

INTRODUCTION TO
THE BEHAVIORAL ECOLOGY OF THE PROTECTION OF
NATIVE FLORAS AND FAUNAS

COMMERCIAL IMPORTATION INTO FLORIDA OF
INVERTEBRATE ANIMALS AS BIOLOGICAL
CONTROL AGENTS

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ABSTRACT

A survey of commercial producers and sellers of biological control agents revealed 49 species of invertebrate animals imported into Florida. Of these, 48 were imported for augmentative biological control of pests, and one for educational purposes. There were 3 species of nematodes, 1 mollusc, 8 mites, and 37 insects. More than half (25) of them were not known to occur in Florida at the time of importation, and some of them might be capable of establishing populations in Florida and might serve as classical biological control agents. Targets were mainly pest insects in the orders Homoptera (41%), Diptera (19%), Lepidoptera (15%) and Thysanoptera (11%). The targets were on or in perennial plants, annual plants, greenhouses, pasture- and turfgrasses, stored products, and feces of domesticated vertebrates. Some targets of commercially-imported biological control agents had been targets of classical biological control research. Some agents ("common") were imported frequently and by several producers, but others ("uncommon") were imported perhaps only once or twice. More targets previously recorded as targets of classical biological control agents were associated with "uncommon" commercially-imported agents than with "common" ones; more of the "common" agents than the "uncommon" ones were released into multiple habitats.

Key Words: Florida, biological control, commercial producers, introduced species, integrated pest management.

RESUMEN

Una encuesta a productores y vendedores comerciales de agentes de control biológico reveló 49 especies de animales invertebrados importadas a Florida. De estas, 48 fueron importadas para control aumentativo biológico de plagas, una con fines educativos. Hubieron 3 especies de nemátodos, 1 molusco, 8 ácaros y 37 insectos. Antes de su importación no se conocía de la existencia en Florida de más de la mitad (25) de ellos, y algunas podrían ser capaces de establecer poblaciones en Florida y servir como agentes de control biológico clásico. Los objetos de control fueron principalmente insectos de los órdenes Homoptera (41%), Diptera (19%), Lepidoptera (15%) y Thysanoptera (11%). Estos objetos de control fueron localizados sobre o dentro de plantas perennes, plantas anuales, en invernaderos, pastos ornamentales y potreros, en productos almacenados y excrementos de animales vertebrados domésticos. Algunos insectos sujetos a control por agentes importados comercialmente, habían sido objetos de investigación de control biológico clásico. Algunos agentes ("comunes") eran importados frecuentemente por varios productores, mientras que otros ("no comunes") se importaban quizás solo una o

dos veces. De los insectos previamente registrados como objetos de agentes de control biológico clásico, estuvieron más asociados a agentes importados comercialmente "no comunes" que a agentes "comunes"; de los agentes en habitats multiples, más fueron del tipo "comunes" que de los "no comunes."

The theme of our symposium is behavioral ecology of the protection of native floras and faunas. This encompasses the behavioral response of native organisms to all sorts of human encroachments, as well as use of behavior of these organisms to protect them. We could have included the behavioral response of native organisms to the use of chemical pesticides, but we did not. At the opposite extreme, we have included the study of how knowledge of behavior of butterflies may be used to protect them. We discuss the subject area further toward the end of this paper.

This introduction continues a theme of the behavioral ecology of biological control, a subject that we began to explore two years ago. In that paper (Frank & McCoy 1992), we asked what are the immigrant insects whose existence has been documented in Florida within the last 20 years, how they arrived in Florida, and what are their likely effects. A year ago (Frank & McCoy 1993), we documented what insects have been introduced to Florida, and discovered that almost all the introduced species were brought to Florida as classical biological control agents of pest insects, most of which, in turn, were of exotic origin. With this paper, we document the invertebrate animals that have been imported into Florida and released for commercial purposes, as augmentative or inundative biological control agents [this is a topic that we excluded from the discussion last year (Frank & McCoy 1993)]. We continue to use our definition (Frank & McCoy 1990) of the word **introduced**. In our view, organisms that arrived by their own volition by flying, walking, swimming, or hitchhiking (stowaways) in cargoes, are **immigrants**. Only those brought here deliberately by humans are introduced. Taken together, these immigrant and introduced organisms are adventive.

METHODS AND MATERIALS

A newsletter called **The IPM Practitioner** publishes periodically a list of names and addresses of companies that sell biological control agents. We devised a questionnaire to mail to all listed companies that we thought might sell insect biological control agents to buyers in Florida. We asked these companies what insect biological control agents they had sold to purchasers in Florida, what were the target pests, and how many individual insects of each species were sold annually within the last 5 years to purchasers in Florida.

Thirty nine companies (see ACKNOWLEDGMENTS) replied, but some did not. Some did not do so because they had gone out of business, others did not do so because they had moved without forwarding addresses, and some presumably did not choose to do so. Therefore, we asked the Division of Plant Industry (DPI) of the Florida Department of Agriculture and Consumer Services, for a list of permits issued to such companies for the importation into Florida of insect biological control agents. This not only gave us information on introduced organisms, but gave us names of additional companies. Florida law in Florida Statutes (1991), applied in Florida Administrative Code (1993), now requires that anyone shipping biological control agents into Florida obtain a permit to do so. Companies whose names appeared on the list of permits issued were contacted by mail if we had not already received information from them.

RESULTS

Targets

Table 1 contains 31 reported targets (27 insects) of imported biological control agents. Many (13) of these targets were listed previously as targets of introduced biological control agents (Frank & McCoy 1993). Well-represented insect orders are Homoptera (41%), Diptera (19%), Lepidoptera (15%), and Thysanoptera (11%). Diptera are better

TABLE 1. REPORTED TARGETS OF THE IMPORTED BIOLOGICAL CONTROL AGENTS, IN FLORIDA OR ELSEWHERE. THOSE NOT KNOWN TO OCCUR IN FLORIDA ARE ANNOTATED. ALMOST ALL THE SPECIES THAT DO OCCUR IN FLORIDA ARE IMMIGRANTS. THIS LIST IS TO SOME EXTENT AN EXPANSION OF INCOMPLETE INFORMATION.

<i>Acarus siro</i> L. (Acarina: Acaridae) - flour mite.
<i>Amyelois transitella</i> (Walker) (Lepidoptera: Pyralidae) - navel orangeworm.
<i>Aonidiella aurantii</i> (Maskell) (Homoptera: Diaspididae) - California red scale.
<i>Aphis gossypii</i> Glover (Homoptera: Aphididae) - cotton aphid.
<i>Aspidiotus nerii</i> Bouche (Homoptera: Diaspididae) - oleander scale.
<i>Bemisia tabaci</i> Gennadius (Hemiptera: Aleyrodidae) - sweetpotato whitefly.
<i>Blissus</i> spp. (Heteroptera: Lygaeidae) - chinch bugs.
<i>Bradysia</i> spp. (Diptera: Sciaridae) - fungus gnats.
<i>Coccus hesperidum</i> L. (Homoptera: Coccidae) - brown soft scale.
<i>Carpocapsa pomonella</i> (L.) (Lepidoptera: Olethreutidae) - codling moth.
<i>Diaprepes abbreviatus</i> (L.) (Coleoptera: Curculionidae) - the "common" names are West Indian sugarcane rootstock weevil, citrus root weevil, Apopka weevil, and Apopka bug.
<i>Epilachna varivestis</i> Mulsant (Coleoptera: Coccinellidae) - Mexican bean beetle.
<i>Frankliniella occidentalis</i> (Pergande) (Thysanoptera: Thripidae) - western flower thrips.
<i>Haematobia irritans</i> (L.) (Diptera: Muscidae) - horn fly.
<i>Heliothrips haemorrhoidalis</i> (Bouché) (Thysanoptera: Thripidae) - greenhouse thrips.
<i>Helix aspersa</i> Müller (Pulmonata: Helicidae) - brown garden snail, native to Europe, immigrant into California and other parts of the USA, twice eradicated from Florida (Dekle 1969); not known at present to occur in Florida (L. A. Stange pers. comm.).
<i>Liriomyza</i> spp. (Diptera: Agromyzidae) - <i>Liriomyza</i> leafminers.
<i>Musca domestica</i> L. (Diptera: Muscidae) - house fly.
<i>Myzus persicae</i> (Sulzer) (Homoptera: Aphididae) - green peach aphid.
<i>Planococcus citri</i> (Risso) (Homoptera: Pseudococcidae) - citrus mealybug.
<i>Plutella xylostella</i> (L.) (Lepidoptera: Yponomeutidae) - diamondback moth.
<i>Pseudococcus longispinus</i> (Targioni-Tozzetti) (Homoptera: Pseudococcidae) - long-tailed mealybug.
<i>Saissetia neglecta</i> DeLotto (Homoptera: Coccidae) - Caribbean black scale.
<i>Saissetia oleae</i> (Bernard) (Homoptera: Coccidae) - black scale.
<i>Scapteriscus</i> spp. (Orthoptera: Gryllotalpidae) - <i>Scapteriscus</i> mole crickets.
<i>Sitotroga cerealella</i> (Olivier) (Lepidoptera: Gelechiidae) - Angoumois grain moth.
<i>Stomoxys calcitrans</i> (L.) (Diptera: Muscidae) - stable fly.
<i>Tetranychus cinnabarinus</i> Boisduval (Acarina: Tetranychidae) - no generally-accepted common name.
<i>Tetranychus urticae</i> Koch (Acarina: Tetranychidae) - two-spotted mite.
<i>Thrips tabaci</i> Lindeman (Thysanoptera: Thripidae) - onion thrips.
<i>Trialeurodes vaporariorum</i> (Westwood) (Homoptera: Aleyrodidae) - greenhouse whitefly.

represented as targets of commercially-imported biological control agents than as targets of classical biological control agents.

Even though our questionnaire asked only for information on insect biological control agents, some companies chose to send us information on nematodes, mites, and molluscs. Because so few species of insects were listed, we decided to include this additional information when it was provided, even though it may be incomplete. At the same time, our list of target organisms was expanded because of this additional range of organisms. To avoid repetition in later text, we listed target organisms and their classification and common names in Table 1.

Arthropod targets of imported biological control agents include tetranychid mites (especially *Tetranychus urticae*), thrips (especially *Frankliniella occidentalis*), whiteflies (*Bemisia tabaci* and *Trialeurodes vaporariorum*), aphids (especially *Myzus persicae*), mealybugs (*Planococcus citri* and *Pseudococcus longispinus*), soft scale insects (*Coccus hesperidum*), armored scale insects (*Aspidiotus nerii*), diamondback moth (*Plutella xylostella*), *Liriomyza* leafminers (*Liriomyza* spp.), fungus gnats (*Bradysia* spp.), and muscoid flies (*Musca domestica*, *Stomoxys calcitrans* and *Haematobia irritans*).

Biological Control Agents

Table 2 contains the information we sought about biological control agents sold in Florida. For each species listed we give a brief account of origin, distribution, and host/prey relations from the literature. For each, after the words IMPORTED VS, we give the intended target as it appeared on forms returned by suppliers and in the DPI records. We have arranged this information in order of precise (specific identification of target), through more general (family or superfamily of target), to very imprecise

TABLE 2. INVERTEBRATE BIOLOGICAL CONTROL AGENTS IMPORTED INTO FLORIDA SINCE 1982 BY COMMERCIAL ORGANIZATIONS.

RHABDITIDA: STEINERNEMATIDAE

Steinernema feltiae (Filipjev): this entomopathogenic nematode is believed to be native to Europe, but occurs also in Australia and New Zealand (Poinar 1990); IMPORTED VS *Scapteriscus* spp.

Steinernema carpocapsae (Weiser): this entomopathogenic nematode is widely distributed in Europe, North America, South America, Australia and New Zealand, its origin obscure (Poinar 1990); IMPORTED VS *Diaprepes abbreviatus*.

Steinernema scapterisci Nguyen & Smart: this entomopathogenic nematode is native to South America and was released in Florida as a classical biological control agent (Parkman et al. 1993) after laboratory screening showed a high level of host-specificity to *Scapteriscus* mole crickets (Nguyen & Smart 1991); IMPORTED VS *Scapteriscus* spp.

PULMONATA: SUBULINIDAE

Rumina decollata (L.): native to the Mediterranean region of Europe and northern Africa, this species was introduced into California for biological control of *Helix aspersa*, which it achieved with some success as a non-specialist predator, though it proved to be a minor plant pest (Auffenberg & Stange 1986); IMPORTED VS *Helix aspersa*.

ACARINA: LAELAPIDAE

Hypoaspis miles (Berlese): this species was described from Europe; we have not discovered published evidence of its feeding habits or that it might be a useful biological control agent; IMPORTED VS *Bradysia* spp.

Hypoaspis sp.: we have not discovered published evidence of feeding habits of "*Hypoaspis* sp." or that it might be a useful biological control agent; however, an undescribed species, mentioned as *Geolaelaps* [nr. *aculeifer* (Canestrini)] was found in potting soil in British Columbia (Canada) and was there shown experimentally using inoculative introductions in a greenhouse to be able as a predator to suppress populations of *Bradysia* sp. and of *Frankliniella occidentalis* (Gillespie & Quiring 1990); these are pests in Florida greenhouses, too; *Geolaelaps* sp. (with no documentation that it is the same as was investigated in British Columbia) was IMPORTED VS "insects"; *Hypoaspis* sp. was IMPORTED VS "invertebrates."

ACARINA: PHYTOSEIIDAE

Galendromus occidentalis (Nesbitt): native to Canada and the northern USA (Moraes et al. 1986), this predacious mite has been used successfully to control *Tetranychus urticae* by inoculative introductions into apple orchards in the northwestern USA (Croft & Mcrae 1992); IMPORTED VS *Tetranychus urticae*, or not given.

Mesoseiulus longipes (Evans): native to Africa (Moraes et al. 1986); IMPORTED VS *Tetranychus urticae*, *Trialeurodes vaporariorum*, or not given.

Neoseiulus barkeri Hughes: perhaps native to Europe (Moraes et al. 1986); is a predator of thrips and has controlled *Thrips tabaci* when released inoculatively, several times per season, into Danish greenhouses (Hansen 1988); IMPORTED VS *Frankliniella occidentalis*, *Thrips tabaci*, *Acarus siro*, "broadmites," and "thrips."

Neoseiulus californicus (McGregor): native to California (Moraes et al. 1986); IMPORTED VS *Tetranychus urticae*, or not given.

Neoseiulus cucumeris (Oudemans): native to Europe (Moraes et al. 1986); is a predator of thrips and has controlled *Thrips tabaci* and *Frankliniella occidentalis* when released inoculatively into Canadian greenhouses (Gillespie 1989); IMPORTED VS *Acarus siro* L. (flour mite), *Tetranychus urticae*, *Frankliniella occidentalis*, "mites," "thrips," and "biocontrol in greenhouses."

Phytoseiulus persimilis Athias-Henriot: native to Africa, and introduced into California (Moraes et al. 1986); IMPORTED VS *Tetranychus cinnabarinus*, *T. urticae*, "phytophagous mites," "spider mites," "spider mites in greenhouse," "vegetable pests," or not given.

COLEOPTERA: COCCINELLIDAE

Cryptolaemus montrouzieri Mulsant: native to Australia, introduced into California in 1891, and is a predator of Coccidae and Pseudococcidae; introduced into Florida from California in 1930 against *Planococcus citri*, and established in the center and south (Gordon 1985, Frank & McCoy 1993); IMPORTED VS *Planococcus* sp., "mealybug on cucumber" and "mealybug."

Delphastus pusillus (LeConte): native to the southern USA and widely distributed in the center and north of Florida; is a predator of Aleyrodidae and to some extent of Coccidae (Gordon 1985); IMPORTED VS *Bemisia tabaci*, and "insects."

Hippodamia convergens Guérin-Méneville: native to the USA and occurring throughout Florida, this species is a predator of Aphididae (Gordon 1985); IMPORTED VS "aphids" or "various," or not given.

Rhyzobius lophanthae (Blaisdell): native to Australia, introduced into California in 1892, and now widely distributed in the southern tier of states across the USA including Florida, this species is a predator of Coccidae, Pseudococcidae, and Diaspididae (Gordon 1985); IMPORTED VS *Aspidiotus nerii*, and "scale insects."

COLEOPTERA: HISTERIDAE

Carcinops sp.: there are at least 16 species in America north of Mexico, and 4 of them occur in Florida, including *C. pumilio* (Erichson) and *C. troglodytes* (Paykull) (M. C. Thomas pers. comm.); adults and larvae of *Carcinops* are predacious, especially on muscid fly larvae in dung and carrion, with interspecific variation in habitat preferences; only *C. pumilio* (which occurs in temperate climates) and *C. troglodytes* (which occurs in tropical climates) include poultry manure in their habitat range (Geden 1990); *C. pumilio* shows potential as a biological control

TABLE 2. (Continued)

agent of muscid fly larvae in poultry houses under certain circumstances (Geden 1990); the effect of *C. troglodytes* on the muscid fauna of poultry dung has not been studied, but it may be better adapted for existence in Florida, or at least southern Florida; IMPORTED VS "insects and mites in greenhouses."

DIPTERA: CECIDOMYIIDAE

Aphidoletes aphidimyza (Rondani): Holarctic, its origin obscure, but at least for many decades has inhabited North America, including Florida, though it is not abundant in the southeastern USA (R. Gagné, pers. comm.); it "has been used as a predator with good results for the control of aphids in many northern climates [but] success obtained with it in Florida has been limited to the cooler months of the year" (Osborne & Oetting 1990); IMPORTED VS *Myzus persicae*, *Aphis gossypii*, "aphids," "biocontrol in greenhouses," "plant pests," and "insects."

HEMIPTERA: ANTHOCORIDAE

Orius insidiosus (Say): native to North America, including Florida, and is known to prey on thrips and mites (Clausen 1940; Herring 1966); IMPORTED VS "vegetable pests," and as "general predator."

Orius tristicolor (White): native to the western parts of North America, excluding Florida (Herring 1966); thrips are preferred prey items, but it will feed on plant materials to maintain itself when prey is scarce (Salas-Aguilar & Ehler 1977); IMPORTED VS "insects," "vegetable pests," "plant pests," "biocontrol in greenhouses," or not given.

HEMIPTERA: PENTATOMIDAE

Podisus maculiventris Say: native to North America, including Florida, and is a predator of larvae of Lepidoptera and of Chrysomelidae (Clausen 1940; Richman & Mead 1980); IMPORTED VS *Epilachna varivestis*.

HYMENOPTERA: APHELINIDAE

Aphytis melinus DeBach: native to India and Pakistan, introduced into California in 1956-1957 as a parasitoid of *Aonidiella aurantii* and became established (Laing & Hamai 1976); there seem to be no records of existence of *A. melinus* in Florida, nor of attempts to introduce it as a classical biological control agent, nor is this surprising, because its host (*A. aurantii*) is not at all common (H. W. Browning, pers. comm.); IMPORTED VS "scale," and "pest management in groves."

Encarsia formosa Gahan: cosmopolitan, its origin obscure, but at least for many decades has inhabited North America including Florida; it is best-known as a parasitoid of *Trialeurodes vaporariorum*, but it also attacks *Bemisia tabaci* (Gordh 1979; Osborne & Oetting 1990; Frank & McCoy 1993); release of this species in greenhouses has achieved effective control of *T. vaporariorum* in several countries, though the methods used are critical to success (Hussey & Scopes 1985; Osborne & Oetting 1990); IMPORTED VS *Trialeurodes vaporariorum*, *Tetranychus urticae*, "vegetable pests," "whiteflies," and "insects."

Eretmocerus mundus Mercet: native to the Mediterranean region of southern Europe, northern Africa, and western Asia (it has also been reported from Illinois), it is a parasitoid of *Bemisia tabaci*, though it has been reported from a few other whitefly species (Lopez-Avila 1986); was imported from Israel and Sudan to Florida in 1990-1991 for classical biological control purposes (Frank & McCoy 1993) and progeny of the material from Sudan subsequently was released in Dade, Hillsborough, Marion, Orange, Palm Beach and Volusia counties, without evidence yet of permanent establishment (R. Nguyen, pers. comm.); IMPORTED VS *Bemisia tabaci*.

HYMENOPTERA: APHIDIDAE

Aphidius matricariae Haliday: a Holarctic species which is a parasitoid of several aphid species (Marsh 1979); attempts were made in the 1950s to establish populations

of it in Florida, apparently without success (Frank & McCoy 1993); IMPORTED VS *Myzus persicae*, or not given.

Lysiphlebus testaceipes (Cresson): widespread in temperate North America (including Florida) and South America, and is a parasitoid of several species of aphids (Marsh 1979); IMPORTED VS "vegetable pests," and "insects and mites in greenhouses."

HYMENOPTERA: BETHYLIDAE

Goniozus legneri Gordh: native to South America, introduced into California in 1979, and became established, for control of *Amyelois transitella* (Legner & Warkentin 1988); there are no records of *G. legneri* being imported into Florida for classical biological control purposes (Frank & McCoy 1993); IMPORTED VS "insects and mites in greenhouses."

HYMENOPTERA: BRACONIDAE

Cotesia plutellae (Kurdjumov): native to Europe, introduced to several countries around the world, and established successfully, for control of *Plutella xylostella*; an insecticide-tolerant strain was introduced to Florida from Malaysia in 1990, but its establishment has not yet been announced (Jansson & Pena 1990); IMPORTED VS *Plutella xylostella*.

Dacnusa sibirica Telenga: native to the Palearctic region, and used in European greenhouses for seasonal inoculative releases for control of *Liriomyza* leafminers (Minkenberg 1992); IMPORTED VS *Liriomyza* spp. leafminers, "leafminers," "insects," "vegetable pests," "thrips" and "broad mites."

HYMENOPTERA: EULOPHIDAE

Diglyphus isaea (Walker): native to the Palearctic region, invades European greenhouses and plays a part in suppression of *Liriomyza* leafminer populations (Minkenberg 1992); IMPORTED VS *Liriomyza* spp. leafminers, "leafminers", and "vegetable pests."

Thripobius semiluteus Bouček: native to the Old World tropics, this species was discovered in the New World (Brazil) for the first time in 1988, and specimens were taken to California for study as a potential biological control agent of *Heliothrips haemorrhoidalis* (LaSalle & McMurtry 1989); IMPORTED VS *Heliothrips haemorrhoidalis*.

HYMENOPTERA: ENCYRTIDAE

Anagyrus fusciventris (Girault): native to the Pacific and known as a parasitoid of *Pseudococcus longispinus*, this species was imported from Hawaii into California and thence into Bermuda (Bartlett 1978; Gordh 1979); IMPORTED VS "mealybugs."

Anagyrus pseudococci (Girault): native to the Mediterranean region of southern Europe and northern Africa, but imported from South America to California in 1953 and established, it attacks several species of *Planococcus* and *Pseudococcus* including *Planococcus citri* (Bartlett & Lloyd 1958; Bartlett 1978b); IMPORTED VS "mealybugs."

Leptomastidea abnormis (Girault): possibly native to the Mediterranean region of southern Europe and northern Africa, with no record of introduction to North America, it nevertheless has been present in Florida for many decades, presumably as an immigrant, and is known primarily as a natural enemy of *Planococcus citri*, though it attacks some other mealybugs (Bartlett 1978b); IMPORTED VS "mealybugs."

Leptomastix dactylopii Howard: native to Brazil and the West Indies, and perhaps also to southern Florida, certainly has been present in Florida for many decades, and is more or less a specific natural enemy of *Planococcus citri*, though it will attack other species of *Planococcus* and *Pseudococcus* in the laboratory (Bartlett 1978b); IMPORTED VS *Planococcus citri*, "mealybug on cucumber," and "mealybugs."

Microterys flavus (Howard): native to eastern North America including Florida, its recorded hosts belong to several genera (*Coccus*, *Lecanium*, *Pulvinaria*, and *Saissetia*) of scale insects (Gordh 1979); IMPORTED VS *Coccus hesperidum*.

TABLE 2. (Continued)

Metaphycus helvolus (Compere): native to South Africa, imported to California as a natural enemy of *Saissetia oleae* and established there in 1937, its recorded hosts belong to several genera (*Coccus*, *Lecanium*, *Parasaissetia*, and *Saissetia*) of scale insects (Bartlett 1978a); it was imported into Florida in 1971 against *Saissetia neglecta*, under the mistaken belief that this pest was *S. oleae*, but there is no evidence that it became established (McCoy 1985; Frank & McCoy 1993); IMPORTED VS "mealybugs," and "scale".

Tachinaephagus zealandicus Ashmead: native to Australia and New Zealand, this species was introduced into California in 1967-1968 as a biological control agent of dung-inhabiting fly larvae, and material of it was shipped also to Virginia (Legner 1978); it is a parasitoid of fly pupae (Gordh 1979); it has been reported from Florida (Butler et al. 1981); material of this species from Mauritius, perhaps with a genetic composition differing from that of feral Florida stock, was imported to Florida for study in 1975 and 1989 but was not released (Frank & McCoy 1993); IMPORTED VS "insects and mites in greenhouses."

HYMENOPTERA: PTEROMALIDAE

Muscidifurax zaraptor Kogan & Legner: native to the southwestern USA (California, New Mexico, Arizona, and Utah) and recorded as a parasitoid of pupae of muscid flies including *Musca domestica* and *Stomoxys calcitrans* (Burks 1979a); there are no records of *M. zaraptor* being imported for classical biological control purposes (Frank & McCoy 1993); IMPORTED VS *Musca domestica*, and "insects and mites in greenhouses."

Nasonia vitripennis (Walker): cosmopolitan, its origin obscure, but at least for many decades inhabiting North America including Florida, is a parasitoid of pupae of calliphorid and muscid flies including *Musca domestica* (Burks 1979a); material of this species from France, Zimbabwe, and Brazil, perhaps with a genetic composition differing from that of feral Florida stock, was imported to Florida for study in 1986-1987 but was not released (Frank & McCoy 1993); IMPORTED VS *Musca domestica*.

Spalangia endei Walker: cosmopolitan, its origin obscure, but at least for many decades inhabiting North America including Florida, is a parasitoid of pupae of calliphorid and muscid flies including *Musca domestica*, *Stomoxys calcitrans*, and *Haematobia irritans* (Burks 1979a); material of this species from Thailand, Mauritius, France, Hungary, India, Australia, and Brazil, perhaps with a genetic composition differing from that of feral Florida stock, was imported to Florida for study in 1984, 1986-1987, and 1989, but was not released (Frank & McCoy 1993); IMPORTED VS *Musca domestica*.

Spalangia nigroaenea Curtis: cosmopolitan, its origin obscure, but at least for many decades inhabiting North America including the eastern USA south to Virginia, is a parasitoid of pupae of muscid flies including *Musca domestica* and *Stomoxys calcitrans* (Burks 1979a); it was reported to occur also in Florida by Morgan & Patterson (1975); material of this species from Zimbabwe, perhaps with a genetic composition differing from that of feral stock, was imported to Florida for study in 1986 but was not released (Frank & McCoy 1993); IMPORTED VS *Musca domestica*.

Sphegigaster sp.: there are 2 species in America north of Mexico, one of which is native to the northern USA (Michigan and Montana), and the other was introduced from England into British Columbia in the mid-1930s; the introduced species [*S. flavigaster* (Walker)] is a parasitoid of leafminers of the genus *Phytomyza*, but the host of the other one is not recorded (Burks 1979a); an unidentified species is a parasitoid of *Musca domestica*, and material of it was introduced from South Africa to California in 1967-1968, apparently without success (Legner 1978); there are no records of any *Sphegigaster* sp. being imported to Florida for classical biological control purposes (Frank & McCoy 1993); IMPORTED VS "insects and mites in greenhouses."

HYMENOPTERA: TRICHOGRAMMATIDAE

Trichogramma minutum Riley: native to southern Canada and the USA except for most southern and southwestern areas, and is a parasitoid of eggs of many species of Lepidoptera and other orders in arboreal habitats (Burks 1979b); IMPORTED VS *Sitotroga cerealella*.

Trichogramma pretiosum Riley: native to southern Canada and the USA except for most southern and southwestern areas, and is a parasitoid of eggs of many species of Lepidoptera and other orders on herbaceous vegetation (Burks 1979b); was imported to Florida from Texas in 1971 and reportedly became established (Martin et al. 1976; Frank & McCoy 1993); IMPORTED VS *Sitotroga cerealella*.

MANTODEA: MANTIDAE

Tenodera aridifolia Stoll: native to Asia, its arrival and liberation at Mt. Airy, Pennsylvania, about 1896, were due to actions by a nurseryman (Blatchley 1920); we presume that it hitchhiked in plant material and thus is an immigrant rather than that the nurseryman introduced it [see Frank & McCoy (1990) for explanation of terms **immigrant** and **introduced**]; it is now distributed widely in the northeastern USA and southeastern Canada (Nickle 1987) but is not established in Florida (M. C. Thomas, pers. comm.); females are flightless, and populations have limited powers of dispersal without the effect of commercial movement of plants and commercial sales of the mantid itself (Hurd & Eisenberg 1984); sold to purchasers in Florida by one commercial organization for "educational purposes" without implication that it will succeed in controlling pest insects.

NEUROPTERA: CHRYSOPIDAE

Chrysoperla carnea (Stephens): native to the Holarctic region, but is rare or absent in the extreme south of Florida (Tauber & Tauber 1983); its rarity in Florida led to introductions into Florida from India in the 1950s against *Myzus persicae*, and other aphids, but the lacewing remained rare or absent where it was introduced, and the introductions were viewed as failures (Frank & McCoy 1993); has a broad host range including Tetranychidae, Aphididae and other Homoptera, Thysanoptera, eggs and larvae of Lepidoptera, and even eggs of Coccinellidae (Balduf 1939); IMPORTED VS "aphids," "insects," and "insects and mites in greenhouses" or not given.

Chrysoperla rufilabris (Burmeister): native to eastern North America including Florida, is more abundant in Florida than is *C. carnea*, is better adapted for the humid conditions of the southeastern USA, and better adapted for use in irrigated crops and in greenhouses than is *C. carnea* (Tauber & Tauber 1983); has a broad range of prey including Tetranychidae, Aphididae, *Blissus*, and eggs of *Carpocapsa* (Balduf 1939); IMPORTED VS "aphids," or not given.

(e.g., "vegetable pests"). It appears that some importers are reluctant to provide precise information.

Naturalization Status. There are 3 levels of status for "naturalization" of the imported biological control agents. First, some of them are native to Florida. Second, some of them which are thought not to be native, were known to occur in Florida at the time of importation. Third, some were not known to occur in Florida. This third group is of especial interest, because it is conceivable that some of them may become established in Florida as a result of the commercial importations. We have attempted in Table 2 (and the Discussion) to distinguish among these levels. Nine of the biological control agents are native to Florida, another nine are naturalized, and five are either native or naturalized. Of the total 48 agents imported, more than half (25), therefore, were not known to occur in Florida at the time of importation.

Habitats. We recognize six groups of habitats into which imported biological control agents have been released. These are perennial plants, annual plants, greenhouses, stored products, grasses (pasture and turf), and vertebrate feces. The distribution of imported biological control agents among habitats is unlike that of their targets (Fig. 1). Specifically, relatively more biological control agents were released into greenhouses than might be expected from the relative number of targets in that habitat, and relatively fewer into perennial plant habitats. This may have been because of the high value of greenhouse-grown plants, the relative inability of the agents to disperse beyond the greenhouse, or a combination of these and other factors.

Greenhouses are mentioned specifically in several places in Table 2. Biological control in greenhouses has received much attention in Europe, somewhat less in Canada and a few states in the USA, and is now receiving attention in Florida. In some ways, biological control in greenhouses resembles classical biological control, because pests in them are in a confining environment which is (in the ecological sense) an island. Some of the pests may only be able to thrive in greenhouses, because the surrounding environment may be inhospitable. Introduction of appropriate natural enemies in appropriate numbers and with appropriate timing into the greenhouse may control the pests during the growth of a crop. One release of agents may suffice to control some pests. Populations of pest and natural enemy alike may die when crop residues are removed or when soil is heat- or steam-sterilized. The ecosystem is then reset only at planting of the next crop, when already-infested seedling plants are used, or when pests invade from outside.

Annual field crops (most field crops) provide another habitat in which biological control is used commercially. Annual ornamental plants are comparable from the ecosystem viewpoint. These habitats are more readily invaded by pests and native natural enemies alike than are greenhouses, and are more subject to the vagaries of climate.

Perennial plants in groves and orchards are a venue of commercial biological control releases. Experience in biological control suggests that these habitats are the ones more

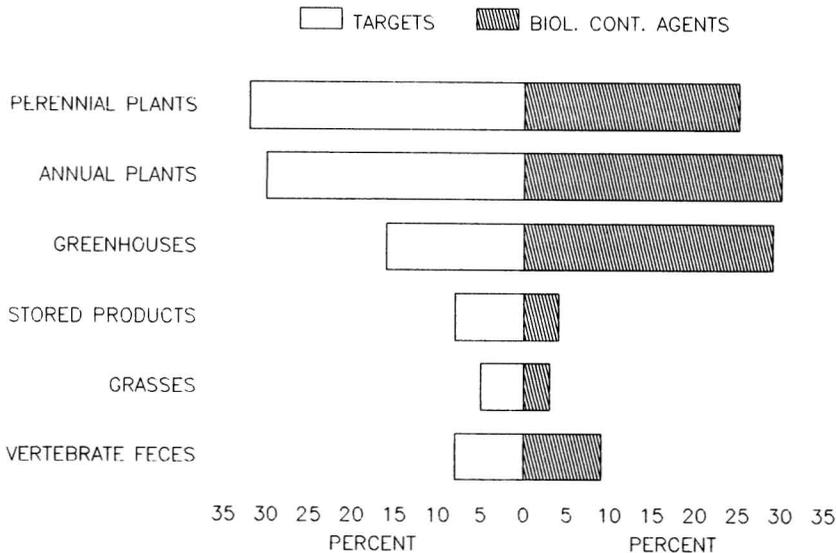


Fig. 1. Relative numbers of targets and imported biological control agents in the 6 habitat types.

TABLE 3. ALTERNATIVE NAMES USED IN THE DOCUMENTATION AND LITERATURE WHICH WAS CONSULTED FOR BIOLOGICAL CONTROL AGENTS LISTED IN TABLE 2. AT LEFT ARE SYNONYMS OR TYPOGRAPHICAL ERRORS FOR NAMES AT RIGHT

<i>Amblyseius californicus</i>	see <i>Neoseiulus californicus</i>
<i>Amblyseius cucumeris</i>	see <i>Neoseiulus cucumeris</i>
<i>Amblyseius mackenziei</i>	see <i>Neoseiulus barkeri</i>
<i>Anagyrus fusiventris</i>	see <i>Anagyrus fusciventris</i>
<i>Aphidius colemani</i> Viereck	see <i>Aphidius matricariae</i>
<i>Geolaelaps</i> sp.	see <i>Hypoaspis</i> sp.
<i>Lindorus lophanthae</i>	see <i>Rhyzobius lophanthae</i>
<i>Metaseiulus occidentalis</i>	see <i>Galendromus occidentalis</i>
<i>Neoseiulus bakeri</i>	see <i>Neoseiulus barkeri</i>
<i>Neoseiulus mckenziei</i>	see <i>Neoseiulus barkeri</i>
<i>Paratenodera sinensis</i>	see <i>Tenodera aridifolia</i>
<i>Phytoseiulus longipes</i>	see <i>Mesoseiulus longipes</i>
<i>Steinernema bibionis</i>	see <i>Steinernema feltiae</i>
<i>Tenodera aridifolia</i>	see <i>Tenodera aridifolia</i>
<i>Tenodera aridifolia</i>	see <i>Tenodera aridifolia</i>
<i>Tenodera aridifolia sinensis</i>	see <i>Tenodera aridifolia</i>
<i>Tenodera sinensis</i>	see <i>Tenodera aridifolia</i>
<i>Thripobius semilutens</i>	see <i>Thripobius semiluteus</i>

amenable to classical biological control, but not necessarily to augmentative biological control.

Use of classical biological control agents against pests of stored products was reviewed by Brower (1990). Storage bins and greenhouses are alike in confining the commodity that is protected, and in forming a barrier to ingress and egress of pests and their natural enemies.

Chemical control of pests has, until recently, been the norm in turfgrass in Florida, but attitudes are changing rapidly. Pasture grasses are now treated relatively little with chemicals because the few chemicals registered for such uses are generally too costly to use routinely.

Poultry houses, stables and dairies provide habitats for muscoid flies whose population control depends in part on physical management of wastes and regulation provided by native natural enemies. Augmentative release of biological control agents can provide additional suppression of the pests.

Patterns

We ranked the biological control agents simultaneously by number of companies importing them into Florida, and number of individuals reported. We then multiplied the rankings together to pool them, and divided the agents into two equally sized groups, "common" agents and "uncommon" agents. We employed only two groups because the data are incomplete and of variable quality; we assume, therefore, that our sample of the data is unbiased. We then asked whether the number of species in any of six categories of targets was distributed disproportionately between the two groups. The categories were: (1) targets, (2) agents, (3) native and naturalized biological control agents, (4) agents released into more than one habitat, (5) agents released into each of the six habitats, and (6) targets of major economic concern (i.e., targets whose effects are estimated to be \$2 million or more annually). Targets of major economic effect were

determined from information provided by Hamer (1985), Schuster (1992), comments by J. E. Funderburk, and our experience.

More targets recorded previously as targets of introduced biological control agents were associated with "uncommon" imported agents than with "common" ones (G test, $G = 9.9$, $P < 0.05$), and more of the "common" agents than the "uncommon" ones were released into multiple habitats ($G = 5.9$, $P < 0.05$). No other disproportionate distributions were detected. The first relationship may indicate that importers focus on supplying biological control agents aimed at targets that are different from those of governmental introduction programs. The second relationship may indicate that importers focus on biological control agents that can be employed in a wide array of circumstances. On the other hand, it may simply indicate that the most useful agents also are the ones that can adapt best to varying environmental conditions.

DISCUSSION

Naturalization Status

The 3 levels of naturalization status of imported organisms are discussed below in light of their possible environmental and economic effects.

Natural Enemies Native to Florida. The ladybird beetles *Delphastus pusillus* and *Hippodamia convergens* are typical of this group. The action of commerce is to release appropriate numbers of them where they may reduce numbers of pest whitefly or aphid species. This action is unequivocally preferable environmentally to the use of chemical pesticides that will kill non-target organisms and perhaps cause other side-effects. Economically, the action is more complex. It is beneficial when its cost is exceeded by the cost (i.e., losses to the grower) of taking no action. Nevertheless, the grower must endeavor to release the appropriate number of agents at the appropriate time(s) to maximize his economic returns. The questions about numbers and time(s) can be answered only by experimentation. Even if a natural enemy provides the best suppression of the pest that it can under any circumstances, the grower still may not make a profit on the crop because the level of suppression was inadequate. The grower under these circumstances has no option but to use other methods of pest control, whether they be additive methods of biological control (several biological control agents), or of a combination of biological and other methods (IPM), or of strict chemical control.

Natural Enemies Naturalized in Florida. The ladybird beetles *Cryptolaemus montrouzieri* and *Rhyzobius lophanthae* are typical of this group. Both were introduced from Australia into North America during the last century as biological control agents, and both are now established in Florida. The action of commerce is to release appropriate numbers of them where they may reduce numbers of a pest mealybug or soft scale insect. This action is unequivocally preferable environmentally to the use of chemical pesticides that will kill non-target organisms and perhaps cause other side-effects. Economically, the action is identical to that of releasing numbers of a native natural enemy.

At an extreme, however, is the decollate snail (*Rumina decollata*) which is established only in very restricted areas of Florida is a generalist predator of other snails and will eat plant materials. Its further dissemination in Florida has not been documented to be beneficial, and it may conceivably be harmful [see Protection of the Native Fauna and Flora].

Natural Enemies Not Yet Established in Florida. Several of the biological control agents being imported into Florida have, to our knowledge, not been introduced for classical biological control purposes. Typical of this group are *Dacnusa sibirica* and *Diglyphus isaea*. It is conceivable that some of them might establish populations and

become useful classical biological control agents. The action of commerce is to release appropriate numbers of them where they may reduce numbers of *Liriomyza* leafminers. This action is unequivocally preferable environmentally to the use of chemical pesticides that will kill non-target organisms and perhaps cause other side-effects. Economically, the action is identical to that of releasing numbers of a native natural enemy.

At an extreme, however, is the "Chinese mantis" (*Tenodera aridifolia*), which is sold in Florida for educational purposes. It is unlikely to have any beneficial effect in Florida's environment because studies elsewhere do not suggest it would make an effective biological control agent (Hurd & Eisenberg 1984).

Protection of the Native Fauna and Flora

There is a range of host-specificity among the imported organisms. At one extreme, some of them are specialized to a target species, but at the other, some are generalists, feeding on a range of organisms not necessarily related to the target. One of the latter is the snail *Rumina decollata*. It is not native to Florida, but has small populations established at 3 localities. The original reason for its importation to California was to combat brown garden snail, a pest of exotic origin. But brown garden snail does not occur in Florida, and we do not understand why *Rumina decollata*, its predator, should have been imported. We think rather that its importation was inadvisable in that it is known to be a minor plant pest, and that it might attack native non-pest molluscs. It can be argued that the species already occurs in Florida so should not be barred from additional entry, but its wider dissemination by commerce for no apparently useful reason is questionable.

Importation of the mantid *Tenodera aridifolia* also is questionable. A native of Asia, it is established in the northeastern USA, but is unable to spread rapidly because females are wingless. Thus, such spread of its population as occurs beyond a few meters is mainly by movement of plants and by commercial sales of *T. aridifolia*. This mantid is not known to be established in Florida and perhaps could not become established in Florida if it is physiologically adapted to more temperate regions. It might be argued that the importation of an insect for educational purposes is harmless, especially if it cannot survive outdoors in Florida, and also if it has little effect as a predator. The counter-argument would state that it might be able to survive outdoors, and might threaten some component of the native fauna, perhaps as a competitor of native mantids. Direct and indirect, but unintended, effects of introduced and imported organisms, including biological control agents, are always a potential risk (Howarth 1991, Simberloff 1992).

Selection of Biological Control Agents. So far as we have determined, there are no Florida-based producers of biological control agents: all agents are being produced elsewhere and imported into Florida. Many of these biological control agents are effective elsewhere according to the literature, but there is little literature on their effectiveness in Florida. Many of the biological control agents are native to temperate climates, and some of them apparently are not well-adapted physiologically to existence in Florida. An example of this is the export to Florida of *Chrysoperla carnea*, when *C. rufilabris* seems better adapted to existence in Florida.

Perhaps natural enemies native to Florida would be superior to some of the natural enemies currently being imported. Producers in northern and western North America, or Europe, may not be aware of the potential of some of these natural enemies native to Florida, and may not have access to stock of them. An example is the predacious mite *Galendromus helveolus* (Chant). This mite, native to Florida, is an effective predator of tetranychid mites, including *Tetranychus urticae* (Caceres & Childers 1991). Yet, we are not aware of any commercial producer even listing *G. helveolus* for sale,

let alone exporting it to Florida. Perhaps it is time for commercial production of biological control agents to begin in Florida.

Commercial Production of Biological Control Agents

Advantages of Commercial Production. The Division of Plant Industry (DPI) releases a very limited range of biological control agents for the public benefit, but these are all classical (inoculative) biological control agents. These releases are based upon perceived need, and are not experimental. The Agricultural Research Service of the Department of Agriculture (USDA-ARS) is involved in releases of classical biological control agents for the public benefit in Florida, but also is involved to a limited extent in releasing augmentative (or inundative) biological control agents, for experimental purposes. The principal releaser of classical biological control agents for experimental purposes is the Institute of Food & Agricultural Sciences (IFAS) of the University of Florida, and it also is involved in experimental trials of augmentative biological control agents. These three organizations do not sell biological control agents to growers for augmentative or inundative purposes.

The governmental organizations in Florida that release classical biological control agents as needed (as contrasted with releases for experimental purposes) are DPI and the Animal and Plant Health Inspection Service of the Department of Agriculture (USDA-APHIS). Such releases are for further dissemination of established natural enemies. Mosquito control districts (which are funded by a combination of state and local taxes) release predacious mosquito larvae and fishes only against pest mosquitoes. No governmental organization sells augmentative and inundative biological control agents to commercial agricultural, horticultural, and livestock producers, or for control of mosquitoes or aquatic weeds. Commercial producers of (augmentative and inundative) biological control agents therefore offer unique services which governments do not duplicate.

What the Customer Needs to Know. The would-be purchaser of a biological control agent needs considerable information before making a purchase, including:

- the correct identity of the pest -
- the current size of the pest population -
- whether effective natural enemies already are present and in adequate numbers -
- what is the damage the pest will cause if left untreated -
- are there effective natural enemies for use against this pest (on this crop) at this time of year in Florida and what are they -
- how many natural enemies are needed, when should they be applied, are they available and at what cost -
- will use of the natural enemy be cost-effective -
- will use of the natural enemy be compatible with other operations being conducted in the same place (crop, etc.), and are there more cost-effective methods than biological control?

This is more information than the would-be purchaser of a chemical pesticide requires (though some uses of chemicals are quite sophisticated), and only part of it can be supplied by a producer of biological control agents at a distant location. If the customer cannot obtain all the necessary information unaided, then he/she will have to contract pest control (or pest control advice) or a scouting service.

Responsibilities of the Producer. The subjects of correct identification of natural enemies, quality control in mass-production, guidelines for use provided to purchasers by producers, and professionalism of the producers, were discussed by Hoy et al. (1991). We have nothing to add beyond emphasizing that the producer of biological control

agents should not be expected to answer all the questions that a customer may need to know about the customer's particular circumstances, **unless** that producer offers a scouting service which will visit the customer's location.

Responsibilities of DPI. In our interpretation, the purpose of statute 581.083 (Florida Statutes 1991) is to protect plants in agriculture and horticulture by (among other things) preventing the movement into Florida of pests of plants, biological control agents, and arthropods, except under permit of the Division of Plant Industry. Arthropods are mentioned specifically, so all seem to be included, whether or not they are pests of plants or are biological control agents. Nematodes and molluscs are not mentioned by name, so presumably are included only if they are pests of plants, or are biological control agents, or will "directly or indirectly affect plant life." Chapter 5B-57 (Florida Administrative Code 1993) specifically excludes Crustacea from Arthropoda and, in our interpretation, broadens agriculture and horticulture to "the environment."

The law does not specifically address the encouragement of biological control vs. other means of pest control, although we believe that it should do so explicitly, and although unwritten administrative policy in DPI is to do so. The law does not discuss its own demise if federal laws should be written to replace it and laws of other states. If many states had their own laws on importation, the burden of paperwork on biological control producers would become overwhelming, and the replacement of state laws by a single, federal, set of laws would be an attractive proposition. We think that existing Florida laws are reasonable, and that they imply a willingness to admit biological control agents to be imported to Florida by commercial organizations.

