during the first generation to achieve ratios of 2:1 for each organism.

The sterile insects are assumed to be fully competitive. The release of 4,000 sterile insects of both sexes would achieve a sterile-to-fertile ratio of 2:1 during generation 1. Therefore only 33.3 percent or 333 of the 1,000 normal females will mate with fertile males. The concurrent presence of 2,000 female parasitoids would mean a parasitoid to host ratio of 6:1. This will have an effect equal to the release of 12,000 female parasitoids alone. A ratio of 2,000 female parasitoids to 333 reproducing female hosts is estimated to cause about 98 percent parasitism. Thus the combined influence would be 67 +.98 (100-67) = 99.3 control.

To inhibit reproduction by 99.3 percent by the release of sterile insects alone the sterile to fertile ratio would have to be about 130:1. This would require the release about 260,000 sterile insects of both sexes. To achieve 99.3 percent parasitism by the release of parasitoids alone, I estimate that it would be necessary to release about 16,000 parasitoids of both sexes.

The advantage of the release of both organisms is not limited to the action during generation 1. Even if no sterile insects were released during generation 2, enough parasitoid progeny would in theory be present to achieve an adult parasitoid-to-host ratio of 49:1 during generation 2. Thus, releases would be necessary for only one pest generation. Earlier we noted that it has not yet been demonstrated that parasitoids alone are capable of eliminating pest populations. But, if even a few sterile insects were released along with parasitoids this would ensure the use of a method of suppression that can lead to eradication of isolated populations.

The degree of enhanced suppressive action depends on the size of the initial ratios of released parasitoids to the natural populations. The higher the ratios, the greater will be the enhanced suppressive action. At ratios as high as 3:1 for each organism - or an overall ratio of 6:1 - the combined suppressive action during the first and second generations would be so high it would be difficult to even calculate. It would require the release of about 2,000,000 sterile insects alone to achieve a ratio of 1,000:1 to equal the effect of a ratio of 6:1 of both organisms. When pest populations are very low due to natural causes or are first suppressed to a very low level by other means, it would not require the production and release of many organisms of both kinds to achieve ratios as high as 10:1 or even 100:1.

In areas subject to the invasion of only a few insects by long distance flight or by way of imported infested commodities the routine release of only a few insects per unit

TABLE 5. INFLUENCE OF THE CONCURRENT RELEASE OF ENOUGH STERILE INSECTS AND PARASITOIDS TO ACHIEVE RATIOS OF 2:1 DURING GENERATION 1 OF A PEST POPULATION OF THE NATURE SHOWN IN TABLE 1.

Parameters	Generation	
	1	2
Normal males	1,000	32
Normal females	1,000	32
Sterile insects, both sexes	4,000	none
Sterile-to-fertile ratio	2:1	—
Females reproducing	333	32
Small larvae per female	80	86
Total small larvae	26,640	2,752
Female parasitoids released, generation 1 only	2,000	1,567
Ratio, female parasitoids to reproducing female hosts	6:1	49:1
Host larvae parasitized per female	52	52
Total larvae parasitized	104,000	29,484
Ratio, larvae parasitized to larvae present	3.9:1	10.7:1
Percent parasitism	98	99+
Larvae parasitized, number	26,107	2,724+
Larvae not parasitized, number	533	27
Survival larvae to adults, percent	12	—
Adult hosts next generation, both sexes	64	—
Adult parasitoids, next generation both sexes	3,133	—

area might ensure overwhelming ratios and protect the area from the establishment of invading pests. This would be a new procedure for preventing the establishment of invading insect pests.

The examples described are merely an indication of the potential benefits that can be realized by combining different insect control methods that have density dependent and mobile suppressive action. In theory, similar enhanced suppressive action can be realized by releasing two parasitoid species that parasitize and complete development in different life stages of the host. The concurrent release of a parasitoid species that parasitizes and completes development in the host eggs and another species that parasitizes and completes development in the host larvae or pupae would be examples of such parasitoids. The concurrent release of a larval and puparia parasitoid would be another example. The use of insect sex pheromones in traps or as attracticides that have long range attraction power plus the release of parasitoids would be another example of the integration of two suppression techniques that could lead to mutually enhanced suppressive action.