Administration of the laws is currently being made more efficient. Response to applications for importation permits is now being made by facsimile transmission (FAX), together with a condensed explanation of Florida laws. Records are now being compiled into a computerized database, so that permits for individual species, once granted, may be reissued very rapidly. We think that the Arthropod and Arthropod Pathogen Introduction Committee (which reviews importation requests) could readily compile a computerized list of all approved biological agents, current and foreseen, even in advance of a request having been made; this would allow rapid action on new applications. The committee could review catalogs of biological control agents offered for sale by commercial companies to decide which items would and would not be permitted for admission to Florida. Companies selling living organisms (which may die within a few days) may need a very rapid response to an application for importation permit. At the same time, any company selling biological control agents in Florida should be willing to send a small sample of organisms to DPI for verification of identification.

Effectiveness. The question of effectiveness of biological control agents is not part of Florida law. It does the customer no good to buy biological control agents which cannot be effective under his circumstances. It does the customer no good to buy potentially-effective biological control agents if he/she lacks the knowledge to release them to best effect (too few, too many, wrong timing, or other incorrect strategy). The customer, by costly trial and error, may learn the necessary release strategies. Alternatively, the customer may hire a scouting company with the necessary knowledge. No body of knowledge exists to provide information to the customer on all biological control agents which may conceivably be imported legally. In Florida, the onus to provide such information falls not upon DPI, but mainly upon the Cooperative Extension Service (CES) of the University of Florida. Although the CES can now provide some information, this is woefully inadequate, because the necessary experimentation has been done for few biological control agents. The basic reason that the research has not been done is because of lack of funds to support experimentation. Traditionally, manufacturers of chemical pesticides have provided funds for field trials of their products, so the CES has knowledge on use of chemicals. Growers' organizations or producers' organizations can fund the necessary studies on biological control agents if they are so inclined; it is

unlikely that public funds will be provided for such studies while public funds are in such short supply that funding even for schools, roads, prisons and welfare, is deemed inadequate in Florida. The senior author will be pleased to answer questions from growers' organizations or producers' organizations about research possibilities.

THIS SYMPOSIUM

We have pointed out that large numbers of insect species arrived in Florida as **immigrants**, and that some of these became pests (Frank & McCoy 1992). We have also pointed out that considerable numbers of insect species were **introduced** for classical biological control of pests (Frank & McCoy 1993). The introduction to this symposium focuses on commercial importations of biological control agents, and completes our review of **introduced** biological control agents. The theme of the symposium is the relationship between biological control and the preservation of native floras and faunas. We are aware that certain segments of the public view "**introduced**" insects as being detrimental to the environment, but we think in the first part that these people confuse those that are **immigrant** with those that are **introduced**, and in the second that they have no clear concept of the benefits of biological control. In our view, the key to this understanding is in the behavioral ecology of the biological control agents and of their targets. We hope that this symposium and the two that preceded it will provide biologists with a background of information on **adventive** insects in Florida. With this background, we may in future be able to examine how introductions of plants and animals (vertebrates as well as invertebrates) for agricultural, horticultural, educational, and trivial purposes, have altered ecosystems.

Exotic plants and animals invade native ecosystems, attacking individual species, or affecting whole communities through crowding, or alteration of ecosystem properties such as soil chemistry or fire frequency. Control of exotic species in native ecosystems over large areas by chemical or mechanical means is costly and potentially damaging to other components of the ecosystems. Roy Van Driesche explains how classical biological control can be used to suppress these exotic species, and he gives examples in the control of weeds and of invertebrate and vertebrate animal pests.

Strawberries are a high-value crop in Florida. Their main arthropod pest is *Tetranychus urticae*, which is most often controlled by use of chemical acaricides. Gordon Decou explains that the pest mites often come with seedling plants from the nursery, and that chemical control can be difficult due to plant density or resistance of the mites to chemical acaricides. However, he has demonstrated that the pest mites can be controlled effectively by the use of the predacious mite *Phytoseiulus persimilis*, when appropriate release strategies are used. He uses these strategies in commercial strawberry production to the economic advantage of growers and himself.

Caribbean fruit fly, *Anastrepha suspensa* (Loew), is an immigrant pest in Florida. It attacks tropical soft fruits and, to some extent, citrus. Several classical biological control agents have been introduced to Florida against it, but their combined effect still is inadequate. Their limitations seem to be due to their inability to track periodic increases in populations of the fly, to the influence of oviposition-detering markers, and to microclimate. John Sivinski (manuscript not submitted) has demonstrated experimentally that augmentative releases of a braconid parasitoid substantially lowered fruit fly populations.

The number of species of rare and endangered vertebrate animals is vastly less than that of invertebrates. Nevertheless, almost all funds for conservation are awarded to vertebrate animals. There are at least two reasons for this, though their limits are blurred. First is the general public's lack of awareness of invertebrate animals unless they bite, sting, or otherwise cause damage. Second is an anthropocentric scale of values in which invertebrates (insects are a prime example) are for the most part viewed

as being pests. Tonya Van Hook sees this situation as a challenge in environmental education.

Butterflies are the prime example of insects which are appreciated by the general public. This appreciation is because of the visual beauty of the adult stage, no matter that the larval and perhaps pupal stages, when noticed, may be viewed as repugnant. Jacqueline Miller discusses behavior of adult butterflies, some of which can be explained in terms of predator avoidance. Differences in behavior of adults from mainland and insular populations accentuate her account. These kinds of behaviors by adults must be considered in designing refugia for rare and endangered butterflies.

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RESISTANCE OF SELECTED INTERSPECIFIC
LYCOPERSICON HYBRIDS TO GREENHOUSE WHITEFLY
(HOMOPTERA: ALEURODIDAE)

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ABSTRACT

Lycopersicon interspecific hybrids and species inbreds were examined for resistance to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleurodidae), in four separate greenhouse studies. The two *L. pennellii* Correll interspecific hybrids (ICR.13 X LA1735 and ICR.13 X LA716) were the most toxic and/or repellent to adult whiteflies. ICR.13 X LA1735 exhibited the most adult and nymphal antibiosis and adult antixenosis, supported the lowest number of eggs and nymphs and developed the smallest second generation of adults. The *L. esculentum* Miller entry (ICR.13) was usually intermediate in all characteristics examined. All the entries in the study were able to support all the whitefly developmental stages which suggests selective pressure could possibly overcome a resistance mechanism based solely on adult antibiosis. This study provides evidence for adult and nymphal antibiosis mediated by trichome exudates and the possibility that a second nymphal antibiosis mechanism is present within the leaves of LA1735.

Key Words: Insecta, *Trialeurodes vaporariorum* spp., tomato.

RESUMEN

En cuatro estudios separados, se examinaron híbridos inter-específicos y líneas endogámicas de *Lycopersicon* para resistencia a la mosca blanca de los invernaderos, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleurodidae). Dos híbridos inter-específicos de *L. pennellii* Correll (ICR.13 X LA1735 y ICR.13 X LA716) fueron los más tóxicos o más repelentes a los aleurodidos adultos. ICR.13 x LA1735 mostró el máximo de antibiósis a los adultos y ninfas a antixenosis de los adultos, sostenía el mínimo número de huevos y ninfas, y desarrolló la más pequeña generación segunda de adultos. La partida *L. esculentum* Miller (ICR.13) usualmente fue intermedia en todas características examinadas. Todas las plantas en el estudio fueron capaces de sostener todos los estados de desarrollo de la mosca blanca, lo cual sugiere que presiones selectivas posib-

lemente podrían vencer a un mecanismo de resistencia basado solamente sobre antibiosis al adulto. Este estudio provee evidencia para antibiosis al adulto y la ninfa basado en exudados de tricomas, y en la posibilidad que un segundo mecanismo de antibiosis a las ninfas está presente en las hojas de LA1735.

The greenhouse whitefly, *Trialeurodes vaporariorum* Westwood, can be a serious pest of greenhouse tomatoes. Whitefly adults and nymphs suck plant sap from leaves and secrete honeydew. This direct damage weakens the plant and can significantly reduce yields (Lindquist et al. 1972). Fruit quality is also affected because the honeydew supports sooty-mold which shades foliage and discolors fruit.

Chemical control of greenhouse whiteflies is difficult because the adult stage is targeted and pesticide resistant strains occur in most production greenhouses. Presently, successful biological control can be achieved with the parasitic wasp *Encarsia formosa* Gahan (Lindquist 1977, van Lenteren et al. 1980) given proper environmental conditions. However, lowering the temperature to conserve energy during the winter months can disturb the equilibrium between pest and parasite, thus forcing a grower to switch back to a chemical control program (Berlinger 1980, Berlinger & de Ponti 1981). Tomato host resistance to whiteflies would provide growers with a means of control when the greenhouse environment cannot be made favorable for *E. formosa*.

Greenhouse whitefly resistance has been reported to exist in selected species accessions of *Lycopersion hirsutum* f. *typicum* Humb. & Bonpl. (Gentile et al. 1968, de Ponti et al., 1975, Lobo et al., 1987b), *L. hirsutum* f. *glabratum* Muller (Gentile et al. 1968, de Ponti et al. 1975) and *L. pennellii* Correll (Gentile et al. 1968, de Ponti et al. 1975, Plage 1975, Lobo et al., 1987a). Research in this area has focused on the toxicity of species accessions to adult whiteflies. However, species accessions that are highly resistant to adult whiteflies are difficult to rank and thus retard progress in understanding the resistance mechanisms involved. In addition, only observational reports (Gentile et al. 1968, Plage 1975, de Ponti & Hogenboom 1980) provide information on how the other developmental stages of whiteflies are affected by different *Lycopersicon* species. The objective of this study was to evaluate interspecific hybrids between *L. esculentum* and wild species accessions for level and type of resistance to all greenhouse whitefly stages. Analysis of whitefly resistance in interspecific hybrids may allow ranking of highly resistant germplasm and the manner in which the insects are affected by the mechanisms involved.

MATERIALS AND METHODS

General Procedures

Four greenhouse studies were conducted using the plant material listed in Table 1. All whiteflies used in these experiments were obtained after completing at least one generation on greenhouse grown 'Tropic' or ICR.13 tomato plants. Adult whiteflies were not sexed and were used 24-48 h after eclosion. Seed was germinated and seedlings or cuttings were grown in a 2:1 mix of Cornell (peatlite) Mix II to Wooster silt loam soil. A randomized complete block design was used for all four studies.

Study 1. The purpose of this study was to screen tomato interspecific hybrids for resistance to whiteflies using detached leaves. Twelve genotypes (Table 1) were clonally-propagated and grown for 2 mo in 3.8 liter containers until leaf-stem sections were removed and used in either a no-choice or choice greenhouse experiment. After trans-

TABLE 1. *LYCOPERSON* SPECIES AND INTERSPECIFIC HYBRIDS USED IN THESE *T. VAPORARIORUM* HOST RESISTANCE STUDIES.

Entry	Species or Cross	Study
ICR.13	<i>L. esculentum</i>	1-4
LA1716	<i>L. pariflorum</i>	3
ICR.13 X LA94	<i>L. esculentum</i> X <i>L. h. f. typicum</i>	1-3
Tropic X PI127826	<i>L. esculentum</i> X <i>L. h. f. typicum</i>	1&2
Tropic X PI126449	<i>L. esculentum</i> X <i>L. h. f. glabratum</i>	1
ICR.13 X LA121	<i>L. esculentum</i> X <i>L. pimpinellifolium</i>	1&2
ICR.13 X LA1735	<i>L. esculentum</i> X <i>L. pennellii</i>	1-4
ICR.13 X LA1716	<i>L. esculentum</i> X <i>L. pennellii</i>	1
ICR.13 X LA1401	<i>L. esculentum</i> X <i>L. cheesmanii</i> ssp. <i>minor</i>	1&2
ICR.13 X LA1627	<i>L. esculentum</i> X <i>L. cheesmanii</i>	1
ICR.13 X LA1500	<i>L. esculentum</i> X <i>L. chmielewskii</i>	1
ICR.13 X LA1958	<i>L. esculentum</i> X <i>L. chilense</i>	1&2
ICR.13 X LA1421	<i>L. esculentum</i> X <i>L. e. var. cerasiforme</i>	1

planting and 1 mo later, 20 grams of Osmocote (N-2.8 g, P-1.2 g, K-2.3 g) were added to each container. Each experiment was run twice (late March and mid-April) with four blocks in the no-choice experiment and six blocks in the choice experiment. The test unit was a fully mature and expanded leaf containing only four leaflets and an 11-cm stem section set in a 270-ml bottle of nutrient solution. A block consisted of one test unit/entry randomly placed in a 48-slot bottle rack in a 0.23 m³ cage. The following nutrient solution was used: N-17.5 mg/liter, P-6.75 mg/liter, K-40 mg/liter, Ca-16.8 mg/liter, Mg-5 mg/liter, Fe-0.13 mg/liter and 5 mg/liter of Peter's Compound 111 (W. R. Grace & Co., Fogelsville, PA). The solution was changed every wk for 3 wks. Greenhouse day/night temperature ranges during the experiment were 30-21°C and 20-16°C.

In the no-choice experiment, leaflets were infested by placing 5-10 adult whiteflies in a 38 cm³ clip-on cage on two leaflets per entry for 24 and 48 h. The large amount of clip-on cages handled did not allow accurate adult whitefly counts. The cages were fastened to the leaflets at random. Adult mortality was determined after 24 and 48 h and nymphal counts were taken after 14 and 21 d. Second generation adult emergence was determined by placing the two leaflets with the most 3rd and 4th nymphal instars from each entry on a moist piece of filter paper in a 9-cm petri dish, 21 d after infestation. The dishes were placed in a 23°C growth room set for a photoperiod of 12:12 (L:D) at 80 μmol s⁻¹m⁻² of photosynthetically active radiation. Every day for 8 d adult eclosion was recorded and each leaflet was misted and placed back on the moistened filter paper.

In the choice experiment, blocks were infested twice with 72 adult whiteflies for 24 h. After the first infestation the racks were turned 180 degrees and re-infested. Nymphal counts were taken 14 and 21 d after the start of the experiment.

Study 2. The purpose of this study was to substantiate the results of Study 1 and to evaluate selected interspecific hybrids for resistance to different whitefly developmental stages. Seven of the 12 plants used in the previous study (Table 1) were clonally propagated and placed in a greenhouse in 15.2 cm pots for six weeks. After transplanting, 20 grams of osmocote (N-2.8 g, P-1.2 g, K-2.3 g) were added to each pot. After the plants had developed 10-12 macroscopic leaves, their shoot tip was removed above the 7th macroscopic leaf from the stem terminal. The plants were pruned to three leaves (7th, 8th and 9th) and four leaflets per leaf before the start of the study. Three separate experiments were conducted, two no-choice (nymphal development and adult survival) and one choice. Only six entries were used in each experiment. ICR.13 X LA121 was

only used in the choice experiment and 'Tropic' X PI127826 was only used in the two no-choice experiments. Greenhouse day/night temperature ranges during the experiment were 35-21°C and 22-16°C.

In the nymphal development experiment, four plants per entry were infested by placing a 38 cm³ clip-on cage containing five adult whiteflies on each leaflet for 48 h. After 2 d (on 14 June), the clip-on cages were removed and adult mortality was determined. In addition, three leaflets from each plant were collected and number of eggs were counted. The two leaflets with the most eggs were placed on a moist piece of filter paper in a 9 cm petri dish. The petri dishes were placed in a growth room and handled the same as in Study 1. After 7 d in the growth room leaflets were removed and eggs and nymphs were counted. The remaining leaflets on the plants were removed in groups of three on 19 June, 27 June and 3 July and respectively, eggs, eggs and nymphs and nymphs were counted. On each date, the two leaflets with the most eggs, eggs and nymphs, or nymphs were placed in a petri dish and handled the same as in Study 1. After 4-7 d in the growth room, the number of eggs, nymphs, pupae and adults were recorded for each leaflet.

In the adult survival experiment, three plants/entry were infested by using the same size clip-on cages and the same number of adult whiteflies per cage as in the nymphal development experiment. The cages were left on the leaflets for either 2, 4, 6, 8, 10 or 12 d. At the end of each period two cages per plant were removed and adult survival was determined.

In the choice experiment, one plant of each entry was placed in each of four 0.23 m³ cages and were infested with 360 adult whiteflies for 48 h. After 2 d all leaflets were removed and number of eggs per leaflet were counted.

Study 3. The purpose of the study was to examine the effect of glandular trichomes on whitefly developmental stages. Four genotypes were examined (Table 1). ICR.13 X LA94 and ICR.13 X LA1735 were vegetatively propagated and ICR.13 and LA1716 were seed propagated. Seedlings and rooted cuttings were transplanted into 3.79 liter containers 6 wks before the start of the experiment. After transplanting and 6 wks later, 20 grams of Osmocote (N-2.8 g, P-1.2 g, K-2.3 g) were added to each container. Each plant developed 14-18 macroscopic leaves before the start of the experiment. The shoot tip and lower leaves of the plants were removed. The 8th, 9th, 10th and 11th macroscopic leaf from the stem terminal on 12 plants/entry were infested. These selected leaves were pruned to four leaflets and six plants/entry were wiped of trichome exudates. ICR.13, LA1716 and ICR.13 X LA94 were wiped 24 h before infesting with whiteflies while ICR.13 X LA1735 was wiped only 1-2 h.

ICR.13 X LA 1735 was wiped of exudate shortly before the start of the experiment because *L. pennellii* possesses type IV trichomes (Luckwill, 1943), which are capable of re-exuding exudate. The exudates were removed by wiping the abaxial surface of each leaflet with a dry Kimwipe[®] followed by two wipes with a 50% ethanol moistened Kimwipe. A distilled water rinse followed each ethanol wipe. These plants were used to conduct two no-choice experiments: an adult survival and a nymphal development. Greenhouse day/night temperature ranges during the experiment were 35-21°C and 22-16°C.

In the adult survival experiment, each entry was infested by placing a 38 cm³ clip-on cage containing five adult whiteflies on one leaflet per leaf. After 4 d the cages were removed and adult mortality was determined. The leaflets were then detached and, after eggs were counted, were used in the nymphal development experiment.

In the nymphal development experiment, six plants of each entry by treatment combination were placed in a 0.74 m³ cage and infested for 3 d with 360 adult whiteflies. The two leaflets per plant from the adult survival experiment with the most eggs were placed on a moistened piece of filter paper in a 9-cm petri dish. The petri dishes were

placed in a growth room and handled the same as in Study 1. After 6 d in the growth room, these leaflets were removed and eggs and nymphs were counted. Two of the three remaining leaflets per leaf on each plant were collected 8 and 15 d after the adult whiteflies were removed from the cages. Eggs and nymphs were counted 8 d after removal of adults, and nymphs and pupae were counted 7 d later. After 6-8 d in the growth room, the number of eggs, nymphs, pupae and adults were recorded for each leaflet.

Study 4. The purpose of this study was to examine in more detail the effect glandular trichomes have on whitefly nymphal development. ICR.13 and ICR.13 X LA1735 were the only genotypes examined. Both entries were vegetatively propagated, fertilized and grown the same as in Study 3. The 8th and 9th macroscopic leaf from the top of three plants of ICR.13 and six plants of ICR.13 X LA1735 were cut back to three leaflets. The abaxial trichome exudates were removed from three plants of ICR.13 X LA1735 as in Study 3. The plants were under natural light conditions until 29 October, the start of the experiment, then given 12 h per day of supplemental light with high pressure sodium lights (400 watts, 3 m spacing) suspended 80 cm above the tops of the plants. Greenhouse day/night temperature ranges during the experiment were 25-23°C and 18-16°C. The 8th and 9th macroscopic leaf on each plant of ICR.13 and ICR.13 X LA1735 (wiped of trichome exudates) were infested by placing a 38 cm² clip-on cage containing 8-10 adult whiteflies on each leaflet. The unwiped leaflets of ICR.13 X LA1735 were infested with clip-on cages containing 10-12 adult whiteflies. The unwiped leaflets of ICR.13 X LA 1735 were infested with more adult whiteflies because results from Studies 1-3 indicated that less eggs would be laid on unwiped ICR.13 X LA 1735. After 3 d the cages were removed and eggs per leaflet were counted by positioning the leaflets under a dissecting scope while the leaflets remained attached. One wk after infestation, eggs were again counted, after 2 wks nymphs were counted and 3 wks following infestation all leaflets were removed and pupae were counted. All leaflets were then placed on a moist piece of filter paper in a 9-cm petri dish and set in a growth room under the same conditions as in Study 1. Adult eclosion per leaflet was counted every day for 10 d.

Statistical Analysis

Analysis of data for all experiments was performed using analysis of variance (SAS Institute 1985) and means were separated by a protected least significant difference (LSD) test.

RESULTS

Study 1

Regardless of the experiment, there was no change in the ranking of entries when the 14- and 21-day nymphal counts were compared. In the no-choice experiment, ICR.13 X LA1735 and ICR.13 X LA716 had the highest percentage mortality of adult whiteflies at 48 h and the fewest nymphs per leaflet (Table 2). The data for percentage adult mortality at 24 h was similar to that at 48 h. There was a tendency for ICR.13 X LA1735 to have fewer adults per leaflet and a lower ratio of adults to nymphs. All the nymphs on ICR.13 X LA1401 and ICR.13 X LA716 were able to develop into adults. All the entries in the experiment were able to produce a second generation of adult whiteflies.

In the choice experiment, the fewest nymphs occurred on ICR.13 X LA716 and ICR.13 X LA1735 and the most on ICR.13 X LA1421, ICR.13 X LA94 and 'Tropic' X PII127826 (Table 2). The *L. esculentum* entry (ICR.13) was intermediate in nymphs per leaflet.

TABLE 2. RESPONSE OF *T. VAPORARIORUM* ADULT AND NYMPHS TO A *L. ESCULENTUM* INBRED (ICR.13) AND SELECTED INTERSPECIFIC HYBRIDS IN DETACHED LEAF EXPERIMENTS (STUDY 1).

Entry	No Choice			Choice	
	% Adult Mortality 48h ¹	Nymphs/ Leaflet ²	Adults/ Leaflet ³	Adults/ Nymphs ⁴	Nymphs/ Leaflet ⁵
ICR.13 X LA94	2	45	37	0.83	18.1
ICR.13 X LA1627	4	40	30	0.82	11.0
ICR.13 X LA121	2	57	42	0.76	6.9
ICR.13 X LA1735	68	18	11	0.62	6.0
ICR.13 X LA1421	2	55	45	0.80	22.9
Tropic X PI127826	10	40	32	0.87	17.5
Tropic X PI126449	5	34	22	0.68	11.0
ICR.13 X LA1401	3	47	54	1.00	7.1
ICR.13 X LA1500	1	38	37	0.97	13.6
ICR.13 X LA716	45	31	33	1.00	2.1
ICR.13 X LA1958	2	48	41	0.91	11.6
ICR.13	2	54	48	0.89	11.3
SE	4	7	9	0.27	3.5
LSD	11	19	ns	ns	9.8

¹LSD test (SAS Institute 1985) (F=6.41, entry df=11, error df=69, P<0.0001). Percentage adult mortality per leaflet was determined 48 h after infestation.

²(F=2.95, P<0.01) Nymphs per leaflet data collected 21 d after infestation.

³(F=1.49, P>0.05) Number of second generation adults.

⁴(F=0.42, P>0.05) Proportion of nymphs that developed into adults.

⁵(F=2.76, entry df = 11, error df = 115, P <0.01).

Study 2

In the nymphal development experiment, ICR.13 X LA1735 had the highest percentage adult mortality and supported the fewest eggs, nymphs, pupae and second generation adults per leaflet (Table 3). ICR.13 was intermediate in number of eggs, nymphs, pupae and second generation adults per leaflet. ICR.13 x LA1735 had the lowest proportion of eggs and nymphs on 21 June (0.54 vs. 0.93 for ICR.13 X LA94, 0.93 for ICR.13 X LA1401, 1.00 for ICR.13 X LA1958, 1.00 for ICR.13, and 0.74 for 'Tropic' X PI127826, SE = ± 0.2); eggs, nymphs and pupae on 1 July (0.29 vs. 1.00 for ICR.13 X LA94, 0.98 for ICR.13 X LA1401, 1.00 for ICR.13 X LA1958, 0.84 for ICR.13, and 1.00 for 'Tropic' X PI127826, SE = ± 0.15); and nymphs, pupae and second generation adults on 9 July (0.60 vs. 1.00 for ICR.13 X LA94, 1.00 for ICR.13 X LA1401, 1.00 for ICR.13 X LA1958, 0.85 for ICR.13, and 0.72 for 'Tropic' X PI127826, SE = ± 0.15). Tropic X PI127826 had the lowest portion of eggs and nymphs on 25 June (0.54 vs. 0.81 for ICR.13 X LA94, 1.00 for ICR.13 X LA1735, 1.00 for ICR.13 X LA1401, 1.00 for ICR.13 X LA1958, and 1.00 for ICR.13, SE = ± 0.2).

In the adult survival experiment, ICR.13 X LA1735 was always the most detrimental to adult whiteflies regardless of the amount of exposure time (Fig. 1). Adult whitefly mortality tended to increase for all the entries as time of exposure increased. After just 6 d, over 90 % mortality occurred in the adult whiteflies caged on ICR.13 X LA1735 and 'Tropic' X PI127826. The next highest level of mortality was over 80 % which occurred on ICR.13 X LA1401 after 8 d of exposure.

In the choice test the fewest eggs were deposited on ICR.13 X LA1735 (Fig. 2). The highest numbers occurred on ICR.13 X LA1401 and ICR.13 X LA94.

TABLE 3. RESPONSE OF *T. VAPORARIORUM* ADULTS AND NYMPHS TO A *L. ESCULENTUM* INBRED (ICR.13) AND SELECTED INTERSPECIFIC HYBRIDS (STUDY 2).

Entry	No choice				
	% Adult Mortality ¹	Eggs/ Leaflet ²	Nymphs/ Leaflet ³	Pupae/ Leaflet ⁴	Adults/ Leaflet ⁵
ICR.13 X LA94	14	28.8	50.2	23.6	5.4
ICR.13 X LA1735	72	10.3	11.7	0.5	0.2
ICR.13 X LA1401	16	27.5	53.0	7.0	1.9
ICR.13 X LA1958	8	18.0	36.5	2.4	6.4
Tropic X PI127826	23	35.2	30.8	5.7	1.2
ICR.13	21	18.0	22.9	4.6	1.2
SE	4	7.6	12.5	2.7	2.3
LSD	12	21.4	35.4	3.9	4.7

¹LSD test (SAS Institute 1985) (F=39.44, entry df=5, error df=15, P<0.0001). Percentage adult mortality per leaflet was determined 48 h after infestation.

²(F=3.08, P<0.05)

³(F=3.74, P<0.05)

⁴(F=4.45, P<0.05)

⁵(F=4.23, P<0.05) Number of second generation adults.

Study 3

The removal of abaxial trichome exudates from ICR.13 X LA1735 significantly increased adult whitefly survival and number of eggs per leaflet and increased the proportion of eggs that developed into nymphs (Table 4) when compared to the unwiped leaflets of ICR.13 X LA1735. In addition, the wiped leaflets of ICR.13 had higher numbers of pupae and adults per leaflet compared to the unwiped leaflets of ICR.13. Conversely, the wiped leaflets of LA1716 had lower numbers of nymphs, pupae and adults and a lower proportion of nymphs that developed into pupae compared to the unwiped leaflets of LA1716. Of all the entry x treatment combinations, the unwiped leaflets of ICR.13 X LA1735 had the lowest adult whitefly survival, the fewest eggs and the lowest proportion of eggs that developed into nymphs (Table 4). These leaflets also tended to have the fewest nymphs, pupae and second generation adults, and the lowest proportion of nymphs and pupae that developed into either pupae or second generation adults.

Study 4

The wiped leaflets of ICR.13 X LA1735 had higher numbers of pupae and second generation adults per leaflet and tended to have higher numbers of eggs and nymphs than the unwiped leaflets of ICR.13 X LA1735 (Table 5). The number of these stages on the unwiped leaflets of ICR.13 was intermediate. The unwiped leaflets of ICR.13 X LA1735 had the lowest proportion of eggs that developed into either nymphs or pupae and nymphs that developed into pupae (Table 6) and tended to have the lowest proportion of eggs that developed into second generation adults. The wiped leaflets of ICR.13 X LA1735 had a lower proportion of eggs that developed into either nymphs or pupae than unwiped leaflets of ICR.13.

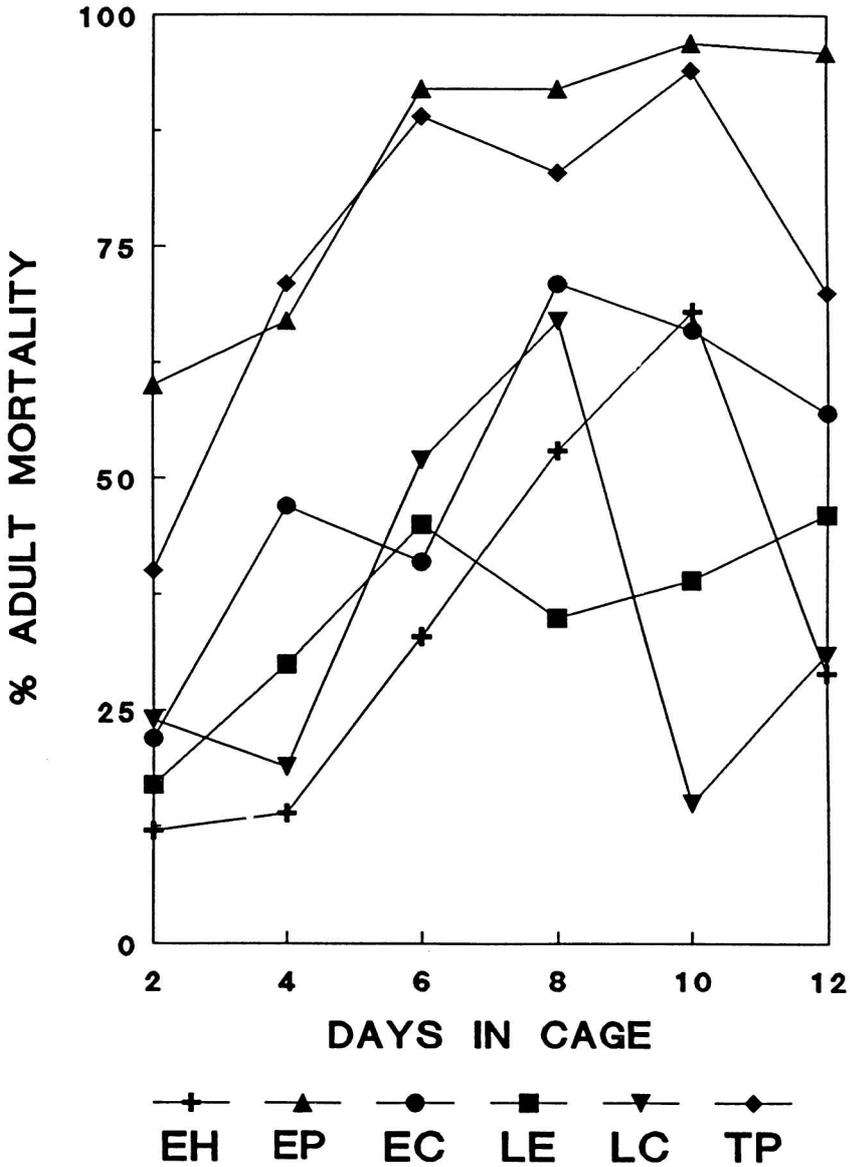


Fig. 1. Percentage adult mortality of *T. vaporariorum* on a *L. esculentum* inbred (LE = ICR.13) and five interspecific hybrids (EH = ICR.13 X LA94, EP = ICR.13 X LA1735, EC = ICR.13 X LA1401, LC = ICR.13 X LA1958, TP = Tropic X PI127826) after 2-12 days in a clip-on cage (SE = ± 13%) (Study 2).

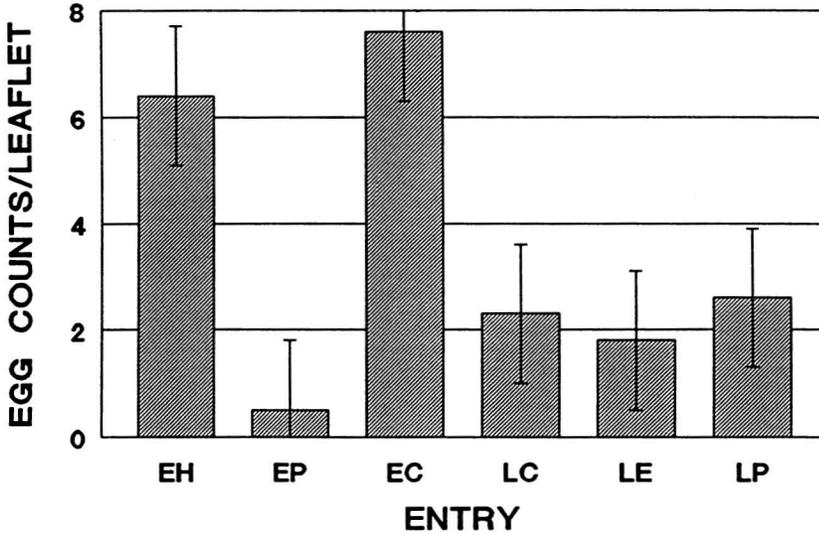


Fig. 2. Egg counts from a choice experiment in which whiteflies (*T. vaporariorum*) were caged with a *L. esculentum* inbred (LE = ICR.13) and five interspecific hybrids (EH = ICR.13 X LA94, EP = ICR.13 X LA1735, EC = ICR.13 X LA1401, LC = ICR.13 X LA1958, LP = ICR.13 X LA121) (Study 2). Bars indicate SE.

DISCUSSION

Of all the genotypes examined, the two *L. pennellii* hybrids (ICR.13 X LA1735 and ICR.13 X LA716) were the most toxic and/or repellent to adult whiteflies. ICR.13 X LA716 was used only in the first study because in Study 1 all the nymphs on this hybrid developed into adults. ICR.13 X LA1735 exhibited the most adult and nymphal antibiosis and adult antixenosis, supported the lowest number of eggs and nymphs and developed the smallest second generation of adults. Another entry that exhibited some adult and nymphal antibiosis was a *L. hirsutum* f. *typicum* hybrid ('Tropic' X PI127826). Both LA1735 and LA716 were screened by Lobo et al. (1987a) for toxicity to adult whiteflies and exhibited 100% adult whitefly mortality. In another study using *L. hirsutum* f. *typicum*, Lobo et al. (1987b) found 99% adult whitefly mortality on PI127826 and no eggs and nymphs. In all four of the present studies, ICR.13 was usually intermediate in all the characteristics examined indicating that it has a higher level of resistance than some of the hybrids studied. In the two choice experiments, ICR.13 X LA94 was preferred more often than ICR.13. All the entries in this study were able to support all the whitefly developmental stages. There were differences in the amount of antibiosis to adults and nymphs and in preference for egg laying. However, even the hybrids that exhibited the highest amount of adult antibiosis were still able to support a second generation of adults. Additional studies need to be conducted to determine the health and feeding preference of a second generation of whiteflies raised on these hybrids.

The trichome exudate of ICR.13 X LA1735 was toxic and/or repellent to adult whiteflies and also affected nymphal developmental stages. The trichome exudate of *L. pennellii* accession LA716 and the *L. hirsutum* f. *typicum* accession PI126826 were reported by Gentile et al. (1968) to be highly toxic to adult whiteflies. However, after they removed trichome exudates oviposition occurred and nymphs developed into adults. Plage (1975)

TABLE 4. RESPONSE OF *T. VAPORIORUM* ADULTS AND NYMPHS TO A *L. ESCULENTUM* INBRED (ICR.13), A *L. PARIFLORIUM* INBRED (LA1716) AND TWO INTERSPECIFIC HYBRIDS, ICR.13 X LA94 AND ICR.13 X LA1735, WIPED OR UNWIPED OF TRICHOME EXUDATES (STUDY 3).

Entry	Treatment	No Choice							
		% Adult Mortality ¹	Eggs/ Leaflet ²	Nymphs/ Leaflet ³	Pupae/ Leaflet ⁴	Adults/ Leaflet ⁵	Nymphs/ Eggs ⁶	Pupae/ Nymphs ⁷	Adults/ Pupae ⁸
ICR.13 X LA94	unwiped	36	76.0	43.5	15.2	6.9	0.97	0.66	0.68
	wiped	22	60.5	25.7	10.2	6.0	0.83	0.65	0.68
ICR.13 X LA1735	unwiped	100	3.9	2.2	1.0	0.2	0.22	0.50	0.15
	wiped	25	38.0	12.8	6.0	2.6	0.87	0.68	0.35
LA1716	unwiped	13	43.9	25.1	21.0	8.1	1.00	0.88	0.56
	wiped	18	30.3	9.4	4.0	2.6	1.00	0.54	0.50
ICR.13	unwiped	15	25.3	6.9	1.7	0.8	1.00	0.80	0.56
	wiped	14	31.0	14.6	9.1	4.7	0.94	0.74	0.59
SE		1.3	8.2	4.0	3.1	1.3	0.05	0.09	0.11
LSD		15	23.7	11.6	6.4	3.8	0.15	0.27	NS

¹LSD test (SAS Institute 1985) (F = 24.17, entry X treatment df = 3, error df = 35, P < 0.0001). Percentage adult mortality per leaflet was determined 4 days after infestation.

²(F = 3.93, P < 0.05).

³(F = 6.99, P < 0.001).

⁴(F = 7.58, P < 0.001).

⁵(F = 4.88, P < 0.01) Number of second generation adults.

⁶(F = 22.8, entry X treatment df = 3, error df = 35) Proportion of eggs that developed into nymphs.

⁷(F = 2.92, P < 0.05) Proportion of nymphs that developed into pupae.

⁸(F = 0.54, P > 0.05) Proportion of pupae that developed into adults.

TABLE 5. RESPONSE OF *T. VAPORARIORUM* NYMPHS TO A *L. ESCULENTUM* INBRED (ICR.13) AND ONE INTERSPECIFIC HYBRID, ICR.13 X LA1735, WIPED AND UNWIPED OF TRICHOME EXUDATES (STUDY 4).

Entry	Treatment	No Choice			
		Eggs/ Leaflet ¹	Nymphs/ Leaflet ²	Pupae/ Leaflet ³	Adults/ Leaflet ⁴
ICR.13 X LA1735	unwiped	24.8	19.4	16.3	12.9
ICR.13 X LA1735	wiped	51.4	43.4	40.2	36.0
ICR.13	unwiped	28.7	27.7	25.1	20.9
SE		6.4	5.2	4.5	3.6
LSD		ns	ns	17.6	14.2

¹LSD test (SAS Institute 1985) (F = 5.02, entry df = 2, error df = 4, P > 0.05).

²(F = 5.43, P > 0.05).

³(F = 7.25, P < 0.05).

⁴(F = 10.54, P < 0.05).

reported that the high degree of adult whitefly mortality seen in LA716 is closely correlated with the amount of leaf stickiness. He also reported that the trichome exudate from LA716 was toxic to adult whiteflies and observed a slight reduction in survival going from the egg to the pupal stage. Different accessions of *L. hirsutum* f. *typicum*, *L. hirsutum* f. *glabratum* and *L. pennellii* were reported by de Ponti et al. (1975) to also be highly resistant to whiteflies, and they suggested that other factors besides the trichome exudates may be contributing to the level of resistance seen in the *L. pennellii* accessions.

In all the studies we conducted with ICR.13 X LA1735, rarely did we observe dead adult whiteflies stuck to leaves. This supports Plage's (1975) suggestion, that it might be possible to breed for toxic materials on tomato leaves that are not sticky. In addition, de Ponti & Hogenboom (1980) reported that some of the F₃ plants from crosses between *L. pennellii* and *L. esculentum* had a high level of resistance but were not as sticky as other resistant plants.

TABLE 6. PROPORTION OF *T. VAPORARIORUM* EGGS THAT DEVELOPED INTO NYMPHS, PUPAE, AND ADULTS AND NYMPHS INTO PUPAE AND PUPAE INTO ADULTS ON A *L. ESCULENTUM* INBRED (ICR.13) AND ONE INTERSPECIFIC HYBRID, ICR.13 X LA1735, WIPED AND UNWIPED OF TRICHOME EXUDATES (STUDY 4).

Entry	Treatment	No Choice				
		Nymphs/ Eggs ¹	Pupae/ Eggs ²	Adults/ Eggs ³	Pupae/ Nymphs ⁴	Adults/ Pupae ⁵
ICR.13 X LA1735	unwiped	0.81	0.68	0.56	0.85	0.82
ICR.13 X LA1735	wiped	0.84	0.81	0.69	0.96	0.86
ICR.13	unwiped	0.96	0.87	0.74	0.91	0.85
SE		0.01	0.01	0.05	0.02	0.07
LSD		0.05	0.03	ns	0.07	ns

¹LSD test (SAS institute 1985) (F = 30.58, entry df = 2, error df = 4, P < 0.05).

²(F = 119.76, P < 0.05).

³(F = 3.43, P > 0.05).

⁴(F = 11.02, P < 0.05).

⁵(F = 0.09, P > 0.05).

Our data reveal that ICR.13 X LA1735 consistently had a lower proportion of eggs that developed into nymphs than any other entry examined which indicates a nymphal antibiosis mechanism mediated through the trichome exudates that is probably operating on the first and second instars. The first instar in whitefly development is a crawler stage which could come in contact with the trichome exudates. The effect the trichome exudates of ICR.13 X LA1735 had on the biology of the whitefly nymphs was not examined. Possible modes of action could be toxicity, repellency and feeding deterrence. ICR.13 X LA1735 may also possess some internal leaf factors that affect nymphal stages because egg to nymph proportions on wiped leaflets in Study 4 were lower than unwiped leaflets of ICR.13. However, more evidence is necessary to either support or refute an internal leaf mechanism because in Study 3 wiped leaflets of ICR.13 X LA1735 and unwiped leaflets of ICR.13 did not differ in the proportion of nymphs that developed on each plant.

The trichome-mediated adult whitefly antibiosis mechanism possessed by ICR.13 X LA1735 may not be an enduring means of control because ICR.13 X LA1735 was able to support a second generation of whiteflies. The second generation developed from ICR.13 X LA1735 suggests a shift in a population of whiteflies could possibly overcome a resistance mechanism based solely on adult antibiosis. Presently this conclusion is tentative because survival on resistant lines has not been demonstrated to be heritable. However, if a nymphal antibiosis mechanism that is different from the adult mechanism could be discovered, and the two mechanisms were combined, a stable form of resistance would be more likely because two stages in the life cycle of *T. vaporariorum* would be targeted.

These studies provide evidence for a trichome exudate mediated adult and nymphal antibiosis mechanism and the possibility that a second nymphal antibiosis mechanism is present within leaves of ICR.13 X LA1735. These studies also provide evidence for the importance of interspecific hybrids in whitefly host resistance studies. Making interspecific hybrids by crossing to a *L. esculentum* inbred allows examination of insect response at different levels of resistance and also permits ranking of highly resistant germplasm. In these studies, survival of a second generation of whiteflies occurred in an interspecific hybrid of *L. hirsutum* f. *typicum* and *L. pennellii*. In earlier reports in which researchers examined only species accessions, all the *L. hirsutum* f. *typicum*, *L. hirsutum* f. *glabratum* and *L. pennellii* examined were reported as being highly resistant and very detrimental to adult whiteflies (Gentle et al. 1968, de Ponti et al. 1975, Plage 1975, Lobo et al. 1987a, 1987b). Because *L. pennellii* has a number of negative attributes (small green fruit, self-incompatibility, unilateral incompatibility and brittle stems, petioles and peduncles), progress towards greenhouse whitefly resistant cultivars could be accelerated if the genes for resistance were identified.

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LABORATORY AND FIELD OLFATORY ATTRACTION OF
THE MEXICAN FRUIT FLY (DIPTERA: TEPHRITIDAE) TO
METABOLITES OF BACTERIAL SPECIES

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ABSTRACT

Bacteria isolated from the Mexican fruit fly, *Anastrepha ludens* Loew, were identified and found to be similar to bacteria isolated from other fruit fly species. Bacteria of the same species as those identified from *A. ludens* were obtained from the American Type Culture Collection (ATCC). These bacteria were cultured and attractiveness to *A. ludens* adults was determined for the whole beer, and for filtered and autoclaved supernatants in laboratory bioassays. All bacterial cultures were attractive to *A. ludens*, and some were significantly more attractive than others. Autoclaved supernatants were significantly more attractive than the whole beer or filtered supernatants. Two strains of *Bacillus thuringiensis* (serovars *finitimus* and *kurstaki*), not previously reported to attract fruit flies, were attractive to *A. ludens*. In field studies, metabolites from bacterial fermentation of two cultures (ATCC #8090 and #13883) captured as many *A. ludens* adults as Torula yeast/borate pellets. Metabolites from these two cultures caught nearly twice as many females as males compared to about equal numbers of males and females captured by Torula yeast/borate pellets and Nulure[®]. Consistent with laboratory bioassays, metabolites from RGM-1 caught significantly fewer *A. ludens* adults than the metabolites from #8090 and #13883.

Key Words: Insecta, *Anastrepha ludens*, bacteria, attractants.

RESUMEN

La identificación de bacteria aislada de moscas de la fruta, *Anastrepha ludens* (Loew), mostró que estas eran similares a bacteria que han sido identificada en otras especies de moscas de la fruta. Los bioensayos se basaron en especímenes de bacteria de la Colección Americana a de Tipos de Cepas (A.T.C.C.). Cultivos de esta bacteria se utilizaron en bioensayos para determinar la actividad del fermento completo, de sobrenatantes filtrados, y de sobrenatantes esterilizados. Todas las cepas resultaron atractivas para los adultos de *A. ludens*. Sobrenatanes esterilizados fueron significativamente más atractivos que los fermentos completos de bacteria o que los sobrenatantes filtrados. Dos cepas de *Bacillus thuringiensis* (serovar *finitimus* y *kurstaki*), no reportadas previamente como atrayentes de moscas de la fruta, fueron atrayentes para los adultos de *A. ludens*. En estudios de campo, metabolitos derivados de la fermentación de cepas ATCC #8090 y

#13883 fueron tan activos como las tabletas de levadura *Torula*/borato para atraer máximas capturas de adultos de *A. ludens*. Estos dos cepas capturaron aproximadamente la misma cantidad de machos y hembras. Consistente con de laboratorio, la preva de campo demostró que metabolitos de la cepa RGM-1 fueron significativamente menos atrayente para los adultos de *A. ludens* que los metabolitos activos #8090 y #13883.

The Mexican fruit fly, *Anastrepha ludens* (Loew), is a serious pest of fruit cultures including citrus as well as other subtropical fruits. For many years, researchers have used proteinaceous baits to trap fruit flies including *A. ludens* (McPhail 1938, Dean 1941, Hanna 1947, Steiner 1952, Lopez-D 1963, Cunningham et al. 1978). It is generally agreed that better attractants are needed for fruit flies.

At the beginning of this century, Petri (1910) suggested that bacteria had a symbiotic relationship with tephritids. Bacteria isolated from fruit flies are usually gram-negative enterics while others are pseudomonads (Fitt & O'Brien 1985, Tsiropoulos, 1976). These bacteria have been isolated from the alimentary tract of fruit fly adults.

Recently, Jang & Nishijima (1990) isolated enteric bacteria from the alimentary tract of lab-reared and wild *Bactrocera dorsalis* Hendel and obtained an olfactory attraction response to the bacterial isolates by *B. dorsalis* adults. McCollum et al. (1992) isolated an enteric similar to *Enterobacter agglomerans* that was attractive to foraging *Rhagoletis pomonella*. Robacker et al. (1991), found that *Staphylococcus aureus*, isolated from the mouth parts of *A. ludens* adults, was highly attractive to *A. ludens*.

In this paper, we report on the identification of bacteria isolated from the alimentary tract of wild *A. ludens* adults as well as from grapefruit (*Citrus paradisi* Macfadyen) leaf imprints and fruit washes from chapote amarillo, *Sargentia greggii* S. Wat. We also report on the attractiveness to *A. ludens* of three types of aqueous preparations of American Type Culture Collection (Rockville, MD) bacterial cultures similar to bacteria identified from *A. ludens*. Additionally, we compared attractiveness to *A. ludens* of two strains of *Bacillus thuringiensis* (Berliner) and *S. aureus* previously tested by Robacker et al. (1991). Moreover, we conducted a field experiment comparing metabolites of bacterial fermentations to the standard proteinaceous baits used in trapping *A. ludens*.

MATERIALS AND METHODS

Isolation and Identification of Bacteria From Native *A. ludens* and Other Sources.

Native *A. ludens* adults were collected in a grapefruit orchard located near Ciudad Victoria, Tampaulipas, Mexico, using McPhail traps containing 10% Nulure® (Miller Chemical and Fertilizer Corp., Hanover, PA). A layer of autoclaved perlite® (Termolita SA, Monterrey, N.L. MX) was placed on top of the Nulure® to prevent the captured flies from coming in contact with the Nulure®.

Approximately 50 *A. ludens* adults were captured with this system. The adults were individually packed in vials and the vials were placed in a freezer. In the laboratory, the adults were disinfected externally using a modified procedure by Martignoni & Steinhaus (1961). A piece of sewing thread (5.08 cm) was used to tie the neck and ovipositor (or anal area) to prevent any of the disinfectant from entering the alimentary tract. Adults were individually placed into 150 x 25 mm test tubes containing 70% percent ethanol and the tubes were capped. The tubes were shaken using a Vortex Genie for approximately 30 s. The ethanol was decanted and sterile distilled water was added. This procedure was repeated three times. A 0.3% hypochlorite solution was

added to each tube and the tubes were shaken for 30 s. The procedure continued as with the ethanol. The disinfected adults were removed from the tubes using sterile forceps and transferred to sterile watch glasses (50 x 15 mm) and a ml of sterile distilled water was added. Adults were dissected and the alimentary tracts were streaked on trypticase soy agar (BBL, Baltimore, MD) plates and incubated at 32°C for 24-36 h. At the end of the incubation period, discrete colonies were aseptically removed using an inoculation loop and re-streaked on trypticase soy agar and incubated at 32°C for 24-36 h. The bacteria were gram stained, subcultured on MacConkey agar (BBL, Baltimore, MD) and incubated at 32°C for 24-36 h. MacConkey agar is a modification of the medium described by MacConkey (1905) and is used to detect enteric bacteria as well as inhibit growth of gram positive organisms. Gram negative pure strains were then streaked in trypticase soy agar slants and refrigerated for further studies. As stated before, all bacteria isolates came from the alimentary tract. A few gram positive cultures were isolated but were destroyed without identification. Identification of the gram negative organisms was conducted using the Analytical Profile Index (API) 20E (Analytab Products, Plainview, NY), additional biochemical tests (oxidase, oxidation/fermentation analysis, and differentiation of gram negative bacilli by their attack on dextrose, lactose, sucrose and the liberation of sulfides), and Bergey's Manual of Systematic Bacteriology (10th ed.).

Chapote amarillo fruit were collected in the Montemorelos, Nuevo Leon, Mexico area and were brought back to the laboratory. The fruit was then rinsed with a 0.08% saline solution and the rinse was plated and bacteria identified using the same procedures used to identify bacteria from the alimentary tract of *A. ludens* adults. To determine microbial populations on grapefruit leaf material, leaves were picked and immediately pressed (smooth side down) on petri plates filled with trypticase soy agar medium. Each leaf was removed and the plates were sealed and incubated at 35°C for 48 h. The procedure for isolation of bacterial colonies was the same as previously described.

Fermentation and Bioassay

The bacteria identified from *A. ludens* were lost in a refrigeration accident. Rather than attempting to re-isolate bacterial colonies from *A. ludens*, we obtained similar bacterial species (i.e. similar by species, but not necessarily isolated from fruit flies) from the American Type Culture Collection. We also obtained three gram positive organisms; two *B. thuringiensis* isolates from the *B. thuringiensis* Cultures, USDA, Peoria, Illinois, and RGM-1 (Robacker et al. 1991). To culture the bacteria, 100 ml of tryptic soy broth (Difco, Detroit, MI) were placed in 250 ml shaker flasks and autoclaved at 121°C for 20 min. The flasks were cooled and seeded with the American Type Culture Collection cultures, *B. thuringiensis* isolates or RGM-1. The flasks were placed in an incubated rotary shaker (31°C., 250 rpm) for 144 h. The 144 h incubation time was chosen because preliminary attractiveness bioassays indicated 144 h yielded a more attractive product than shorter fermentations. During and/or after fermentation, all cultures were subjected to microscopic examination and API 20E (Analytab Products) testing to ensure purity and verify species identification. At the end of the time period, a 10 ml sample was transferred to a 100 ml flask and labeled whole beer. The remaining 90 ml were centrifuged at 10,000 rpm for 15 min. Forty-five ml of the supernatant were autoclaved at 121°C. for 20 min., while the other 45 ml were filtered using a 0.45µ polypropylene encased syringe filter (Alltech, Deerfield, IL). The whole beer and the autoclaved and filtered supernatants were then tested for attractiveness to *A. ludens* adults. In another experiment, cells were spun down and the supernatant removed, saving the pellets (sediment). The pellets were rinsed with sterile distilled water, centrifuged and resuspended four times. After the fourth time, the cells were suspended in sterile, distilled water and tested for attractiveness.

All attractiveness bioassays were conducted in the laboratory using cage-top bioassays like those used by Robacker et al. (1991). The bioassay consisted of placing two filter paper (Whatman No. 1, Whatman, Hillsboro, OR) triangles (3 cm per side) loaded with 10 μ l bacterial preparation and two with 10 μ l of tryptic soy broth on top of an aluminum-framed, aluminum-screened cage (0.3 x 0.3 x 0.3 m) containing 200 flies (sex ratio about 1:1). The numbers of flies beneath the papers were counted once each min for 10 min. Filter papers containing treatments were placed diagonally from each other on two corners of the cage as were the papers containing sterile tryptic soy broth. The filter papers were raised 0.5 cm above the cage top using a washer-like ring (O.D. 4.3 cm, 0.3 cm thick) to ensure that olfaction was solely responsible for attraction of flies. Flies used in the bioassay were age 10-14 days post eclosion. The ratio of the total count beneath the treatment papers to the count beneath the tryptic soy broth papers was defined as the T/C ratio.

Field Study

The field study was conducted in the spring of 1993 in an orange grove in the Huerta Altamira located in the municipality of Allende, Nuevo Leon, Mexico. Test baits were autoclaved supernatants from the American Type Culture Collection bacterial cultures #13883 and #8090 and from RGM-1. Aside from the test baits, *Torula* yeast/borate pellets (5 pellets per 500 ml water) and 10% Nulure[®] without borate were included in the study. There were a total of 50 McPhail traps (10 traps each of 5 baits) used in the experiment per replicate (week). The traps were hung on individual trees in a 7 x 7 + 1 (7 traps per 6 rows; the last row having 8 traps) block of trees in the grove in a repeating sequence of the five baits. Traps were rebaited and rotated weekly so that all trap sites held each of the five baits once. Captured *A. ludens* adults were sexed, counted and recorded each week.

Statistical Analysis

The bacteria were not fermented or tested at the same time, thus comparisons of attractiveness of bacteria to each other were confounded with the time of the year when each bacterium was tested. However, the effect of the confounding was probably minimal because all bioassays contained tryptic soy broth as an internal control to standardize attractiveness of the various bacterial preparations. Thus, the data were combined and analyzed as a completely randomized experiment. Each bacterium was grown three times over a two-month period. Attraction variability from fermentation to fermentation was nested within effects of attractant type (original beer, autoclaved supernatant and filtered supernatant) and bacterial species. The main effects of bacterium species and attractant type and the interactions of these effects were tested using the "fermentation nested within the attractant type by bacterial species interaction" as the error term. Analysis was conducted using the ANOVA procedure of PC SAS (SAS Institute, 1988). T/C ratios were calculated and used as data. The relative attractiveness of the whole beer and autoclaved and filtered supernatants to each other were not affected by time-of-year confounding. Paired t-tests were conducted to compare the attractiveness of each bacterial sample with tryptic soy broth controls. These tests also were not affected by time-of-year confounding.

Statistical analysis of the field test was conducted assuming the placement of the 50 traps per week was at random. The ANOVA procedure of PC SAS (SAS Institute, 1988) was implemented with the treatment effect partitioned into effect of the bait, the week the test was performed, and the interaction of bait with week. Analyses were conducted after transforming counts into percentages of total males, females, and males

plus females captured during the week. This was done to eliminate effect of population size, which decreased dramatically during the five-week experiment, on bait means. The decrease in the number of flies captured each week suggested that our traps were removing flies from a stagnant population so that weekly 'replications' were not independent. Therefore, F values required to establish significance were chosen based on a reduced degrees-of-freedom approach suggested by Box (1954) for cases where repeated measures are taken on the same subject, which in this case is the orchard. The F values were chosen using the most conservative (higher F values required for significant differences) assumptions about lack of independence from week to week. Consequently, the degrees-of-freedom for the five baits were reduced from 4 to 1, those for the bait \times week interaction were reduced from 16 to 4, and those for the experimental error were reduced from 299 to 45.

RESULTS AND DISCUSSION

Identification of Bacteria

Forty-seven bacterial isolates were cultured from wild *A. ludens* adults (Table 1). Thirty-six of the strains were gram negative rods while 11 were gram positive rods and cocci. The gram negative bacteria belonged to the family Enterobacteriaceae, according to the identification techniques utilized. Enteric bacteria isolated from *A. ludens* were similar to the bacteria isolated from other tephritids (Gow 1954, Fitt & O'Brien (1985), Lloyd et al. (1986).

The most prevalent bacterial species observed was *Citrobacter freundii*, which was isolated from the alimentary tract, chapote amarillo washings and citrus leaf imprints, followed by *Klebsiella pneumoniae* and *Erwinia herbicola*. Although the API 20E iden-

TABLE 1. BACTERIA ISOLATED FROM THE GUT AND ALIMENTARY TRACT OF MEXICAN FRUIT FLY, CITRUS LEAF IMPRINTS AND CHAPOTE AMARILLO FRUIT.

Bacteria	No. of Isolates	Source
<i>Citrobacter freundii</i>	9	crop, alimentary tract ¹ chapote amarillo, leaf material
<i>Klebsiella pneumoniae</i>	5	alimentary tract ¹
<i>Erwinia herbicola</i> ²	5	leaf material
<i>Proteus vulgaris</i>	4	crop, alimentary tract ¹
<i>Pseudomonas maltophilia</i>	3	leaf material
<i>Klebsiella oxytoca</i>	2	crop, alimentary tract ¹
<i>Pseudomonas aeruginosa</i>	2	crop
<i>Serratia marcescens</i>	1	crop
<i>Enterobacter sp.</i>	1	crop
<i>Pseudomonas sp.</i>	1	crop
<i>Serratia liquefaciens</i>	1	crop
<i>Acinetobacter calcoaceticus</i> <i>var anitratus</i>	2	crop, alimentary tract ¹
Gram positive bacteria	11	leaf washes and imprints crop, alimentary tract ¹

¹Alimentary tract other than crop.

²Isolates are from leaf material, most probably identification is *E. herbicola* which is identified as *E. agglomerans* in the API 20E identification system.

tified *E. herbicola* as *Enterobacter agglomerans*, it came from plant material and the most likely identification is *E. herbicola*. According to Bergey's Manual of Systematic Bacteriology (10th ed.), *E. agglomerans* and *E. herbicola* are synonymous. However, Ewing & Fife (1972) proposed that clinical sources should be designated as *E. agglomerans* because the characteristics of the organisms conform with the genus *Enterobacter*. Additionally, the API 20E profile index indicates that *Erwinia* should be strongly suspected if the organism was isolated from plant material.

Attractancy Bioassays in the Laboratory

Table 2 lists all the bacterial cultures used in this study. All bacteria strains were significantly more attractive to *A. ludens* adults than the tryptic soy broth control. The least attractive strain was *K. oxytoca* (ATCC # 43075) ($t = 14.3$; $df = 26$; $P < 0.001$ for whole beer, autoclaved and filtered supernatant combined). It is apparent that bacteria do not have to be isolated from fruit flies to be attractive to *A. ludens*. These are very important findings since they suggest that attraction of fruit flies to bacteria may be a nearly ubiquitous phenomenon, at least when bacteria are cultured on tryptic soy broth.

Overall, autoclaved supernatants were significantly more attractive than the filtered supernatants or whole beer ($K=100$; $P < 0.05$) according to Waller-Duncan K ratio t

TABLE 2. BACTERIAL CULTURES USED IN ATTRACTANCY STUDIES WITH MEXICAN FRUIT FLY ADULTS.

<i>Bacterial Cultures</i>	
Code	American Type Culture Collection
17903	<i>Acinetobacter calcoaceticus</i>
43608	<i>Acinetobacter calcoaceticus</i>
8090	<i>Citrobacter freundii</i>
8454	<i>Citrobacter freundii</i>
29063	<i>Citrobacter freundii</i>
8724	<i>Klebsiella oxytoca</i>
43075	<i>Klebsiella oxytoca</i>
9591	<i>Klebsiella pneumoniae</i>
13883	<i>Klebsiella pneumoniae</i>
19181	<i>Proteus vulgaris</i>
21719	<i>Proteus vulgaris</i>
14885	<i>Pseudomonas aeruginosa</i>
14886	<i>Pseudomonas aeruginosa</i>
13283	<i>Pseudomonas sp.</i>
15165	<i>Pseudomonas sp.</i>
11367	<i>Serratia liquefaciens</i>
	Northern Regional Research Laboratory (USDA, ARS; Peoria, IL)
HD-1	<i>Bacillus thuringiensis</i> Subsp <i>kurstaki</i>
HD-3	<i>Bacillus thuringiensis</i> Subsp <i>finitimus</i>
	Robacker et al. (1991).
RGM-1	<i>Staphylococcus aureus</i>

test ($F = 6.6$; $df = 2, 114$; $P < 0.002$). The reason for the greater attractiveness of the autoclaved preparations to *A. ludens* is unknown but may be due to attractive artifacts formed during autoclaving. The data clearly demonstrate that the attractant volatiles produced by the bacteria remained in solution after the bacteria had been filtered or destroyed. The attractiveness of the three preparations was not significantly affected by the bacterial species (preparation by species interaction: $F = 0.8$; $df = 36, 114$; $P = 0.8$).

For 15 strains where washed cells were tested, their attractiveness to *A. ludens* was well below that of the tryptic soy broth control. The highest T/C ratio was $0.67 (\pm \text{S.E.} = 0.26)$ obtained for *C. freundii* (ATCC #29063). This strain was not significantly less attractive than tryptic soy broth. The lowest mean T/C ratio was $0.21 (\pm \text{S.E.} = 0.06)$ obtained for *K. pneumoniae* (ATCC #9591). In this case, the bacterial cells were significantly less attractive than tryptic soy broth ($t = 4.8$; $df = 2$; $P < 0.05$).

Table 3 ranks the bacteria according to their attractiveness to *A. ludens*. *K. pneumoniae* (ATCC #13883), *C. freundii* (ATCC #8090) and two strains of *Proteus vulgaris* (ATCC #19181 and #21719) were the most attractive bacteria ($K=100$; $P < 0.05$) according to Waller-Duncan k ratio t test ($F = 4.1$; $df = 18, 114$; $P < 0.0001$). *B. thuringiensis*, known for its effective control of lepidopteran, coleopteran and dipteran larvae, is not known to attract fruitflies. Nevertheless, the autoclaved supernatant of HD-3 (serovar *finitimus*) was very attractive to *A. ludens* adults when compared to most of the enterics tested (Table 3). The other *B. thuringiensis* culture, HD-1 (serovar *kurstaki*), was slightly less attractive but not significantly different than HD-3.

The relationship between the culturing medium and the bacteria that results in the attractiveness to *A. ludens* is unknown. However, sufficient information is available to infer that the attraction is caused by heat stable chemical(s), one or more of which appear to be amines (Robacker et al. 1993). Most likely, the bacteria produce these chemicals as by-products of the metabolism of nutrients in the medium.

TABLE 3. ATTRACTION OF MEXICAN FRUIT FLY ADULTS TO VARIOUS BACTERIAL ODOR PREPARATIONS.

ATCC#	Species	Beer ¹	Autoclaved ¹	Filtered ¹	Overall + S.E. ²
13883	<i>K. pneumoniae</i>	2.9	4.2	3.7	3.62 ± 0.27 a
8090	<i>C. freundii</i>	3.4	3.5	3.8	3.54 ± 0.26 ab
19181	<i>P. vulgaris</i>	3.8	3.5	3.3	3.53 ± 0.20 ab
21719	<i>P. vulgaris</i>	3.1	3.6	3.5	3.39 ± 0.21 abc
HD-3	<i>B. thuringiensis</i>	2.8	3.4	2.8	3.00 ± 0.19 bcd
14885	<i>P. aeruginosa</i>	2.6	3.3	3.0	2.93 ± 0.22 cd
8454	<i>C. freundii</i>	2.7	3.3	2.8	2.93 ± 0.16 cd
17903	<i>A. calcoaceticus</i>	2.9	3.3	2.4	2.89 ± 0.18 cd
15165	<i>Pseudomonas</i> sp.	2.9	3.1	2.6	2.87 ± 0.20 cd
29063	<i>C. freundii</i>	3.1	2.7	2.7	2.83 ± 0.17 cd
9591	<i>K. pneumoniae</i>	2.6	3.3	2.5	2.80 ± 0.16 d
11367	<i>S. liquefaciens</i>	2.9	2.7	2.7	2.76 ± 0.15 d
RGM-1	<i>S. aureus</i>	3.1	2.5	2.5	2.70 ± 0.15 de
14886	<i>P. aeruginosa</i>	2.6	2.6	2.5	2.58 ± 0.14 de
17903	<i>A. calcoaceticus</i>	2.4	3.0	2.3	2.55 ± 0.16 de
43608	<i>A. calcoaceticus</i>	2.3	3.2	2.0	2.51 ± 0.21 de
HD-1	<i>B. thuringiensis</i>	2.3	2.5	2.6	2.48 ± 0.15 de
13283	<i>Pseudomonas</i> sp.	2.2	2.7	2.3	2.43 ± 0.13 de
43075	<i>K. oxytoca</i>	2.4	2.4	1.8	2.17 ± 0.12 e

¹T/C ratios (n = 9) for beer, autoclaved and filtered bacterial preparations.

²Overall T/C ratios (n = 27) followed by the same letter are not significantly different ($K = 100$; $P = 0.05$) by Waller-Duncan k ratio t test (SAS Institute 1988).

Field Tests

The results of the field test were complicated by a large decrease in the number of flies captured from the first (2303 flies) to the last (95 flies) week of the experiment. As described in the methods, the effect of this change in population size was eliminated by transforming the actual counts of flies captured in traps into percentages of flies captured each week. Reduced degrees-of-freedom analysis of variance (Box 1954) of the resulting percentage data, performed because 'replications' over time were not independent, showed that bait efficacies changed along with the population size. This was demonstrated by large bait x week interactions for males ($F = 5.3$; $df = 4,5$; $P < 0.01$), females ($F = 2.8$; $df = 4,45$; $P < 0.05$), and males + females ($F = 5.1$; $df = 4,45$; $P < 0.01$). Examination of bait x week means revealed that the principal reason for the interactions was that Nulure® was the least attractive bait during the first two weeks when fly populations were highest and the most attractive bait during the last three weeks when populations were lowest. The reason for this change in Nulure® efficacy with changes in population size is not known.

Table 4 shows the percentages of flies captured by the five baits over the five-week experiment. Reduced degrees-of-freedom analysis of variance (Box 1954) indicated that significant bait effects occurred for males ($F = 9.4$; $df = 1,45$; $P < 0.01$), females ($F = 8.4$; $df = 1,45$; $P < 0.01$), and males + females ($F = 8.9$; $df = 1,45$; $P < 0.01$). Nulure® and Torula yeast caught significantly more males than any of the bacterial metabolites. However, metabolites produced by bacterial cultures #8090 and 13883 and Torula yeast caught the most females. Torula yeast, metabolites from #8090, and Nulure® caught the highest percentages of males + females. Consistent with results of laboratory bioassays presented in Table 3, RGM-1 was significantly less attractive than the metabolites from #8090 and #13883.

Over the course of the five-week experiment, all the baits except Torula yeast caught more females than males (Table 4; Female/Male ratio), a fact that is not apparent from the percentages discussed above. Metabolites from #13883 and #8090 caught nearly twice as many females as males. This suggests that volatile(s) produced by these bacteria may contain chemical(s) that are more specific for attracting females compared to volatile(s) from Torula yeast and Nulure®.

TABLE 4. PERCENTAGE CAPTURES OF MEXICAN FRUIT FLIES IN MCPHAIL TRAPS BAITED WITH METABOLITES FROM BACTERIAL FERMENTATION OR STANDARD PROTEINACEOUS LURES.¹

Bait	Males ²	Females ²	Males + Females ²	Ratio of Females to Males
RGM-1 (<i>S. aureus</i>)	10.4 b	10.9 c	10.7 c	1.3
3883 (<i>K. pneumoniae</i>)	13.8 b	21.9 ab	19.1 b	1.8
8090 (<i>C. freundii</i>)	18.1 b	25.9 a	23.1 ab	1.8
Nulure®	28.9 a	17.1 b	21.1 ab	1.3
Torula yeast	28.8 a	24.2 a	26.0 a	1.0

¹Means in a column followed by the same letter are not significantly different ($K=100$; $P = 0.05$) by Waller-Duncan k ratio t test (SAS Institute, 1988).

²Mean percentages of total males, females or males + females captured each week.

Our investigation follows the work of other researchers (Jang & Nishijima 1990, McCollum et al. 1992) in attempting to identify bacterial isolates as alternative attractants to those presently used for fruit fly trapping. Lures currently used in trapping *A. ludens* include Nulure® and Torula yeast-Borax pellets in bulky, fragile McPhail traps. Although these lures can be effective, there exists a need to locate and identify improved attractants to monitor *A. ludens* populations. We feel that chemical(s) produced by bacteria provide a potential source to develop an attractant that functions like proteinaceous baits, but which can be incorporated into slow-release dispensers for use in standard or modified sticky traps.

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ANALYSIS OF CARIBBEAN FRUIT FLY
(DIPTERA: TEPHRITIDAE) TRAPPING DATA, DADE COUNTY,
FLORIDA, 1987-1991

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ABSTRACT

Records of Caribbean fruit flies, *Anastrepha suspensa* (Loew), captured in McPhail traps were analyzed from 48 trapping locations in Dade County (Port of Miami and Homestead) from 1987-1991. Greatest numbers were trapped over all locations in May, June, and July 1987 and 1989-1991, and in November 1988. Thirteen species of Caribbean fruit fly host trees were represented among the 48 trap locations. Numbers of flies trapped weekly in all traps or just those in conspecific host trees were not linearly correlated with weekly mean temperatures or weekly precipitation. Weekly trap catches were not correlated among conspecific host tree sites or between the Port of Miami and Homestead areas.

Key Words: *Anastrepha suspensa*, populations, sampling, host.

RESUMEN

Se analizaron los registros de las trampas tipo "McPhail" de la mosca de la fruta del Caribe *Anastrepha suspensa* (Loew), en 48 sitios diferentes en el condado Dade (Puerto de Miami y Homestead) de 1987 a 1991. El aumento máximo en el número de moscas atrapadas ocurrió en todos los lugares en mayo, junio y julio de 1987 y 1989-1991, y en noviembre de 1988. Trece especies de árboles hospederos de la mosca de la fruta del caribe fueron representados en los 48 sitios donde se encontraron las trampas. El número de moscas atrapadas semanalmente en todas las trampas o en aquellas localizadas en hospederos de la misma especie, no estuvieron relacionadas linealmente con el promedio semanal de la temperatura y la precipitación. El promedio semanal de moscas atrapadas

no estuvo relacionado ni entre los sitios con árboles hospederos de la misma especie ni entre las áreas del Puerto de Miami y Homestead.

McPhail trapping with hydrolyzed torula yeast and borax bait pellets to detect exotic tephritids at ports of entry has been carried out by the Florida Department of Agriculture and Consumer Services since the 1970s in Dade County, Florida, (Anonymous 1989). From these trapping data, the numbers of Caribbean fruit fly [*Anastrepha suspensa* (Loew)] adults, an introduced and established quarantine pest, have been recorded.

The effects of temperature, precipitation, wind, humidity, and host availability on trapping of adults of several species of fruit flies (not Caribbean fruit fly) have been investigated outside of Florida. In general, catches of fruit flies increased with increasing host availability and the occurrence of temperature and rainfall favorable to host and fly development (Baker & Chan 1991, Drew & Hooper 1983, Harris & Lee 1986, Harris & Lee 1987, Jiron & Hedstrom 1991, Wong et al. 1985). Fehn (1982) found a negative correlation between rainfall and numbers of flies (*Anastrepha* spp.) captured in peach groves in Brazil but no correlation between numbers of flies captured and temperature, wind, or humidity. Herrera A. & Vinas V. (1977) determined that numbers of flies [*Anastrepha* spp. and *Ceratitis capitata* (Wiedemann)] captured were positively correlated with temperature but negatively correlated with humidity in mango groves in Peru. Inayatullah et al. (1991) determined a predictive model for density of *Bactrocera cucurbitae* Coquillett, in Pakistan based on a positive correlation between trap catches and temperature. Studies on species other than the Caribbean fruit fly which have associated high numbers of trapped adults with increased host availability include those of Fletcher (1974), Houston (1981), Harris & Olalquiaga (1991), and Vargas et al. (1983a, b). The effects of temperature and precipitation on trap catches of Caribbean fruit fly adults have not been reported.

Effects of host availability on Caribbean fruit fly trapping or larval density in Florida have been investigated. Burditt (1982) found no differences in numbers of flies trapped concurrently in loquat, guava, and tamarind trees and concluded that population fluctuations were probably synchronous in all areas of Dade County, irrespective of location of trap or availability of host. Mason & Baranowski (1989) speculated that high trap catches corresponded to suitable environmental factors, host availability, or mass synchronous adult eclosion in guava groves in Dade County. Von Windeguth et al. (1973) observed that high larval populations were maintained for most of the year in tropical almond, common guava, calamondin, and sapodilla. They also observed that loquat and Suriname cherry supported very high populations of larvae during their short fruiting seasons, and that movement of populations among hosts was imperceptible due to overlapping of fruiting seasons. Swanson & Baranowski (1972) determined monthly larval density for 6 hosts of the Caribbean fruit fly in Dade County and observed that loquat, rose apple, and Suriname cherry were among the few fruits available during winter and early spring which supported high populations during that period leading to an annual adult peak in late spring. In comparing citrus-growing areas with tropical fruit-growing areas in Indian River County, Nguyen et al. (1992) found that Caribbean fruit flies reproduced in different hosts as they became available over the year but did not heavily colonize citrus groves because citrus was not a preferred host. They captured greatest numbers of flies in McPhail traps during summer months in their 4 year study.

The objectives of the present research were to determine, through McPhail trap sampling, the time of year when the Caribbean fruit fly was captured in greatest numbers in Dade County, Florida, and any correlations between (1) trap catches and temperature

and rainfall, (2) catches among traps in conspecific host trees in different areas, and (3) between traps from mixed hosts in 2 widely separated areas, Miami and Homestead.

MATERIALS AND METHODS

During 1987-1991, McPhail traps at 50 trapping locations, 25 in each of the Port of Miami and Homestead areas, were monitored by Florida Department of Agriculture and Consumer Services personnel. All but 2 traps were maintained in their original positions during the 5-year period. Data from the 2 traps which were moved were excluded, leaving 48 traps (24 in each area) for analysis. There were 252 weekly sampling dates between January 1987 and December 1991.

Traps in the Port of Miami (PM) were all located within 0.2 km of either Biscayne Bay or the Atlantic Ocean (Fig. 1). Four traps were located in Miami Beach, 6 in Miami, 4 on Dodge Island, 2 each on Watson and Palm Islands, and 1 each on Belle Isle, San Marco, Dilido, Rivo Alto, Hibiscus, and Star Islands. One trap was located in each tree. Host tree species names and numbers of each were: *Citrus paradisi* MacF., grapefruit (5); *Coccoloba diversifolia* Jacq., pigeon plum (1); *Coccoloba wifera* (L.) L., sea grape (8); *Eriobotrya japonica* (Thunb.) Lindl., loquat (1); *Mangifera indica* L., mango (3); *Manilkara zapota* van Royen, sapodilla (2); *Psidium guajava* L., common guava (2); *Syzygium jambos* Alston, rose apple (1); and *Tamarindus indica* L., tamarind (1). All of the above plants, excepting tamarind and pigeon plum, are hosts of the Caribbean fruit fly (Norrbom & Kim 1988). Distances between traps ranged from 0.1 km to 6.0 km. The area was highly urbanized, with numerous dooryard hosts near trap sites, far from agricultural areas and forests containing feral common guava, and located at a major seaport for agricultural produce.

Traps in the Homestead Air Force Base (HAFB) area were all located about 36 km SW of the PM traps and 4-9 km inland from Biscayne Bay (Fig. 1). Sixteen traps were located on HAFB and 8 to the NE in adjacent Leisure City and Princeton. Host tree species names and numbers of each were: *Callistemon* sp., bottlebrush (1); *Citrus aurantium* L., sour orange (1); sea grape (4); *Dovyalis hebecarpa* Warb., Ceylon gooseberry (1); loquat (7); *Ficus* sp., fig (1); mango (3); sapodilla (1); *Persea americana* Mill., avocado (1); *Pouteria campechiana* Baehni, egg fruit (1); rose apple (1); *Terminalia catappa* L., tropical almond (1); and X *Citrofortunella mitis* Ingram & Moore, calamondin (1). All plants, except for bottlebrush and probably fig (species unidentified) are hosts of Caribbean fruit fly (Norrbom & Kim 1988). The distance between traps ranged from 0.2 km to 6.0 km. The area was rural, with relatively low density of dooryard hosts (compared with PM), and located near agricultural areas and forests containing feral common guava.

Elevations (0-5 m), soils (mostly loamy on level terrain, well-drained, shallow, over Miami oolite), temperatures, and rainfall were considered to be very similar at all trapping sites. Monthly rainfall and maximum and minimum temperatures for the eastern Dade County region were averaged (Fig. 2) from 6 National Oceanic and Atmospheric Administrations (National Climatic Data Center 1987-1991) weather stations (Miami Beach, Hialeah, Miami International Airport, Royal Palm Ranger Station, University of Florida TREC [Homestead Airport after May 1990], and USDA Miami [Perrine after May 1989]).

Fruiting periods of the 13 species of host trees in which traps were located were delineated by Morton (1987) and confirmed by personal observation in the field (Fig. 3).

Trapping data were transformed to $(x + 0.5)^{1/2}$ and analyzed by PROC CORR (Pearson correlation) and PROC GLM (ANOVA, LSD) programs for personal computer (SAS Institute 1990).

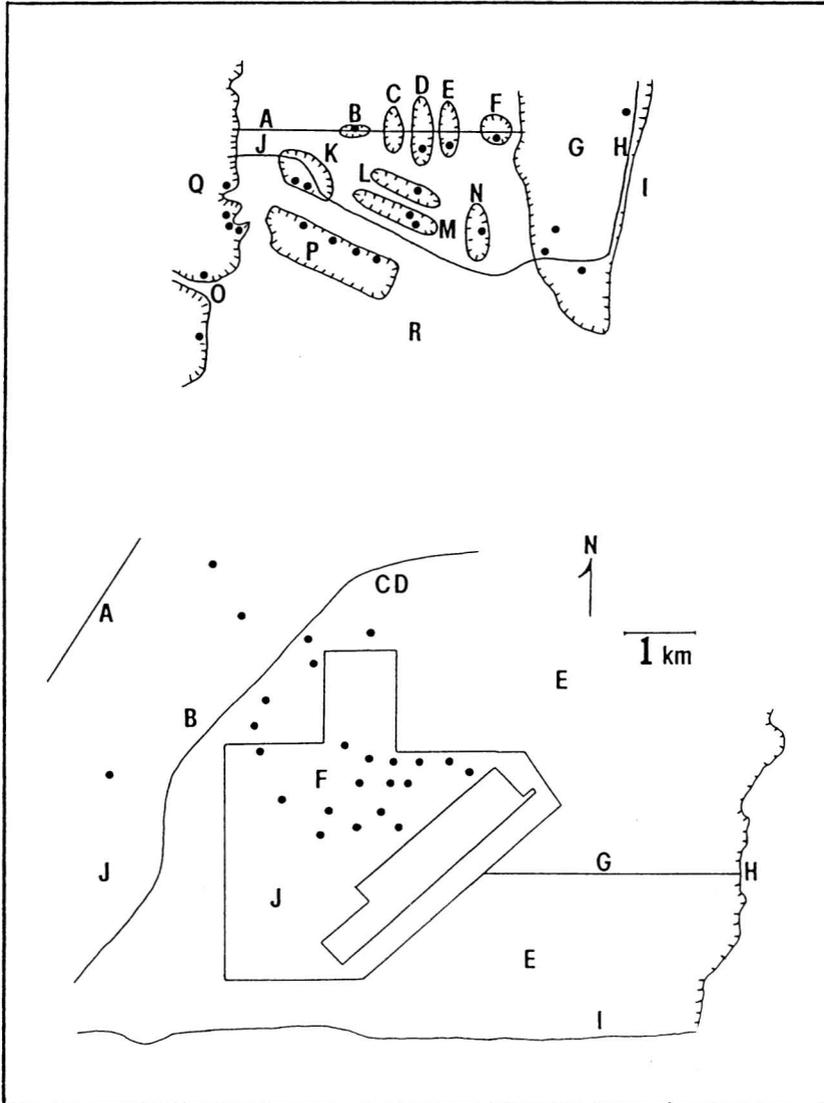


Fig. 1. Map of McPhail trap sampling locations, Dade County Florida, 1987-1991, black circles are trap locations. Upper map is Port of Miami: A, Venetian Causeway; B - F, San Marco, San Marino, Dilido, Rivo Alto, Belle Isle Islands; G, Miami Beach; H, route A1A; I, Atlantic Ocean; J, MacArthur Causeway; K - N, Watson, Hibiscus, Palm, Star Islands; O, Miami River; P, Dodge Island, Port of Miami; Q, Miami; R, Biscayne Bay. Lower map is Homestead Air Force Base: A, route US1; B, Leisure City; C, Florida Turnpike; D, Princeton; E, agricultural and forest area; F, Homestead Air Force Base; G, Military Canal; H, Biscayne Bay; I, Mowry Canal; J, residential area. Scale applies to both maps.

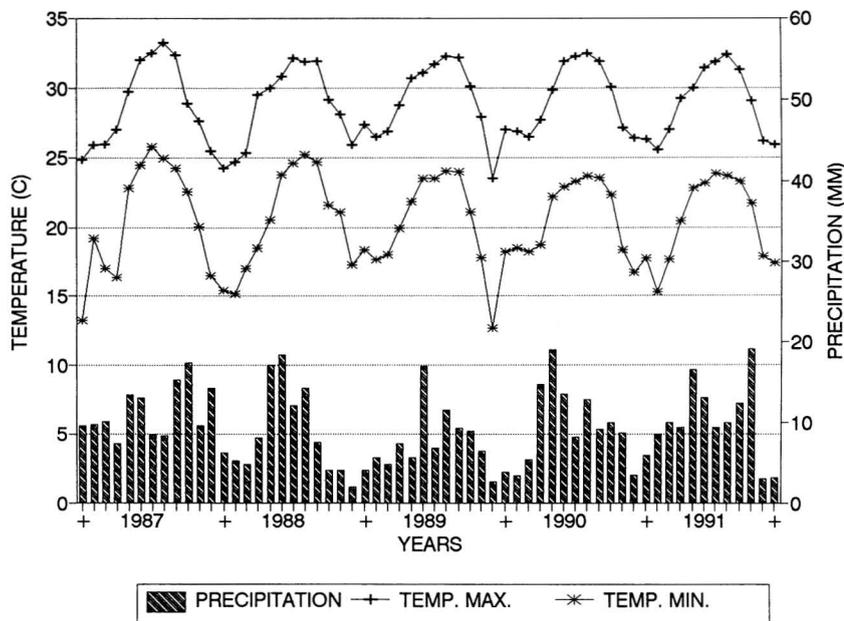


Fig. 2. Monthly average maximum and minimum temperatures and precipitation for eastern Dade County, Florida, 1987-1991.

RESULTS AND DISCUSSION

Analysis of Fig. 3 indicated that 6-9 of the 13 host species were fruiting in each month in the trapping areas. Fruiting periods for the various hosts overlapped and oviposition and development sites were available year-round in various fruits. Individual trees probably varied from year to year in the amount of fruit produced depending on available water, fertilization, pesticide applications, and other management practices, which were not documented.

Monthly average temperatures ranged from 13 °C to 33 °C over the 5 years (Fig. 2). Temperatures dipped below freezing for 2 nights during week 52 of 1989, but flies were trapped the week after the freeze (Fig. 4). Sixty-eight percent of the flies captured that week were located in a trap in a tropical almond tree at HAFB. Flies were also trapped that week in grapefruit, guava, loquat, and rose apple trees.

The mean number (\pm SEM) of Caribbean fruit flies captured per week and per trap over 5 years in each species of tree was: tropical almond (13.1 ± 4.4); calamondin (10.0 ± 2.0); grapefruit (8.0 ± 0.9), rose apple (7.0 ± 1.5); guava (6.6 ± 0.9); loquat (4.7 ± 0.8); egg fruit (3.2 ± 0.7); mango (1.9 ± 0.3); and sea grape (0.9 ± 0.2). Fewer than 0.9 flies per week per trap were caught in avocado, Ceylon gooseberry, pigeon plum, sapodilla, sour orange, and tamarind.

Weekly trap catches (Fig. 4) appeared to mirror temperature fluctuations (Fig. 2). Four of the 5 highest weekly trap catches were in May, June, or July (Fig. 4) except for 1988 when the greatest number of flies was captured in November. Weeks each year in which greatest mean numbers ($\alpha = 0.05$, LSD) of flies per trap were caught over all

HOST	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
AVOCADO	+	+				+	+	+	+	+	+	+
CALAMONDIN	+	+	+	+	+	+	+	+	+	+	+	+
CEYLON GOOSEBERRY			+	+	+				+	+	+	
EGGFRUIT	+	+	+								+	+
GRAPEFRUIT	+	+	+	+	+				+	+	+	+
GUAVA	+	+			+	+	+	+	+			
LOQUAT		+	+	+								
MANGO					+	+	+	+				
ROSE APPLE					+	+	+					
SAPODILLA					+	+	+	+	+			
SEA GRAPE	+	+	+	+	+	+	+	+	+	+	+	+
SOUR ORANGE	+	+	+	+	+	+						+
TROPICAL ALMOND									+	+	+	+

HOST PRESENT 

Fig. 3. Fruiting phenologies of the 13 hosts of the Caribbean fruit fly in which McPhail traps were placed in Dade County, Florida, 1987-91.

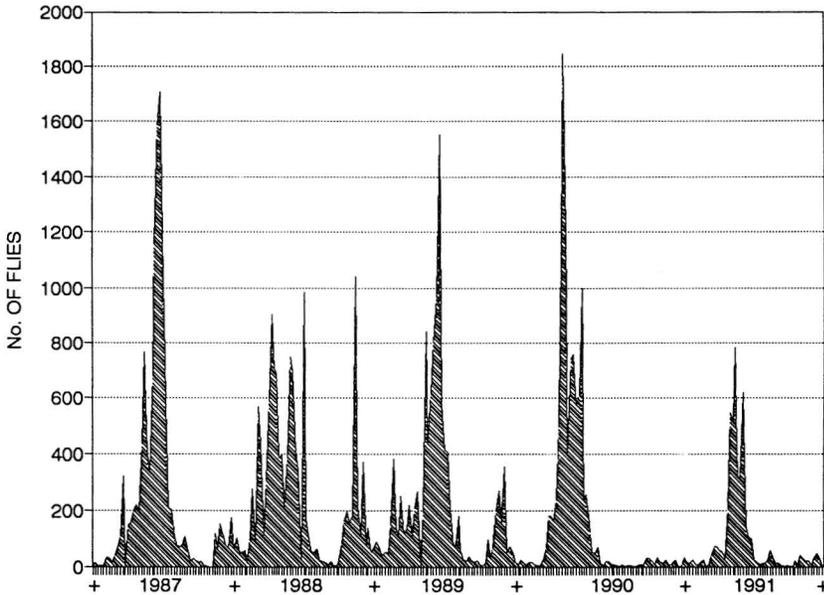


Fig. 4. Weekly Caribbean fruit fly adult captures in McPhail traps (each week represents a total of 48 traps), Dade County, Florida, 1987-1991.

locations were: 1987, week 26 (34 per trap); 1988, week 46 (21 per trap); 1989, week 25 (32 per trap); 1990, week 18 (38 per trap); 1991, week 20 (16 per trap). Smaller peaks in the winters of 1987 and 1989 reflected captures in the tropical almond trap.

Weekly fly catches from all traps together and mean temperatures for the same weeks were correlated significantly ($\alpha = 0.05$) in 1987, 1989, and 1991, but the correlations were not linear in those years, given the extremely small correlation coefficients (1987, $P = 0.0001$, $r = 0.01$; 1989, $P = 0.004$, $r = 0.003$; 1991, $P = 0.0003$, $r = 0.005$). In 1988 and 1990, correlations were not significant (1988, $P = 0.33$; 1990, $P = 0.06$). These results agreed with findings of Fehn (1982) who found no correlation between temperature and trap catches (*Anastrepha* spp.) in Brazil but were in contrast to the findings of Herrera A. & Vinas V. (1977), who found a positive correlation between temperature and trap catches (*Anastrepha* spp.) in Peru.

Rainfall was generally heaviest in summer or early fall months during all years (Fig. 2). While the correlations between weekly fly catches from all traps together and total rainfall from the same weeks were significant ($\alpha = 0.05$) in 1989 and 1990, they were not linear in those years (1989, $P = 0.0001$, $r = 0.008$; 1990, $P = 0.003$, $r = 0.001$). Correlations between fly catches and rainfall were not significant for the other 3 years (1987, $P = 0.66$; 1988, $P = 0.06$; 1991, $P = 0.15$). Analyses were also run for weekly fly catches and rainfall from 1, 2, and 3 weeks prior to trapping weeks to determine if there was a lagged response of fly activity to precipitation, but correlations were not higher.

Correlations of weekly fly catches from all traps together with rain and temperature together were significant ($\alpha = 0.05$) for 1987, 1989, 1990, and 1991, but were not linear for those years (1987, $P = 0.0001$, $r = 0.01$; 1989, $P = 0.0001$, $r = 0.008$; 1990, $P = 0.01$, $r = 0.004$; 1991, $P = 0.0001$, $r = 0.008$). The factors were not significantly correlated in 1988.

In general, catches in traps within each host tree species did not have a high linear correlation with rainfall and temperature. The best linear correlation of a host with rainfall and temperature together was common guava ($P = 0.0001$, $r = 0.32$). As has been suggested by Harris & Lee (1986, 1987) for other tropical fruit flies, weather probably affected the fruiting period and yields of hosts more than it affected fly trap catches. The present results support Fehn's (1982) conclusion that environmental factors and availability of hosts interact to affect trapping frequency.

Weekly mean (\pm SEM) numbers of flies per trap, over all locations and weeks, were 4.7 ± 0.5 (1987), 4.6 ± 0.6 (1988), 4.3 ± 0.4 (1989), 3.9 ± 0.7 (1990), and 1.8 ± 0.2 (1991). More flies were trapped weekly per trap in 1988 than in other years ($P = 0.05$, LSD) and the fewest were trapped in 1991. Significant ($P < 0.05$) correlation coefficients between weekly mean captures over all locations and years ranged from 0.34 to 0.83. The catch patterns of 1990 and 1991 were highly correlated ($P = 0.0001$, $r = 0.83$), which may be confirmed by visual comparison of the trapping curves for both years (Fig. 4).

A mean (\pm SEM) of 3.6 ± 0.5 flies were taken weekly per trap in the PM and 4.1 ± 0.5 flies were taken in the HAFB over the 5 years. The difference between the means was not significant ($P > 0.05$). PM and HAFB weekly trap catch means were not significantly correlated ($P > 0.05$) for any year. Visual comparison of weekly fly catches in the PM (Fig. 5) and the HAFB (Fig. 6) confirms the disparity between catch patterns in the 2 areas.