It is difficult to anticipate just what this potentially powerful mechanism of suppression can mean to insect pest management if it is exploited and applied for the regulation and eradication of insect pests. When the pest populations are very low for any reason and if relatively few insects would have to be released to achieve high ratios the cost can be very low. The release of biological organisms that have density depen-

dent suppressive action and which also have mobility and pest detection mechanisms would combine several characteristics that can result in a very powerful method of insect control and eradication. And we should keep in mind that we would be using methods of control that would be highly pest specific and would permit all other natural control factors to operate in a near normal manner. If these principles are confirmed and exploited it could dramatically alter future insect pest management and eradication programs with great economic and environmental benefits.

Practical Implications for Specific Insect Pests

I have described various mechanisms and principles of insect control and the results to expect from different control procedures. However, what agricultural executives and farmers want to know is what does all this mean in terms of dealing with specific insect pest problems and what will be the costs and benefits compared with current control procedures.

Any one of a dozen insect pests could be selected to make such analysis. However, I will describe in a general way the procedure that could be followed in making use of insect parasitoids and sterile insects for regulating total populations of two of our most important insect pest species; the corn earworm, *Helicoverpa zea*, and the tobacco bud worm, *Heliothis virescens*.

The two pests differ somewhat in their biology and host plant preferences, but they will be regarded as one pest entity. To relate the theoretical results we have presented to practical utilization several estimates and assumptions must be made. The released organisms will be directed against the insects that emerge from the overwintering pupae. Most of the reproduction by this first generation normally occurs on wild host plants. But most of the wild hosts are in cultivated areas.

A vitally important parameter that will determine the feasibility of regulating populations of the two pests is the number of insects that emerge from the overwintering population. I have, with the help of some of my colleagues, made estimates of the number of adults that are likely to emerge from the overwintering puparia. I estimate that the overwintering population will normally consist of about 1 billion moths of both sexes. Emergence and reproduction by the overwintered population are assumed to occur primarily in cultivated areas comprising about 75,000 square miles or about 50 million acres of cultivated lands. The suppressive measures will be applied in the United States and northern Mexico where most overwintering occurs. Biologists have obtained information which suggests that many of the insects that reproduce early in Mexico will emigrate to the United States. Therefore, international cooperation would be necessary.

Thorough surveys and monitoring of the pest populations will be an essential aspect of such a program. The biological organisms should be released at the proper time and in appropriate numbers as emergence of the natural population occurs. It no doubt would be advantageous to release more than one parasitoid species. Promising parasitoids would include the hymenopterous larval parasitoid, *Microplitis croceipes* and the tachinid larval-pupal parasitoids, *Archytas marmoratus* and *Eucelatoria bryani*. As depicted in table 5, good control will result if sufficient numbers of a parasitoid are released for one generation to achieve an adult parasitoid to adult host ratio of 3:1. Thus the release of 3 billion parasitoids is proposed. Releases in the different regions would begin, perhaps in February in Mexico. Then as the season advances the parasitoids would be released to coincide with the emergence of the pests from the overwintering pupae.

I assume that the parasitoids will be released in each area at 1 mile intervals every five days for 40 days or about 8 releases. If reproduction of the first generation is

largely inhibited this would minimize the number of immigrant moths that normally disperse for several hundred miles to supplement the overwintering populations. While such program may seem to be of unprecedented scope, it would not be much larger than the screwworm program that has been conducted in the United States and Mexico for the past 25 years.

As depicted in table 4, an adult parasitoid to adult host ratio of 3:1 is estimated to cause virtually complete control within several cycles. A high degree of control of the overwintering population could be expected in the United States and northern Mexico the first year. If so, very few moths should be available to migrate into the agricultural areas north of the normal overwintering areas and thereby avoid the heavy losses the pests cause each year in the northern states.