Numbers of flies trapped weekly were compared among hosts of the same species in each year. Only 2 (from among 450 possible trap pairs) of the sea grape trap catches were highly linearly correlated ($r = 0.85$, $P = 0.01$). There were no correlations ($P > 0.05$) between trap catches for any 2 mango, rose apple, guava, loquat, sapodilla, grapefruit, or sour orange trees within any year. Thus, a high trap catch in a tree did not

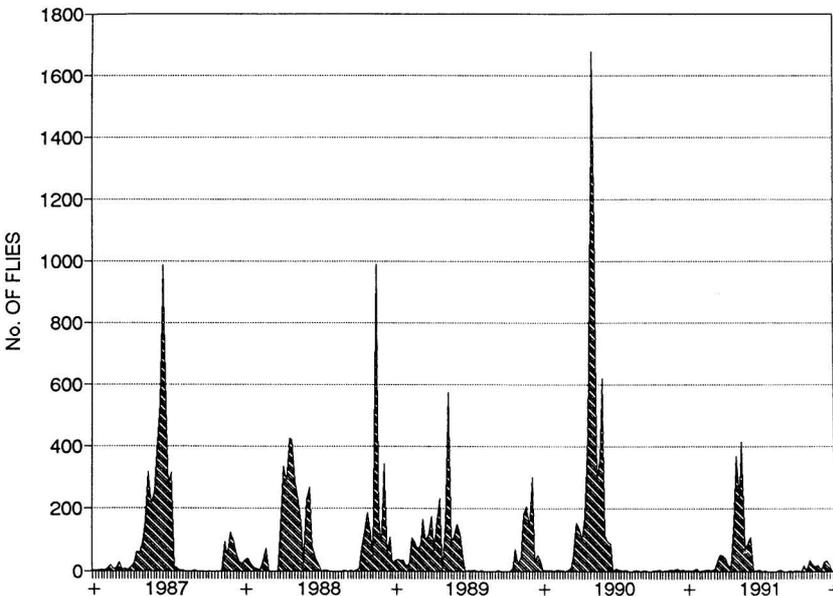


Fig. 5. Weekly Caribbean fruit fly adult captures in McPhail traps (each week represents a total of 24 traps), Port of Miami, Dade County, Florida, 1987-1991.

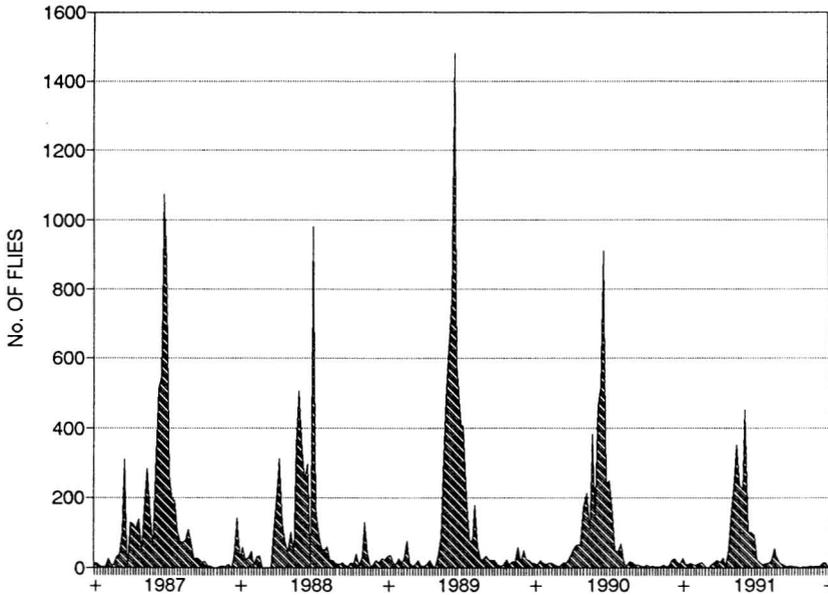


Fig. 6. Weekly Caribbean fruit fly adult captures in McPhail traps (each week represents a total of 24 traps), Homestead Air Force Base, Dade County, Florida, 1987-1991.

allow a prediction that there would be a high trap catch in another tree of the same species during the same sampling period. Individual trap catches were, therefore, essentially independent of each other in this trapping scheme. These results conflict with those of Burditt (1982) who concluded that Caribbean fruit fly activity was synchronous over an area irrespective of host in which traps were placed.

ENDNOTE

I thank R. Pantaleon (Agricultural Research Service, Miami) for tabulating the data and preparing the Spanish abstract, and D. Chalot (Florida Department of Agriculture and Consumer Services, Miami) for providing the trapping records. Mention of a proprietary product does not constitute endorsement by the USDA.

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NEW SPECIES AND RECORDS OF PREDACEOUS MIDGES OF
THE GENUS *PROBEZZIA* FROM FLORIDA AND ALABAMA
(DIPTERA: CERATOPOGONIDAE)

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ABSTRACT

Three new species of *Probezzia* Kieffer are described from one locality, Florida Caverns State Park in Jackson County, Florida: *fairchildi* New Species, *meadi* New Species, and *weemsi* New Species. A fourth species, *glicki* New Species, is described from two localities in Alabama. Florida distribution records are presented for five additional previously described species. The midges from Blackshear, Georgia, previously reported as *Probezzia nigra* Wirth, were misidentified, and are now reported as *Macropeza blantoni* Wirth and Ratanaworabhan (New Georgia State Record). A new key is provided to the 23 known North American species of *Probezzia*, as well as diagrammatic illustrations of the color patterns of femora and tibiae of females.

Key Words: Predaceous midges, *Probezzia*, Ceratopogonidae.

RESUMEN

Se describen tres especies nuevas de *Probezzia* Keiffer de una localidad, el Parque Estatal Cavernas Floridaanas en el condado de Jackson, Florida: *fairchildi* Especie Nueva, *meadi*, Expecie Nueva, y *weemsi* Especie Nueva. Una cuarta especie, *glicki* Especie Nueva, se describe de dos localidades en Alabama. Registros de distribución para la Florida se presentan para cinco especies previamente descritas. Las mosquitas de Blackshear, Georgia, previamente reportadas como *Probezzia nigra* Wirth, fueron el identificadas erroneamente, y ahora se reportan como *Macropeza blantoni* Wirth y Ratanaworabhan (Nuevo Registro para Georgia). Se presenta una nueva clave para las 23 especies norteamericanas conocidas de *Probezzia*, ademas unas ilustraciones de las configuraciones de colores de los femures y las tibias de las hembras.

The large, conspicuously marked, predaceous midges of the genus *Probezzia* Kieffer are common and characteristic inhabitants of the psammolittoral zone of the lakes and larger streams of the northern United States, southern Canada, and Eurasia. They have not been found south of northern Florida, Texas, and northern California. Williams (1955) and Wirth (1971) reported on the habits of the larvae and pupae. Mature larvae migrate from their shallow water habitat up the stems and leaves of cat-tails and other emergent plants where pupation occurs within a few inches of the water surface. Pupae secure themselves to the plants by means of secretory adhesive discs on some of the abdominal sternites. When disturbed, the pupae are able to move forward by wriggling movements and, using these discs, as well as the strong segmental spines on the abdomen, secure themselves.

Downes (1978) reported in detail the feeding habits of *Probezzia* females. The females are predaceous on small, soft-bodied insects (wing length 2-7 mm) such as mayflies and chironomid midges. Most remarkably, females of *Probezzia* will feed on the males of

their own species while mating is in progress, piercing the body wall and sucking the haemolymph. The shrivelled body of the male drops off later on, but the genitalia often remain attached to the female abdomen.

After two taxonomic revisions by Wirth (1951, 1971) the systematics of the North American *Probezzia* species is fairly satisfactory. An exception to this became apparent, however, when I made large collections of *Probezzia* adults at the Florida Caverns State Park in Jackson County, Florida, in 1970, 1973, and 1981. I collected two described species, *P. albitibia* Wirth and *P. smithii* (Coquillett), as well as three additional species which I am here describing as new. In addition I am describing a fourth species collected by Jayson Glick in Alabama, that may also occur in northern Florida. The midges from Blackshear, Georgia, reported by Wirth (1971) as *Probezzia nigra* Wirth, were misidentified, and are in fact *Macropeza blantoni* Wirth and Ratanaworabhan (1972a), previously known only from Florida (New Georgia State Record). See discussion under *Probezzia fairchildi* n. sp.

The genus *Probezzia* has been adequately diagnosed in the revision by Wirth (1971), to which the reader is referred for a full discussion of taxonomic characters and a summary of biological information. Downes & Wirth (1981) gave a more up-to-date discussion of taxonomic characters in the family Ceratopogonidae. In *Probezzia*, structural characters have not proved very useful except in a few exceptional species, and as previously, I rely heavily on features of coloration, especially of wings, halteres, legs, antennae, and abdominal tergites. Structure of the male genitalia is remarkably uniform among species and has not been used taxonomically, contrary to practice in the study of most other ceratopogonid genera.

The types of the new species here described are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C.

KEY TO NORTH AMERICAN SPECIES OF *PROBEZZIA*

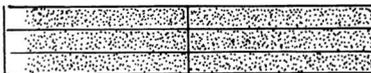
(See Figs. 1, 2)

1. Wing entirely pale, veins and membrane whitish 2
- Wing entirely infuscated or whitish with broad dark band, veins in infuscated portion darkened (if faint, infuscation may be seen more clearly by viewing the wing from the base or apex at a slight angle) 12
2. Scutum entirely yellow or pale brown, or yellow on anterior half 3
- Scutum entirely shining black or dark brown 4
3. Scutum entirely yellow or pale brown; legs entirely yellow to pale brown (northeastern N. Amer.) *pallida* Malloch (female)
- Scutum yellow on anterior half, shining black posteriorly; legs with distal halves of all femora and broad median ring and narrow apex of hind tibia brown (New York) *unica* (Johannsen)
- 4(2). Halter knob dark; tibiae and at least distal halves of femora black 5
- Halter knob pale; usually not more than distal third of all femora black; abdomen entirely yellowish white 6
5. Abdomen entirely dark; trochanters and bases of femora dark; scutum and scutellum dark brown with very fine short setae (Michigan) *atriventris* Wirth
- Abdomen pale, segments 8-9 dark; trochanters pale, femora usually pale on proximal fourth to half; scutum black with long, stouter setae (eastern N. Amer.) *albiventris* (Loew)
- 6(4). Legs entirely pale except for black 5th tarsomeres (northeastern N. Amer.) *pallida* Malloch (males)
- Legs with black markings on femora and tibiae 7
7. Hind tibia extensively dark-banded; fore tibia various 8

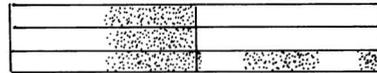
- Hind tibia yellow except extreme narrow base and apex black; fore femur usually dark on distal third to half (northeastern N. Amer.). *xanthogaster* (Kieffer)
8. Hind tibia with broad sub-basal band and narrow apex black; fore tibia various 9
- Hind tibia black on distal 2/3; fore tibia pale except narrow base and apex black (Florida) *weemsi* new species
9. Fore femur dark on distal third to half 10
- Fore femur dark only on extreme apex 11
10. Fore and mid tibiae without dark sub-basal bands (northeastern N. Amer.) *sabroskyi* Wirth
- Fore and mid tibiae with bases extensively infuscated (northeastern N. Amer.) *jamnbacki* Wirth
- 11(9). Fore and mid tibiae with sub-basal dark bands (northeastern N. Amer.) *williamsi* Wirth
- Fore and mid tibiae dark only on extreme bases and apices (Europe, northwestern N. Amer.) *seminigra* (Panzer)
- 12(1). Wing entirely dark, or pale only at extreme base 13
- Wing with at least proximal fourth pale 17
13. Femora and tibiae entirely dark (southeastern U.S.) 14
- Femora dark at most only on distal third; tibiae dark with broad subapical pale band (northeastern N. Amer.; USSR) *fuscipennis* Wirth
14. Large species, wing length 2.66 mm; wing lightly infuscated; abdomen pale, segments 8-9 dark brown; antenna extremely elongated, antennal ratio 0.52; segment 11, 216 microns long; claws short, stout, and evenly curved (Florida) *fairchildi* new species
- Smaller species, wing length 1.7-2.3 mm; wing deeply infuscated; abdominal coloration various; antenna shorter, antennal ratio 1.4-1.5; segment 11, 125-147 microns long; claws slender, straighter 15
15. Antenna short, antennal ratio 1.55; segment 11, 125 microns long, segments 3-15 brownish; abdomen entirely brownish; wing length 1.7 mm (Florida) *meadi* new species
- Antenna long and slender, antennal ratio 1.36; segment 11, 147 microns long, segments 3-10 pale, 11-15 dark; wing length 2.3 mm; abdominal coloration various 16
16. Wing slightly infuscated; halter dark; abdominal tergites 4-5, 8-9 dark (Louisiana) *ludoviciana* Wirth
- Wing deeply infuscated; halter pale; abdominal tergites all dark (southeastern U.S.) *nigra* Wirth
- 17(12). Wing with dark band covering middle third of wing and centered just distad of r-m crossvein, distal portion of wing pale; broad apices of femora and broad sub-basal band on hind tibia dark; halter knob pale 18
- Wing with at least distal two-thirds dark; leg markings and halter color various 19
18. Fore and mid tibiae pale except bases and apices in female, entirely dark in male (northeastern N. Amer.) *albitibia* Wirth
- Fore and mid tibiae with basal third to half dark in female (male unknown) (Louisiana) *rosewalli* Wirth
- 19(17). Halter knob dark; tibiae and distal third to half of femora black (northeastern N. Amer.) *infuscata* Malloch
- Halter knob pale 20
20. Tibiae entirely and femora except extreme bases black (eastern N. Amer.) *smithii* (Coquillett)

- Fore and mid tibiae with only extreme apices dark; femora with extensive pale markings 21
- 21. Hind tibia pale except at extreme apex (Florida, Alabama) . *glicki* new species
- Hind tibia with broad sub-basal dark band 22
- 22. Femora extensively black, at least on mid and hind legs 23
- Femora almost entirely pale, only narrow knee spots dark (western N. Amer.)
..... *flavonigra* (Coquillett)
- 23. Femora black nearly to base of fore leg and on distal half to third on mid and
hind legs (Texas) *bottimeri* Wirth
- Femora black on narrow apex of fore leg and on distal fourth on mid and hind
legs (Europe; western N. Amer.) *concinna* (Meigen)

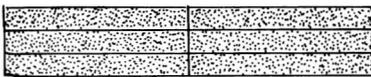
SECTION A



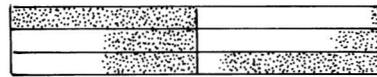
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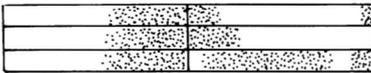
UNICA



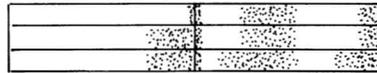
ATRIVENTRIS



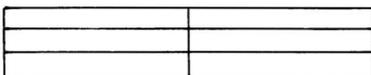
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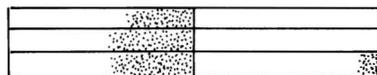
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WILLIAMSII

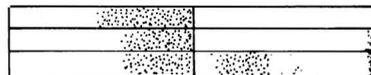


PALLIDA

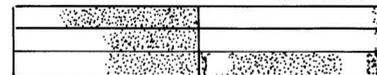


XANTHOGASTER

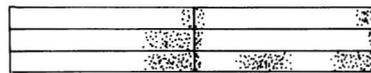
SECTION B



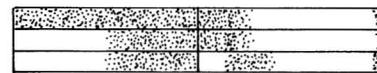
SABROSKYI



ALBITIBIA



SEMINIGRA



ROSEWALLI

Fig. 1. Diagram of pale and dark markings of femora (left) and tibiae (right) of (top to bottom) fore, mid, and hind legs of species of *Probezzia* (Section A, species with wing entirely whitish; Section B, species with dark band over midportion of wing).

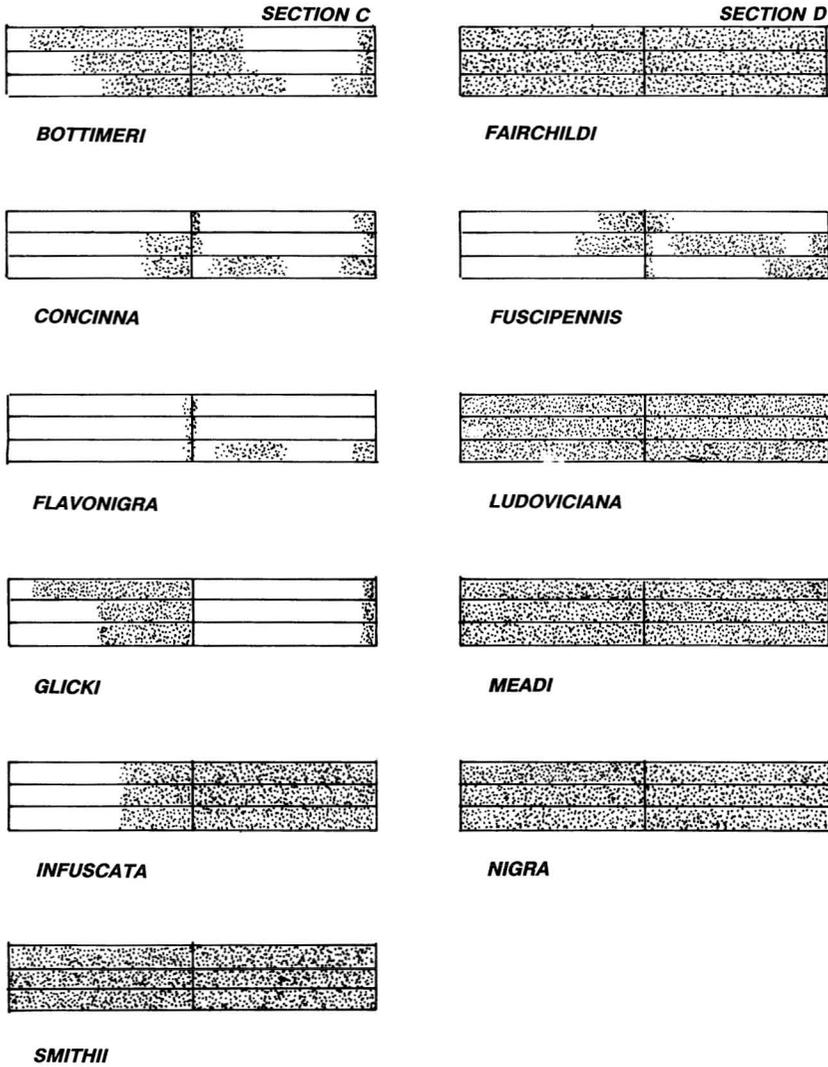


Fig. 2. Diagram of pale and dark markings of femora (left) and tibiae (right) of (top to bottom) fore, mid, and hind legs of species of *Probezzia* (Section C, species with wing infuscated on distal one-half to three-fourths; Section D, species with wing entirely infuscated).

Probezzia albitibia Wirth

Probezzia albitibia Wirth, 1971: 732 (male, female; Virginia, Wisconsin to Quebec, south to Virginia); Wirth & Grogan, 1979: 884 (male, female, pupa; Potomac River Valley records).

DIAGNOSTIC CHARACTERS OF FEMALE. Wing length about 2.7 mm. Antenna with segments 3-10 whitish, 11-15 dark brown. Thorax dark brown. Legs yellowish; fore

femur dark brown except at extreme base; distal 1/2 of mid femur and distal 1/3 of hind femur dark brown; fore and mid tibiae with faint basal and apical brown bands; hind tibia dark brown with pale brown sub-basal and subapical bands (these often entirely absent). Wing whitish including veins; a prominent transverse band across mid portion of wing, 1/4 as wide as wing is long, the veins in this area dark brown. Halter pale. Abdomen pale, tergites 3-5 dark brown.

DISTRIBUTION. Eastern North America, Wisconsin to Quebec, south to Alabama and Florida.

FLORIDA RECORDS. **Florida**, Jackson Co., Florida Caverns State Park, 4.v.1970, W. W. Wirth, light trap, 6 females; same, 26.v.1973, 7 females.

NOTES. The type series of *Probezzia albitibia* was mixed. Females from Maryland, Michigan, New York, and West Virginia resemble the holotype from Dead Run, Fairfax Co., Virginia, in having two pale bands on the hind tibia. Females from Falls Church, and Scott Run, Potomac River, Fairfax Co., Virginia, and the series recorded above from Jackson Co., Florida, differ in having the hind tibia entirely dark. No other differences could be found and it is unknown whether this difference represents variation in one species or whether a second species is involved. The males are sexually dimorphic in having all the tibiae dark; in all other *Probezzia* leg color is virtually the same in males and females (Wirth & Grogan 1979: 886).

Probezzia albiventris (Loew)

Ceratopogon albiventris Loew, 1861: 311 (Cent. I, no. 7) (female; Georgia).

Probezzia albiventris (Loew); Malloch, 1914: 138 (combination); Wirth, 1951: 28 (diagnosis; distribution); Wirth, 1971: 733 (taxonomic notes; distribution); Wilkening et al., 1985: 528 (Santa Rosa, Florida record).

DIAGNOSTIC CHARACTERS OF FEMALE. A large black and pale yellow species, wing length 2.7 mm. Antenna brown, segments 3-10 pale, 11-15 brown. Palpus brown. Legs dark brown; trochanters, bases of femora variably, and tarsomeres 1-3 pale; tarsomeres 4-5 black; female claws short and curved, 110 microns long. Wing entirely whitish hyaline including veins. Halter dark. Abdomen pale, segments 8 and 9 dark brown.

DISTRIBUTION. Eastern North America, Wisconsin to New Brunswick, south to Texas and Florida.

FLORIDA RECORDS. **Florida**: Santa Rosa Co., Jay v.1962, T. W. Boyd, light trap, 3 females.

Probezzia sabroskyi Wirth

Probezzia sabroskyi Wirth, 1951: 31 (male, female; Michigan; fig. male genitalia); Wirth, 1971: 736 (Distribution; correction of Wirth 1951 misdeterminations); Wilkening et al., 1985 (Santa Rosa Co., Florida record).

DIAGNOSTIC CHARACTERS OF FEMALE. Wing length about 2.7 mm. Antenna brown, segments 3-10 whitish. Thorax dark brown. Legs pale yellow; distal 1/3 of all femora, a sub-basal band at 1/3 length of hind tibia, and narrow apex of hind tibia dark brown. Wing milky white including veins. Halter pale. Abdomen yellowish white (tergites 3-5 dark in Florida specimens).

FLORIDA RECORDS. **Florida**: Santa Rosa Co., Blackwater River, Florida A. & M. Biological Station, 23.v.1973, W. W. Wirth, light trap, 1 female.

Probezzia smithii (Coquillett)

Ceratopogon smithii Coquillett, 1901: 600 (female; New Jersey).

Probezzia smithii (Coquillett); Malloch, 1914: 138 (combination); Wirth, 1951: 29 (diag-

nosis; distribution); Wirth, 1971: 737 (distribution; taxonomic notes); Wirth & Grogan, 1979: 888 (male, female, pupa; Potomac River Valley records); Wilkening et al., 1985: 529 (records from Jackson, Leon, Santa Rosa Counties, Florida).

DIAGNOSTIC CHARACTERS OF FEMALE. A small blackish species; wing length 2.0 mm. Antenna pale, segments 11-15 brownish. Legs with femora and tibiae blackish, extreme bases of femora paler. Wing dark, whitish on proximal 1/4. Halter pale. Abdomen with variable dark markings, usually dark on tergites 2-8.

DISTRIBUTION. Eastern United States, Kansas and Wisconsin to New Jersey, south to Louisiana and Florida.

FLORIDA RECORDS. **Florida:** Jackson Co., Florida Caverns State Park, 4.v.1970, 26-29.v.1973, 24.iv.1981, W. W. Wirth, light trap, 47 females. Leon Co., 5 mi N Tallahassee, v.1970, WWW, light trap, 1 female. Santa Rosa Co., Blackwater River State Park, 25.v.1973, WWW, light trap, 1 female.

Probezzia fairchildi Wirth, **New Species**

DESCRIPTION. Female Holotype. Wing length 2.66 mm; breadth 0.98 mm. Antenna much elongated, segments 4-10 each as long as those in 11-14 series; segments 4-10 yellowish white, 11-12 dark except at base, 13-15 entirely dark brown; lengths of flagellar segments 262-180-216-310-210-180-195-180-216-198-114-186-238 microns; antennal ratio (11-15/3-10) 0.52. Palpus pale brown, lengths of segments 36-54-118-58-72 microns. Thorax black. Legs with femora and tibiae entirely blackish; claws relatively stout, curved. Wing uniformly infuscated, veins pale brown. Halter dark. Abdomen pale yellow, segments 8-9 entirely dark brown. Spermathecae slightly ovoid, slightly unequal, 144 x 115 microns and 129 x 97 microns; tapering slightly to slender necks.

Male Allotype. Wing length 1.55 mm; breadth 0.50 mm; costal ratio 0.81. Color markings as in female, but abdomen entirely brown. Antenna brown, segments 12-15 darker, plume pale; lengths of flagellar segments 115-57-57-57-57-57-57-57-100-129-186-226 microns. Genitalia typical of the genus.

DISTRIBUTION. Florida.

TYPES. Holotype female, allotype male, Jackson Co., Florida, 26.v.1973, W. W. Wirth, light trap. Paratypes, 21 males, 21 females, as follows:

Florida: Jackson Co., same data as types, 21 males, 15 females; same but 4.v.1970, 1 female; same but 24.iv.1981, 3 females. Baker Co., Glen St. Mary, v.1971, F. S. Blanton, light trap, 1 female. Leon Co., Tall Timbers Res. Station, iv.1978, F. W. Mead, light trap, 1 female.

ETYMOLOGY. This species is dedicated to G. B. Fairchild in recognition of his important contributions to Diptera taxonomy, especially of the families Psychodidae and Tabanidae, and in appreciation of his friendship and good will as a retired colleague at the Florida State Collection of Arthropods, Gainesville, Florida.

DISCUSSION. *Probezzia fairchildi* is unique in the genus in the unusual length and stoutness of the proximal antennal segments, readily distinguishing it from all other *Probezzia* species. In size and color markings this species greatly resembles the North American species of *Macropeza*, a closely related Sphaeromiine genus (Wirth & Ratanaworabhan 1972a, Knausenberger & Wirth 1980). In *Macropeza*, however, the female fifth tarsomeres have fewer ventral batonnets; the female claws are short and curved, stout at the base and pointed apically; the r-m crossvein is elongate; and the hind tarsi are often greatly elongated.

Probezzia glicki Wirth, **New Species**

DESCRIPTION. Female Holotype. Wing length 2.08 mm. Antenna slender, pale yellow, segments 11-15 infuscated; lengths of flagellar segments 107-90-90-90-98-90-90-107-

126-137-144-155-159 microns; antennal ratio 0.95. Palpus whitish, lengths of segments 28-43-72-44-43 microns. Thorax dark brown; coxae and trochanters yellowish white. Legs yellowish white, fore femur dark brown on distal 3/4, mid and hind femora dark on distal 1/2; tibiae with narrow bases and apices brown. Tarsal claws moderately long and slender. Wing pale on proximal 1/2, faintly infuscated on distal 1/2. Halter pale. Abdomen pale, segments 7-8 brown. Spermathecae greatly unequal, the larger elongate oval, tapering distally to stout neck; the smaller short oval, not tapering, with short slender neck; measurements 143 x 83 microns including neck, and 86 x 65 microns.

Male. Unknown.

DISTRIBUTION. Alabama.

TYPES. Holotype female, **Alabama**, Tallapoosa Co., 2.2 mi SW Camp Hill at Hwy. 34, 15.vi.1988, W. E. Garrett. Paratype, 1 female, **Alabama**, Dallas Co., Marion Junction, Black Belt Substation, 21-23.v.1978, J. I. Glick; 1 female, same data but 25-27.vi.1978.

ETYMOLOGY. This species is named for Jayson I. Glick in recognition of his superb but unpublished taxonomic study of the Ceratopogonidae of Alabama as a graduate student at Auburn University.

DISCUSSION. *Probezzia glicki* resembles *P. xanthogaster* in leg markings, pale abdomen, and pale halter, but *P. xanthogaster* differs in having the wing and abdomen entirely whitish.

Probezzia meadi Wirth, New Species

DESCRIPTION. Female Holotype. Wing length 1.65 mm; breadth 0.58 mm. Antenna relatively short, entirely brown; lengths of flagellar segments 90-51-51-47-47-47-62-125-125-136-136-169 microns; antennal ratio 1.55. Palpus brown; lengths of segments 14-32-57-47-47 microns. Thorax black. Legs with femora and tibiae dark brown; femora with bases slightly paler. Claws long and slender, slightly curved, the basal tooth unusually slender, nearly half as long as claw. Wing entirely infuscated, the veins dark brown. Halter pale. Abdomen pale brown, segments 8-9 dark brown. Spermathecae oval, unequal, measuring 108 x 80 microns and 87 x 67 microns.

Male. Unknown.

DISTRIBUTION. Alabama, Florida.

TYPES. Holotype female, **Florida**, Jackson Co., Florida Caverns State Park, 4.v.1970, W. W. Wirth, light trap. Paratypes, 25 females, as follows: **Alabama**: Tallapoosa Co., Sandy Creek, 3.5 km WSW of Camp Hill at Hwy 34, 15.vi.1988, W. E. Garrett, 1 female. **Florida**: Escambia Co., Walnut Hill, vi.1969, F. S. Blanton, light trap, 1 female. Jackson Co., same data as holotype, 9 females; same data but 26.v.1973, 12 females. Leon Co., 3 mi N Tallahassee, v.1970, FSB, light trap, 1 female. Santa Rosa Co., Jay, v.1962, T. W. Boyd, light trap, 1 female.

ETYMOLOGY. This species is dedicated to Frank W. Mead, Florida State Department of Agriculture and Consumer Services, in recognition of his many years of dedication to the collection and study of Florida Diptera, and in appreciation of his long and close friendship.

DISCUSSION. *Probezzia meadi* resembles the Neotropical species of the genus *Neobezzia* Wirth and Ratanaworabhan (1972b) in its long, slender claws of the female, but *Neobezzia* species lack the strong mesonotal spines, the costa does not reach the wing tip (costal ratio 0.87-0.95), and the male parameres are fused on the distal half. *Probezzia meadi* resembles *P. nigra* Wirth and *P. ludoviciana* Wirth, but the two related species are larger and the female antennal segments 3-10 are pale.

Probezzia weemsi Wirth, New Species

DESCRIPTION. Holotype Female. Wing length 1.95 mm; breadth 0.57 mm. Antenna long and slender, segments 2-10 pale, 11-15 infuscated; lengths of flagellar segments

93-72-72-72-72-72-90-143-143-143-162-180 microns; antennal ratio 1.41. Palpus pale, lengths of segments 18-36-65-36-43 microns. Thorax dark brown; coxae and trochanters pale; femora dark brown distally, pale at extreme base on fore leg, on proximal 1/3 to 1/2 on mid and hind legs; tibiae dark at extreme base, fore tibia dark at extreme tip; distal 1/3 of mid tibia and distal 2/3 of hind tibia brownish. Wing entirely pale, appearing hyaline rather than whitish. Halter pale. Abdomen entirely yellowish white. Spermathecae slightly unequal, slightly ovoid, tapering slightly to short slender necks; measuring 102 x 78 microns and 80 x 62 microns.

Male Allotype. Wing length 1.18 mm; costal ratio 0.73. Coloration as in female, but hind tibia infuscated on distal 1/3. Antenna with plume and segments 3-12 pale, 13-15 brown; lengths of flagellar segments 72-43-43-43-43-43-57-80-90-126-143. Genitalia typical of the genus.

DISTRIBUTION. Northern Florida.

TYPES. Holotype female, allotype male, Florida, Jackson Co., Florida Caverns State Park, 26.v.1973, W. W. Wirth, light trap. Paratypes, 20 females, same data as types.

ETYMOLOGY. This species is dedicated to Howard V. Weems of the Florida Department of Agriculture and Consumer Services, in recognition of his many years of enthusiastic leadership in the development of the Florida State Collection of Arthropods, and in appreciation of his close and long lasting friendship.

DISCUSSION. *Probezzia weemsi* resembles the northeastern species, *P. xanthogaster* Kieffer, with its pale wing, halter, and abdomen, but differs in leg markings, the tibiae in *P. xanthogaster* being entirely pale except for the extreme tip of the hind pair.

NOTES ON GEOGRAPHIC DISTRIBUTION

The genus *Probezzia* presently is known only from 23 North American species, three of which also occur in Eurasia. The distribution of the genus is primarily in the northeastern United States and eastern Canada (12 species); while three species (*concinna*, *fuscipennis*, and *seminigra*) occur in Eurasia, western Canada, and northwestern United States; four species (*bottimeri*, *ludoviciana*, *nigra*, and *rosewalli*) occur only in the Gulf Coast states; and four species (*fairchildi*, *glicki*, *meadi*, and *weemsi*) occur only in Alabama and northern Florida.

The occurrence of three undescribed species of *Probezzia*, along with two known species, *P. albitibia* Wirth and *smithii* (Coquillett), in the same collections at Florida Caverns State Park, and a fourth new species in nearby parts of Alabama, points to this area as a probable center of endemism for this genus in the southeastern United States. Berner (1950) stated in his monograph on the Florida mayflies (Ephemeroptera): "The Apalachicola River drainage has without doubt been the main highway of ingress to Florida for the great majority of animals which require flowing water or hardwood forest." Rogers (1933) found that the ecological conditions existing in the Apalachicola drainage would admirably explain the distribution of many northern craneflies (Tipulidae) in Florida. Neill (1957) gave a valuable summary of plant and animal distribution illustrating "northern disjuncts" in the Florida panhandle. Carr (1940) reported that the most extensive invasion of Florida by the northern element is encountered in that portion of the panhandle which is drained by the Apalachicola River.

Hubbell (1936: 354) stated that "in this peculiar environment [the deep ravines of the Apalachicola region] a great many Northern plants occur, evidently the remnants of a Northern flora left as relicts from Pleistocene times in these deep, moist, cool ravines . . . It has also been noted that many Northern plants reach their southernmost limits in these ravines and that many typically Southern plants intermingle here with the Northern species. Not only is this true of plants, but such has proved to be the case in the craneflies, the Odonata, the Opilionids, the Orthoptera, the crayfish, the amphibians, and the reptiles. Many of the species of mayflies which have entered the state have spread out from the Apalachicola drainage and now occupy rather wide ranges in

Florida, but there are certain forms which seem to be more or less confined to this region."

ACKNOWLEDGMENTS

I am grateful to B. V. Peterson, Systematic Entomology Laboratory, U. S. Department of Agriculture, for assistance in arranging the loan of the holotypes and other material of *Probezzia* in the National Museum of Natural History, Smithsonian Institution, Washington, D. C. I am also indebted to Gary R. Mullen and Jayson I. Glick for the opportunity to study Glick's *Probezzia* material in the collection of Auburn University, Alabama. I also acknowledge the kindness and assistance of the superintendents and staff of the Florida Caverns State Park during my visits in 1970, 1973, and 1981.

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EFFECT OF TRAP COLOR ON SPECIES COMPOSITION OF ALATE APHIDS (HOMOPTERA: APHIDIDAE) CAUGHT OVER WATERMELON PLANTS

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ABSTRACT

The species composition and abundance of alate aphids caught in water traps containing green or yellow tiles were compared. Traps were operated in a watermelon field during the spring and autumn growing seasons of 1992. *Aphis spiraeicola* Patch, a vector of watermelon mosaic virus 2 (WMV-2), accounted for 79% of the aphids caught in the spring and 91% of those caught in the autumn in yellow traps. However, this species accounted for only 6% and 11% of aphids caught in green traps in the spring and autumn, respectively. *Uroleucon pseudambrosiae* (Olive), also a vector of WMV-2, was the most abundant aphid in green traps in the spring but was absent in the autumn. *Aphis gossypii* Glover (16% of aphids in green traps) and *Aphis craccivora* Koch (31%) were more common in the autumn than in the spring and may be important vectors of cucurbit potyviruses at that time.

Key Words: Epidemiology, watermelon mosaic virus 2, *Uroleucon pseudambrosiae*, *Aphis* spp.

RESUMEN

La composición y abundancia de especies de áfidos alados capturados en trampas de agua de color verde y amarillo en una plantación de sandía durante la temporada de primavera y otoño fueron comparadas. *Aphis spiraeicola* Patch fue colectado en cantidades muy altas en trampas amarillas durante la primavera y otoño. Esta especie representó el 6% y 11% de los áfidos capturados en trampas verdes durante la primavera y el otoño, respectivamente. *Uroleucon pseudambrosiae* (Olive), otro vector del virus mosaico de la sandía tipo 2 (VMS-2), fue el áfido más abundante en trampas verdes durante la primavera; sin embargo, este vector no se atrapó en la temporada del otoño. *Aphis gossypii* Glover (16% de los áfidos capturados en trampas verdes) y *Aphis craccivora* Koch (31%) fueron más comunes en el otoño, indicando que pueden ser importantes vectores en epidemias causadas por potivirus en cucurbitáceas en esa estación.

Watermelon mosaic virus 2 (WMV-2), a potyvirus, is the most important virus affecting watermelon in the spring in Central and North Florida (Purcifull et al. 1988). WMV-2 is nonpersistently transmitted by many species of aphids (Coudriet 1962, Yamamoto et al. 1982, Adlerz 1987) and is thus difficult to control. Early infection can stunt plants and reduce fruit set (Demski & Chalkley 1974). Fruit from infected plants may develop ringspots on the rind and pale green varieties become bleached in appearance.

In our studies of the epidemiology and management of this virus we have used green tile water traps, first described by Irwin (1980), to estimate aphid landing rates. Peaks in the number of aphids caught in green tile traps correlated well with the first appearance

of WMV-2 in the spring in Florida (Webb & Linda 1993). Green tiles have also been used to monitor landing rates of aphid vectors in peppers, tobacco, and potatoes (Raccah *et al.* 1985, Gray & Lampert 1986, Boiteau 1990). The spectral reflectance properties of our tile closely match those of watermelon leaves and, theoretically, should trap only aphids that would be landing in the crop (Irwin & Ruesink 1986).

Adlerz trapped aphids at the Central Florida Research Center for many years, using yellow sticky boards, yellow water pan traps, and a suction trap (Adlerz 1974, 1976, 1978, 1987). Because much of what we know about locally important vectors is based on his research, we thought it essential to know how our green tile trap catches differed from yellow pan catches in terms of species composition and abundance.

A second cucurbit crop is often grown in the autumn when there are two additional potyviruses present, zucchini yellow mosaic virus (ZYMV) and the watermelon strain of papaya ringspot virus (PRSV-W). These viruses share many of the same vectors but may be transmitted with different efficiencies (Adlerz 1987). There are no published data available on the species composition of alate aphids landing in watermelon fields in the autumn. We thus compared green and yellow traps during the autumn growing season, not only to collect additional data on differences between traps, but to also identify the species of aphids landing in the crop at that time.

MATERIALS AND METHODS

The green tile used in our traps was chosen because its spectral reflectance closely matched that of watermelon leaves, specifically a young, but expanded leaf from the cultivar 'Charlee'. The reflectance of several green tiles and leaves was measured with an optical microreflectometer (Materials Science Center, University of Florida, Gainesville 32611).

Traps were constructed by using clamps to attach a clear plastic sandwich box (12.5 x 12.5 x 5 cm) to a metal rod, as described by Irwin (1980). Dark green ceramic tiles (made in England by H&R Johnson Tiles Ltd, a company now owned by ABC Tiles, Orlando, FL 32805), 10.8 x 10.8 cm, were placed in the box which was filled with water containing a small amount of detergent to break the surface tension. Yellow tile traps were identical to the green except that a yellow plastic tile (supplied by D. J. Schuster, University of Florida, Gulf Coast Research and Education Center, Bradenton) was used. No reflectance data were available for this tile.

In the spring, we placed five traps of each color within a 1.5-ha watermelon breeding field planted in early March. Black plastic mulch and drip irrigation were used in this field. One pair of traps was placed within each corner of the field and one pair near the center. Yellow and green traps were placed at least 5 m apart within a row of plants. Trap height was adjusted to canopy level. In the autumn (watermelon planted in mid August), two green traps were placed with each yellow trap (randomly arranged within a location but at least 5 m apart). Because green traps were not highly attractive to aphids, we hoped to increase our chances of trapping less abundant aphids by increasing the number of traps. For analysis, the number of aphids caught per trap location was divided in half.

We collected aphids five times a week for 12 wk in the spring (17 Mar. - 8 June) and for 9 wk in the autumn (21 Sept. - 20 Nov.) and stored them in 70% ethanol. Collected specimens that could not be identified in ethanol were cleared and mounted on microscope slides following the procedure outlined by Hille Ris Lambers (1950). Identifications were made or confirmed by the third author. Voucher specimens are housed in the Florida State Collection of Arthropods, Gainesville.

Aphids collected were identified for each date and totaled for each season by species and trap color. Those species that accounted for at least 3% of the total aphids caught

were compared within a season by trap color using *t*-tests. The number of aphids caught in green tile water traps in the autumn was divided in half before analysis, but total numbers caught are presented in Table 1.

RESULTS

The spectral reflectance of the dark green tile we chose to use matched that of watermelon leaves both in position of peaks (550 nm for the leaves and 540 nm for tiles) and in percent reflectance (Fig. 1). Both leaves and tiles showed an additional peak in

TABLE 1. APHIDS COLLECTED IN WATER PAN TRAPS, LAKE COUNTY, FL, 1992

Aphid Species ^c	Spring ^a		Autumn ^b	
	17 Mar. - 8 June Green	Yellow	21 Sept. - 20 Nov. Green	Yellow
<i>Acyrtosiphon pisum</i> (Harris)	0	1	1	0
<i>Aphis coreopsidis</i> (Thomas)	0	1	0	1
<i>Aphis craccivora</i> Koch*	3	5	67	95
<i>Aphis fabae</i> -Scopoli complex	0	4	0	0
<i>Aphis gossypii</i> Glover*	1	5	34	46
<i>Aphis helianthi</i> Monell complex	0	3	1	3
<i>Aphis middletonii</i> (Thomas)*	7	43	11	30
<i>Aphis nerii</i> Boyer de Fonscolombe*	0	5	0	1
<i>Aphis rubifolii</i> (Thomas)	0	2	0	0
<i>Aphis sambuci</i> L.	0	12	0	0
<i>Aphis spiraeicola</i> Patch*	7	1143	26	2349
<i>Aphis</i> sp.	0	3	2	0
<i>Brachycaudus helichrysi</i> (Kaltenbach)	0	1	0	0
<i>Geopemphigus flocculosus</i> (Moreira)	0	0	0	1
<i>Hayhurstia atriplicis</i> (L.)	2	2	0	0
<i>Hyalopterus pruni</i> (Geoffroy)	1	1	0	0
<i>Hysteroneura setariae</i> (Thomas)*	1	0	0	0
<i>Lipaphis erysimi</i> (Kaltenbach)	2	14	1	0
<i>Macrosiphum euphorbiae</i> (Thomas)*	0	1	0	0
<i>Microparsus olivei</i> Smith and Tuatay	0	0	0	1
<i>Myzocallis multisetis</i> Boudreaux and Tissoth	0	1	2	0
<i>Myzus persicae</i> (Sulzer)*	3	48	0	7
<i>Rhopalosiphum cerasifoliae</i> (Fitch)	0	2	0	0
<i>Rhopalosiphum maidis</i> (Fitch)	0	3	4	6
<i>Rhopalosiphum nymphaeae</i> (L.)	0	0	1	1
<i>Rhopalosiphum padi</i> (L.)*	1	5	1	0
<i>Rhopalosiphum rufiabdominalis</i> (Sasaki)	2	9	1	1
<i>Sarucallis kahawaluokalani</i> (Kirkalady)	0	0	0	2
<i>Schizaphis</i> sp.	0	0	2	0
<i>Sipha flava</i> (Forbes)	1	1	2	1
<i>Tetraneura nigriabdominalis</i> (Sasaki)	20	20	55	35
<i>Therioaphis riehmii</i> (Boerner)	0	2	0	0
<i>Uroleucon pseudambrosiae</i> (Olive)*	59	115	0	0
<i>Uroleucon</i> sp.	3	0	0	0
Unknown	0	1	0	0

^aTotal aphids caught in five traps of each color.

^bTotal aphids caught in five yellow tile traps or 10 green tile traps.

^cSpecies followed by * are known vectors of WMV-2 (Coudriet 1962, Yamamoto et al. 1982, Adlerz 1987, Webb & Yokomi 1993).

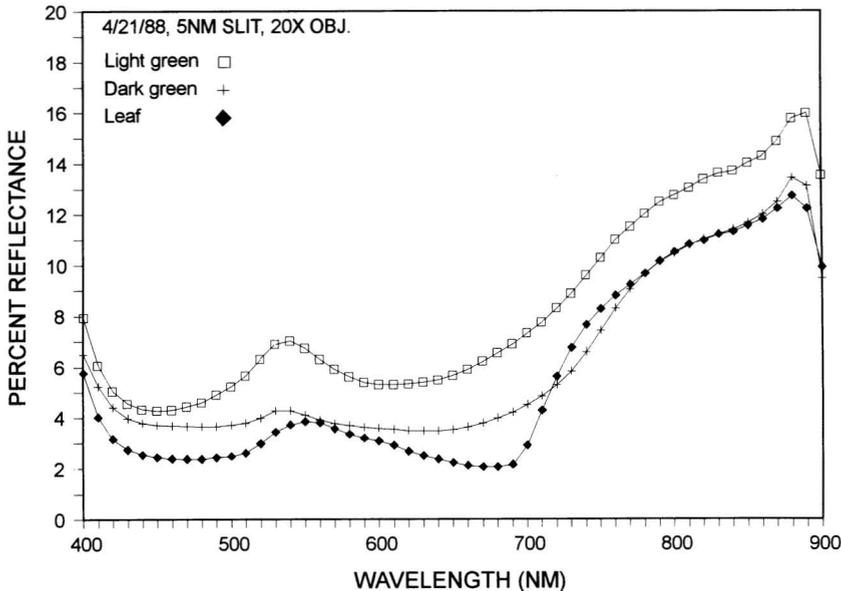


Fig. 1. Spectral reflectance of dark and light (lime) green tiles and a watermelon leaf.

the infrared region of the spectrum. A lighter, more yellow-green tile was also measured but was brighter (higher percent reflectance) than the leaves measured.

A total of 32 species was collected in both seasons from yellow tile traps (Table 1). More species were collected in the spring than in the autumn (28 versus 15), even though the total number of aphids was higher in the autumn (2579 versus 1453). Eight species in the spring and six in the autumn were represented by only one individual. Eleven species were trapped in both seasons.

A total of 23 species was collected from green traps (Table 1). Fifteen species were found in the spring and 17 in the autumn. In the spring, 113 individuals were collected from five traps versus 212 from 10 traps in the autumn. Only nine species were caught in both seasons. In a few cases, species represented by few individuals were caught in green tile pan traps in one season and yellow in the other. Three species [*Hysteronneura setariae* (Thomas), a *Schizaphis* sp., and a *Uroleucon* sp.] were collected only from green tile traps.

In the spring, *Aphis spiraeicola* Patch (= *A. citricola* van der Goot) was the most abundant aphid caught in yellow tile traps (Table 1, Fig. 2), constituting 79% of the total aphids collected. We caught more *Aphis* spp. (11 versus 4) with yellow traps than with green, although most were not abundant. *Myzus persicae* (Sulzer) also appeared to be attracted to yellow. *Tetraneura nigriabdominalis* (Sasaki), a species that feeds on the roots of grasses, was found in equal numbers in yellow and green traps (Table 1). Other grass-feeding species [*Rhopalosiphum* spp., *Sipha flava* (Forbes)] were not abundant, and there were no apparent differences between green and yellow traps.