Obviously we are dealing with rough estimates and assumptions that would have to be investigated intensely. However, for the purpose of this gross analysis I estimate that the eventual cost of rearing suitable parasitoids will average $10 per 1,000 or $10 million per billion. The cost for distributing the organisms is estimated to be $2 per mile of flight for the aircraft. It is assumed that the biological agents will be distributed at 1 mile intervals in about 75,000 square miles of territory. The cost for distributing the organisms each release period would amount to only about $150,000 or $1.2 million for 8 releases. Based on a rearing cost estimate of $10 million per billion parasitoids, the cost for 3 billion parasitoids would be $30 million. Other costs including thorough surveys, general supervision and other costs are assumed to increase the cost during the first year to about $35 million. This is about what the screwworm programs have cost during the past 25 years.

Recognizing that there are unavoidable inefficiencies in such operations, it would seem more rational to assume the need for producing and distributing 6 billion parasitoids rather than 3 billion during year 1. Other costs would be about the same regardless of the number of parasites released. Therefore, we might assume that the costs during year 1 would be about $65 million. *This would be less than 10 percent of the losses the pests now cause under current management procedures.*

In dealing with insect pest populations from a total population perspective using control methods that have pest density dependent suppressive action the major benefits should be realized after the first year. The elimination of the population is out of the question. Some adults of both species no doubt can immigrate several hundred miles from other regions. Some of the insects will be present in the management areas each year even though most of the reproduction is inhibited. However, if we assume that the normal overwintering and immigrating population will be as low as 100 million as few as one billion parasitoids should achieve a parasitoid to host ratio as high as 10:1. In that event the annual cost for management of the pests might be below $25 million.

In considering the feasibility of dealing with the corn earworm and the tobacco budworm by the procedure described it should be kept in mind that under current control procedures the two pests are estimated to cost agriculture in the United States more than $1 billion per year (King et al. 1989). They are also responsible for much of the insecticides required for agricultural purposes.

Some or all of the estimates I have made may be too liberal. The normal overwintering population might be higher than 1 billion and the parasitoid-to-host ratio may have to be higher than 6:1 to achieve adequate control. On the other hand, it is also possible that one or more of my estimates are too high. If the overwintering population is normally as low as 667 million and the parasitoids could eventually be reared at a cost as low as $5 million per billion, the estimates I have made for the first year would be too high even if the parasitoid to host ratio would have to be as high as 10:1. The continuing annual cost might be less than half the cost during the first year.

From a national and worldwide standpoint, it is probable that no insect pest complex has been investigated as intensively as has the Helicoverpa/Heliothis complex. In my opinion about all of the basic technology needed has already been developed. No new discoveries are necessary. Nature has created the organisms. However, scientists and agriculturalists must accept the holistic approach and focus on making the transition from basic information to practical application. I see no obstacle to making this transition other than failure of our agriculture executives in both the public and private sectors to accept the concept and unwillingness of our scientists to undertake the research challenges that would be involved in perfecting the technology and proving its performance.

The same principles and the same techniques of control should apply for many other insect pests. Other important species that I consider good candidates for total population management in a similar cost effective manner include such major pests as the bollweevil, *Anthonomus grandis*; European corn borer, *Ostrinia nubilalis*; sugarcane borer, *Diatraea saccharalis*; the medfly, *Ceratitis capitata*, and other tropical fruit fly species; Colorado potato beetle, *Leptinotarsa decimlineata*; codling moth, *Laspeyresia pomonella*; and numerous other species. For some of the species the costs during year 1 might be quite high and other methods of control may be needed to reduce the normally high natural populations to a level that can be managed by parasitoids and/or sterile insects.