Uroleucon pseudambrosiae (Olive) (formerly *Dactynotus*) was the most abundant species caught in green tile traps in the spring (Table 1, Fig. 2). The number of *U. pseudambrosiae* caught in green traps in the spring was not significantly different, however, than the number caught in yellow, based on season totals per trap ($t = -1.6403$,

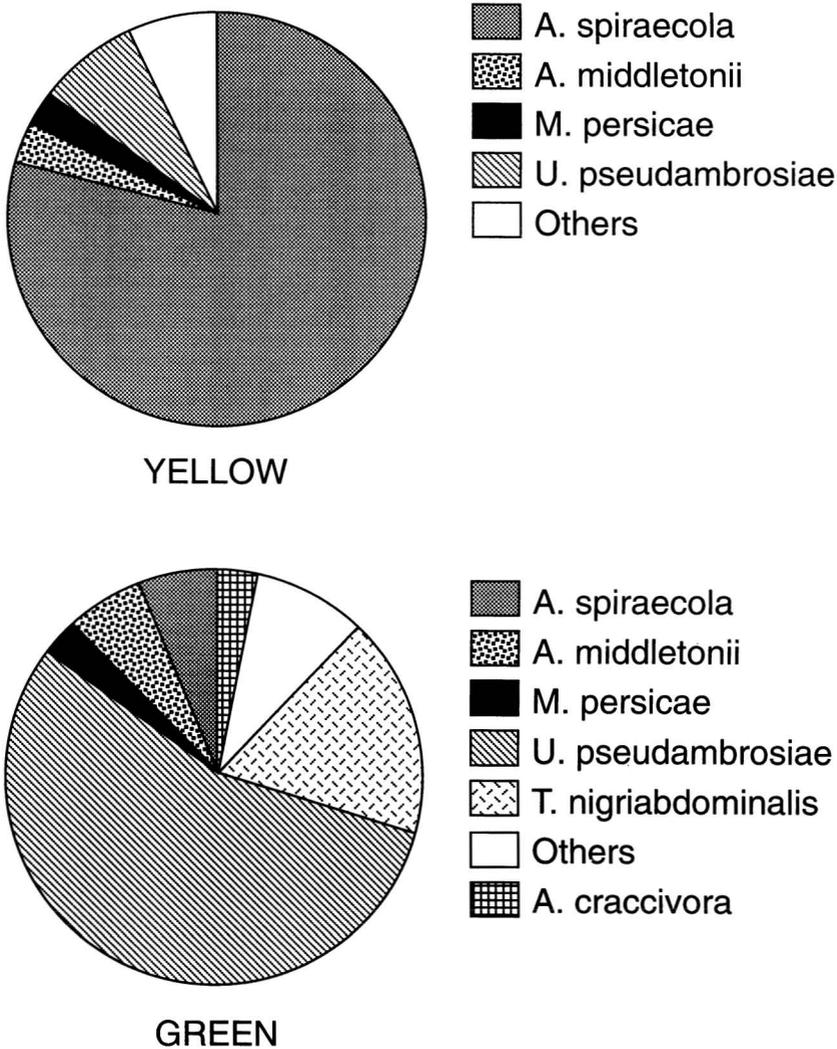


Fig. 2. Species composition of aphids caught in five yellow or five green tile water pan traps from 17 Mar. to 8 June 1992. For yellow tiles, $n = 1453$; for green, $n = 113$.

$df = 4.5$, $P = 0.1697$). The number of aphids caught in yellow traps varied more among traps than did the number caught in green traps (Fig. 3).

In the autumn, *A. spiraecola* accounted for 91% of aphids collected from yellow tile traps and for 11% of those from green tile traps (Table 1, Fig. 4). *T. nigriabdominalis* was also caught in both seasons, again in approximately equal numbers from the two traps (Table 1). Most of the *A. craccivora* Koch and *A. gossypii* Glover were collected in the autumn (Table 1). There were no significant differences in the number of *A. gossypii* caught in green versus yellow traps ($t = -1.514$, $df = 8$, $P = 0.1685$), but *A.*

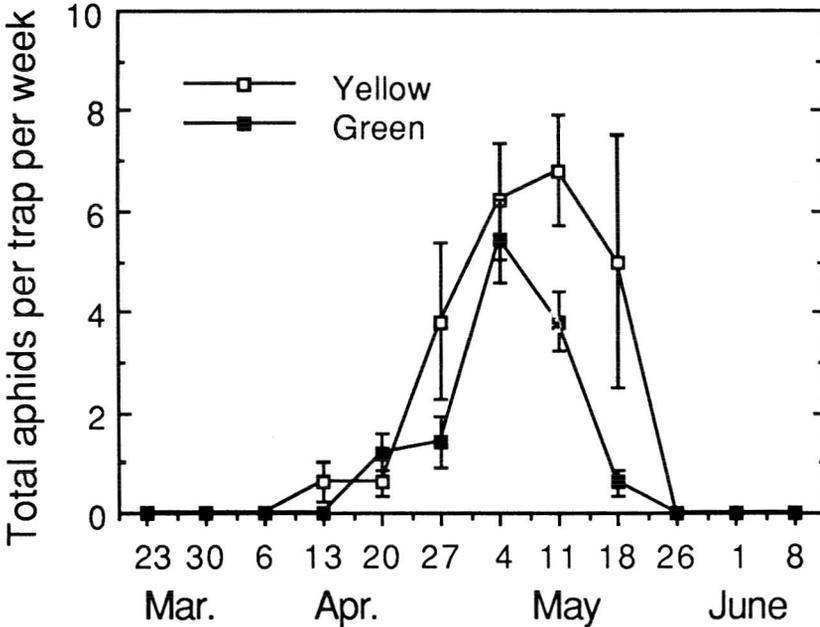


Fig. 3. Mean number of *U. pseudambrosiae* caught per trap in yellow and green tile traps.

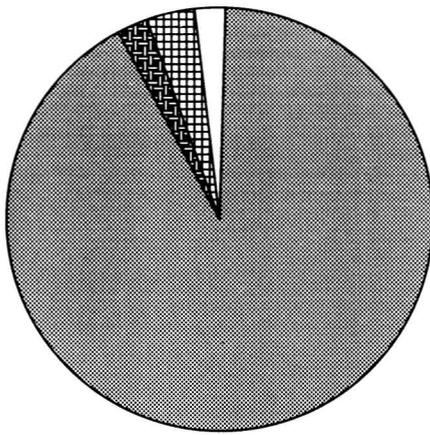
craccivora was caught more often in yellow traps ($t = -2.4733$, $df = 8$, $P = 0.0385$). No *U. pseudambrosiae* and very few *M. persicae* or *Lipaphis erysimi* (Kaltenbach) were caught in either trap in the autumn.

Of aphid species trapped in the spring, 39% of those caught in yellow traps and 47% in green traps were known vectors of WMV-2. The percentage of total aphids (individuals rather than species) caught that were potential vectors was much higher for both traps. Yellow trap catches were dominated by *A. spiraeicola*, a known vector. Thus, 95% of the total number of aphids trapped were theoretically capable of vectoring WMV-2. Fewer total vectors were caught in green traps (73%), even though the number of vector species trapped was higher, because *T. nigriabdominalis*, a non-vector (Adlerz 1987), accounted for 18% of the aphids caught.

In the autumn, 40% of the species trapped in yellow traps and 47% of those in green traps were potential vectors. Again, total numbers were much higher. Of the *A. spiraeicola* collected in yellow traps, however, 84% were trapped after 26 Oct. when most watermelon plants had senesced. These aphids thus had no role in the viral epidemic in the crop. In contrast, approximately 60% of aphids identified as *A. gossypii*, the only aphid to colonize watermelon, were collected by 6 Oct. (from both green and yellow traps). Differences between total aphids and total vectors in green traps were due to the presence of *T. nigriabdominalis*.

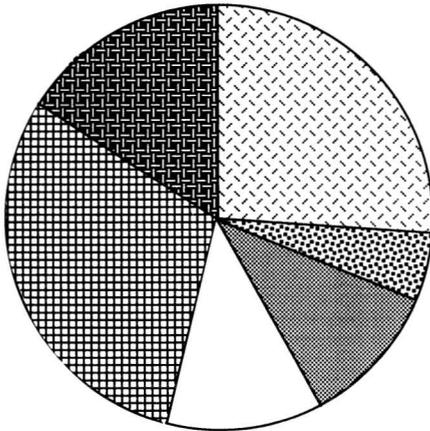
DISCUSSION

Yellow is highly attractive to many species of aphids (Taylor & Palmer 1972). Taylor & Palmer (1972) summarized data from three studies comparing yellow traps with



YELLOW

-  A. craccivora
-  A. gossypii
-  A. spiraecola
-  Others



GREEN

-  A. craccivora
-  A. gossypii
-  A. spiraecola
-  A. middletonii
-  T. nigriabdominalis
-  Others

Fig. 4. Species composition of aphids caught in five yellow or ten green tile water pan traps from 21 Sept. to 20 Nov. 1992. For yellow tiles, n = 2579; for green, n = 212.

non-selective traps. They concluded that yellow was generally attractive to species feeding on dicotyledons but not to those feeding on grasses and sedges. In one of the studies they summarized, *A. spiraecola* was more than 700 times more attracted to yellow than *R. padi*. In our study we also found that yellow was no more attractive to grass-feeding species than green (*T. nigriabdominalis*, for example) and was much more attractive to species feeding on dicotyledons, especially *A. spiraecola* and *M. persicae*. Both of these species are highly polyphagous. *A. spiraecola* has host plants in over 20 families, with citrus the most important crop plant (Blackman & Eastop 1984).

Halbert et al. (1986) found no differences in the number of *A. spiraecola* caught in yellow pan traps and in mosaic green tile pan traps. In addition to possible differences between our yellow traps and theirs, it is also possible that the mosaic green tile was more attractive to this species than the dark green tile used in our study. The spectral reflectance of our tiles matched leaves not only in the position of peaks, but in percent reflectance. Mosaic green tiles had a higher percent reflectance than soybean (Irwin & Ruesink 1986) or potato leaves (Boiteau 1990) and may be somewhat more attractive for this reason. The percent reflectance that we measured at each wavelength for watermelon leaves is not directly comparable to those for soybean and potato leaves (due, we assume, to different methods of measurement) but the peak wavelengths match and the overall pattern is relatively similar.

Our results matched those of Adlerz (1978) who stated that, in most years at Leesburg, *A. spiraecola* accounted for 79% to 99% of the aphids caught on yellow sticky traps or in water pan traps. The overwhelming numbers of this species caught by yellow tiles in our study accounted for a large part of the difference in total numbers of aphids caught by yellow and green tiles.

Although the number of aphids trapped with green tile water traps appears low, it is comparable to the number of aphids trapped in ermine lime tile traps by Gray & Lampert (1986) in North Carolina. The area of our green traps (117 cm²) was approximately equal to one large, or two or three small, watermelon leaves. If, as theorized, green traps mimic the leaf surface, then one should be able to estimate the number of aphids landing on a plant if the number of leaves or the total surface area is known (Gray & Lampert 1986). For example, from 12 to 18 May, five *A. middletonii* were caught in green tile traps, equivalent to 5 divided by (7 days x 6 traps) or 0.12 aphids per trap per day. We have found that by 8 wk after planting, or approximately at fruit set, a watermelon plant can have between 300 to 500 leaves with an average leaf area of 58 cm² per leaf (S.E.W., unpublished data). Thus 18 to 30 *A. middletonii* per day could be landing on one plant at a time when viral infection could still result in serious damage to the crop.

In this paper we have presented data for two seasons of one year. Adlerz reported many of the same species caught in yellow traps in earlier years (spring only) at the Central Florida Research Center, with differences mainly among those species of which he collected only one or two individuals per season (Adlerz 1974, 1987). He did report year-to-year differences in the abundance of *A. spiraecola* and *A. middletonii*, species thought to play a significant role in virus spread (Adlerz 1976, 1978, 1987). In the spring of 1993, many more *A. middletonii*, a root-feeding aphid, were present in green tile traps, and the increase of *U. pseudambrosiae* was delayed, probably because of a mid-March freeze which destroyed the flower stalks of its host, *Lactuca graminifolia* Michaux (unpublished data).

For epidemiological studies we think that green tile traps offer important advantages over yellow tiles. Although it is simple to trap aphids, it is expensive and time-consuming to identify them. Traps that attract large numbers of aphids create extra labor and potentially misleading information (Taylor & Palmer 1972).

The differential attractiveness of yellow also makes it difficult to draw conclusions about the relative abundance of a potential vector. Adlerz (1987) noted that yellow pans caught proportionately more *A. spiraecola* than a suction trap operated at plant height. In 1982, this species constituted 38% of total aphids trapped in pans versus 11% of aphids caught by suction trap (Adlerz 1987). In the same study, he also noted that most of the *Uroleucon* sp. were caught by the suction trap (27% versus 3% of total aphids in pans). We have found *U. pseudambrosiae* to be as efficient a vector as *A. spiraecola* in arena tests (Webb & Kok-Yokomi 1993) and suggest that its role in epidemics of WMV-2 may have been overlooked, partly because of the trapping methods used previously. Conversely, the importance of *A. spiraecola* may have been overemphasized.

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POPULATION ECOLOGY OF TWO SPECIES OF *PASIMACHUS*
(COLEOPTERA: CARABIDAE) IN THE SANDHILL HABITAT
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ABSTRACT

The population ecology of *Pasimachus subsulcatus* Say and of *P. strenuus* LeConte was studied with beetles captured by pitfall trapping. We searched for patterns in: (1) activity/density, (2) reproduction, (3) body size, and (4) parasitization. Females and males of both species were most active/dense in spring and autumn; females of both species were especially active/dense, relative to males, in late summer-early autumn; few females of both species bore post-vitellogenic eggs in summer; and males of *P. subsulcatus* produced mature sperm in spring and autumn. It was concluded that mating occurs in spring and autumn for both species, and oviposition in summer-early autumn. Our data suggest that relatively high percentages of both female and male *P. subsulcatus* trapped in late summer-early autumn were relatively large. In most months, females of *P. subsulcatus* were, on average, larger than males, but the two sexes of *P. strenuus* were similar in size. About 1.4% of *P. subsulcatus* and 3.3% of *P. strenuus* were parasitized by tachinid flies. Parasitization of both species peaked in late summer-autumn, and there was no evidence that parasitization was influenced by sex, size, or female gravidity, with one exception. Small individuals of *P. subsulcatus* were parasitized more often than one would expect from their representation among captured individuals.

Key Words: Carabidae, Florida, ground beetles, reproduction, parasitization, mating.

RESUMEN

Se estudió la ecología poblacional de *Pasimachus subsulcatus* Say y de *P. strenuus* LeConte con escarabajos capturados en trampas de suelo. Buscamos patrones en (1) actividad/densidad, (2) reproducción, (3) tamaño del cuerpo, y (4) parasitización. Las hembras y los machos de ambas especies fueron más activos/densos durante la primavera y el otoño; las hembras de ambas especies fueron especialmente activas/densas, al compararse a los machos, en los fines del verano y los principios del otoño; pocas hembras de ambas especies cargaban huevos post-vitelogenéticos en el verano; y los machos de *P. subsulcatus* produjeron esperma madura en la primavera e el otoño. Se concluyeron que aparear ocurre en la primavera y el otoño para ambas especies, y la oviposición ocurre en el verano y los principios de otoño. Nuestros datos sugieren que porcentajes relativamente altos de hembras y machos de *P. subsulcatus* atrapadas en los fines del verano y los principios del otoño fueron de relativamente grandes tamaños. En la mayoría de meses, las hembras de *P. subsulcatus* tenían tamaños más grandes, por el promedio, que los machos, pero los dos sexos de *P. strenuus* fueron semejantes en tamaño. Cerca de 1.4% de *P. subsulcatus* y 3.3% de *P. strenuus* fueron parasitados por moscas tachinidas. El apogeo de parasitización de ambas especies fue en los fines de verano y en el otoño, y no hubo evidencia que la parasitización fue influido ni por el sexo, el tamaño, o la gravidad de las hembras, con una excepción. Los individuos pequeños de *P. subsulcatus* fueron parasitados más frecuentemente que se hubiera esperado basado en su representación entre individuos capturados.

The ground beetle genus *Pasimachus* includes about 25 large, flightless, xerophilic species, all restricted to North America (see Nichols 1988). The most thoroughly-studied species is *P. elongatus* LeConte (e.g., Cress & Lawson 1971, Calkins & Kirk 1974), probably because it is a predator of false wireworms and other agricultural pests (Barney & Armbrust 1980, Wise 1985). Another species, *P. punctulatus* Haldemann, also has been studied in detail (Nelson 1969, 1970). In Florida, several species of *Pasimachus* are common in xeric upland habitats, such as scrub and sandhill, but very little is known about them.

In this paper, we address the population ecology of *P. subsulcatus* Say and of *P. strenuus* LeConte. Trapping data were used to search for patterns of activity/density. Similar activity/density studies of *P. punctulatus* in Texas (Nelson 1970) and of three species of *Evarthrus* (Coleoptera: Carabidae) in Florida (Harris & Whitcomb 1971) indicated peaks in both spring and autumn. The activity/density of *P. elongatus* in more northern locations, Arkansas (Allen & Thompson 1977) and South Dakota (Calkins & Kirk 1974), peaks only in summer. These observations, and others (see Thiele 1977), led us to predict that the activity/density of the two species of *Pasimachus* that we studied would peak in either spring or autumn, or in both seasons.

We used measurements of large numbers of individuals to search for patterns of body size, because the body size of many ground beetle species vary over time, as ecological conditions change (Thiele 1977). We predicted, therefore, that the body sizes of the two species of *Pasimachus* that we studied would vary, and that this variation would be attributable to an environmental cause. We also predicted that females would be larger than males of the same species, simply because this is the case for most animals (Cockburn 1991). However, males might be similar in size to, or larger than, females, particularly if they competed for access to females (Alcock & Gwynne 1991).

Finally, we used internal examinations of individual beetles to search for patterns of reproduction and parasitization. It was predicted that peaks in reproduction would coincide with peaks in activity/density, because ground beetle behaviors often are interdependent and triggered by similar environmental cues (Thiele 1979). We also predicted that rates of parasitization would be low, because parasites and parasitoids are thought to play only minor roles in governing the density and distribution of ground beetle populations (Thiele 1977). Predators, on the other hand, are thought to play a major governing role (Thiele 1977, Murdoch 1966, Parmenter & MacMahon 1988); so much so that conspicuous anti-predator adaptations have been induced (Thiele 1977). We cite, for example, the defensive secretions of some species of *Pasimachus* (Nelson 1970, Davidson et al. 1989, Witz & Mushinsky 1989).

MATERIALS AND METHODS

Totals of 2280 individual *P. subsulcatus* and 545 individual *P. strenuus* were captured in pitfall traps located in The University of South Florida's Ecological Research Area. The traps were open from November 1982 to May 1984 (see McCoy 1987). The site had been divided into approximately 1 ha plots for the purpose of studying the effects of burning on resident organisms. Because burning regimes differ among plots, the sandhill habitat (see Myers 1990) at this site varies from virtually open wiregrass, to wiregrass-turkey oak woodland, to near xeric oak woodland. More detailed information about the site is available in Mushinsky (1985), McCoy (1987), and Mushinsky & Gibson (1991).

The traps were 60 5-gal buckets arranged in pairs connected by an aluminum drift fence 7.5 m long and 0.5 m high. Ten traps each were distributed among six plots, four of which were sampled for the entire 19 months, one for 16 months from February, 1983 to May, 1984, and one for 14 months from April, 1983 to May, 1984. Within a plot, traps were overdispersed (mean distance between traps = 30 m), to minimize the possibility

that traps would sample overlapping areas of habitat. We checked all traps at least twice weekly, but combined individuals captured in the same month for analysis.

We recognize that data can be mis-interpreted when using pitfall trapping to monitor ground-dwelling arthropods (e.g., Mitchell 1963, Greenslade 1964). To minimize mis-interpretation in this study, we neither made comparisons between species (cf. Halsall & Wratten 1988) nor computed estimates of absolute numbers (cf. Baars 1979). We also recognize that removal trapping may affect population structure and we assumed that the low density of traps reduced the possibility that any patterns we detected were caused by method of sampling.

Beetles collected from the traps were frozen immediately upon return to the laboratory and then stored in 70% isopropanol. Each individual was dissected to determine its sex, its gravidity (presence of post-vitellogenic eggs; cf. Mitchell 1963, Dawson 1965), the number of eggs, and the occurrence of parasites. The numbers and identities of parasites were recorded. The size of each individual beetle was measured, using interocular distance (transverse distance across the dorsum of the head, between the compound eyes at their longitudinal midpoints). Measurements were made with an ocular micrometer installed in a dissecting microscope (120X). Interocular distances were measured precisely, and were highly correlated with other measures of size, such as length of elytron.

We collected 64 males of *P. subsulcatus* in November–December 1988, January 1989, and July 1989, and examined them for sperm production (see Witz 1990). These males were collected in pitfall traps, as described above. In the laboratory, the abdominal cavities of decapitated individuals were flooded immediately with a 1.5% glutaraldehyde, 2.0% tannic acid fixative solution in 0.05M sodium cacodylate buffer (Seagull & Heath 1979). The reproductive tracts were removed while still emersed in fixative. The testes were separated and placed individually in vials of fixative solution for two hours. Post-fixation was in cold 1.5% osmium tetroxide, 2.5% potassium ferrocyanide solution for one hour (Russell & Burguet 1977). We dehydrated the testes in a graded alcohol series, embedded them in Spurr's plastic (Spurr 1969), sectioned them on a Sorvall MT-2 ultramicrotome, and double-stained sections with uranyl acetate and lead citrate (Venable & Coggeshall 1965), prior to examining them with an Hitachi H500 transmission electron microscope. Insufficient *P. strenuus* males were collected to examine sperm production.

RESULTS AND DISCUSSION

Activity/Density

Individuals of both species were captured most frequently in spring from April to May and in autumn from September to October (Fig. 1). The frequency of capture of females was correlated positively with the frequency of capture of males of the same species (Spearman's Rank Correlation; $r = 0.89$, $p < 0.05$, $n = 19$ (*P. subsulcatus*); $r = 0.88$, $p < 0.05$, $n = 16$ (*P. strenuus*)). The sex ratios of both species varied over time (G Test of Independence; $G = 28.47$, $p < 0.10$, $df = 18$ (*P. subsulcatus*); $G = 16.32$, $p < 0.10$, $df = 9$ (*P. strenuus*)), indicating that the magnitude of the changes in activity/density between months were not similar for the two sexes. In most months, the numbers of males captured exceeded the numbers of females; some late summer-early autumn months were the only important exceptions (Table 1).

Reproduction

Gravid females usually bore a single post-vitellogenic egg (72% of *P. subsulcatus* with one egg, 25% with two eggs, and 3% with three eggs; 50% of *P. strenuus* with one egg, 31% with two eggs, 13% with three eggs, and 3% each with four and five eggs).

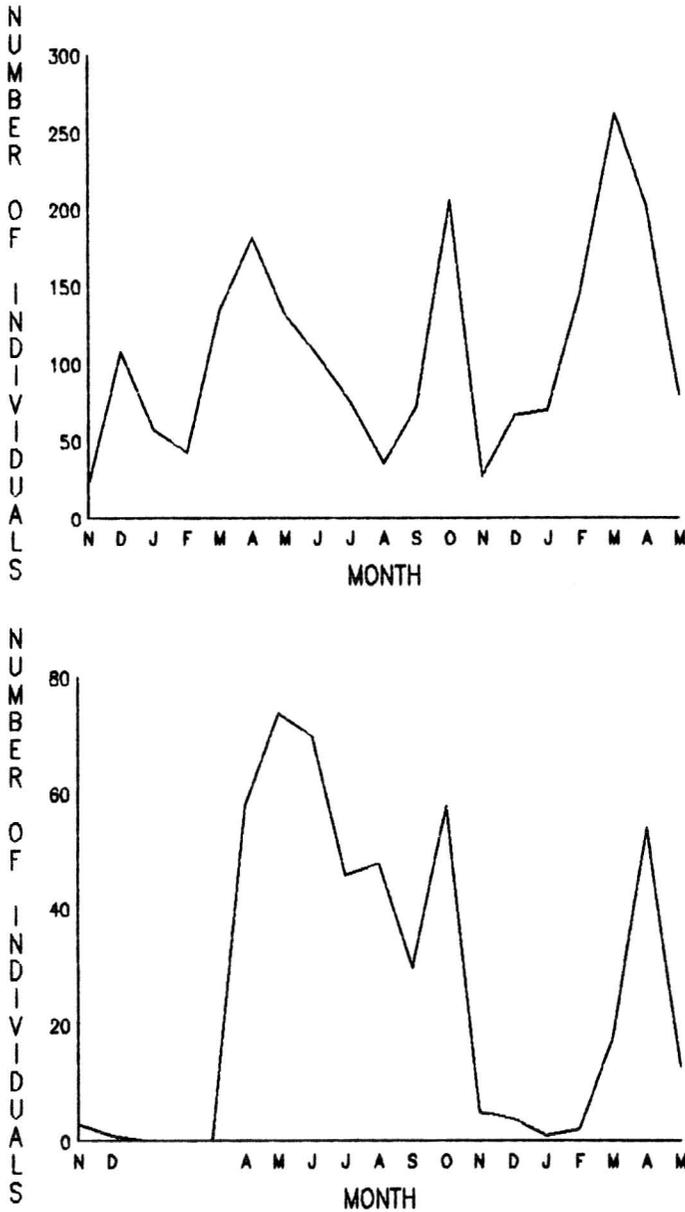


Fig. 1. Number of individual *Pasimachus subsulcatus* (upper) and *P. strenuus* (lower) captured in each of the 19 months of sampling.

There was no apparent seasonal pattern in the tendency of gravid females to bear more than one egg. We also saw no apparent tendency for females bearing more than one egg to be especially large.

TABLE 1. DATA DERIVED FROM BEETLES CAPTURED DURING A 19-MONTH STUDY. FIRST ENTRY IS *PASIMACHUS SUBSULCATUS* AND THE SECOND IS *P. STRENUUS*. PERCENTAGES ARE REPORTED ONLY FOR N = 10 OR GREATER.

Month	No. of Females	No. of Males	Gravid (%)	Parasitized (%)
Nov.	7/ 2	15/ 1	-/ -	0/ -
Dec.	38/ 1	70/ 0	63/ -	0/ -
Jan., 1983	20/ 0	38/ 0	65/ -	0/ -
Feb.	13/ 0	30/ 0	61/ -	0/ -
Mar.	37/ 0	98/ 0	65/ -	3/ -
Apr.	49/25	133/33	53/48	3/ 0
May	49/28	84/46	57/43	2/ 0
Jun.	41/26	65/44	46/46	0/ 1
Jul.	30/22	46/24	67/14	1/ 2
Aug.	20/23	16/25	25/30	14/12
Sep.	41/27	32/35	49/52	5/ 6
Oct.	86/39	120/19	58/69	7/ 9
Nov.	12/ 3	16/ 2	42/ -	4/ -
Dec.	25/ 1	42/ 3	64/ -	1/ -
Jan., 1984	23/ 0	48/ 1	56/ -	1/ -
Feb.	49/ 1	97/ 1	82/ -	1/ -
Mar.	86/10	177/ 8	76/30	0/
Apr.	75/25	127/29	68/28	1/ 0
May	31/ 7	50/ 6	52/ -	0/ 0

The percentage of females with post-vitellogenic eggs for both species appeared to decrease early in the year to a low in summer and then to increase later (Table 1). To test this apparent relationship, we separated the data by plot to expose between-plot variation and correlated the percentages of females with post-vitellogenic eggs with the rank-order of months. For *P. subsulcatus*, correlations were performed separately for the months of January to August, 1983 (apparent decrease) and August to December, 1983 (apparent increase). For *P. strenuus*, correlations were performed separately for the months of April to July, 1983 (apparent decrease) and July to October, 1983 (apparent increase). The apparent decrease was confirmed (Spearman's Rank Correlation, $r = -0.54$, $p < 0.05$, $n = 44$) for *P. subsulcatus*, but the apparent increase could not be confirmed (Spearman's Rank Correlation, $r = 0.27$, $p > 0.10$, $n = 27$). On the other hand, both the apparent decrease (Spearman's Rank Correlation, $r = -0.43$, $p < 0.10$, $n = 20$) and the apparent increase (Spearman's Rank Correlation, $r = 0.64$, $p < 0.05$, $n = 22$) were confirmed for *P. strenuus*. For either species, pooling data among plots to avoid possible pseudoreplication did not alter the results.

Spermatocytes and spermatids were present, and mature sperm were absent, in all *Pasimachus subsulcatus* males ($n = 31$) collected in January 1989; mature sperm were present, and spermatocytes and spermatids were absent, in all males ($n = 24$) collected in November and December, 1988. Spermatogonia were present, and spermatids and mature sperm were absent, in all males ($n = 9$) collected in July 1989. Although these results must be viewed cautiously, they suggest that a first cycle of spermatogenesis is initiated early in the year and culminates by mid-year. It is then followed immediately by a second cycle that culminates late in the year.

Our data suggest that at least parts of the reproductive phenologies of the two species are apparent. Four conclusions are particularly relevant: (1) both sexes were most active/dense in spring and autumn (both species), (2) females were especially active/dense, relative to males, in late summer-early autumn (both species), (3) few females bore post-vitellogenic eggs in summer (both species), and (4) males produced mature

sperm in spring and autumn (*P. subsulcatus*). Taken together, these conclusions indicate for both species that matings occur in spring and autumn, and oviposition in summer-early autumn.

Body Size

The median size (interocular distance) of females of *P. subsulcatus* appeared to be larger than the median size of males in every month and was significantly larger (Wilcoxon Rank Sum Test, $W^* = 2.0-9.1$, $p < 0.05$, $m = 13-80$, $n = 30-174$) in every month, except occasionally between August and January (Fig. 2). The median size of males of *P. strenuus* appeared to be larger than the median size of females in seven of eight months, but was significantly larger only in May 1983 (Wilcoxon Rank Sum Test, $W^* = 5.1$, $p < 0.05$, $m = 26$, $n = 46$).

No seasonal pattern in body size was obvious to us. Both the mean and median sizes of males of *P. subsulcatus* declined over the entire 19-month sampling period (Spearman's Rank Correlation; $r = -0.65$, $p < 0.05$, $n = 19$ (mean); $r = -0.70$, $p < 0.05$, $n = 19$ (median)), as did the mean size of females (Spearman's Rank Correlation, $r = -0.51$, $p < 0.05$, $n = 18$). The median size of females also appeared to decline over the sampling period, but we could not confirm this tendency (Spearman's Rank Correlation, $r = -0.35$, $p > 0.10$, $n = 18$). We did not attempt similar analysis with *P. strenuus*, because large numbers of beetles of both sexes were captured in only a few months.

Although females of *P. subsulcatus* tended to be larger than males during most of the year, this size distinction was conspicuously reduced in late summer-early autumn (Fig. 2). Furthermore, although the median size of females of *P. subsulcatus* usually appeared to exceed the mean size, the disparity was greatest in late summer-early autumn (Fig. 2). We concluded from these observations that relatively high percentages of the females and males of *P. subsulcatus* trapped at this time were large individuals. Data from additional years would be needed to test this conclusion.

Parasitization

Only two types of internal parasites were found. The first was an unidentified species of nematode which we removed from a single female of *P. subsulcatus* captured in February 1983. The second was a species of Tachinidae (Diptera), which we have tentatively identified as *Sitophaga* sp. (Arnaud 1978 and included references). Immature stages of this parasitoid were removed from both species. About 1.4% of individual *P. subsulcatus* and 3.3% of individual *P. strenuus* were parasitized. The mean number of parasitoids per host was 1.4 (SD = 0.7) for *P. subsulcatus*, and 3.4 (SD = 3.9) for *P. strenuus*.

We found no evidence, for either species, that one sex was parasitized disproportionately. For *P. subsulcatus*, the expected number of parasitized females, based on the percentage of females, was 13.3, and the observed number was 14; for *P. strenuus*, the expected and observed numbers were 7.4 and 7, respectively. We also found no evidence that certain sizes of *P. subsulcatus* were parasitized disproportionately (Kolmogorov-Smirnov Test, $D = 0.07$, $p > 0.10$, $n = 23$). *P. strenuus* with an interocular distance of 8.8 mm or less were parasitized more heavily than individuals of other sizes (Kolmogorov-Smirnov Test, $D = 0.37$, $p < 0.10$, $n = 12$): Beetles of this small size were expected to comprise only about 46% of parasitized individuals, but actually comprised about 83%. Finally, we found no evidence, for either species, that gravid females were parasitized more frequently. For *P. subsulcatus*, the expected number of parasitized gravid females, based on the percentage of gravid females, was 8.6, and the observed number was 6; for *P. strenuus*, the expected and observed numbers were 3.1 and 3, respectively.

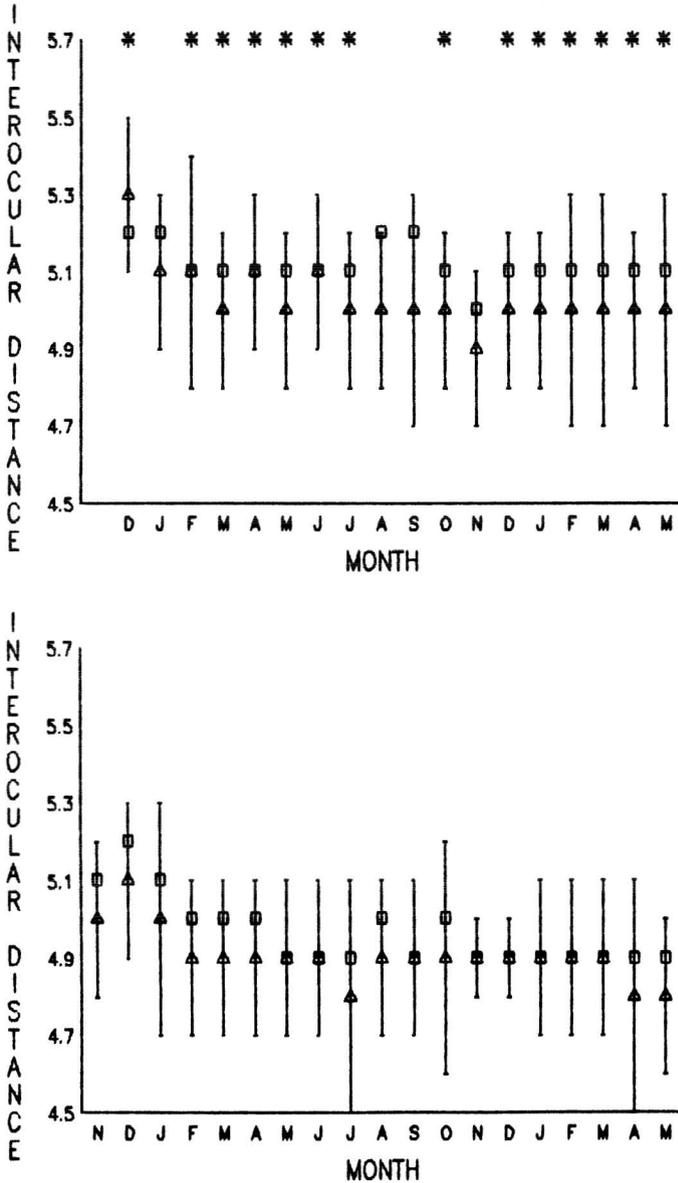


Fig. 2. Mean (triangles) and median (squares) inter-ocular distances of female (upper) and male (lower) *Pasimachus subsulcatus* in each of the 19 months of sampling. Vertical bars are one standard deviation and asterisks at the top of the upper graph designate months of which median sizes of females and males differed significantly ($p < 0.05$). Sizes are compared only for months in which at least ten individuals of each sex were captured.

Parasitization of both species appeared to peak in late summer-autumn (Table 1), but because of the small number of parasitized individuals, this result must be viewed cautiously. It suggests that relatively high levels of parasitization coincided with relatively high levels of activity of both species of *Pasimachus* (see Fig. 1). The number of parasitized individuals was correlated strongly with the total number captured for *P. strenuus* (Spearman's $r = 0.50$, $p < 0.05$, $n = 16$), but not for *P. subsulcatus* (Spearman's $r = 0.29$, $p > 0.10$, $n = 19$). The difference between species may simply reflect a better match of the seasonal activity/density of *P. strenuus* (see Fig. 1) with the life cycle of the parasitoid.

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FIELD RESPONSE OF *RHYNCHOPHORUS CRUENTATUS*
(COLEOPTERA: CURCULIONIDAE) TO ITS AGGREGATION
PHEROMONE AND FERMENTING PLANT VOLATILES

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ABSTRACT

Semiochemicals from 2.5 kg of chopped stem tissue from cabbage palmetto, *Sabal palmetto* (Walter), frozen or fresh stem tissue from sugarcane, *Saccharum officinarum* L., or syncarp tissue from pineapple, *Anana comosus* (L.), were equally suitable for field attraction of *Rhynchophorus cruentatus* (F.) when used with 0.4 mg/d of its aggregation pheromone, 5-methyl-4-octanol (cruentol). Twenty-eight different chemicals known to be fermentation products from palm sap were screened with 0.4 mg/d cruentol for field attraction of *R. cruentatus* adults. Good chemically-mediated field trapping of *R. cruentatus* was achieved with cruentol plus ethyl acetate (852 mg/d) and to a lesser degree with each of the following: (S)-(-)-ethyl lactate (release rate not determined; ND), ethyl isobutyrate (40 mg/d), ethyl butyrate (255 mg/d), or ethanol (51 mg/d). However, none of the test chemicals with cruentol were as effective as 1.5 kg of fermenting sugarcane or *S. palmetto* tissue plus cruentol. Also, none of these chemicals were attractive by themselves at the rates tested. A combination of individually released ethanol (48 mg/d), ethyl acetate (131 mg/d), ethyl butyrate (34 mg/d), ethyl isobutyrate (40 mg/d), and (S)-(-)-ethyl lactate (ND) with cruentol was as effective for the capture of *R. cruentatus* as cruentol plus any of the individual components at the rates tested. Several trap designs were evaluated for future research and implementation of semiochemically-mediated monitoring and management of *R. cruentatus*.

Key Words: Chemical ecology, palmetto weevil, semiochemicals, field trapping.

RESUMEN

Semioquímicos de 2.5 kg de tejido picado del tallo del palmetto de col, *Sabal palmetto* (Walter) tejido de caña de azúcar, *Saccharum officinarum* L. o congelado o fresco, y tejido de sincarpo de piña, *Anana comosus* (L.) fueron igualmente satisfactorios para atracción en el campo de *Rhynchophorus cruentatus* (F.) cuando fue usado con 0.4 mg/d de su feromona de agregación, 5-metilo-4-octanol (cruentol). Veintiocho diferentes químicos conocidos como productos de la fermentación de la savia de las palmeras fueron examinados con 0.4 mg/d cruentol para atracción en el campo de los adultos de *R. cruentatus*. Se logró buen atrapamiento de campo de *R. cruentatus* con cruentol más acetato de etilo (852 mg/d), y a un nivel menos con cada uno de las combinaciones siguientes: (S)-(-) lactato de etilo (razon de liberar no determinado; ND), isobutirato de etilo (40 mg/d), butirato de etilo (255 mg/d), etanol (51 mg/d). Sin embargo, ninguno de los químicos con cruentol fueron tan efectivo como 1.5 kg de caña en fermentación o tejido de *S. palmetto* más cruentol. Además, ninguno de estos químicos fueron atractivos

por si mismo a las concentraciones examinadas. Una combinación de etanol (48 mg/d), acetato de etilo (131 mg/d), butirato de etilo (34 mg/d), isobutirato de etilo (40 mg/d) y (S)-(-)-lactato de etilo (ND) liberados individualmente con cruentol fue efectivo para la captura de *R. cruentatus* como cruentol más cualquiera de los componentes individuales por las razones examinadas. Se evaluaron varios diseños de trampas para investigaciones futuras y para implementación de monitoreo y control de *R. cruentatus* basado en semioquímicos.

Rhynchophorus cruentatus (F.) is a pest of stressed palms in the southeastern United States (Giblin-Davis & Howard 1989). Feeding damage by the larvae of this weevil is difficult to detect before the regenerative apical meristem (bud) of the palm has been destroyed (Giblin-Davis & Howard 1988). The congeneric palm weevil, *R. palmarum* (L.) is the major vector of the red ring nematode, *Bursaphelenchus cocophilus* (Cobb), which causes the lethal and economically important red ring disease of coconut (*Cocos nucifera* L.) and African oil palm (*Elaeis guineensis* Jacq.) in the southern Caribbean, Mexico, and Central and South America (Giblin-Davis 1993). Other species of *Rhynchophorus* may be capable vectors of the red ring nematode as well (Giblin-Davis 1993).

Recently, male-produced aggregation pheromones have been identified for six species of *Rhynchophorus* (Gries et al. 1993, Hallet et al. 1993, Oehlschlager et al. 1992, 1993b, Rochat et al. 1991, 1993, Weissling et al. 1994). The aggregation pheromone for *R. cruentatus* has been identified as 5-methyl-4-octanol (cruentol) (Weissling et al. 1994). Semiochemicals from fermenting host tissue and male-produced aggregation pheromones interact synergistically to provide enhanced trapping of *Rhynchophorus* spp. (Gries et al. 1993, Hallet et al. 1993, Oehlschlager et al. 1992, 1993a,b, Weissling et al. 1994). In nature, *Rhynchophorus* spp. are normally attracted to wounded, stressed, or dying palms (Wattanapongsiri 1966) and male-produced aggregation pheromones apparently aid in recruitment of weevils of both sexes to patchily distributed resources.

Identification of host-derived semiochemicals for *Rhynchophorus* spp. would allow for the development and production of longer lasting and more easily implemented traps when used with their specific aggregation pheromones. Chemically-mediated traps would have applications in monitoring and management attempts for red ring nematode-infested *R. palmarum* or other species of *Rhynchophorus*.

The cabbage palmetto, *Sabal palmetto* (Walter), is the most frequently reported host of *R. cruentatus* (Giblin-Davis & Howard 1989). Freshly chopped *S. palmetto* crown and stem tissue is a reliable bait for trapping *R. cruentatus* and is most attractive 24-72 h after harvest (Weissling et al. 1992). However, *S. palmetto* is labor and time consuming to procure for short duration field attractancy studies. A more convenient alternative plant tissue with similar attractancy when released with cruentol is needed for future work. In addition, we wanted to see if there was something unique about fermenting *S. palmetto* tissue or if ubiquitous fermentation products from a variety of plant tissues would be attractive with cruentol for *R. cruentatus* adults.

The purpose of this study was to field-evaluate the attraction of different fermenting plant tissues with cruentol to *R. cruentatus* adults. We also took a pragmatic approach to field-evaluating the attractancy of a number of volatile fermentation products when used alone or released with cruentol for the capture of *R. cruentatus* adults. Lastly, several trap designs were evaluated for future experiments with semiochemically-mediated trapping of *R. cruentatus*.

MATERIALS AND METHODS

Field Response of Weevils to Fermenting Plant Tissues and Cruentol

A trap for capturing and retaining live *R. cruentatus* adults (Weissling et al. 1992) was used for comparisons of the attractancy of different fermenting plant tissues with cruentol. Briefly, each trap consisted of a 19-liter black, high density polyethylene (HDPE) bucket (United States Plastic Corp., Lima, OH) with a 32-cm diam composite PVC pipe lid (2.4 cm ID for each individual PVC tube). Each trap had two 5-mm diam holes drilled into the bottom for drainage and was suspended in a *S. palmetto* tree with nylon cord so that the bottom of the bucket was about 0.5 m from the ground.

Experiment No. 1 was conducted 11-18 May 1992 and the treatments were 2.5 kg of chopped tissue from the following fresh sources; 1) *S. palmetto* stem and crown, 2) sugarcane, *Saccharum officinarum* L., stem, 3) pineapple, *Anana comosus* (L.), syncarp, and 4) saw palmetto, *Serrenoa repens* (Bartram), stem (Table 1).

Racemic 5-methyl-4-octanol (cruentol) was synthesized (> 95% purity) and released from four 40 μ l capillary tubes with 10 μ l each of pheromone. Each capillary tube was cut 1 cm above the meniscus and placed into a 300 μ l microcentrifuge tube with two 3-mm holes drilled 5 mm below the sealed top (release rate 0.4 mg/d @ 27-34° C) as described by Weissling et al. (1994) for all experiments in this paper.

Experiment No. 2 was conducted 5-12 June 1992 and the treatments were the same as for experiment No. 1 except that chopped frozen sugarcane stem replaced the saw palmetto stem (Table 1).

Traps for both experiments were arranged in a randomized complete block design in a 300 ha pasture interspersed with *S. palmetto* and *S. repens* at the A. Duda & Sons, Inc. citrus unit, 12 km south of La Belle, Hendry Co., FL. Traps were spaced about 20 m apart within blocks and blocks were separated by \geq 300 m. There were four blocks for experiment No. 1 and five for experiment No. 2. Total numbers of adult male and female *R. cruentatus* collected per trap for each 7-day trapping period were used for analysis. Data were transformed $(x + 0.5)^{0.5}$ and a Statistical Analysis System general linear models procedure (SAS Institute 1985) for unbalanced analysis of variance (ANOVA) was used. Untransformed means are presented. A Waller-Duncan *k*-ratio *t*-test ($k = 100$, $P \leq 0.05$) was used for mean separations.

Weevil Attraction to Fermentation Products and Cruentol

Chemicals were chosen for preliminary evaluations, with or without cruentol, for attractancy to *R. cruentatus* from a list of empirically-tested chemicals that (1) elicited *R. palmarum* electroantennogram (EAG) activity greater or equal to the response to 72 h fermented sap from African oil palm (Rochat 1987), and/or (2) from a list of characterized volatiles from fermented African oil palm sap (palm wine) (Nagnan et al. 1992), and/or (3) from a list of major volatiles from Sri Lankan arrack (coconut palm wine distillate) (Samarajeewa et al. 1981). The chemicals were obtained from Aldrich Chemical Co. (ACC), Eastman Kodak Co. (EKC), Fisher Scientific (FS), Matheson, Coleman & Bell Manufacturing Chemists (MCB), or Sigma Chemical Co. (SCC) and were \geq 85% chemically pure.

Preliminary studies included Y-tube screening of certain chemicals versus air (zero grade) for *R. cruentatus* attraction (N = 10 or 20 weevils of each sex) (see Weissling et al. 1993 for Y-tube methods). The following chemicals were tested in the Y-tube olfactometer: *cis*-2-hexen-1-ol (92%; ACC), citronellal (93%; EKC), 95% ethanol, ethyl butyrate (99%; ACC), ethyl isobutyrate (99%; ACC), ethyl (S)-(-)-lactate (98%; ACC), 1-hexanol (98%; EKC), isoamyl acetate (99%; SCC), and 2-methyl-1-propanol (99.9%; FS).

TABLE 1. ATTRACTION OF *RHYNCHOPHORUS CRUENTATUS* ADULTS TO FIELD TRAPS DESIGNED FOR LIVE INSECT CAPTURE AND BAITED WITH DIFFERENT PLANT TISSUES (2.5 KG) AND SYNTHETIC 5-METHYL-4-OCTANOL (RACEMIC MIXTURE OF CRUENTOL RELEASED AT 0.4 MG/DAY) IN HENDRY CO., FLORIDA FOR 7-DAY SAMPLING PERIODS.

Treatment	No. of Replicates	No. Weevils Per Trap (Mean + S.E.) ¹	
		Females	Males
<i>Experiment no. 1 (11-18 May 1992)</i>			
Chopped <i>Sabal palmetto</i> stem	4	3.8 ± 2.3ab	2.8 ± 1.3a
Chopped fresh sugarcane stem	4	5.8 ± 1.3a	2.5 ± 2.3a
Fresh pineapple (quartered)	4	2.3 ± 0.6ab	3.5 ± 0.9a
Chopped <i>Serrenoa repens</i> stem	4	0.0 ± 0.0b	0.0 ± 0.0b
<i>Experiment no. 2 (5-12 June 1992)</i>			
Chopped <i>Sabal palmetto</i> stem	4	15.4 ± 2.7a	6.9 ± 2.1a
Chopped fresh sugarcane stem	5	15.2 ± 6.1a	7.2 ± 4.0a
Fresh pineapple (quartered)	5	10.4 ± 2.5a	4.2 ± 1.2a
Chopped frozen sugarcane stem	4	7.0 ± 1.1a	3.8 ± 1.8a

¹Means followed by the same letter are not significantly different according to a Waller-Duncan *k*-ratio *t*-test on ($x + 0.5$)^{0.5} transformed data ($k = 100$, $P \leq 0.05$). Untransformed means are presented.

All chemicals except citronellal and 1-hexanol were screened for *R. cruentatus* attraction in combination with cruentol (0.4 mg/day) in single replicate field response trials during September 1992. In addition, the following chemicals were screened for attraction with cruentol; acetaldehyde (99%; FS), 1-butanol (99.9%; FS), *n*-butyl acetate (99%; ACC), ethyl acetate (99%; MCB), ethyl caprate (99%; ACC), ethyl caproate (99%; ACC), ethyl caprylate (99%; ACC), glacial acetic acid (99.7%; FS), hexanoic acid (99%; ACC), isobutyric acid (99%; ACC), isopropyl acetate (99.9%; EKC), isovaleric acid (99%; ACC), lactic acid (85%; FS), methanol (99%; FS), 3-methyl-1-butanol (99%; FS), 1-pentanol (99%; FS), octanoic acid (99.5%; ACC), 1-propanol (99%; FS), and α -terpineol (98%; ACC). One ml of each test chemical was placed in a 2-ml Gold Brand[®] ampule (designated AMP) with a 4 mm diam opening (Wheaton, Millville, NJ). The AMP was put into a 25.9 ml polystyrene vial with wires for hanging it in the trap.

The lethal trap described by Weissling et al. (1993) was used for these preliminary studies and modified for the subsequent replicated field studies. The trap consisted of a 19-liter black HDPE bucket with a composite PVC pipe lid. In the preliminary screenings, a 4.8-liter, tapered, beige, two-part flower pot (opening covered with a galvanized hardware mesh cone with 6 mm openings) was used to house the test stimulus. Tissue controls or test chemicals were placed inside the inverted flower pot and it was suspended 3 cm from the composite lid by two wires. The buckets were positioned in the field, filled with about 2 liters of tap water and 50-60 g of Alconox detergent (Alconox, Inc. New York, NY), and anchored with two metal bars through the composite lid into the ground. Traps were arranged in a completely randomized design in the pasture at A. Duda & Sons, Inc. and spaced ≥ 20 m apart.

Chemicals that elicited significant attraction from *R. cruentatus* in the Y-tube olfactometer and/or lured ≥ 6 weevils per trap after 7 days in the field during September 1992 were selected for a replicated field evaluation. These were ethanol, ethyl acetate,

ethyl butyrate, ethyl caproate, ethyl caprylate, ethyl isobutyrate, ethyl (S)-(-)-lactate, isopropyl acetate, lactic acid, *n*-butyl acetate, and octanoic acid. Each of these chemicals was tested using the AMP release device with or without 0.4 mg/d of cruentol.

Three other chemical release devices were used besides the AMP design to modulate release rates for selected chemicals: 1) 5 ml of test chemical in a 14.8 ml glass vial (OD x H = 21 x 70 mm) with a screw top with a 4 mm diam hole (designated 4DH), 2) 5 ml of test chemical in a 14.8 ml glass vial without a top (11.4 mm diam opening) (designated 4NT), and 3) 25 ml of test chemical in a 40.7 ml glass vial (OD x H = 28 x 108 mm) without a top (17.8 mm diam opening) (designated 11NT). Release rates were quantified gravimetrically at the end of each 7-day trapping period. Transportation of chemicals to and from the field was done with lids tightly sealed onto vials or with plastalina modeling clay (Van Aken International, Rancho Cucamonga, CA) which was used to plug ampules. Chemicals were placed in a 120-ml HDPE specimen container (Fisher Scientific Co., Pittsburgh, PA) (4DH, 4NT, and 11NT designs) or a 25.9 ml polystyrene vial (AMP design) which was suspended from the inside of the test stimulus container by wires.

Chemicals with relatively high weevil counts in the preliminary study were tested using at least one additional release device to the AMP device with and without cruentol. These chemicals and the release devices used were: ethanol (4DH, 11NT), ethyl acetate (4DH, 11NT), ethyl butyrate (4NT, 11NT), ethyl isobutyrate (4NT), and ethyl (S)-(-)-lactate (4NT).

The previously described lethal trap design was modified slightly for this experiment. The stimulus container was changed from the flower pot to a translucent white, 946 ml capacity, HDPE container (Fisher Scientific Co., Pittsburgh, PA). An 8.5-cm diam hole was cut in the lid of the container and a 9.5-cm diam piece of aluminum screening (1.5 mm square openings) was glued to the inside circumference of the lid. These lids were used to retain 0.5 kg of chopped *S. palmetto* stem and crown tissue within the inverted container. The controls were 0.5 kg of *S. palmetto* tissue with or without cruentol and an empty trap with or without cruentol. Traps of the old design with an inverted flower pot stimulus container with 1.5 kg of chopped *S. palmetto* tissue with or without cruentol were also included for comparison with previous studies of *R. cruentatus* attraction (Weissling et al. 1993, 1994).

Traps were spaced 20 m apart in a completely randomized design and treatments were replicated weekly for ten consecutive 7-day sampling periods starting 6 October 1992 and running through 15 December 1992 at the pasture at A. Duda & Sons, Inc. Total trap counts of *R. cruentatus* adults were transformed and analyzed as previously described.

The lethal trap was modified again for a field experiment to test the efficacy of cruentol and ethanol (AMP), ethyl acetate (4DH), ethyl butyrate (4NT), ethyl isobutyrate (AMP), ethyl (S)-(-)-lactate (4NT), and a combination of each of these chemicals released separately from 2 ml ampules in a 120 ml HDPE specimen holder. The stimulus container was changed to a translucent white, 4.9 liter capacity, HDPE container (Fisher Scientific Co., Pittsburgh, PA). A 13.0 cm diam hole was cut from the lid of the container and a 17.5 cm diam piece of galvanized hardware cloth (6 mm square openings) was glued to the inside circumference of the lid. These lids were used to retain 1.5 kg of chopped fresh sugarcane stem tissue within the inverted container which was suspended 2 cm from the opening of the bucket with a PVC crossbar capped with PVC cap and tee. A metal post was driven through the PVC tee into the ground to help prevent damage by raccoons and cattle. A bungee chord was used to secure the bottom of the trap to the post. The previously used PVC composite lid was not used (see Fig. 1C for approximate trap design). Sugarcane tissue with or without cruentol and an empty trap with or without cruentol served as controls. Traps were arranged in a randomized complete

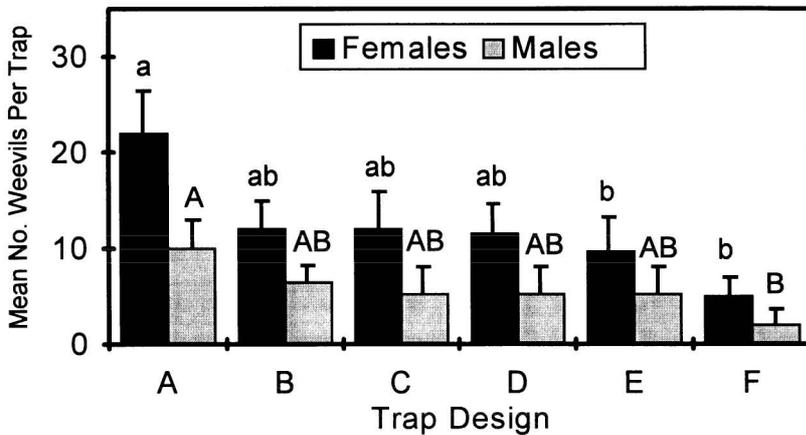
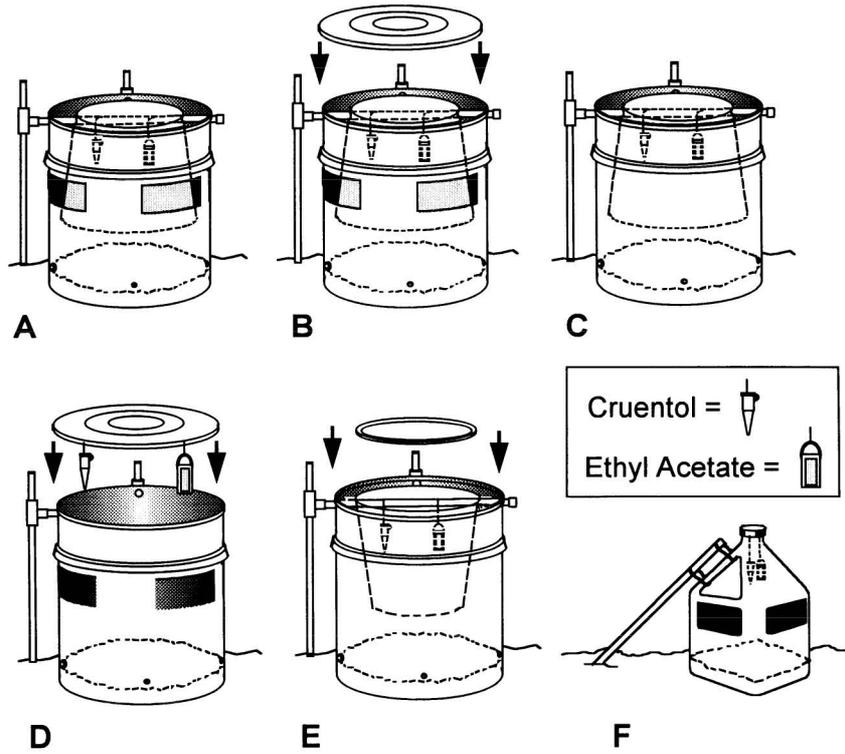


Fig. 1. Comparisons of mean 7-day trap counts of adult female and male *Rhynchophorus cruentatus* from six different semiochemically-mediated lethal traps, each baited with 0.4 mg/d 5-methyl-4-octanol (cruentol) and 742.3 mg/d ethyl acetate ($n = 7$). Means followed by the same letter are not significantly different according to a Waller-Duncan k -ratio t -test on $(x + 0.5)^{0.5}$ transformed data ($k = 100, P \leq 0.05$). Untransformed means are presented. Error bars indicate standard error of the mean.

block design in the pasture at A. Duda & Sons, Inc. and spaced ≥ 20 m apart within each block and blocks were separated by ≥ 50 m. Studies were conducted 29 June-6 July 1993 and 6-13 July 1993. Treatments within each block were rerandomized between sample periods. Adult male and female counts of *R. cruentatus* were transformed and analyzed as previously described.

Modifications of Semiochemically-Mediated Traps

Several modifications of the lethal trap were field-tested with cruentol and ethyl acetate (4DH release device with 8 ml of ethyl acetate) as the semiochemical bait to determine the best trap design for future research (Figs. 1A-F). The basic trap design involved the 19-liter black HDPE plastic bucket with drainage holes and contained detergent solution as previously described (Figs. 1A-E). In three designs, three 4 x 13 cm openings were cut and spaced 10 cm apart and 21 cm from the bottom around the circumference of the 19-liter bucket (Figs. 1A, B, D). The black lids for these 19-liter buckets were used to prevent excessive rainfall and tampering in two designs (Figs. 1B, D). In the design pictured in Fig. 1D, two eye bolts were attached through the lid for hanging baits. A translucent white, 4.9-liter, HDPE stimulus container was inverted and suspended 2 cm from the opening of the bucket with a PVC crossbar capped with a PVC cap and tee in three designs (Figs. 1A-C) and not inverted in one design (Fig. 1E). In this design (Fig. 1E), the bottom of the stimulus container was removed and the lid was used to keep rain and animals away from the semiochemical baits while allowing easier access for changing semiochemicals. PVC tees were attached through each bucket to a small PVC piece and capped at 90° from the crossbar. No crossbar was needed in the design pictured in Fig. 1D which had 2 PVC tees attached through the bucket at 90° from each other. Metal posts were driven through the PVC tees into the ground to anchor the traps and prevent tampering (Figs. 1A-E). One lethal trap design (Fig. 1F) consisted of a clean 3.78-liter HDPE milk container with three 4 x 10 cm openings cut 12 cm from the bottom. The trap was attached to a metal rod by the handle with duct tape. This design had an eye bolt through the top for suspending semiochemicals and was filled with about 600 ml of tap water and 20 g of Alconox detergent (Alconox, Inc. New York, NY).

Traps were arranged in a randomized complete block design in the pasture at A. Duda & Sons, Inc. and spaced ≥ 20 m apart within each block and blocks were separated by ≥ 50 m. The experiment was conducted 25 August to 1 September 1993 with 7 replicates. Adult male and female counts of *R. cruentatus* were transformed and analyzed as previously described.

RESULTS AND DISCUSSION

Field Response of Weevils to Fermenting Plant Tissues and Cruentol

In experiment No. 1, fermenting *S. palmetto* plus cruentol, sugarcane plus cruentol, and pineapple plus cruentol were equally attractive for *R. cruentatus* females, but sugarcane plus cruentol was more attractive than *S. repens* plus cruentol ($F = 4.43$; $df = 3$; $P = 0.0358$) (Table 1). Fermenting *S. palmetto* plus cruentol, sugarcane plus cruentol, and pineapple plus cruentol were equally attractive for *R. cruentatus* males, but more attractive than *S. repens* plus cruentol ($F = 4.44$; $df = 3$; $P = 0.0355$) (Table 1). The lack of attractancy of *S. repens* plus cruentol is probably indicative of a lack of moisture in this tissue which may have affected the quality of fermentation and the quantity of attractive volatiles released. *Serrenoa repens* is a host of *R. cruentatus* (R.M.G.-D. unpublished data, Giblin-Davis & Howard 1989) and under different condi-

tions from this experiment may release attractive volatiles. Sugarcane stem and fermenting pineapple syncarp are suitable larval food sources for *R. cruentatus*, although these plants are usually not observed as natural hosts (Giblin-Davis et al. 1989).

In experiment No. 2, cruentol plus fermenting *S. palmetto*, fresh and frozen sugarcane, and pineapple were equally attractive for *R. cruentatus* females ($F = 1.19$; $df = 3$; $P = 0.3537$) and males ($F = 0.45$; $df = 3$; $P = 0.7190$) (Table 1). This study shows that semiochemicals from fermentation (≤ 7 days) of a variety of plant tissues are equally suitable for attraction of *R. cruentatus* when cruentol is present. Our results are similar to those reported by Diegado & Moreno (1986) with *R. palmarum*. They found that tissue from fruits of papaya, banana, pineapple, and orange, and stem tissue from African oil and coconut palms were attractive to adults of *R. palmarum* (Diegado & Moreno 1986).

Weevil Attraction to Fermentation Products and Cruentol

An average of eight times more *R. cruentatus* adults were captured in lethal traps baited with *S. palmetto* tissue (0.5 kg) and cruentol than with tissue alone (0.5 kg) or cruentol alone; no weevils were captured in unbaited traps (Table 2). These results corroborate previous studies (Weissling et al. 1994). *Sabal palmetto* tissue (1.5 kg) with cruentol was nearly three times more effective for trap capture of *R. cruentatus* than 0.5 kg of tissue plus cruentol (Table 2). The palm tissue pieces for the 0.5 kg treatment were tightly packed into the 946 ml containers and retained with a fine screen which reduced the efficiency of volatile release. Fermenting *S. palmetto* tissue (0.5 and 1.5 kg) plus cruentol are equally attractive when used in the flower pot stimulus holder or in a 4.9-liter HDPE container with a coarse screen and greater surface area for volatile release (R.M.G-D., unpublished data).

None of the chemicals with cruentol were as effective as the 1.5 kg of *S. palmetto* tissue plus cruentol (Table 2). Also, none of the chemicals tested were attractive alone, although ethyl acetate (1971 mg/d) captured about 1 weevil per trap (Table 2). Adults of *R. cruentatus* responded to cruentol combined with either ethyl acetate (1843 and 482 mg/d) or ethyl (S)-(-)-lactate (4NT) equally as well as to *S. palmetto* (0.5 kg) plus cruentol (Table 2).

Ethyl (S)-(-)-lactate with cruentol was significantly more attractive to *R. cruentatus* adults when released from the 4NT device than from the AMP device (Table 2). Antennae from males of *R. palmarum* gave the strongest EAG response to ethyl lactate compared with 72 h fermented African oil palm sap (Rochat 1987). Isopropyl acetate elicited an EAG response from *R. palmarum* similar to African oil palm sap (72 h) (Rochat 1987). However, it was not attractive when released to *R. cruentatus* at 67 mg/d with cruentol compared with cruentol alone (Table 2). Ethanol elicited a small relative EAG response from *R. palmarum* male antennae (Rochat 1987) but was attractive at 34 and 564 mg/d with cruentol to *R. cruentatus* (Table 2).

Ethyl isobutyrate (30 mg/d) was attractive with cruentol, but not attractive when released at about 276 mg/d compared with cruentol alone (Table 2). Ethyl butyrate at 229 mg/d with cruentol was equally as attractive as ethyl isobutyrate at 30 mg/d with cruentol and slightly more attractive than ethyl butyrate at 17 or 449 mg/d with cruentol (Table 2). Ethyl butyrate was detected in the distilled extract of fermented African oil palm sap but not in methylene chloride extracted sap (Nagnan et al. 1992). Octanoic acid and its ethyl ester (ethyl caprylate), ethyl caproate, *n*-butyl acetate, lactic acid, and isopropyl acetate, which appeared attractive with cruentol in our preliminary studies, were not as attractive as cruentol alone at the rates used (Table 2).

Good chemically-mediated trapping of *R. cruentatus* was achieved with cruentol plus ethyl acetate (852 mg/d) and to a lesser degree with cruentol plus (S)-(-)-ethyl lactate (4NT), ethyl isobutyrate (40 mg/d), ethyl butyrate (255 mg/d), and ethanol (51 mg/d)

TABLE 2. ATTRACTION OF *RHYNCHOPHORUS CRUENTATUS* ADULTS TO LETHAL FIELD TRAPS IN HENDRY CO., FLORIDA BAITED WITH SELECTED CHEMICALS, CHOPPED *SABAL PALMETTO* STEM TISSUE, AND/OR SYNTHETIC 5-METHYL-4-OCTANOL (RACEMIC MIXTURE OF CRUENTOL RELEASED AT 0.4 MG/DAY) FOR 7-DAY SAMPLING PERIODS (6 OCTOBER THROUGH 15 DECEMBER 1992).

Treatments [Release Device] ¹	Cruentol (+ or -)	No. of Traps	Total No. Weevils/Trap (Mean ± S.E.) ²
Chopped <i>Sabal palmetto</i> stem (1.5 kg)	+	10	32.0 ± 5.1a
Chopped <i>Sabal palmetto</i> stem (0.5 kg)	+	10	11.7 ± 3.7b
Ethyl acetate [11NT] (1843.1 ± 124.4 mg/day)	+	8	9.9 ± 3.5bc
Ethyl (S)-(-)-lactate [4NT]* (hygroscopic; release rate not quantified)	+	4	9.5 ± 4.0bc
Ethyl acetate [4DH] (482.4 ± 21.9 mg/day)	+	7	8.6 ± 2.0bc
Ethyl isobutyrate [AMP]* (30.3 ± 2.5 mg/day)	+	8	7.1 ± 2.1cd
Ethyl butyrate [4NT]* (229.4 ± 35.9 mg/day)	+	4	6.8 ± 4.1cd
Ethyl acetate [AMP]* (107.8 ± 7.4 mg/day)	+	8	6.1 ± 2.2cde
Ethanol [AMP] (34.0 ± 2.4 mg/day)	+	8	5.8 ± 1.4cdef
Ethanol [11NT]* (564.1 ± 50.3 mg/day)	+	4	5.8 ± 1.7cd
Ethyl butyrate [AMP] (17.1 ± 1.0 mg/day)	+	8	4.4 ± 1.3defg
Chopped <i>Sabal palmetto</i> stem (1.5 kg)	-	10	4.3 ± 1.3defg
Ethyl butyrate [11NT]* (448.6 ± 87.8 mg/day)	+	4	3.5 ± 1.3defg
Ethyl caprylate [AMP]* (0.9 ± 0.5 mg/day)	+	5	3.0 ± 0.8defgh
Octanoic acid [AMP]* (hygroscopic; release rate not quantified)	+	5	2.8 ± 1.3fghi
Ethyl (S)-(-)-lactate [AMP]* (hygroscopic; release rate not quantified)	+	8	2.6 ± 0.8efghi

TABLE 2. (Continued)

Treatments [Release Device] ¹	Cruentol (+ or -)	No. of Traps	Total No. Weevils/Trap (Mean ± S.E.) ²
Isopropyl acetate [AMP]* (67.0 ± 1.9 mg/day)	+	5	2.4 ± 0.8ghij
Ethanol [4DH]* (169.9 ± 23.5 mg/day)	+	4	2.3 ± 1.0ghijk
Ethyl caproate [AMP]* (2.5 ± 0.1 mg/day)	+	5	1.6 ± 0.4ghijkl
Chopped <i>Sabal palmetto</i> stem (0.5 kg)	-	10	1.4 ± 0.7hijklm
No treatment	+	9	1.2 ± 0.7hijklm
Ethyl isobutyrate [4NT]* (275.6 ± 26.3 mg/day)	+	4	1.0 ± 1.0ijklm
Ethyl acetate [11NT] (1971.4 ± 156.5 mg/day)	-	8	0.8 ± 0.5ijklm
<i>N</i> -butyl acetate [AMP]* (14.6 ± 0.7 mg/day)	+	5	0.4 ± 0.4klm
Lactic acid [AMP]* (hygroscopic; release rate not quantified)	+	5	0.4 ± 0.2jklm
Ethyl acetate [4DH] (509.9 ± 38.3 mg/day)	-	7	0.1 ± 0.1lm
Ethanol [AMP] (33.6 ± 2.0 mg/day)	-	8	0.1 ± 0.1lm
Ethyl butyrate [AMP] (17.8 ± 1.0 mg/day)	-	8	0.1 ± 1.0lm
No treatment	-	10	0.0 ± 0.0m

¹Chemicals were released from one or more of the following different kinds of containers to modulate release rates; (AMP) = 1 ml of test chemical in a 2 ml Gold Brand ampule with a 4 mm diam opening (Wheaton, Millville, NJ), (4DH) = 5 ml of test chemical in a 14.8 ml glass vial (OD x H = 21 x 70 mm) with a screw top with a 4 mm diam hole, (4NT) = 5 ml of test chemical in a 14.8 ml glass vial without a top (11.4 mm diam opening), and (11NT) = 25 ml of test chemical in an 40.7 ml glass vial (OD x H = 28 x 108 mm) without a top (17.8 mm diam opening). Release rates were quantified gravimetrically.

Treatments ranked according to total weevils captured per trap.

²Means followed by the same letter are not significantly different according to a Waller-Duncan *k*-ratio *t*-test on (x + 0.5)^{0.5} transformed data (*k* = 100, *P* ≤ 0.05). Untransformed means are presented.

*No male or female weevils were captured using this same treatment but without cruentol. Data for the treatment without cruentol is not shown but is equal to the no treatment without cruentol.

(Table 3). Release rates from the same release devices were higher in this experiment (Table 3) than in the previous experiment (Table 2) because of seasonally higher ambient temperatures. The ethyl acetate release device (4DH) ran dry at about 6 days under these summer conditions and data in Table 3 probably underestimate the 7-day weevil counts. None of the rest of the chemicals tested ran dry during the experiment. Sex ratios were skewed towards females when cruentol was present, but not when either *S. palmetto* or sugarcane was used without pheromone (Table 2 data not shown, Table 3).

TABLE 3. ATTRACTION OF *RHYNCHOPHORUS CRUENTATUS* ADULTS TO LETHAL FIELD TRAPS IN HENDRY CO., FLORIDA BAITED WITH SELECTED CHEMICALS, CHOPPED SUGARCANE STEM TISSUE, AND/OR SYNTHETIC 5-METHYL-4-OCTANOL (RACEMIC MIXTURE OF CRUENTOL RELEASED AT 0.4 MG/DAY) FOR 7-DAY SAMPLING PERIODS (29 JUNE-6 JULY 1993 AND 6-13 JULY 1993).

Treatments [Release Device] ¹	Cruentol (+ or -)	No. of Replicates	No. Weevils Per Trap (Mean ± S.E.) ²	
			Females	Males
Chopped sugarcane (1.5 kg)	+	10	37.0 ± 6.4a	20.3 ± 3.9a
Ethyl acetate [4DH] (852.4 ± 34.9 mg/day)	+	10	26.7 ± 3.2b	9.7 ± 1.8b
Combination*	+	9	21.7 ± 3.1bc	7.7 ± 2.0bc
Ethyl (S)-(-)-lactate [4NT] (hygroscopic; release rate not quantified)	+	10	16.0 ± 2.0cd	6.5 ± 1.1bc
Ethyl isobutyrate [AMP] (40.2 ± 1.3 mg/day)	+	10	13.1 ± 2.4de	5.8 ± 1.5c
Ethyl butyrate [4NT] (254.5 ± 13.6 mg/day)	+	10	13.1 ± 1.6de	4.4 ± 1.1c
Ethanol [AMP] (51.0 ± 2.0 mg/day)	+	10	10.3 ± 1.8ef	5.1 ± 0.9c
Chopped sugarcane (1.5 kg)	-	10	5.3 ± 1.7g	4.9 ± 1.1c
No treatment	+	10	5.6 ± 0.6fg	1.8 ± 0.5d
No treatment	-	10	0.1 ± 0.1h	0.0 ± 0.0e

¹See legend of Table 2 for description of release devices. Treatments ranked according to total weevils captured per trap.

²Means followed by the same letter are not significantly different according to a Waller-Duncan *k*-ratio *t*-test on $(x + 0.5)^{0.5}$ transformed data ($k = 100$, $P \leq 0.05$). Untransformed means are presented.

*Combination = ethanol (48.4 ± 4.9 mg/d), ethyl acetate (131.2 ± 1.9 mg/d), ethyl butyrate (34.0 ± 7.7 mg/d), ethyl isobutyrate (39.6 ± 1.0 mg/d), and ethyl lactate (release rate unknown) each released separately from an AMP device.

Ethyl acetate was one of the most attractive chemicals that we tested with cruentol (Tables 2,3). Trap counts appeared to be dose related for ethyl acetate and cruentol. However, there were no significant differences among the 108, 482, and 1843 mg/d release rates for ethyl acetate with cruentol (Table 2). Ethyl acetate, ethyl lactate, and ethanol were among the list of major volatiles identified by Samarajeewa et al. (1981) from coconut palm wine distillates and arrack and performed well in our study when released with cruentol (Tables 2, 3). The other major components, acetaldehyde, amyl-alcohol, methanol, 2-methyl-1-propanol, and 1-propanol were not attractive with cruentol to *R. cruentatus* at the rates tested in our study (unpublished data). Samarajeewa et al. (1981) found ten-fold increases in the concentrations of ethyl acetate and ethyl lactate

in naturally-fermented samples of coconut sap compared with controlled fermentations with commercial strains of *Saccharomyces* yeasts. The role of mixed microflora in the qualitative and quantitative profiles of host-plant fermentation products for attraction of *Rhynchophorus* spp. has not been studied. It could prove interesting. Also, the role of host-plant volatiles in host apparency to *Rhynchophorus* spp. has not been studied. It could be important in understanding management practices that encourage red ring nematode transmission in African oil palm and coconut palm plantations by *R. palmarum* or establishment of other species of *Rhynchophorus* in host palms.

The combination treatment [ethanol + ethyl acetate + ethyl butyrate + ethyl isobutyrate + (S)-(-)-ethyl lactate] with cruentol was as effective for the capture of *R. cruentatus* as any of the individual components with cruentol at the rates tested (Table 3). This suggests that an important class of semiochemicals may be missing or that further optimization of release rates and ratios is needed. Jaffé et al. (1993) have recently shown that a mixture of 68% ethanol, 27% ethyl acetate, and 5% pentane was as attractive to *R. palmarum* in a laboratory movement assay as odors from red ring-diseased coconut palm stem. Unfortunately, 2-methyl-5(E)-hepten-4-ol (male-produced aggregation pheromone of *R. palmarum*) plus ethanol, ethyl acetate, isoamyl acetate, 3-methyl-1-butanol, hexanal, or pentane alone (release rates undetermined) and as mixtures were not effective in the field.

Modifications of Semiochemically-Mediated Traps

There were no significant differences in the release rates of ethyl acetate among the six different trap designs ($F = 0.49$; $df = 5$; $P = 0.7792$) and the pooled release rate was 742.3 ± 7.9 mg/d (mean \pm S.E.). Trap counts of females and males of *R. cruentatus* were equal for all but one of the five 19-liter black bucket designs (Fig. 1). The design pictured in Fig. 1E did not catch as many males and the 3.78-liter milk container design (Fig. 1F) did not catch as many females or males as the 19-liter black bucket design pictured in Fig. 1A. Future research with semiochemically-mediated trapping of *R. cruentatus* should utilize the designs pictured in Figs. 1B,D because these traps are the simplest to make and use. The trap designated in Fig. 1B could be used when a trap baited with tissue is to be compared with a trap (Fig. 1D) baited with only chemicals.

Currently, we are identifying and quantifying EAG active semiochemicals for *R. cruentatus* from perfusions of fermenting *S. palmetto*, sugarcane, and pineapple. Work is in progress on the optimization of ratios of plant-derived semiochemicals to be used with cruentol in a chemically-mediated trap for *R. cruentatus* that is equal to, or better than, fermenting sugarcane or *S. palmetto* tissue plus cruentol.

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SCIENTIFIC NOTE

CALLING BEHAVIOR OF THE MOTH *COPITARSIA CONSUETA*
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Copitarsia consueta (Walker) is a noctuid moth distributed across Mexico and Central and South America (Gutierrez & MacGregor 1985, Castillo & Angulo 1991). In Mexico *C. consueta* is an important pest of cabbage, although on occasion it infests other cultivated plants (Gutierrez & MacGregor 1985). Few studies have been carried out on the biology and behavior of this species. Recently Rojas et al. (in press) have studied its mating behavior and the chemical identification of the female sex pheromone is in progress. The purpose of this study was to determine the effect of age, mating, and photoperiod on the calling behavior of *C. consueta*.

The colony of *C. consueta* was started from 30-40 larvae collected from cabbage in the field. The larvae were reared on an artificial diet (Rojas et al., in press) at 25 ± 2 °C, $65 \pm 5\%$ RH and reversed 14: 10 (L:D) photoperiod with scotophase beginning at 0600 hours.

The females were held singly in plastic containers (5 x 7 cm) and observed with a red light (7.5-w bulb) at 15 min intervals during each scotophase until the last female stopped calling in the following photophase. Calling females were recognized by the extended terminal abdominal segments. The daily onset of calling time (time after lights off), and length of calling of each female were recorded.

In order to determine the effect of age on calling behavior, 28 virgin females were observed during the first six scotophases at 25 ± 2 °C, $65 \pm 5\%$ RH and reversed 14: 10 (L:D) photoperiod.

The influence of mating on calling behavior was studied in 17 females. Three-day-old moth pairs were placed in glass cages and observed until copulation occurred. After mating, the females were placed individually into plastic containers and observed during the following three scotophases at 25 ± 2 °C, $65 \pm 5\%$ RH, and reversed 14: 10 (L:D) photoperiod.

The influence of photoperiod on calling of virgin females was studied in virgin females. Three groups of 24 pupae were conditioned under three different photoperiodic regimes (16L: 8D, 14L: 10D, and 12L: 12D). After emergence the adults were maintained under similar photoperiodic regimens. At each photoperiod, observations were made during the fourth scotophase at 25 ± 2 °C and $65 \pm 5\%$ RH.

The data were log transformed so that the variance among means was stabilized, subsequently subjected to analysis of variance (ANOVA). The level of probability considered significant was $P < 0.05$.

Of the 28 females observed, no individual called the day following their emergence, the most females (23) called for the first time during the second day, and the rest (5) the third day after eclosion (2.2 ± 0.39 days). Because not all individual called at the same chronological age, we used the calling age (Turgeon & McNeil 1982) for comparing calling behavior. Calling behavior occurs in the latter third of the scotophase. The

TABLE 1. CHANGES IN MEAN ONSET OF CALLING TIME AND MEAN LENGTH OF CALL WITH CALLING AGE OF *C. CONSUETA*.

Calling Age (day)	Mean (\pm SD) Onset Calling Time (min after lights off)	Mean (\pm SD) Length of Calling Period (min)
1	444 \pm 29	77 \pm 42
2	415 \pm 20	138 \pm 40
3	391 \pm 20	179 \pm 35
4	391 \pm 40	208 \pm 42
5	386 \pm 41	210 \pm 54

duration of calling bouts increased significantly with age although the number of bouts did not change significantly ($F = 0.66$, $df = 4, 130$; $P > 0.05$) with calling day. The mean daily onset of calling time differed significantly with age ($F = 17.10$; $df = 4, 130$; $P < 0.001$). As moths aged, they initiated calling earlier in the scotophase (Table 1). The mean length of the daily calling period varied significantly with age (Table 1). Other females had a longer duration of calling ($F = 43.3$; $df = 4, 135$; $P < 0.01$), and began calling earlier and with prolonged calling bouts.

The dissection of moths showed that 16 of 17 females had mated. A general trend was observed, as the time after copulation increased, the calling began earlier ($F = 5$; $df = 2, 42$; $P < 0.05$) and lasted longer ($F = 4.71$; $df = 2, 42$; $P < 0.05$). Thirteen females resumed the calling during the first scotophase after copulation. The mean onset of calling time was 422 ± 27 min, and the mean length of calling period was 136 ± 55 min. Two days after mating 15 females called. The calling began at 414 ± 33 min and had a duration of 171 ± 67 min. Seventy-two h after copulation 16 females called, the mean onset of calling time was 379 ± 29 min, and the mean length of calling period was 211 ± 70 min. The mean length of the non-calling period in *C. consueta* was 30 ± 10 h.

The mean onset of calling time differed significantly among the three photoperiod regimens ($F = 111.7$; $df = 2, 69$; $P < 0.001$). Females called earlier under short photophase conditions. The calling began at 318 min in the females maintained at 16L:8D, whereas moths that adapted at 14L:10D and 12L:12D called at means of 390 and 400 min after "light off", respectively. The differences between 14L:10D and 12L:12D are not significant ($P > 0.05$). The mean length of calling period varied significantly among the three groups of females held under different photoperiodic regimens ($F = 16$; $df = 2, 69$; $P < 0.01$). The longer the scotophase, the longer the time females spent calling. The calling duration for females maintained at 16L:8D was 156 min, whereas in photoperiodic regimens of 14L:10D and 12L:12D the females called 174 and 246 min, respectively.

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SUMMARY

The influence of age, mating and photoperiod on calling behavior of the moth *Copitarsia consueta* was investigated under laboratory conditions.

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EFFECTS OF FEEDING OF BROAD MITE (ACARI: TARSONEMIDAE) ON VEGETATIVE PLANT GROWTH

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The broad mite, *Polyphagotarsonemus latus* (Banks), is a polyphagous pest that has been reported on more than 100 different plant species including crops such as cotton, beans, citrus, potatoes, mango, papaya and several ornamental plant species (Schoonhoven et al. 1978, Beattie & Gellatley 1983, Aubert et al. 1981, Hooper 1957, Nemestothy et al. 1982, Laffi 1982). Because of this mite's short generation time (approx. 5 days), high fecundity, small size and protected habitat, the injury it produces is often confused with diseases and phytotoxicity. Jeppson et al. (1975) reported that some of the plant symptoms following broad mite attack were formerly considered to be due to various diseases including plant viruses (Aubert et al. 1981). Broad mite damage has also been confused with herbicide toxicity or micronutrient deficiency (Beattie & Gellatley 1983, Cross & Bassett 1982).

Gerson (1992) stated that the variety of symptoms on different hosts reflects specific plant reactions to the pest's feeding and putative toxins. Broad mites reduce market yield and injure plants by reducing and deforming leaves, flowers and fruits (Schoonhoven et al. 1978, Gerson 1992). Plants under heavy attack cease growing and die (Moutia 1958). Despite extensive descriptions of broad mite injury (Gerson 1992) the quantitative relationship between broad mite injury and reduction of vegetative plant growth has not been studied extensively.

The objective of this study was to relate broad mite injury to vegetative growth of potato (*Solanum tuberosum* L.), bean (*Phaseolus vulgaris* L.), lime [*Citrus aurantifolia* (Christ.) Swingle] and sour orange (*Citrus aurantium* L.).

Bean, potato, lime and sour orange plants were individually grown in 1 liter containers and kept in an air conditioned greenhouse with a temperature of $26 \pm 2^\circ\text{C}$ and relative humidity of 85-90%. Plant age at infestation was 3 and 4 weeks for bean and potato, respectively, and 3 and 4 months for lime and sour orange, respectively. Broad mite stock colonies were reared on pinto bean plants maintained under similar conditions as the treatment plants. Ten broad mite males and female pupae were individually transferred to all apical leaves of the treated plants. A set of uninfested plants of each species

was used as a control. The number of motile mites present on a bean and potato upper leaf or on a lime and sour orange apical shoot were counted 1 week after infestation and infested again if less than 20 mites appeared per leaf.

The number of leaves per plant and plant height was assessed weekly for 4 consecutive weeks. Four weeks after infestation, leaf damage indices (Table 1), leaf area, fresh

TABLE 1. EVALUATION SCALES FOR BROAD MITE INJURY TO POTATO, BEAN, LIME AND SOUR ORANGE.

Plant Species	Injury Level	Type of Injury
Potato	0	No injury
	1	Light injury, some leaves curling, leaves show bronzing.
	2	Moderate injury, curling, leaves show bronzing.
	3	Heavy, leaf curled, necrosis, wilting.
	4	Death of terminal and lateral growing points.
Bean	0	No Injury
	1	Distal and adjacent leaves with a few faint silver spots.
	2	Shoot and/or nearby leaves slightly deformed or curled.
	3	Leaves curled, lower leaf surface, silvery.
	4	Leaves curled, necrotic spots, trifoliate upper leaves, severely deformed or reduced in size.
Lime	0	No injury, no mites observed.
	1	Mites observed, leaf dark green.
	2	Leaf margins slightly rolled downward, leaf yellowish-green.
	3	Leaf light yellow and withering; shoot deformed.
	4	Leaves turning brown, defoliation, death of shoots.
Sour Orange	0	No Injury
	1	Distal leaves slightly deformed.
	2	Distortion of leaves and/or shoots.
	3	Shoots completely deformed.
	4	Distortion of terminal and lateral growing points; death of shoots.

weight and dry weight of leaves were estimated. Leaf area was determined with a leaf area meter (LI-COR, Lambda Instruments Corporation, Lincoln, NE) and water content was determined by subtracting leaf dry weight from leaf fresh weight. Amount of vegetative growth was determined by dividing the dry leaf weight by the total leaf area. The increases in height and number of leaves were determined by subtracting the plant height and number of leaves observed on a given week from the numbers recorded during the prior week.

Differences in these parameters for infested and uninfested plants were determined by student t-test and a linear regression model (SAS 1987) was used to determine the relationship between leaf injury index and leaf area, number of leaves or shoots per plant, plant height and water content.

The responses of the different plant species to broad mite injury varied. Of the physical characteristics studied, leaf area was influenced most by broad mite injury, followed by water content, plant height and numbers of leaves per plant.

Potato. Mean height of plants exposed to broad mite was significantly less than the control plants through week 4 of the post-exposure period. Two weeks after infestation, more leaves were observed on the infested plants than on the control plants. This plant response might indicate that the broad mite reduces apical dominance on the infested plant two weeks after infestation, inducing lateral shoot growth. The number of leaves produced in infested or uninfested plants was similar 3-4 weeks after treatment. The average leaf area of uninfested potatoes was 2.01 times greater than the infested ones (Table 2). The results of the regression analysis of the visual injury index on vegetative growth are shown in Table 3. The slopes of the significant regressions were all negative, showed a reduction on potato height and leaf area, but indicated a poor fit ($r^2 = 0.14$ and 0.41 , respectively). The levels of significance associated with number of leaves per plant and water content were inadequate ($P > 0.05$). Additional studies with other variables, e.g., photosynthesis and nitrogen leaf content (Schaffer et al. 1986, Van de Vrie et al. 1972) are necessary to confirm these results.

TABLE 2. MEAN LEAF AREA AND LEAF WATER CONTENT FROM FOUR PLANT SPECIES INFESTED WITH BROAD MITE.¹

Plant Species	Treatment	Leaf Area ² (cm ² ± SE)	Leaf Water Content ² (g ± SE)
Potato	Infested	9.85 ± 1.74	6.63 ± 1.25
	Uninfested	19.83 ± 1.81***	7.58 ± 1.34 n.s.
Bean	Infested	36.21 ± 2.25	7.69 ± 0.85
	Uninfested	47.26 ± 3.34**	6.36 ± 0.42 n.s.
Lime	Infested	51.10 ± 8.76	1.00 ± 0.17
	Uninfested	146.24 ± 14.71*****	2.78 ± 0.31*****
Sour Orange	Infested	36.91 ± 3.33	0.55 ± 0.07
	Uninfested	52.72 ± 5.99*	1.17 ± 0.15*****

¹Numbers followed by an asterisk were significantly different; t-test;
*P=0.02; **P=0.01; ***P=0.003; ****P=0.001; *****P=0.0001.

Bean. Exposure of bean to broad mites resulted in an immediate increase in plant height 1 week after exposure compared to control plants, but the infested plants were shorter than the control plants 2 through 4 weeks after treatment. The number of leaves per plant increased for infested plants two weeks after treatment and declined sharply 4 weeks after treatment for control and infested plants. In general, there were no differences in the amount of vegetative growth between infested and non-infested plants, but the mean leaf area was 1.30 times greater in non-infested plants than in the infested plants (Table 2). The results from this experiment indicated a significant ($r^2 = 0.43$; $P < 0.0001$) relationship between leaf area and injury level, and a poor fit between the visual injury index and number of leaves per plant ($r^2 = 0.12$; $P < 0.05$) (Table 3).

Lime. All lime plants exposed to broad mites grew and exhibited similar vegetative growth increases in comparison with the control plants. More leaves were observed on non-infested plants than on infested ones. The leaf area and water content per leaf was higher on mite-free lime plants than on mite-infested plants (Table 2). Linear regression analysis showed that the slopes of regression lines were negative for the different parameters, but the relationships were only significant for lime leaf area, water content and broad mite injury ($r^2 = 0.53$; $P < 0.001$ and $r^2 = 0.49$; $P < 0.0001$) (Table 3).

Sour Orange. No vegetative growth was observed for infested and non-infested sour orange plants 2 weeks and 5 weeks after treatment. Broad mite infested plants showed no increase in number of leaves 3 weeks after infestation but leaf number increased thereafter. The leaf area and water content were higher for the mite-free sour orange plants than for the infested ones (Table 2). However, a significant but poor relationship ($P < 0.05$; $r^2 = 0.20$) was only obtained between leaf water content and broad mite injury (Table 3). The results of the regressions were not significant for leaf area, leaves per plant and height.

Our investigation has shown that broad mite feeding appears to be an important factor in development of leaf area and amount of leaf water content of the plant species

TABLE 3. RELATIONSHIP BETWEEN BROAD MITE VISUAL INJURY INDEX (X) AND VEGETATIVE GROWTH OF FOUR HOST PLANTS.

Host Plant	y	a + bx	r^2	P	F
Potato	Height (cm)	23.16-1.31x	0.14	**1	8.54
	Leaves/plant	10.39-0.49x	0.03	ns	1.54
	Leaf area(cm ²)	21.12-3.49x	0.41	***	33.19
	Water content(g)	8.93-0.83x	0.06	ns	2.90
Bean	Height (cm)	25.26-0.32x	0.01	ns	0.67
	Leaves/plant	4.51-0.44x	0.12	**	6.48
	Leaf area(cm ²)	50.08-7.17x	0.43	***	36.17
	Water content(g)	6.94-0.18x	0.03	ns	0.19
Lime	Height (cm)	81.03-0.92x	0.01	ns	0.78
	shoots/plant	11.80-1.12x	0.01	ns	0.17
	Leaf area(cm ²)	151.00-40.81x	0.53	***	75.28
	Water content(g)	2.85-0.76x	0.49	***	63.21
Sour Orange	Height (cm)	35.29-0.99x	0.03	ns	1.55
	Leaves/plant	21.07-0.76x	0.07	ns	3.56
	Leaf area (cm ²)	45.19-2.40x	0.02	ns	1.2
	Water content (g)	0.68-0.15x	0.20	**	10.64

¹Significant level of regression; ns, not significant, $P < 0.05$ **, $P < 0.005$ ***, $df = 48$.

studied. With the exception of potato, broad mite injury does not show a significant relationship with plant height or the number of leaves per plant. Differences in injury among the different plant species may be due to the ability of different species (i.e., woody plants versus herbaceous plants) to regenerate new leaves, to form new shoots if the species is injured or to the inherent ability of broad mites to induce damage response from these plant species. These hypotheses merit further research. We propose the delay in plant growth for some species was caused by reduction of photosynthetic area, stomatal conductance and leaf transpiration (Schaffer et al. 1986) due to feeding by broad mite. Because all experiments were terminated 5 weeks after exposure period, no effect on later stages of plant growth or yield was determined.