Much research will have to be conducted to obtain the needed ecological information and to perfect the technology. Research on managing or eradicating total insect pest populations will be costly and demanding. It will be necessary to demonstrate that the proposed procedure will perform as expected. It might cost several million dollars to conduct one trial experiment involving a single pest. But we are dealing with techniques and strategies that have the potential of benefitting agriculture by several billion dollars per year and also make a major contribution to the goals of greatly reducing the need for costly and ecologically disruptive insecticides. Considering these large potential benefits, an expenditure of $25 million per year for research and development focused on the holistic approach to insect control by biological procedures would be very small. It could be one of the best research investments that agriculture could make. I cannot envision any alternative techniques and strategies that would even approach the economic and environmental benefits that could be realized by the holistic approach using mobile biological organisms.

Insect Pest Problems Especially Relevant For the State of Florida

The principles and mechanisms of suppression that I have described in this lecture are basic and fundamental. They will apply for a wide range of insect pests. Entomologists in Florida could do a great deal to advance the principles and concepts that have been discussed. Your state is a well isolated ecosystem. It could take unilateral action and benefit more than could other states that are not as well isolated from long range insect immigration.

The probability is high that at least two of your important pest problems could be readily resolved by the parasitoid release technique especially if supplemented by the release of sterile insects. I refer to the Caribbean fruit fly, *Anastrepha suspensa*, and the sugarcane borer. Excellent parasitoids of both of the pests are known and efficient mass rearing procedures have been developed for them. Also considerable research has been conducted on parasitoid releases that have given promising results against the sugarcane borer, (Summers et al. 1976). The sterile insect technique has been shown to be an effective means of suppressing several tropical fruit fly and lepidopter-

ous pests. Parasitoid releases have also shown promise for suppressing tropical fruit flies, (Wong, et al. 1992 and Sivinski 1996). I can see no reasons for permitting the Caribbean fruit fly to continue to exist in your state and cause the problems it does for your fruit industry. Also, I can see no reason why the sugarcane borer should be costing sugarcane growers $25 to $50 per acre or more in losses year by year. The first year costs might be considerably higher, but I am confident that after sugarcane borer populations have been reduced to very low levels, they could be maintained below the level of damage at a cost of $2 to $3 per acre per year by the release of relatively few parasitoids per acre perhaps supplemented by the release of some sterile moths.

However, there are a number of other insect pests in your state that are of national significance and which find refuge in your state during the winter months. Each spring and summer enough of the pests spread northward into other agricultural regions and cause damage to a variety of crops before season's end. Those pests include the fall armyworm, *Spodoptera frugiperda*; the beet armyworm, *Spodoptera exigua*; cabbage looper, *Trichoplusia ni*; and diamondback moth, *Plutella tylostella*.

The number of insects of these species that reproduce only in Florida during the winter months has not been determined. But there is little question that the populations that emigrate from your state can increase by 25 to 50 fold during the growing season and threaten losses on perhaps 25 times the crop acreage in other states before season's end.

What the total losses due to these pests amount to per year in the states north of Florida is difficult to say, but they probably aggregate several hundred million dollars per year. I am greatly indebted to Dr. F. A. Johnston who made a special effort to obtain information on the annual cost of control and losses caused by the fall armyworm, beet armyworm, corn earworm, diamondback moth and cabbage looper in Florida. Insecticides now provide the only way to control these pests. I was amazed at the amount that growers spend per year controlling these pests. On most crops it amounts to as much as $100 per acre or more.

From time to time I have discussed with various scientists the feasibility of rigidly controlling such pests during the winter months in Florida to avoid the losses the pests cause other states after they spread northward. But research programs to investigate the feasibility of dealing with the pests during the winter in Florida have not yet materialized.

Since I have been interested primarily in the possible use of the sterile insect and parasitoid release techniques I have made gross estimates of the probable size of the overwintering populations in Florida. It is difficult to say how accurate they are, but I feel confident that it would be feasible to rigidly manage populations of the pests mentioned during the winter primarily by the use of parasitoids at costs of only a fraction of the losses they cause under present methods of control. Mandatory cultural measures such as the destruction of host plants within a certain period after the host crops are harvested should be integrated into a total population management system. This would cost farmers very little, but it can be of major importance in an integrated program. This alone might reduce the number of parasitoids or sterile insects required by half and still result in a more effective program.