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SUMMARY

Injury of vegetative growth of plants by the broad mite, *Polyphagotarsonemus latus* (Banks) has become a significant problem worldwide. A visual rating system was used to relate broad mite injury to potato, bean, lime and sour orange leaf area, height, water content and number of leaves per plant. In general, leaf area and leaf water content was reduced for most of the infested plant species, but the number of leaves per plant and plant height was not significantly related to broad mite injury.

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NATURAL PARASITISM OF *SPODOPTERA FRUGIPERDA*
AND *HELI COVERPA ZEA* (LEPIDOPTERA: NOCTUIDAE)
EGGS IN CORN BY *TRICHOGRAMMA PRETIOSUM*
(HYMENOPTERA: TRICHOGRAMMATIDAE) IN BRAZIL

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The efficiency of field released *Trichogramma* spp. is dependent upon the population dynamics of the targeted host, the host plant phenology and the density of the host insect. Population dynamics of corn pests have been studied in the State of São Paulo (Carvalho 1970, Lara & Silveira Neto 1978), but almost all the data are related to light trap captures of adults (Deary et al. 1964, Everly & Barret Junior 1965, Silveira Neto et al. 1979) with only a few studies related to egg dynamics of corn pests. Latin American literature concerning *S. frugiperda* is reviewed by Andrews (1988). There are only a few records of natural parasitization of *S. frugiperda* eggs by *Trichogramma* species (Sá 1991), and these indicate that the levels achieved are low. Conversely, natural parasitization of *H. zea* by *Trichogramma* spp. has been reported to reach high levels by Vargas & Nishida (1982). Factors affecting the *Trichogramma* parasitism of *H. zea* were reviewed by Oatman (1966) in the USA.

This paper reports on the population dynamics of eggs of *S. frugiperda* and *H. zea*, and their parasitism by *T. pretiosum*. They are correlated with the phenology of the dent corn variety C555 to determine the best conditions for conducting field releases of the parasitoid.

The study was conducted in three field corn plots located in Santo Antônio de Posse, State of São Paulo planted in November 1989 and March and May 1990, respectively. Each plot was about 10,000 m². Sampling was done every third day, starting about 11 days after planting and concluding just before harvest. At each sampling date, groups of 10 plants adjacent to each other were randomly taken for analysis at each of 10 sites, also randomly chosen within each plot. The whole plant was surveyed for eggs of *S. frugiperda*, whereas only the tips of the silks were inspected for eggs of *H. zea*.

In the laboratory, *H. zea* and *S. frugiperda* eggs were counted and incubated in Petri dishes at 25±1°C. Because *S. frugiperda* egg masses contain more than one egg layer, the number of eggs in the upper layer was counted and this value was then multiplied by the number of layers; the exposed single egg layers were added according to the method proposed by Leuck & Perkins (1972) and Nalin (1991). The parasitoid was identified by Dr. R.A. Zucchi, Department of Entomology, Escola Superior de Agricultura "Luiz de Queiroz", University of Sao Paulo and the specimens were deposited at the Department of Entomology *Trichogramma* strain collection.

S. frugiperda egg masses were found in all experimental plots, starting approximately 11 days after germination, between December 1989 and mid July 1990 (Fig. 1-A). The peak egg populations occurred 12 to 71 days after germination (Fig. 1-A₂ and A₃). The

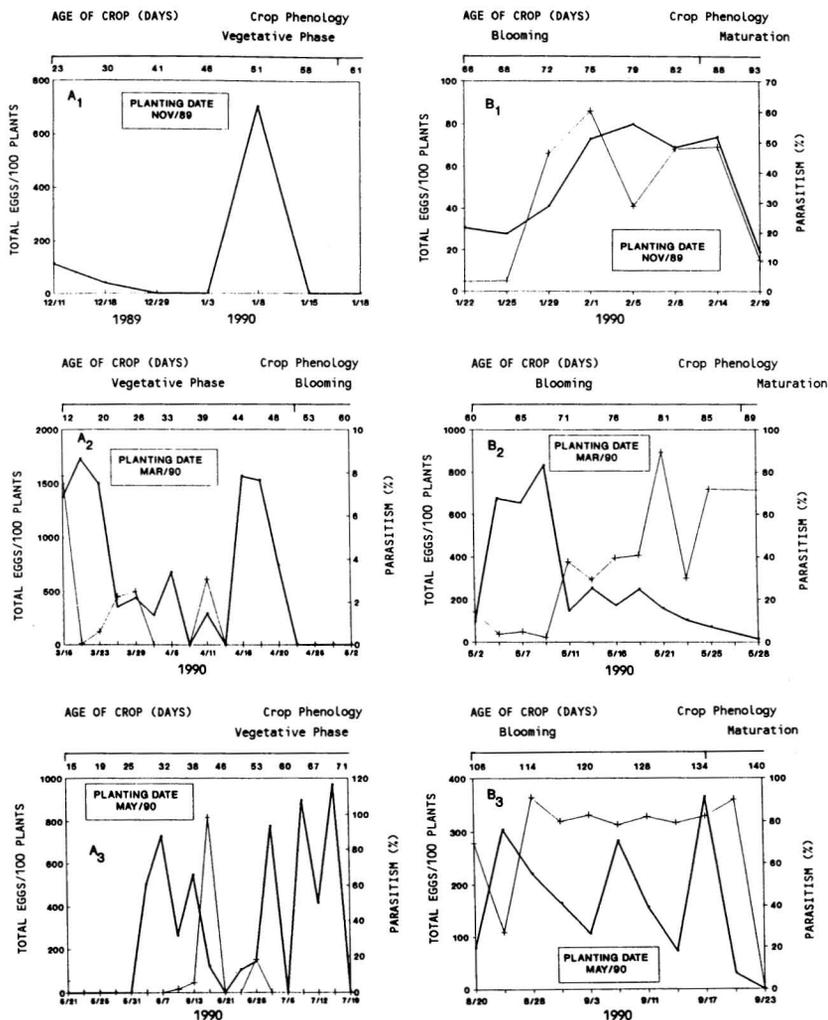


Fig. 1. Numbers of *Spodoptera frugiperda* eggs in (A₁, A₂ and A₃) and *Helicoverpa zea* eggs (B₁, B₂ and B₃) in the corn variety C555 and the percent parasitism by *Trichogramma pretiosum* in Santo Antônio de Posse - State of São Paulo, Brazil.

—————total eggs, +-----+ parasitism (%)

highest egg population occurred when corn (variety C555) was planted in March 1990 (Fig. 1-A₂). The thermal temperature requirements suggested the possible occurrence of 2 generations during the crop season (Sá 1991).

Natural parasitism of *S. frugiperda* by *T. pretiosum* was observed only when corn was planted in March 1990 or later. The highest two levels occurred in March and June 1990. In the sample taken in June 1990, 98.3% of the 120 eggs collected were parasitized (Fig. 1-A₃). However, this should be considered as an exception, because those eggs

were laid in a single layer, whereas the normal oviposition of this pest is done in 2 or 3 overlapping layers. Parasitism was observed between 12 and 53 days after the crop was planted (Fig. 1-A). According to Andrews (1988), Loya (1978) attempted to control *S. frugiperda* with mass releases of an unspecified species of *Trichogramma* without success. Parasitism levels of 0.18% in fields where no releases were made increased to only 0.56% in treated fields. Another attempt to use mass releases of *Trichogramma* spp. in Tamaulipas resulted in less than 15% average parasitism (Peralta et al. 1981).

H. zea was also found in all experimental plots, when the first silks appeared [January and September 1990 (Fig. 1-B)]. The first eggs were found 66 days after the crop was planted (Fig. 1-B₁). As observed for *S. frugiperda*, the highest *H. zea* egg populations occurred when corn (variety C555) was planted in March and May 1990 (Fig. 1-A₂ and A₃). The thermal temperature requirements suggested the possible occurrence of 1 or 2 *H. zea* generations during the crop season (Sá 1991). These results are similar to those reported by Trujillo (1942).

Natural parasitism of *H. zea* eggs by *T. pretiosum* was relatively high, reaching 90.1% in August 1990 (Fig. 1-B₃). Frequently, more than 50% of the eggs were parasitized. However, most often the rates of parasitism peaked after the *H. zea* population had reached high levels and larval damage to silks had already occurred (Fig. 1-B).

The unsuitability of eggs of *S. frugiperda* as hosts for *T. pretiosum* has been previously reported in the literature (Sparks 1979, Pinto et al. 1986). Because the eggs are laid in overlapping layers and are covered with large amounts of scales, *Trichogramma* spp. are prevented from reaching many of the eggs in the mass. Noldus (1989) verified that eggs of *S. frugiperda* are rarely attacked by *T. pretiosum*, and that *T. pretiosum* does not respond to chemical compounds produced by *S. frugiperda*.

High levels of natural parasitism of eggs of *H. zea* by *T. pretiosum* have also been reported previously on different crops (King et al. 1986, Ridgway et al. 1988, King & Coleman 1989). Noldus (1989) reported that *T. pretiosum* respond positively to chemicals produced by *H. zea*, which is considered a preferred host for the parasitoid.

The results of this study indicate that *T. pretiosum* is not an effective parasitoid of *S. frugiperda*, and its practical use under field conditions for control of this species is not very promising. Conversely, it seems that timely periodical releases of *T. pretiosum* for the control of *H. zea* might result in effective control. Further studies should be conducted to compare the effectiveness of introduced and native biotypes and to determine details of the releasing process, i.e., the appropriate timing for releases and number of parasitoids to be released. The results suggest that the field releases of *Trichogramma* should be done when the first silks appear (Fig. 1-B).

SUMMARY

Natural parasitization of *Spodoptera frugiperda* (J. E. Smith) and *Helicoverpa zea* (Boddie) eggs by *Trichogramma* spp. occurred in all corn test plots. The highest levels occurred when corn was planted in March. Parasitism of *S. frugiperda* by *Trichogramma pretiosum* Riley was usually less than 20%, while parasitism of eggs of *H. zea* commonly exceeded 50%. Parasitism of singly laid eggs of *H. zea* was higher than eggs of *S. frugiperda*, which are laid in overlapping layers and protected by scales.

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BOOK REVIEWS

SCOBLE, N. J. 1992. *The Lepidoptera. Form, Function and Diversity*. Oxford University Press (Natural History Museum Publications), xi + 404 p. ISBN 0-19-854031-0. Hardback. \$78.00.

There have been few attempts to create a general volume on the form, function, and diversity of the Lepidoptera. Most of these were written near the start of this century, and published in German or French. Now, N. J. Scoble has created a new synthesis in English which deals with the Lepidoptera on a global basis. The author devotes the first half of the volume to a general introduction to the group's biology, while the second half deals with the major taxa in the Lepidoptera. As such, this single volume constitutes a useful compilation of information on this important insect order, and allows the reader to obtain an excellent overview of the biological diversity of the group.

The book is divided into three principal parts. Part 1, dealing with the anatomy of the Lepidoptera in six chapters, concentrates on external anatomy of the adult head, thorax, and abdomen, and then reviews the egg, larva, and pupa, before completing its survey with discussion of hearing organs, sound production, and scent. After dealing with the basic external morphology of each body division, the function of the various structures is discussed. However, a little discussion of internal anatomy is provided. This first section covers 168 pages.

Part 2 is composed of one chapter on the environmental and ecological importance of Lepidoptera. The 14 pages of text consider a limited selection of topics such as the potential of Lepidoptera for environmental impact, the diversity of plants eaten by lepidopteran caterpillars, and the evolutionary consequences of herbivory (e.g., plant defenses). Brief discussions of Lepidoptera as environmental indicators, as prey, and as useful organisms in silk production, are included in this chapter.

Part 3 represents a guide to the major taxa of Lepidoptera, including a treatment of 41 recognized superfamilies. Scoble provides a summary of the structure, diversity, and general biology of each superfamily, using available information from the literature. The first chapter in this part includes a brief discussion of the historical background of lepidopteran classification and critically addresses some of the problems with existing taxonomic schemes. Usually, each family is illustrated by one half-tone illustration, though in larger families more than one species has been illustrated. The book concludes with an extensive reference section and an index to major topics and taxa.

Overall, the stated purposes of the book are reached. The discussions of most of the taxonomic group are quite dry. Illustrations are adequate but not abundant. This is not a book for the amateur to read for pleasure or inspiration. Instead, it is a reference suitable for finding summaries of most of the important basic information about the Lepidoptera. As such, the line drawings are generally satisfactory and complete in their coverage of the discussed structures. Occasional SEM photographs, half-tone photographs, and four ganged plates of color photographs make the book a useful reference for anyone interested in the general characteristics and biological diversity of the order Lepidoptera. On this basis, I would recommend this book for the professional library of anyone working with Lepidoptera.

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RAUPP, M. A., R. G. VAN DRIESCHE, AND J. A. DAVIDSON. 1993. *Biological Control of Insect and Mite Pests of Woody Landscape Plants: Concepts, Agents and Methods*. 39 pages, including references. Contribution number 8575 of the Maryland Agricultural Experiment Station, Maryland Cooperative Extension Service, University of Maryland, College Park, Maryland. For sale by the University of Maryland, Agricultural Duplicating Service, 6200 Sheridan Street, Riverdale, MD 20727. The price is \$22.00 with volume discounts at purchases of over 10 and 20 copies. Slide series (56 slides, same as plates in manual) \$50.00.

Biocontrol goes glossy! Indeed if biocontrol is to catch the eye as effectively as the pizzazz of pesticide ads, this manual has made an inroad. The bright glossy cover, effective use of computer graphics, and excellent color plates catches the eye. The readability should hold the attention of even the mildly interested. Unfortunately, as in the case of the shinier apple, and the bigger tomato, something may have been compromised.

All in all this is a nicely presented introduction to some biological control considerations for the nursery producer and landscaper. As the forward states, the manual's purpose is to provide a reference that "serves to expand and facilitate the practical use of biological control in landscapes and nurseries." Its brevity (22 pages of text), provides the nursery producer or landscaper a concise and understandable presentation of just what "biological control" is, and partially addresses the "how-to" of implementation. The concepts of conservation, importation and augmentation, as well as the use of formulated biological organisms are discussed in terms of their roles in biological control and integrated pest management. A brief discussion on why biological control should be considered is presented, citing pesticide resistance, pest stimulation, pesticide-induced outbreaks, effects of pesticides on nontarget organisms, and human health risks attributed to exposure to pesticides.

The majority of the manual is rightly devoted to the description and discussion of the natural enemies commonly encountered, and of special interest to landscape and nursery production. The descriptions of the arthropods are reasonably specific, highlighting some important distinctions that allow the untrained to differentiate between pest and beneficial. The accompanying set of excellent color plates allows the reader to clearly see representatives of these natural enemies at various life stages.

I was looking forward to reading the section entitled "Methods For Implementation," hoping to find concise instruction that provides the grower with some concrete methodology to implement a biological control program. I found the manual to provide some excellent pointers, especially in the area of conservation of natural enemies. In the area of augmentation of natural enemies, however, a lack of information available on specific methods prevails. The authors recognize this deficiency and refer the reader to other sources. Considering the relatively narrow scope of the manual's title I was a little disappointed not to find more applicable information regarding augmentative releases. One important area that was entirely overlooked was the need for a scouting program, without which any attempt at implementation of a biocontrol program is probably futile.

The eye-catching manual is printed on sturdy glossy paper, and spiral bound. The slide series, which is a duplication of the color plates in the manual, is numbered rather than labeled; requiring the use of the manual for explanation of the slide contents.

This manual and slide series will certainly be a valuable tool for the introduction of biological control to an audience in need of pest control reform, but I hope that the next "how-to" manual of biological control comes closer to achieving its objective. Onward ho, in search of the elusive shiny apple that tastes as great as it looks!

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DELFOSSÉ, E.S. (ed.). 1993. *Pests of Pastures: Weed, Invertebrate and Disease Pests of Australian Sheep Pastures*. Melbourne; CSIRO, Information Services, x + 434 p. ISBN 0-643-05140-6. Paperback. \$60.00

Have you ever wondered about pest problems and pest management "Down Under"? Here is your chance to get a broad overview of one production system. Delfosse has compiled an excellent set of papers reviewing the state-of-the-art as it relates to pasture production. Australian sheep producers are faced with some of the same problems confronting American livestock and crop producers, but with a distinctly Aussie flavor. Because many Australian pastures are improved, which means that grasses, legumes, or a combination of grasses and legumes have been sown, the pastures are not unlike crop systems. Many of the problems discussed in this book have been brought about by conversion from natural to crop-like systems, or by overgrazing, so a common theme among many of the papers is enhanced understanding of pest ecology. As in North America, invasion of pastures by exotic organisms is a common problem. However, the pests are usually different from those we face in North America. While there is discussion of some cosmopolitan species such as spotted alfalfa aphid and cowpea aphid, there also is information on unique problems. The reader will learn about such exotica as redlegged earth mite (a seedling pest), corbie (Lepidoptera: Hepialidae), doublegee (a weed in legume pastures), and Paterson's curse (a serious pasture pest in Mediterranean-like climatic areas).

The editor was faced with a formidable task in assembling 75 contributions from 115 authors into a coherent volume. The book is organized into 7 sections, each of which receives about equal treatment: an overview of sheep and pasture production, including the economic impact of pests; pest ecology; cultural control; chemical control; biological control; integrated control; and technological and social limitations on pest management in the future. The organization works fairly well, although some placement of papers seems arbitrary. Also, the reader should be aware that treatment of the pest disciplines is not equal, undoubtedly reflecting differential impact of the pests. There are about 30 papers on weeds, as opposed to 13 on invertebrates, 3 on diseases, and 13 on a combination of pest problems. The remainder of the chapters are concerned with economics and research priorities. A novel and very useful element of the book is inclusion of papers by sheep farmers. This may reflect appreciation of the so-called "Rapid Rural Appraisal" system of problem identification (contribution by Ampt and Ison) in which producers participate more fully in problem identification and research planning. Apparently not everything in Australia is done "rapidly," however. It seems that the authors and editor anticipated a 1992 publication date, as they refer to the various papers within the book using 1992 instead of the actual 1993 date.

With so many contributors and so broad a subject, there is risk of superficial treatment. Indeed, with the exception of some comprehensive review chapters, the average length of papers is only about 5 pages. However, the editor and authors have done an outstanding job of providing quality coverage of most topics; despite their short length, the contributions are very informative. Most important to this reader, though, were the accompanying bibliographies. Australians seem to be less prone to publish in widely accessible journals. About one-half of the citations are from workshops, conference proceedings, or State Department of Agriculture or CSIRO publications. While these probably gain good distribution in Australia, it is sometimes difficult for those of us "Up Above" (is this the opposite of Down Under?) to be aware of important developments and to access the documents. Thus, this book goes a long way toward increasing our knowledge of Australian agricultural science. At least from my perspective, there is a lot of quality research in Australia, and a great deal of it is encapsulated in this document.

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MORON, M. A. (ed.) 1993. *Diversidad y Manejo de Plagas Subterráneas*. Sociedad Mexicana de Entomología and Instituto de Ecología; Xalapa, Veracruz, 261 p. Paperback. Price outside Mexico US \$10.00 plus \$3.00 for shipping (by airmail) from Sociedad Mexicana de Entomología, A.C., Atención: Dr. Miguel A. Morón, Apartado Postal 63, Xalapa, Veracruz 91000, Mexico.

This book has a subtitle: *Memorias de la IV Mesa Redonda sobre Plagas Subterráneas* [-] 14 y 15 de octubre de 1993 [-] Instituto de Ecología, A.C. Xalapa, Veracruz, México. As the title implies, the subject is diversity and management of soil-dwelling pests, and the book is the product of authors attending a meeting. The 19 chapters, which are assembled into 3 sections, are the work of 26 authors: 13 from Mexico, 5 from New Zealand, 4 from Costa Rica, 3 from Colombia, and 1 from Brazil. Seventeen of the chapters are in Spanish, 2 in English, and each has a resúmen in Spanish and an abstract in English.

Diversity, ecology, and distribution, the subject of the first section (6 chapters), deals with faunal lists and seasonality of Scarabaeidae in habitats in Mexico, Colombia, and Costa Rica. *Phyllophaga* is the most prominent genus [some of the authors treat it as a member of a family (Melolonthidae) independent from Scarabaeidae], but *Anomala*, *Ligyrrus*, *Cyclocephala*, and numerous others are also considered. One of the authors also deals with *Diabrotica* (Chrysomelidae), and another mentions *Anoplisthius* and *Pyrophorus* (Elateridae), with collection data on members of various other families of Coleoptera collected but not identified. The habitats sampled are by no means limited to agroecosystems.

Agricultural importance is the subject of the next section (8 chapters). Crops damaged by larvae of Scarabaeidae and considered in this section include (principally) maize, but also cassava, peanuts, sugarcane and (briefly) wheat, barley, and oats. Agricultural methods destructive to these pests are pointed out, and these include crop rotation, the use of lime, fire, and specific planting methods for seed. There also is ranking of efficacy of chemical pesticides used for control, and passing mention of natural enemies: some Carabidae and Elateridae which were seen to feed on scarab larvae, and some unidentified Staphylinidae whose role is not understood. One brief chapter deals with 8 species of Acaridae (Acarina) found among roots of various cultivated plants; five species, belonging to the genera *Schwiebia*, *Histiogaster*, *Rhizoglyphus*, and *Sarcassania*, appear to cause damage, but there are interspecific differences in feeding habits by members of *Tyrophagus*, such that while 2 species may cause damage, *T. putrescentiae* (Schränk) appears to be a fungivore.

The final section (5 chapters) is on pest management methods under development for the control of Scarabaeidae (and some Chrysomelidae). These methods range from the development of strains of maize tolerant to attack by larvae of *Phyllophaga*, *Cyclocephala*, and *Diabrotica*, through the use of pathogenic fungi (*Beauveria* and *Metarhizium*) and bacteria (*Serratia* and *Bacillus*), to the cloning of genes causing pathogenicity by *Serratia*. One chapter describes an experimental study in the laboratory showing interaction of soil type (proportion of organic matter) and the effect of *Serratia* on scarab larvae.

The pests considered in this volume are native to the areas where they cause problems. The crops considered are also, for the most part, native. This association of native pest with native crop probably explains why classical biological control is not even considered in this volume. The future seems to hold a rationalization of current agronomic practices together with plant breeding, genetic engineering, and the use of biopesticides as the methods most likely to succeed in reducing damage. An investment in the last two decades, especially by Mexico, in systematics and ecology of Scarabaeidae, is now being teamed with agronomy and insect pathology to solve a serious agricultural problem.

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CLASSICAL BIOLOGICAL CONTROL OF ENVIRONMENTAL PESTS

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ABSTRACT

Exotic species commonly invade areas of conservation concern. Such species may threaten native species or ecosystems, either attacking individual species, or changing ecosystem characteristics in ways that make them less suitable for the continued existence of one or more native species. Among the potential effects of exotic species are crowding, changes in water table levels, fire frequency or intensity, altered soil fertility or chemistry, and altered levels of predation or disease. Chemical, mechanical and biological methods each may be used to control exotic species in some cases. Chemical and mechanical methods are difficult to apply to large areas and must be repeated periodically to prevent pest resurgence. Classical biological control often has high initial costs but is permanent in nature and self propagating, such that large areas can be treated economically. Risks of biological control are minimal if agents are appropriately screened to determine host range prior to introduction and if introductions are conducted using appropriate quarantine procedures. Biological control is a useful approach for control of a variety of kinds of environmental pests that threaten the conservation of native species and ecosystems, including exotic plants, herbivorous and predacious arthropods, other invertebrates, and in some instance vertebrates.

Key Words: Biocontrol, nature conservation, exotic species.

RESUMEN

Especies exóticas frecuentemente invaden las áreas de interés de conservación. Tales especies pueden amenazar a los ecosistemas o las especies nativas, o atacar especies particulares o cambiar características del ecosistema en maneras que lo hacen menos apropiado para la existencia continuada de una o más especies nativas. Entre los efectos potenciales de las especies exóticas se incluyen densidad desfavorable de organismos, cambios en el nivel hidrostático o en la intensidad o la frecuencia de fuegos, química o fertilidad alterada del suelo, y niveles alterados de predación o enfermedades. Métodos químicos, mecánicos o biológicos se pueden usar para controlar especies exóticas en unos casos. Métodos químicos y mecánicos son difíciles aplicar a áreas grandes y tienen que repetirse periódicamente para prevenir resurgimiento de la plaga. El control biológico clásico frecuentemente tiene costos iniciales altos, pero es de un carácter permanente y se propaga por sí mismo, por eso, se pueden tratar económicamente a áreas grandes. Los riesgos de control biológico son mínimos si se examinan los agentes adecuadamente para determinar el rango de organismos hospederos antes de introducirlos, y si se conducen las introducciones usando métodos apropiados de cuarentena. El control biológico es un enfoque útil para controlar una variedad de plagas ambientales que amenazan la conservación de especies y ecosistemas nativos, incluyendo plantas exóticas, artrópodos herbívoros y predadores, otros animales invertebrados, y animales vertebrados.

Biological reserves and other undeveloped lands and water of conservation importance are regularly invaded by exotic plant and animal species. Such invasions reflect the level of human activity in a region because many invasions are assisted by the movement of people and commercial trade in plants and other products. Aggressive exotic species may threaten native flora or fauna by competition or direct attack. In other cases, exotic species may alter basic properties of the ecosystems they invade, rendering them less suitable for the continued existence of broad sets of native species. Efforts to combat such invading species by chemical or mechanical means are often unsatisfactory, the former because of the risk of chemical pollution and cost, and the latter because of cost and the difficulty of applying mechanical remedies to any large undeveloped region. Additionally, neither chemical nor mechanical control provides a permanent solution and areas must be re-treated periodically to prevent pest resurgence. Biological control, through the introduction of natural enemies specialized to attack the undesired exotic species, offers a method to control some exotic pests, over wide areas, permanently. In this article, I discuss the kinds of impacts exotic species can have on native species and ecosystems and define the potential that classical biological control has to address this important conservation issue.

IMPACT OF EXOTIC SPECIES

Exotic species become environmental pests when they attack and threaten the continued existence of particular native species or alter ecosystems on a broadscale in ways that they threaten the continued existence of whole biological communities.

Single Species

Exotic species affect individual native species either because they are pre-adapted to attack them or they simply heighten the competition for resources in ways that are

damaging to native species. Rare species, which by virtue of their precarious small populations or limited distributions, may not be resilient to additional competition or mortality. The Bermuda "cedar" (*Juniperus bermudiana* L.), for example, once widespread on Bermuda, has been nearly eliminated following the invasion of the island by two exotic scales, *Carulaspis minima* (Targ.) and *Insulaspis pallida* (Maskell) (Cock 1985) (Figs. 1,2). Similarly, the introduction of the European starling, *Sturnus vulgaris* L., to North America caused a serious decline in the eastern bluebird, *Sialia sialis* (L.), through competition for nesting cavities. Also, the arrival of the exotic pathogen *Cryphonectria parasitica* (Murr.) Barr which caused a blight of the American chestnut, *Castanea dentata* (Marsh.), all but eliminated this tree, which once dominated forests throughout much of eastern North America. In Florida, native bromeliads are currently threatened by the arrival in Florida (via importation of bromeliads from Central America or Mexico) of weevils in the genus *Metamasius* (Frank, in press) (Figs. 3,4).

Communities

In many cases, exotic species do not directly attack native forms but, rather, outcompete or dispossess them for space and resources by various broad effects that alter the ecosystem or preempt their living space (Vitousek 1986). Among these effects are: (1) crowding and smothering, (2) changes in water tables, (3) altered fire frequency or intensity, (4) changes in soil fertility or chemistry, and (5) enhanced predation or disease.

Crowding. One of the more common effects of introduced environmental plant pests is the formation of dense stands of single species that cover a high percentage of the available habitat. The floating fern *Salvinia molesta* D. S. Mitchell, for example, was spread as an aquarium plant by Europeans to the Old World tropics (from a homeland in southern Brazil). The mats of this plant have covered hundreds of square kilometers



Fig. 1. Bermuda cedar (*Juniperus bermudiana* L.) stands damaged by exotic scales (photo by F. D. Bennett).

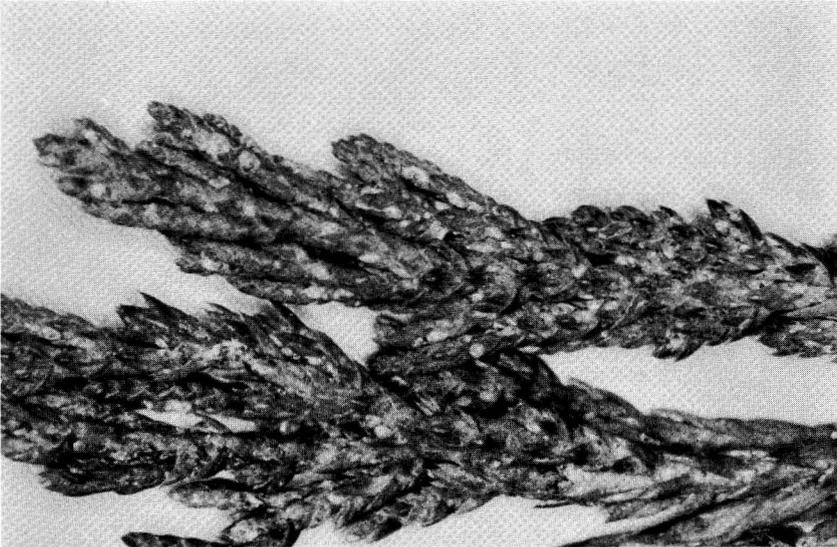


Fig. 2. *Carulaspis minima*, one of two exotic scales attacking Bermuda cedar (photo courtesy of Division of Plant Industry, Florida Dept. of Agriculture & Consumer Services).



Fig. 3. Bromeliad in Florida damaged by immigrant weevil, *Metamasius callizona* (Chevrolat) (photo by J. L. Castner).

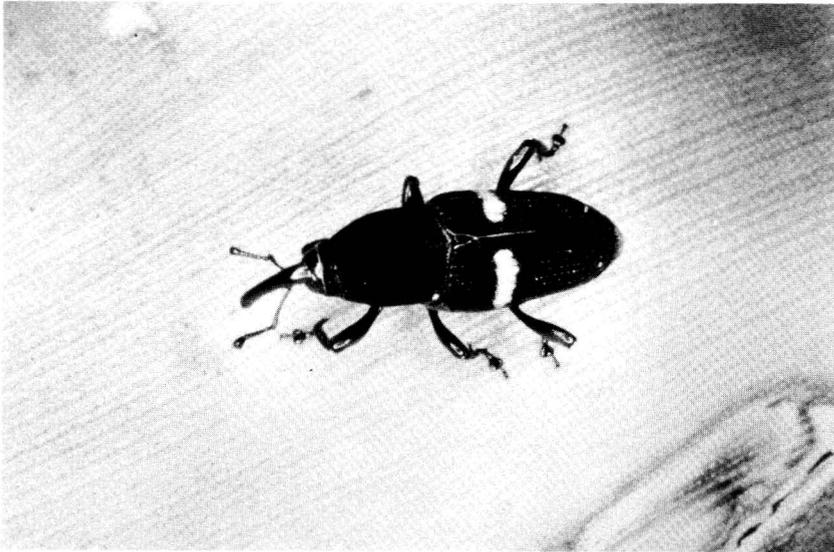


Fig. 4. *Metamasius callizona*, an immigrant weevil damaging native bromeliads in Florida (photo by J. L. Castner).

of rivers and lakes with a continuous layer up to a meter thick in spots (Mitchell et al. 1980). Herbivorous arthropods were sought in the native range of the plant and their subsequent importation caused dramatic reductions in weed densities in India, Papua New Guinea and Namibia (Figs. 5, 6) (Thomas & Room 1986, Forno 1987). Reduction of floating fern densities has allowed environmental conditions to revert to ones favorable for the pre-existing, largely native, vegetation in many areas. In the northeastern U.S., wetland ecosystems have been significantly altered in many states by an invasion of the garden flower purple loosestrife (*Lythrum salicariae* L.) (Fig. 6). This plant displaces the native vegetation in such habitats as cattail (*Typha* spp.) marshes, to the detriment of muskrats, ducks and native plants (Thompson et al. 1987). In Hawaii, interest is strong in maintaining the integrity of the native forest habitats upon which much of the endemic bird fauna depends. Introduced plants, such as the banana poka [*Passiflora mollissima* (Humbolt, Bonpland & Kunth)], are currently degrading the quality of the forest. Banana poka aggressively envelopes native trees in bags of foliage, leading to tree death (Fig. 7, LaRosa 1992). Biological control projects are currently under way against both purple loosestrife and banana poka, but are in their early stages and have not yet controlled the pest. In both cases, funding for the projects has been obtained specifically because of the environmental benefits of the projects, rather than for economic reasons.

Altered Water Tables or Fire Characteristics. In addition to physically taking possession of space, exotic species, especially plants, may alter the physical character of the habitat. Among these alterations are changes in the depth of the water table and the propensity toward fire. Salt-cedars (*Tamarix* spp.), for example, have invaded the riparian areas in the southwestern United States from their original home in Asia (Fig. 8). Because the plant is deeply rooted and does not restrict its evapotranspiration rate, it draws heavily on soil water reserves causing the water table to fall (Vitousek 1986). This

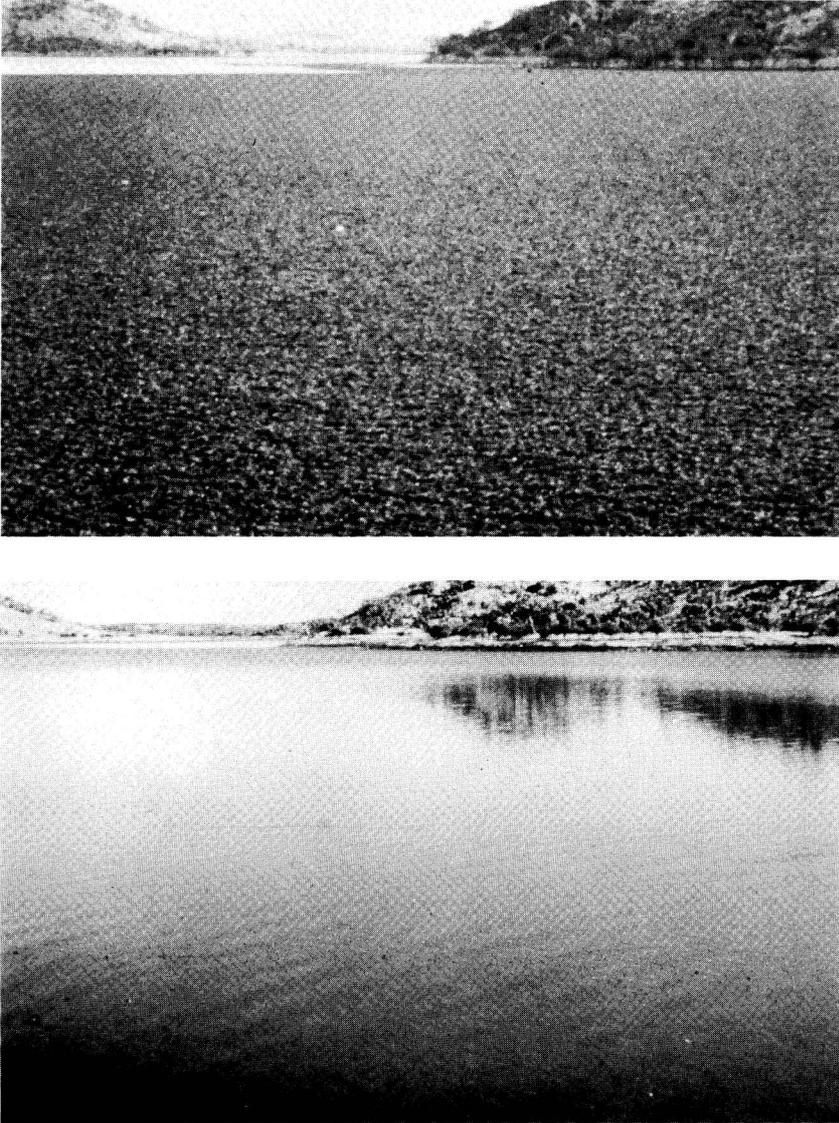


Fig. 5. Mat of the floating fern *Salvinia molesta* (a) before and (b) after biological control by the weevil *Cyrtobagous salviniae* (photo courtesy of CSIRO, Australia).

significantly affects shallow-rooted native riparian species that otherwise flourish in seeps and wet meadows. In areas with heavy concentrations of *Tamarix*, these native riparian communities have largely disappeared. In addition, *Tamarix* is more prone to fire than the native vegetation, and its dominance in an area increases the effects of fire. In South Africa, invasion of native fynbos habitat by the woody shrub *Hakea sericea*



Fig. 6. Stand of purple loosestrife, *Lythrum salicariae*, invading North American temperate wetlands (photo by Richard Malecki).

Schrader has caused a 60% increase in fuel loading at study sites (Versfeld & van Wilgen 1986), increasing fire intensity and perhaps frequency.

Altered Soil Fertility or Chemistry. Soil fertility, salinity and other chemical characteristics are important factors in determining a site's suitability as habitat for plants.



Fig. 7. The exotic vine banana poka (*Passiflora mollissima*) smothering native forests in Hawaii (photo by Clinton Campbell).



Fig. 8. Stands of salt-cedar (*Tamarix* sp.) in riparian areas in the southwestern United States (photo by Jack DeLoach).

If these are altered by an invading plant species, some former occupants of the site may disappear. For example, rare native plants in the nutrient poor soils of the volcanic caldera of Hawaii depend on their ability to survive under such harsh conditions in order to mediate competition with more aggressive plants which require higher fertility levels. The exotic plant *Myrica faya* Ait. is a nitrogen-fixing species that has invaded this habitat and is raising soil nitrogen levels, with the likely outcome that the native species will lose their competitive advantage.

Annual iceplant, *Mesembryanthemum crystallinum* L., which was introduced to California for use as an ornamental, invades grasslands in various coastal areas in California, for example, Santa Barbara Island. The plant accumulates salt which is released upon death of the plant. Important native species in these dune communities are less salt tolerant than annual iceplant, which benefits from the altered soil chemistry allowing it to invade and hold its ground in competition with native species (Vivrette & Muller 1977, Kloot 1983). Exotic species that produce high concentrations of allelopathic chemicals in their root zones also may alter soil chemistry in ways that suppress native plants.

Altered Levels of Predation or Disease. Predacious (or parasitic) species that exhibit high densities and broad host ranges can have important indirect impacts on the densities and species evenness of herbivores or other organisms in the communities which they invade. Adding a dominant predator to a system formerly without one, or removing one from a system shaped by the presence of such a predator, can lead to major changes in competitors and lower trophic level organisms. Invasions of fynbos communities in South Africa, for example, by the Argentine ant, *Iridomyrmex humilis* (Mayr), displaced most of the indigenous ant fauna (Breytenbach 1986). Similarly, introduction of new species of predacious fish, such as the Nile perch (*Lates* sp.) in Lake Victoria, has had vast impact on fish communities, causing extinctions of many species and making many other once common species rare (Goldschmidt et al. 1993). Similarly, diseases can shape com-

munities. Introduction of avian malaria, for example, is believed to be a significant factor in the narrowing of the distributions of native birds in Hawaii (van Ripper et al. 1986).

METHODS FOR THE CONTROL OF EXOTIC SPECIES

Depending on the physical extent of the area affected by an exotic species, mechanical, chemical or biological controls may be employed successfully. When areas infested are small, it may be feasible to destroy the colonizing organisms mechanically or chemically (especially larger plants of species that have limited seed production) (e.g., Santos et al. 1992). Such controls are likely to require periodic repetition, increasing their cost and limiting the size of area which may be cleared of an exotic organism. When large areas are infested, extensive seed banks exist, or the organism is too small or hidden from attack by mechanical or chemical methods, biological control should be considered.

Biological control is limited in its environmental pest applications because developmental costs for new projects, especially against plants, are large and most expenses occur at the beginning of the project during exploration for, and host specificity testing of, new agents (Markin et al. 1992). Harris (1979), for example, estimates that in Canada a complete biological control program for one weed species could cost as much as 1.5 million Canadian dollars. These costs, however, are very low compared to those for developing new pesticides, or long term herbicide weed suppression projects. Also, when a biocontrol agent of a given weed has been employed successfully in one location, its use in similar projects in other countries or locations can be repeated at a much lower cost.

Another important feature of biological control is that the release of biological control agents is a permanent change. It is difficult, if not impossible, to "take back" a released organism once it has been liberated. Sufficient pre-release screening must, therefore, be done to ensure that only suitable organisms are approved for release. Given these constraints, biological control has great application for the control of widespread environmental pests because the natural enemies once released, if effective, remain effective permanently at no further annual cost. Because natural enemies do not need to be released repeatedly, and because they are able to spread to additional areas, the method can be applied even when infested areas are large (thousands to millions of hectares).

Risks from release of properly screened biological control agents are minimal, but each case must be carefully considered because actions that may be safe in one habitat may be undesirable in another (Harris 1990, Gould 1991, Howarth 1991). Rigorous efforts should be made to identify local biological resources of special significance so that these rare, local or unusual life forms are not threatened. Different types of natural enemies vary in the degree of risk that they may pose, and some groups, such as vertebrates, are generally unsuitable for introduction beyond their historical ranges without compelling circumstances (Legner 1986). While some environmental risks may remain in any natural enemy introduction program, even following careful host-range testing, these small, often conjectural, risks must be balanced against the risk of doing nothing. In many cases, uncontrolled populations of environmental pests have had, and continue to have, important impact on native species and ecosystems, including a threat to endangered forms that might contribute to their extinction.

EXAMPLES OF BIOLOGICAL CONTROL OF ENVIRONMENTAL PESTS

Biological control efforts have either been made, are in progress, or have future potential, for many kinds of environmental pests. In the following section I present some examples of biological control of environmental pests. These have been selected from a wide range of organisms in order to demonstrate the scope of biological control.

Aquatic Plants

Several species of tropical or subtropical plants growing in freshwater habitats have invaded other parts of the world. Often they are being spread as ornamental plants for use in ponds or aquaria. One of these is *Salvinia molesta*, a major pest in Africa, India, Papua, New Guinea and Australia. It has recently been controlled successfully, and impressively, with *Cyrtobagous salviniae* Calder & Sands (Forno 1987). Water hyacinth, *Eichhornia crassipes* [Martius (Solms-Laubach)] is another aquatic plant that has created problems around the world following its deliberate spread (for ornamental purposes) from its native Brazil (Gopal 1987). Mats of this plant may be so thick that in addition to economic damage to dams, navigation and fisheries, native fauna and flora are severely affected by reduced levels of dissolved oxygen and increased eutrophication (Harley 1990). Many biological control agents have been assessed for water hyacinth control. The weevils *Neochetina bruchi* Hustache and *Neochetina eichhorniae* Warner and the moth *Sameodes albipunctalis* Warner have been found to be the most effective (Harley 1990). Other important aquatic weeds which have been controlled through biological control, or which have high potential to be controlled, include alligator weed, *Alternanthera philoxeroides* (Martius) Grisebach; water lettuce, *Pistia stratiotes* L.; and Eurasian watermilfoil, *Myriophyllum spicatum* L. (Harley et al. 1990, Madsen et al. 1991).

Terrestrial plants

More than 87 species of terrestrial plants have been targets for biological control (Julien 1992). Most of these were selected because of the damage they caused to grazing and forest lands. However, many of these plants invaded extensive areas of natural habitat and, through the formation of dense, highly competitive weed stands, reduced the value of the habitat for native species, for example, klamath weed (*Hypericum perforatum* L.) in California and prickly pear cactus (*Opuntia stricta* Haworth) in Australia (DeBach et al. 1976).

In other instances, projects have been undertaken specifically for conservation purposes, as for example the control of weeds in the native forests of Hawaii (Markin 1982, Markin et al. 1992). Important terrestrial weeds of environmental concern against which biological control is being attempted or has potential are: banana poka (*Passiflora mollissima*), a forest weed in Hawaii (Waage et al. 1981); giant sensitive plant (*Mimosa pigra* L.), a woody shrub rapidly forming vast monospecific stands in northern Australia (Braithwaite et al. 1989); gorse (*Ulex europaeus* L.) in New Zealand; kudzu [*Pueraria lobata* (Willd.)] in the southeastern United States; and *Sesbania punicea* (Cav.) Benth. in South Africa (Hoffmann & Moran 1991).

Herbivorous Arthropods

Herbivorous arthropods are the most common organisms against which biological control has been employed (e.g., Laing & Hamai 1976, Clausen 1978). Relatively few of these projects, however, have been directed against pests attacking native plants that are not themselves economically valuable as crops, timber or forage. Exceptions include efforts to control scales damaging to the Bermuda cedar (Cock 1985), and weevils attacking native Floridian bromeliads (Frank, in press). Insect damage to native plants is not lacking, but rather, until recently, such ecological damage has not created sufficient public concern to generate funding of control projects.

Predacious or Parasitic Arthropods

Some species of predacious, social Hymenoptera such as the Argentine ant, *Iridomyrmex humilis*, several fire ants (*Solenopsis* spp.) and vespids [e.g., *Vespula pensylvanica* (Saussure)] have invaded various parts of the world. Because of their aggressive, generalist feeding habits and high numbers per ha, they often exert significant impacts on native invertebrates (e.g., Gagne & Howarth 1982, Gambino et al. 1990, Beggs & Wilson 1991). For such species, in forests or conservation lands, biological control holds some potential. Few past efforts, however, have been made against this class of pests.

Non-Arthropod Invertebrates

Relatively little use has been made of biological control for non-arthropod invertebrates, with the exception of molluscs that are herbivorous crop pests, or aquatic species that are intermediate hosts of liver flukes that attack man or domestic animals. No projects against this class of organism have been attempted solely for conservation purposes. Serious environmental pests do exist in this category, however. The zebra mussel, *Dreissena polymorpha* Pallas, has recently invaded North American fresh waters and is spreading rapidly (Ram et al. 1992). While this species is of great economic concern because of its ability to clog water intake pipes, it also is likely to cause significant environmental damage. Densities of this species are extraordinarily high and its presence is likely to place at risk much of the rich North America fresh water clam fauna once the major river systems of the continent are colonized.