The feasibility of managing these pests in the winter by the release of parasitoids and/or sterile insects will depend on the number of the pests that reproduce in your state during the winter and early spring. In my opinion, research to determine as accurately as possible the actual number of the different species that exist in the natural population would be of the highest priority. Certainly through joint efforts by the state and federal scientists, it should be possible to obtain good information on the actual number of the different pests that reproduce in Florida during that period and the source of the reproduction. Until such information is obtained, there is likely to be

little that anyone can or will do to develop and make use of the proposed biological techniques for dealing with these pest problems.

I raise the question, however, whether agriculture can afford to be so dogmatic and intransigent in meeting its insect pest problems. Is there any justification for or does it make any sense to continue to rely year by year on costly and ecologically disruptive insect control methods when the prospects are so favorable for dealing with the pest problems at very low cost and in an environmentally safe manner? Will the time come when society will demand the use of environmentally safe ways to deal with pest problems especially if it will also greatly benefit producers and consumers? What can we do as entomologists to gain the interest and support needed to achieve these goals.

LOOKING TO THE FUTURE

The world's leading scientific institutions are projecting that agriculture within 30 years must produce two times as much food as it now produces to meet the demand of an expanding world population and economy. This will require that agriculture worldwide become more efficient in a number of ways. Protecting crops and livestock from insect damage will be one of the ways to meet the monumental tasks that agriculture faces within the short span of a few decades. People will and *should* demand that the food that is produced be safe and that the quality of the environment in which we live will not be jeopardized.

The methods of insect control that have evolved during the past 50 years have contributed to the highly productive agriculture that we now enjoy. However, this in part has been accomplished by relying primarily on costly and ecologically disruptive insecticides for insect control. The prospects seem dim to me that our present defensive system of management can be greatly improved, if at all. Insects continue to develop resistance to insecticides. People continue to be concerned over the environmental hazards insecticides can produce and more restrictions are being placed on their use. Agriculturists are beginning to wonder if we can maintain the standards of control that have been achieved in the past.

A study of the dynamics of many of our major insect pests and an analysis of the suppression characteristics of various methods of control clearly indicate to me that the preventative measures applied against total insect pest populations would be a much more rational way to deal with many of our major insect pests than to rely on the largely defensive procedures that have been followed for half a century. Two biological control procedures involving mobile organisms offer the best hopes of accomplishing this objective in an effective, economical and environmentally safe manner: the mass-rearing of key parasitoid species and their release throughout the pest ecosystem in adequate numbers and at strategic times in the pest's seasonal cycle; and the release of sterile or genetically altered insects in the same way.

The holistic approach to the management of insect pests by these two biological procedures offers almost unlimited potential for dealing with insect pest problems in an environmentally safe manner and at very low cost. Mass producing the biological organisms should pose no serious technical problems in view of the outstanding progress that insect-rearing scientists and engineers have made in rearing many kinds of insects in large numbers.

The time will come, and sooner than we realize, when it will be necessary for agriculture worldwide to produce the maximum amount of food on diminishing agricultural lands and water for irrigation. This will require greater efficiency and productivity from every aspect of agriculture. Better protection of crops and livestock from insect attack will be one of the ways to achieve these objectives. This will be the responsibility of entomologists and our associated scientists.

I am confident that we already have or could readily develop the technology that will be needed to deal with most of our major insect pest problems in a much less costly and a more ecologically acceptable manner during the next half century than we have done during the last few decades. But it will require that our agricultural leaders in both the public and private sectors make provisions for developing and implementing the type of technology that will permit maximum efficiency and yields and which will also be environmentally acceptable.

We need more positive decisions and bold actions by our scientists and agricultural leaderships in both the public and private sectors that will lead to many other programs as successful and practical as the screwworm program that your society has honored today.

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