Vertebrates

Options for the biological control of vertebrates are limited because their natural enemies are less specific and comprised of fewer species than those of arthropods and plants. Vertebrates that prey on other vertebrates are generally inappropriate for introduction outside of their historical range as the specificity of this group of agents is not usually sufficient to ensure safety to other species. Pathogens may be one group of organisms that may be sufficiently specific for such use. Myxoma virus has been used in several countries to reduce densities of the European rabbit [*Oryctolagus cuniculus* (L.)] (Ross & Tittensor 1986). Context can determine the degree of specificity needed. For example, the feline panleucopaenia virus has been used against feral house cats on Marion Island in South Africa to reduce numbers of seabirds killed by offspring of cats released by a lighthouse keeper (Rensburg et al. 1987). This project was feasible because the island was uninhabited and isolated from populated areas where domestic cats would be at risk. Dobson (1988) suggests that the damage from feral goats on oceanic islands - one of the worst environmental pests in the world - could be reduced by employing a highly specific venereal disease of goats caused by a protozoan in the genus *Trichomonas*. Again, this would be feasible only on islands lacking domestic goat populations.

CONCLUSION

Biological control, unlike mechanical or chemical control, offers a potential mechanism for controlling environmental pests which occupy large ranges in the country of invasion. While initially expensive, results are cost effective over the long term because control, if achieved, is permanent. Biological control has been employed with safety in the vast majority of cases. An adherence to quarantine and host-range testing procedures, a knowledge of locally rare or unique species that might be affected, and a thorough understanding of the biology of the agents to be introduced, should provide the means

to ensure safe application of the method. It is broadly applicable to many types of environmental pests, but has been used so far mainly against plants. Other categories of organisms against which the method has potential application include arthropods, other types of invertebrates and, to a limited degree, vertebrates. Environmental pest creation is a function of the volume of human travel and commerce and should be expected to increase. It is well documented that not controlling such environmental pests puts native species and ecosystems at risk. Organized programs to identify and implement biological control projects against environmental pests are currently lacking with few exceptions. Such an approach is needed if the integrity of native ecosystems is to be protected around the world in the coming century.

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**BIOLOGICAL CONTROL OF THE TWO-SPOTTED SPIDER
MITE (ACARINA: TETRANYCHIDAE) ON COMMERCIAL
STRAWBERRIES IN FLORIDA WITH *PHYTOSEIULUS*
PERSIMILIS (ACARINA: PHYTOSEIIDAE)**

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ABSTRACT

Biological control of *Tetranychus urticae* Koch in Florida's commercial strawberry fields is possible by use of the predacious mite *Phytoseiulus persimilis* Athias-Henriot. A low and stable population of both species is maintained after about 2 months. Immigration of local parasitoids and predators contributes stability. The cost is likely to be lower than that of chemical control, and strawberry yields are not reduced.

Key Words: Biocontrol, *Tetranychus urticae*, predacious mites.

RESUMEN

Control biológico de *Tetranychus urticae* Koch en campos comerciales de fresas en la Florida se logra con el uso del ácaro predador, *Phytoseiulus persimilis* Athias-Henriot.

Una población baja y estable de ambas especies se mantiene después de 2 meses. La inmigración de parasitoides y predadores locales contribuye a la estabilidad. Usualmente, el costo es más bajo que el de control químico y no se reduce el rendimiento de fresas.

Two-spotted spider mites, *Tetranychus urticae* Koch (Acarina: Tetranychidae), are the most economically important arthropod pests in commercial strawberry production in Florida (Jepson et al. 1975, Hochmuth 1988). Spider mites often infest strawberry plants from the nursery, and their control by chemicals can be difficult due to plant density and resistance of the spider mites to acaricides (Smith & Fulton 1951, Helle 1965, Cranham & Helle 1985). Spider mite populations can be controlled by seasonal inoculative release of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae), a predacious mite, with proper release strategies and techniques. Once control has been achieved, the predator and prey populations remain stable.

COMMERCIAL STRAWBERRY PRODUCTION

Traditional strawberry production methods in central Florida include control of spider mites by application of various acaricides. These chemical applications often are made prophylactically and tend to be overused. The cost of controlling spider mites chemically totals \$100-400 per acre (Prevatt 1991, author's experience), depending upon perceived levels of damage caused by spider mites and/or on perceived need for treatment.

To minimize chemical treatments, and to avoid induction of resistance to chemicals, Agri-Tech developed procedures to monitor spider mite populations and to predict onset of economic thresholds. They also developed integrated pest management for spider mites in strawberries in Florida, using biological control whenever feasible. This method of integrated pest management is effective in controlling spider mite populations, and in reducing use of chemicals. It also provides a substantial cost saving to growers and a reduction in development of resistance to chemicals in spider mite populations during each growing season.

An integrated management approach to pest control in strawberries has operated for 10 years or more in central Florida, but it still accounts for only several hundred of the total of 5,000 acres planted. Our experiments with the predacious mite *Phytoseiulus persimilis* to improve management of spider mites were in collaboration with the University of Florida's Gulf Coast Research & Education Center. We were successful in developing a system which controls *T. urticae* in commercial strawberry fields, and this system was implemented during the 1992-1993 growing season on >200 acres of strawberries.

MANAGEMENT

Ensuring that mite-free strawberry plants arrive from the nursery is the first step in controlling *T. urticae* infestations. This allows plants time to develop enough foliage to ensure successful establishment of *P. persimilis* during releases without risking extremely high spider mite populations that may otherwise have to be controlled by use of acaricides.

Proper weekly scouting procedures for spider mites in the field, and thresholds for release of *P. persimilis*, are essential for success. The system developed for the 1992-1993 season involved inspection of ≥ 50 mature strawberry leaflets per block of 7-10 acres. Mature leaflets were chosen because *T. urticae* tend to establish there first. Leaflets

were inspected using a 14× hand lens, noting presence of all stages of spider mites. The percentage of spider-mite-infested leaflets was recorded, and 10% infested leaflets was considered to exceed this threshold. Much higher levels of infestation by spider mites were too high to be overcome by release of *P. persimilis* without risking considerable damage to the crop.

When it was determined that the threshold had been reached, *P. persimilis* was introduced, by hand, at one per plant or approximately 20,000 per acre. Cost of the mites, for one release, was about \$100 per acre plus application costs. In most fields one release was sufficient, although occasionally a few extra predacious mites accelerated control in critical situations. A second release of *P. persimilis* was required about 25% of the time to ensure that control was obtained before noticeable damage had occurred to the plants. Situations requiring the second release were always due to infested nursery stock plants arriving for transplant.

RELEASE TECHNIQUES AND STRATEGIES

Fields must be prepared for introduction of *P. persimilis* before the threshold of spider mites is reached. The use of predacious mites requires complete commitment from the grower in two ways. First, any spray program must use only compatible chemicals. Second, growers must have patience to allow the predators to stabilize the spider mite population more slowly than with chemicals. Without this commitment, mite control will fail.

Any spray program must be adjusted in several ways; even the use of fungicides is important. A spray program that proved successful was a twice-weekly fungicide application of captan 80WP (liquid captan proved to be harmful to *P. persimilis*) with a weekly *Bacillus thuringiensis* Berliner application. Use of most other chemicals is discouraged, although research on compatible pesticides continues. The acaricides Vendex (fenbutatin-oxide) and Agri-mek (abamectin) at half of the standard dosages were safe to *P. persimilis*; this allows use of these chemicals when control by predacious mites is delayed. Our preference for biological control, with use of chemicals only when strictly needed, will help reduce the use of acaricides and avoid resistance.

The predacious mites are shipped from a producer/vendor at 2,000 mites per plastic bottle in a vermiculite medium with a limited food supply. There is a screened air vent in the cap of the bottle which we replace with a ¼ in washer. During application, we rotate the bottles gently to ensure a uniform distribution of mites throughout the bottle because they tend to climb up toward the cap. Occasional inversion of the bottle reduces the chance of releasing too many mites at once. To release the mites, the bottle is held directly over each strawberry plant while the foliage is opened to allow the vermiculite to penetrate the crown of the plant as deeply as possible. One shake of the bottle over every plant releases the *P. persimilis* at approximately 1 per plant. It is necessary to monitor workers closely as they exhaust bottles, and to recalibrate from time to time as necessary. It is important to remember that this process is performed only once per season and that it must receive the close attention it deserves to ensure its success.

Purchasing *P. persimilis* mites is not without complication. When dealing with distant insectaries, it helps to allow for possible shipping delays or lack of availability. Usually the predacious mites are available without any delay, but it is worthwhile giving advance notice when in need of a large order. Most shipping can be done overnight. We found that preparing for an order when 5% of the leaflets are infested with spider mites usually allows sufficient time for release when thresholds are reached.

Once releases are complete, it is critical that the population of both species of mites continue to be monitored weekly, even twice a week if needed, during the crucial initial 4 weeks after release. The most important aspect of determining whether *P. persimilis*

is thriving is discovering the presence of eggs, larvae and nymphs. These other life stages are recorded and included in the weekly leaf counts, allowing the progress of the population to be monitored.

The predator-prey relationship of this system is typical of many in nature. Although the prey population is high initially, the predator mite quickly establishes itself and reproduces so rapidly that it overtakes the prey. At this point, both populations collapse and nearly disappear, only to remain at very low, oscillating densities. At this time the classic predator-prey relationship has been achieved, and biological control is established for the remainder of the growing season. The stability of this system is further enhanced by migration into the fields of locally-occurring predators and parasitoids. In all fields we found invasion by lacewings, *Aphidius*, ladybird beetles, and some local species of predacious mites. This contributes toward the control of aphids, thrips, caterpillars and mites and may reduce the need for chemicals.

RESULTS

To demonstrate the effect of biological control using *P. persimilis*, data from several farms that experienced varying circumstances will be reviewed. The first example illustrates events on a farm with very high spider mite populations during the initial scouting visit (Fig. 1). Although the spider mite population was well over threshold from the start, releases of *P. persimilis* were made on 19 November, and followed by a second release on 16 December when it appeared that the predacious mites were taking too long to achieve control. The second release seemed to be an immediate success. I am

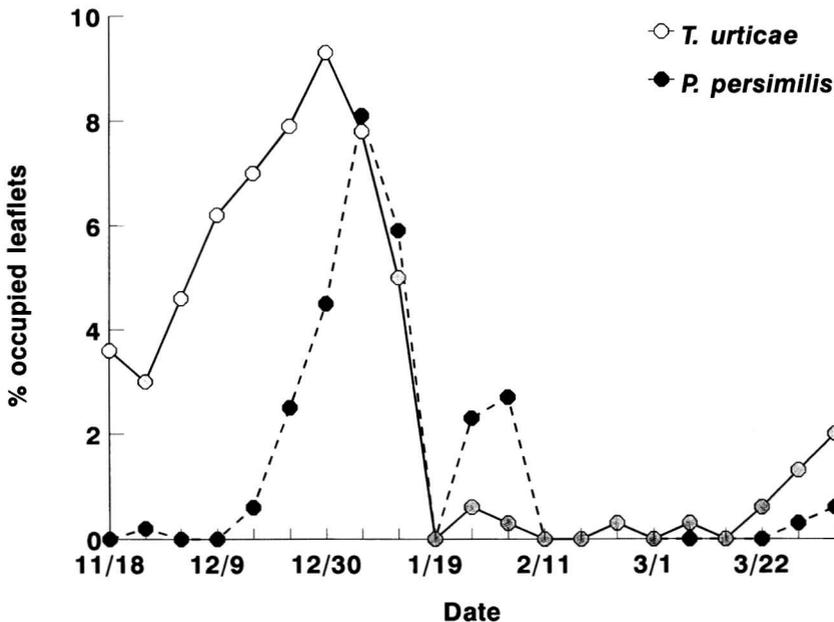


Fig. 1. Percent of strawberry leaflets inhabited by one or more *P. persimilis* or spider mites from November 1992 to March 1993 in field 1. Two releases of predacious mites were made, each at 20,000 per acre.

not sure whether this nearly instant response was due to the additional release of predators or was just a coincidence as progeny of mites from the original release became abundant. Ultimately, control of spider mites was achieved on this farm as both populations rose, then peaked, only to fall as the classic predator-prey relationship endured through the remainder of the growing season.

One of the difficult periods in achieving control by *P. persimilis* follows within the first 10-14 days after release. Experience has shown that it can be difficult to find many predacious mites soon after release using standard scouting techniques. To calm fears of possible failure, dig deeply into the strawberry plants to find evidence of the predacious mites. Usually there is just enough evidence of the predators to be encouraged. The predacious mites appear to move downward, deeply into the plant at first, even when spider mites are readily available near the top of the plant, then slowly disperse toward the top of the plant. This dispersal characteristic, along with others, is a subject for further research.

Another example of biological control, along with one application of an acaricide, is shown in Figs. 2-3. The initial spider mite population was over threshold, but an attempt was made to control the population with predacious mites. A release of *P. persimilis* was made in both fields on 11 November, but within the next two weeks it became apparent that damage to the strawberry plants would occur if an acaricide were not employed. Since the predators were reproducing steadily, but not quickly enough due to the spider mites' early high density, Vendex was applied at half of the standard treatment dose to both fields on 26 November or 3 December. Following the Vendex application, a temporary decrease in spider mite numbers was observed in field 2, but

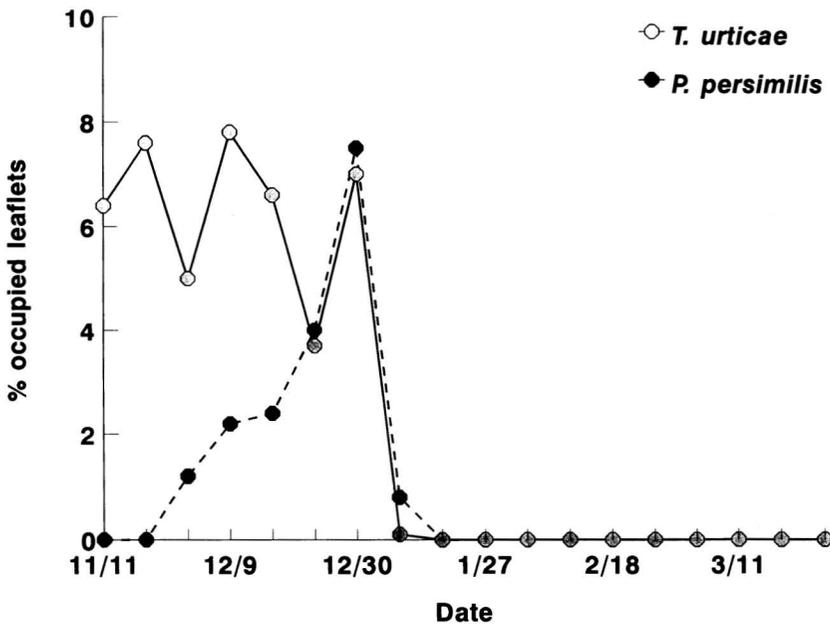


Fig. 2. Percent of strawberry leaflets inhabited by one or more *P. persimilis* or spider mites from November 1992 to February 1993 in field 2. Predacious mites were released at 20,000 per acre, and one acaricide treatment was applied.

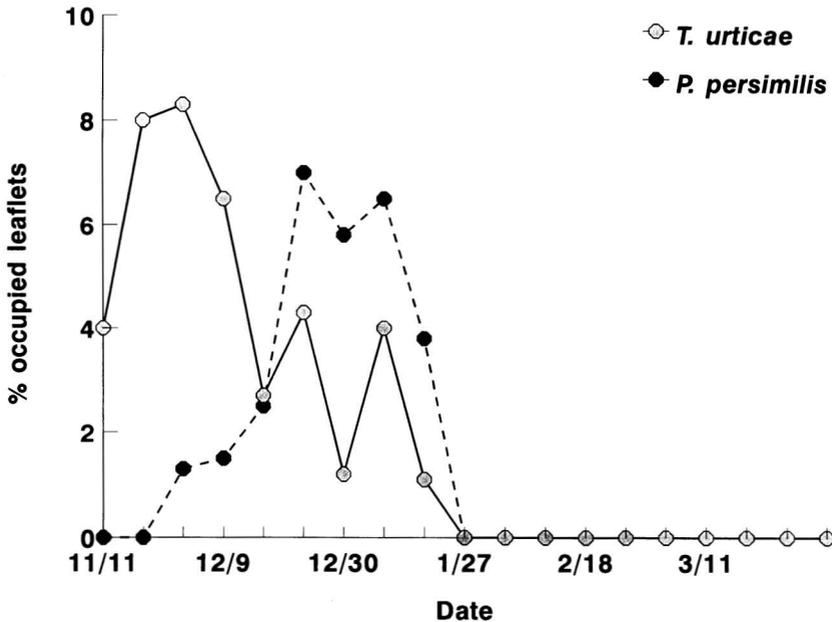


Fig. 3. Percent of strawberry leaflets inhabited by one or more *P. persimilis* or spider mites from November 1992 to February 1993 in a field 3. Predacious mites were released at 20,000 per acre, and one acaricide treatment was applied.

this break afforded just enough control over the next 2 weeks. The population of spider mites in field 3 continued to decline as *P. persimilis* quickly increased in numbers two weeks after the acaricide application. Again, control of *T. urticae* was attained. The two fields exhibited a stable predator-prey relationship between the two mite populations for the remainder of the growing season, as few of either species could be detected.

Two important features of the system were demonstrated on these farms. One is that use of some acaricides, in emergency situations, at low levels, will not jeopardize the control afforded by *P. persimilis*. This is important to commercial growers who can not afford to wait for delayed biological control and to risk loss of yield. The other is that populations of spider mites shown in Fig. 1-3 were too high for reasonable, prompt control in commercial fields using *P. persimilis*, without risking damage. Hence, the threshold of 10% of the leaflets infested is realistic.

Releases of *P. persimilis* were also tried at a reduced level of 10,000 mites per acre (Fig. 4). Control was achieved, although the system took longer to reach stability. A release was made when 12% of the leaflets were infested, but *P. persimilis* had already entered the field from a neighboring field, occupying 2% of the strawberry leaflets by the time a deliberate release was made. The presence of *P. persimilis*, even in such low densities before the release, may have assisted its success. Both populations increased slowly until they reached the same high density observed in the other examples before finally collapsing and achieving stability.

Importantly, the plants had matured fully by the time of this late-season release. The increased amount of foliage provided much more of a chance for *P. persimilis* to move from the vermiculite medium to the leaves, during release, before being disturbed by wind. The outcome of releases on plants with little foliage (i.e., early in the growing

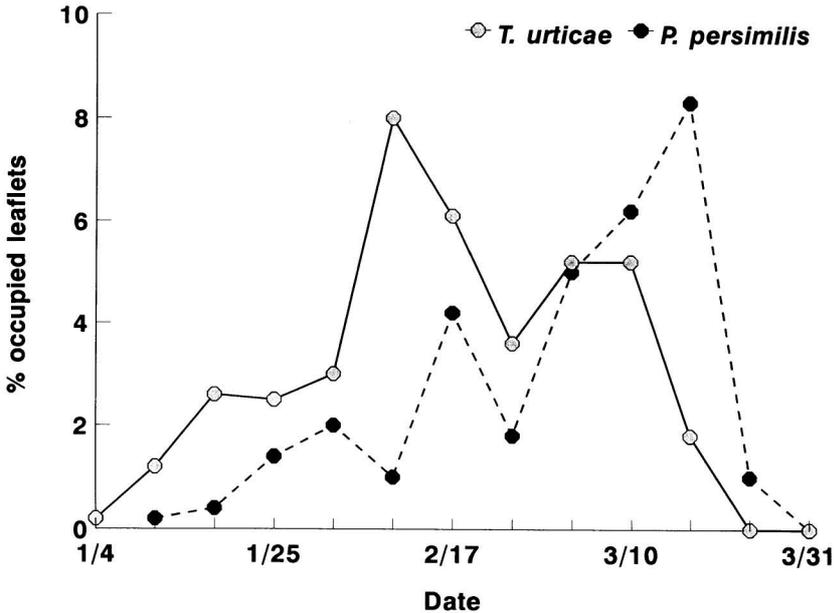


Fig. 4. Percent of strawberry leaflets inhabited by one or more *P. persimilis* or spider mites from January to March 1993 in field 4. Predacious mites were released at 10,000 per acre.

season) can be uncertain. It is preferable to wait for the development of 4-5 fully-expanded leaves.

In the fields under biological control by *P. persimilis*, I have observed stronger plant growth and healthier, denser foliage, possibly due to the absence of chemical treatments (see also Trumble et al. 1988). The growers observed larger fruit size, and reported equal, or larger, yields under biological control compared to chemical control. The cost of chemical control in strawberry fields usually rises through the growing season as mites become more difficult to control. In contrast, an early expenditure on predacious mites stabilizes spider mite densities throughout the season. Every grower realized a cost saving compared to chemical control of mites, and more so when savings of additional, unnecessary, chemical treatments are included in the balance.

Costs for acaricides in two of the fields the previous year were \$375 (Fig. 5) and \$300 (Fig. 6) per acre. These totals do not include labor, fuel, depreciation, etc. This is much higher than the average cost of \$100-150 per acre for *P. persimilis*.

For comparison, we plotted the spider mite populations from two of the farms from the previous year (1991-2) under chemical control (Fig. 5-6). Although actual counts of spider mites were made per complete trifoliolate leaf at the time, we divided the counts by 3 in an attempt to bring the value closer to the rating method we now employ while using biological control methods. This allows a rough comparison of spider mite population movements under both systems. The threshold for treatment under chemical control was 5 mites per trifoliolate leaf or 1.7 per leaflet. The farm data shown in Fig. 5 shows mite populations over threshold nearly the entire season and demonstrated poor response to repeated applications of various acaricides.

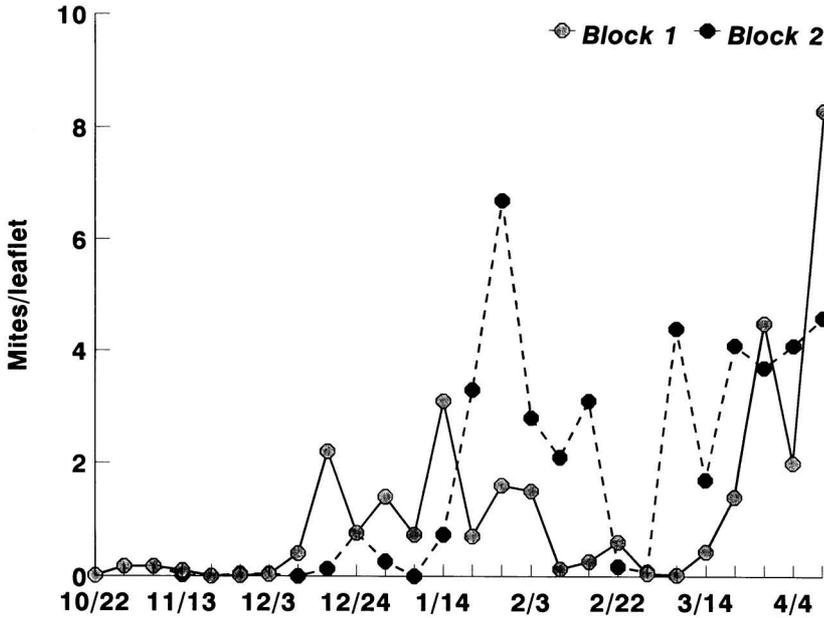


Fig. 5. Number of two-spotted spider mites per strawberry leaflet from October 1991 to April 1992 in field 5. The spider mites were treated with chemicals.

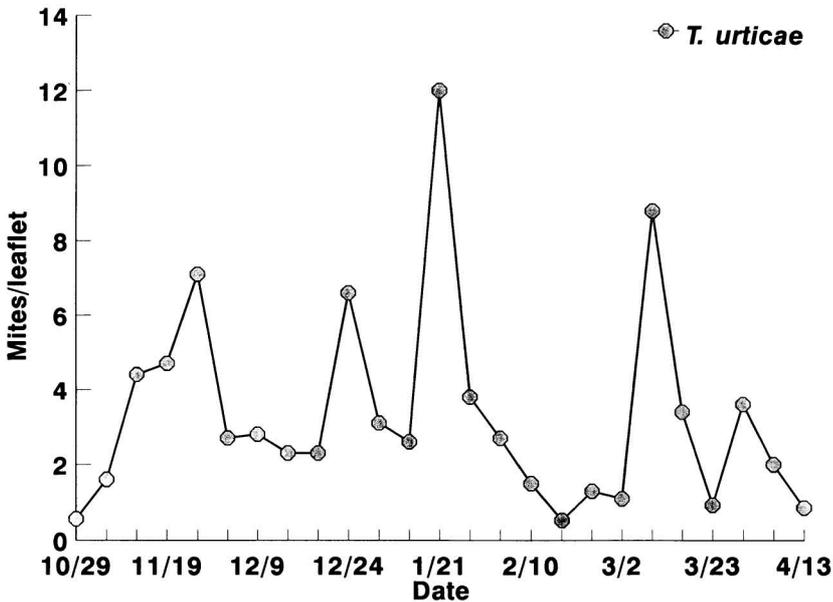


Fig. 6. Number of two-spotted spider mites per strawberry leaflet from October 1991 to April 1992 in field 6. The spider mites were treated with chemicals.

The farm data shown in Fig. 6 provide a more typical view of spider mite response under chemical control. The population remained low initially as the colder weather and early success in spraying provided an effective combination. As temperatures rose in the spring, and reproduction by spider mites increased accordingly, chemical control became increasingly ineffective. This disadvantage was accelerated by the effect of resistance to chemical acaricides. After several weeks of chemical applications, resistance became an increasing problem until the end of the season when all control was finally lost. The opposite is true under biological control: the stability of the predator/prey system provides a field which can be harvested until the market determines otherwise, not because spider mite control fails. Biological control by predacious mites allows commercial growers to take advantage of a late-season market that would be impossible under chemical control.

CONCLUSION

Research on the following subjects would be helpful. Can spider mites be controlled by predacious mites on strawberry plants at the nursery? What would be the effect of travel from the nursery to the farm on the predator/prey relationship? What is the feasibility of using "banker" plants, held as stock at the farm during the fallow season? Can effects of various chemical pesticides on the predator/prey relationship be characterized more adequately? Why do the predacious mites (*P. persimilis*) move downward into leaf axils of strawberry plants when they are released, what can be done to counterbalance this, and what are the other effects of migration by the predacious mites?

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THE CONSERVATION CHALLENGE IN AGRICULTURE AND THE ROLE OF ENTOMOLOGISTS

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ABSTRACT

Conservationists and agriculturists must work together toward the common goal of satisfying growing human population needs while maintaining natural resources and ecological processes critical to long-term human survival. The study of invertebrates has perhaps the greatest potential for contributing to this goal through theoretical, practical, and educational advancements. I discuss my view of the resulting challenge to entomologists with emphasis on insect conservation, sustainable agriculture, and environmental education.

Key Words: Insect conservation, sustainable agriculture, landscape ecology, environmental education.

RESUMEN

Los conservacionistas y los agricultores deben trabajar juntos hacia el objetivo común de satisfacer las necesidades crecientes de la población humana mientras mantienen los recursos naturales y los procesos ecológicos críticos para la supervivencia humana a plazo largo. El estudio de los animales invertebrados tiene el máximo potencial para contribuir a este objetivo por adelantamientos teóricos, prácticos y educacionales. Yo discuto mi punto de vista del reto resultante para los entomólogos con un énfasis en la conservación de los insectos, la agricultura sostenible, y la educación ambiental.

Agriculturists are attempting to feed the world's population in a sustainable manner. Conservationists are attempting to halt the exponential increase in the loss of species and the ecological processes they perform. These goals can be seen as the flip sides of the human population growth problem. Recent changes in the scale of environmental degradation have resulted in a philosophical shift in both groups. History, methods, language, lack of knowledge, and political, economic, and social constraints have kept conservation biologists and agriculturists antagonistic until very recently. In this paper I will discuss the negative effects of these factors on natural and managed ecosystems, and future prospects for attaining sustainable agricultural practices while maintaining biological diversity. The success of conservationists and agriculturists hinges on the cooperation and success of each other. Neither can succeed in the long run without reducing human population growth and per capita resource use.

The rate of human-induced species extinction is considered unacceptable and thought to threaten ecological processes necessary to sustain human food, water, shelter, recreation, and aesthetic needs (Ehrlich & Wilson 1991, Wilson 1985, 1988). Predictions of future worldwide species extinction rates range up to 50,000 species per year (Mann & Plummer 1992). This rate is over 400 times that recorded throughout geological history (Wilson 1985). At this rate we would lose almost one-tenth the number of extant described species over the next 20 years (Paoletti et al. 1992, Reid & Miller 1989). As detrimental

as these losses may be in terms of direct and indirect benefits of biological diversity, conservation concerns simply cannot be addressed in the absence of fulfilling human needs.

Modern agricultural practices are major contributors to the loss of biological diversity and environmental degradation. Agricultural land managers, including farming, rangelands, animal production and forestry systems, manipulate approximately 70 percent of terrestrial ecosystems. Human settlements co-opt another 25 percent, leaving less than 5 percent for primarily conservation-directed management (Reid & Miller 1989, Pimentel et al. 1992, Western & Pearl 1989). Clearly we cannot maintain biological diversity and ecological processes without broadening agricultural practices to include more conservation concerns, and vice versa (Gall & Orians 1992).

Combining agricultural and conservation goals will not be easy. Humans are already co-opting about 40 percent of terrestrial biological productivity, and that percent is rising (Vitousek et al. 1986). Yields of staple food crops must soon more than double just to maintain current per capita consumption. To meet the growing demand for food, approximately 16 million hectares of forests are currently being converted to agricultural lands each year (Pimentel et al. 1986). This land conversion is necessary not only because there are more and more people to feed but because currently managed agricultural lands are deteriorating under modern agricultural practices (Corson 1990, Soulé et al. 1990). We cannot continue this strategy. We are already approaching the limits of arable land conversion and increasing productivity on those lands (de Zeeuw 1988, Ehrlich & Ehrlich 1991, Pimentel et al. 1992, Plucknett 1993, Soulé & Piper 1992).

Although the short term goals of agriculture and conservation are more and more in opposition due to human population pressures, they remain interdependent. Successful management of preserved areas is dependent on surrounding, mostly agricultural, land practices. And ultimately, the success of agriculture depends on the maintenance of surrounding and distant natural systems. Short-term goals have kept these two camps from cooperating. Long-term interdependence has just recently been appreciated in terms of policy, research and education, and is our hope for the future.

Entomologists should take a leading role in combining agriculture and conservation biology. We have an obligation, as resource managers, to the conservation of nature (Dourojeanni 1990, Noss 1989, Summer 1921). Our responsibility rests on three conditions. First, entomologists must contribute to the development of ecologically-based management strategies if we are to meet future challenges of food and fiber production. Second, insects represent most species diversity and are key players in ecosystem structure and function, and so, deserve our attention. Third, the study of insects provides unique, diverse, and relatively unexplored opportunities to develop public environmental literacy necessary to support future conservation and agriculture goals.

THE ENDANGERED SPECIES ACT

In the U.S., conservation policy rests on the Endangered Species Act (ESA) of 1973. The federal list of endangered or threatened species is over 1,000, with 3 times that many awaiting sufficient study for listing (Salwasser 1991, Scott et al. 1987). This species by species approach to conservation focuses on those species on the verge of extinction (McIntyre et al. 1992). It is costly, slow, and biased, and does not adequately address the loss of biological diversity.

Many practical problems limit the ESA. It rests on concepts such as species, habitat, and minimum viable population. These are critical, yet undefined concepts (e.g., see Rojas 1992). The act generally focuses on taxonomic species without considering genetic distinctiveness of individuals or populations making up those species (Crother 1992, Ehrlich 1988). Populations and metapopulations are protected only in special circumstances. It does not provide strong enough habitat protection (Murphy 1991, Rohlf

1990, Sidle & Bowman 1988). Ecosystem function is not effectively addressed using the single species approach (Csuti et al. 1987, Hutto et al. 1987, McIntyre et al. 1992, Salwasser 1991, Scott et al. 1987). Long-term and far-reaching factors are not included in the listing process (Rohlf 1990). Legally, the ESA considers all species of equal value, but, practically, efforts are highly biased toward more glamorous species that may be of little significance ecologically. There is no means to address particular species that are considered especially significant ecologically. Recovery plans, required by the ESA, are high-tech, costly, slow to be developed, approved, and implemented. These obstacles often prevent population recovery. To date, only five species have been taken off the ESA list (U.S. General Accounting Office 1988, in Wilcove et al. 1992), while global species loss continues to rise exponentially. Recovery success will continue to decline as the list grows rapidly.

Support for the ESA has been weakened by political ploys that focus on individual glamorous species to save larger systems (Mann & Plummer 1992). Also, human affinities for large, cuddly, vertebrates have dominated support for conservation and negatively affect the efforts of the U.S. Fish and Wildlife office. We cannot hope to expand such emotionally-based consideration to the number or variety of species that we must address in future conservation efforts.

Time, information, and resource limitations prevent the ESA from addressing the loss of biological diversity and ecosystem function (Noss 1991). The conservation community now generally advocates a hierarchical approach to the conservation of biological diversity, addressing all biological heterogeneity, from genes to landscapes. This approach broadens the scope of the ESA and includes monitoring and managing the composition, structure, and function of ecological systems at multiple levels of biological organization. These include genetic, population and species, community and ecosystem, and landscape levels (Noss 1990b).

The major reasons advanced for concerns about the loss of biological diversity are ecological (Cairns 1993, Ricklefs et al. 1984, Wilson 1988). Ecological processes include physical and biological processes that influence ecosystem diversity, dynamics, and evolutionary pressures that in turn act on the biological components of the system (Ricklefs et al. 1984).

Conservation biology grew out of wildlife and park management, where managing small populations of animals of game interest was a primary objective (Ginsberg 1987). As a result, ecosystem conservation has been aimed at habitat protection for particular species, usually large animals. Rarely are ecological processes objectively considered in land preservation. If we are to devote most attention to those species making up most biological diversity, and those that are most important to the persistence of higher levels of biological organization and ecological function, we must focus more on invertebrates.

Salwasser (1991) lists 4 elements necessary to build a successful ecosystem approach to conserving biological diversity. These include, 1) integrative research, technology and development, 2) design of adaptive management and monitoring strategies, 3) policy development, and 4) public education beyond glamour species. This larger-scale approach in conservation biology reinforces the need for conservation biologists and agriculturists to work together. Not only does most biological diversity occur on agricultural and other managed lands, but management practices directly affect the success of conservation efforts across multiple levels of organization and spatial scales.

INSECT CONSERVATION

"If insects (and other arthropods) were the size of birds, or people the size of mice, 'bugwatchers' would be as prevalent as bird watchers, and entomologists would command the budget of the Defense Department." (H. E. Evans 1985)

Arthropods represent approximately 90 percent of all species including plants (Pimentel et al. 1992b), with insects accounting for approximately 80 percent of all animal species diversity (Samways 1992). Together with micro-organisms, insects make up most animal biomass, and they show, by far, the greatest diversity of ecological roles (Coulson & Crossley 1987). They are also known to be especially vulnerable to small-scale habitat destruction (Ehrlich & Murphy 1987, Murphy et al. 1990). Yet, until recently, this group has been neglected by conservation biologists (Dourojeanni 1990). This neglect has some just bases. Insect life histories are generally characterized by short lifetimes, rapid and high reproductive rates, and high re-colonization rates (IUCN 1983). These attributes contribute to their resilience and recovery potential from human disturbance.

Unjust biases have also contributed to the neglect of this significant group. Invertebrates fare particularly poorly under the ESA. The law provides for listing and protection of any threatened or endangered species of plant or animal. Yet, to date only 28 species of insects, 11 crustaceans, 3 arachnids, and 68 gastropods receive federal protection. These account for only about 26 percent of animal species listed, underrepresenting their importance in species diversity. Unlike vertebrates, distinct populations of invertebrates are not given protection (Murphy 1991).

As with vertebrates, expenditures are not consistent among species. Glamour-species, mostly butterflies, receive disproportionate attention from conservationists and the general public (Pyle 1976). Public support of the ESA will diminish as the listing process includes more and more 'ugly' insects. This will further undermine the single species approach.

Although approximately 1,200 invertebrates have been proposed for listing, practical obstacles will likely limit their inclusion (Bean 1993). These include a lack of information on diversity, abundance, ecological roles, and methods for monitoring them. These obstacles limit the rate of data processing and increase the likelihood of mistakes in identification. For most invertebrates, data necessary to demonstrate a decline in the population size or the spatial distribution are not available, even for relatively well-studied species. Many life histories have not previously been considered. Methods for data collection and interpretation are not well developed. And finally, human effects on invertebrates are often less well understood.

To date, no invertebrate species has recovered to population levels sufficient to be taken off the list. In fact, as of 1990, only 2.5 percent of the then-listed 81 invertebrate species were regarded as improving, while 41 percent were still declining (Bean 1993). This is partly a reflection of a vertebrate-biased expenditure of funds for recovery plans.

There are important moral problems with the species approach to conservation that become evident when we focus on insects. Without an ecological perspective we cannot expect the general public to understand and support the need to eradicate one pest species, import another alien species for biological control, and spend a lot of money and time to preserve yet another.

The Value of Insects

Insects have long been valued for the goods and services they provide to humans. These are reviewed in IUCN (1983), Morris et al. (1991), Murphy (1991), Pyle et al. (1981), and include scientific models in research, medicine, and education, genetic resources, foods, products, wildlife trade, and agricultural services. Beyond direct and indirect economic uses, insects continue to be valued for aesthetic and cultural benefits.

Unlike vertebrates, which are better valued economically and aesthetically (Morris et al. 1991), invertebrates are most important in conservation biology because of the ecological services they provide. Most are neutral or beneficial, and some crucial to agriculture. Their services include pollination, biological control, and waste management.

Yet entomologists focus primarily on the relatively few, but important pests. As agriculture becomes more diversified, entomologists will focus more on insects in natural systems and therefore will contribute more to invertebrate conservation.

The value of invertebrates as environmental monitors is only beginning to be appreciated (Magurran 1988, Oliver & Beattie 1993, Pearson & Cassola 1992). Indicator species are used to assess environmental effects of human activities, to determine regional patterns of biological diversity, to measure changes in community structure and function, and to estimate land value (Hutto et al. 1987, Murphy et al. 1990, Noss 1990b, Pearson & Cassola 1992). Insects show great potential as environmental indicators because they are often specialized, easily observed and monitored in the field, and their needs are often correlated with other species needs (Samways 1989b, Wilson 1988). The abundance and diversity of aquatic insects as an indicator of water quality is probably the most established monitoring system. Butterflies are currently receiving much attention in conservation because of their potential as indicator species. They may provide good indicators of landscape structure necessary for land acquisition and reserve planning (Kremen 1992, Murphy 1991, Pyle et al. 1981). Their value rests in their familiarity, aesthetic qualities, established systematics, developed monitoring techniques, and close association with plants characteristic of this group (IUCN 1983, Pyle et al. 1981, Thomas 1991).

According to Oliver & Beattie (1993), the major shortcomings of using invertebrates as indicators are the shortage of taxonomists, the undeveloped systematics characteristic of most groups, lack of distributional knowledge, and lack of monitoring techniques. They suggest a method for rapid assessment of biological diversity that is based on recognizable taxonomic units assessed by trained technicians. This method saves time and reduces costs without significantly sacrificing accuracy. Such new developments in monitoring methods, together with increased focus on large scale conservation approaches, will increase the need for input by entomologists in conservation.

Insects as Key Players in Ecosystems

The diverse and pervasive ecological roles of invertebrates are sometimes subtle, generally little understood, and often difficult to value economically. It is their significance in the composition, structure and function of ecosystems that most clearly ties them to conservation biology (Ricklefs et al. 1984, Wilson 1987). These influences occur primarily through the direct and indirect effects of insects on primary production, consumption, and decomposition.

Invertebrates are the most abundant and diverse herbivores and detritivores in most terrestrial ecosystems, and most parasite-host and predator-prey associations involve invertebrates. Furthermore, insect specialization and diverse ecological associations are believed to affect larger scale structure and function (Ehrlich & Mooney 1983, Price 1988, Seastedt & Crossley 1984). They are thought to contribute significantly to stability and resilience of many communities (Morris et al. 1991, Wilson 1987). A better understanding of the ecological roles of insects, and their broader influences on ecosystems and landscapes, are crucial to the future development of viable conservation strategies and sustainable agricultural practices.

Human Threats to Insects

Invertebrates face the same general human threats that vertebrates face. These include, 1) changes to the land, including conversion for agriculture, urbanization and industrialization 2) changes to the water, including drainage and impoundment, 3) pollution to the air or water, 4) critical community changes, such as the loss of a host or

invasion by exotics, and 5) specific threats to species, including over-collection and pesticide applications (IUCN 1983, Pyle et al. 1981). Modern agricultural practices are considered major contributors to all of these threats.

Based on distribution estimates for tropical species, a large number of insect species is thought already to be extinct (Dourojeanni 1990). Of the threats in common with vertebrates, over-collecting and non-target effects of pesticide applications are generally considered negligible to invertebrates (Pyle et al. 1981). Over-collecting is thought to be a potential problem only in unique circumstances (e.g., when the species is already at the brink of extinction due to severe habitat loss), or when a species life-history strategy makes it especially vulnerable (e.g., species that are relatively sessile, long-lived, and/or with low regeneration rates) (IUCN 1983).

Habitat loss is considered to be by far the most significant threat to insect conservation, and agricultural conversion is considered the most significant contributor (Samways 1992). Lovejoy (1980, in Dourojeanni 1990) estimates that approximately one-third of all tropical insect species may be extinct by the year 2000 due to deforestation. Eighty percent of worldwide deforestation is to clear land for agriculture (Pimentel et al. 1986). Although such land conversion is thought to represent a great threat in the tropics, it is considered of little importance in temperate areas due to the lower incidence of precinctivism (*sensu* Frank & McCoy 1990). Prairie adapted insects of North America may be especially vulnerable to population decline when those lands are converted to agriculture (IUCN 1983, Pyle et al. 1981). Island invertebrate fauna, such as in Hawaii, may be especially vulnerable to extinctions resulting from land conversion to agriculture (Howarth 1991). Reforestation practices that reduce diversity can also threaten insect species.

Small-scale habitat loss, including overgrazing or changes in grazing ecology associated with animal production, can lead to the loss of associated insects. For example in Europe, myxomatosis was introduced in the 1950s to control rabbit grazing. Resulting changes in grass ecology led to a decrease in at least three lepidopteran species. Likewise, over-grazing by sheep in Australia has threatened an uncommon grasshopper (IUCN 1983). Small-scale and highly specialized adaptations in insects point to the problems of managing an area 'for' certain species. Errors in management scale can lead to unforeseen and unwanted changes in community structure.

Agricultural management practices that disrupt water systems, such as drainage of forest bogs, can threaten insect populations (IUCN 1983). Extensive pesticide and fertilizer use and associated landscape simplification are thought sometimes to harm beneficial insects. However, invertebrate extinctions resulting from pesticide application, except through their association with hosts or symbionts, appear to be rare. This is probably partly a reflection of relatively low insect diversity in monocultures, and methodological problems of documenting extinctions (Morris et al. 1991, Pyle et al. 1981). Because agricultural lands are disrupted and simplified, they can be especially vulnerable to invasion by exotics, which in turn leads to reduced populations of native negative insects (Carroll 1990).

Unique Needs of Insects for Reserve Management

Besides vulnerabilities in common with vertebrates, recent work has shown that insects have unique needs that must be considered in land management planning. Insects are successful because of their small size, short life cycles, and ability to locate and adapt to specific environments (Wilson 1987). These same specializations make them generally susceptible to abiotic population regulation factors (Murphy et al. 1990). Endangered insects may therefore be more likely to become extinct than vertebrates, and require larger minimum viable populations (Thomas 1990). Ecological specializations,

such as a close evolution with particular plant species, sometimes distinct and specific needs during different life stages, and often small distributional ranges, can also contribute to vulnerability to extinction when these local habitats are destroyed (Dourojeanni 1990, Gilbert 1980, Moore 1991, Murphy 1991, Pyle et al. 1981). Insect specialization and small-scale habitat needs can also make them good candidates for relatively inexpensive, conservation efforts (IUCN 1983).

Insects differ significantly from vertebrates in their population dynamics, ecological roles, and habitat requirements. The importance of temporarily unoccupied habitat for invertebrate recolonization is little understood, but likely differs from that of vertebrates. Furthermore, many natural areas have been reduced and fragmented to the extent that they do not possess vertebrate species of similar range and habitat needs as invertebrates and plants (Murphy 1991). If land management strategies do not take into account these differences, important invertebrates may be lost in otherwise legitimate efforts to manage land for the conservation of larger, broader-ranging vertebrates (Ehrlich & Murphy 1987, IUCN 1983, Murphy 1991).

Ehrlich & Murphy (1987) list research needs for development of management strategies aimed at invertebrates. These include investigations of, 1) demography and gene flow, including migration and recolonization by ecologically connected reservoir populations, 2) the importance of habitat diversity and specific habitat requirements, including host requirements, and habitat linkages, and 3) the role of abiotic and biotic factors in population regulation. They also stress the need for long-term studies of representative invertebrate groups, and the need to educate the public about the need to focus on populations rather than species. Thomas (1990) also suggests that minimum viable population estimates should be an order of magnitude above those for vertebrates to ensure comparable protection. Establishing safety margins is especially difficult because of the paucity of data on invertebrate abundance and distribution.

The Future

Insects are most important because of their ecological roles. Disruptions of these roles are not directly tied to the currency of species or extinctions. With limited resources, knowledge, and time, we cannot expect to discover, let alone save, the smaller organisms using a laundry list approach; even with improved methods taking into account differences in extinction threats and land management needs.

Ginsberg (1987) noted a bias toward larger animals by authors presenting at the first Society for Conservation Biology's inaugural meeting in 1987. Excluding aquatic organisms, of 53 papers and posters, there was an evident bias toward birds (10%) and mammals (18%). Plants (8%) and insects (4%) received little attention. Clearly, insects receive too little consideration by conservationists. This is largely a reflection of traditional conservation strategies that are vertebrate-based, as evidenced by the bias toward glamorous butterfly species (Pyle 1976).

Insect conservation will be best addressed by larger-scale research and management strategies that combine conservation and agricultural goals. As conservation biologists develop ecosystem approaches to conservation, they will seek to understand natural systems, what makes them resilient, how do they recover from stress, and how do we monitor these systems. As agriculturists attempt to develop sustainable land management practices, they will model natural systems and include natural areas in their management strategies. In both cases the most important animal group to study will be the insects. These changes in philosophy of both conservationists and agriculturists will provide unique opportunities and challenges for entomologists to contribute to insect conservation efforts (Dourojeanni 1990).

MODERN AGRICULTURE

Humans influence biological diversity primarily through habitat loss and fragmentation, over-exploitation, the introduction of exotic species, pollution, and climate change (Soulé 1991). Modern agricultural practices, including farming, fishing, animal production, and forestry systems, are significant contributors to all of these problems. Biological diversity is also threatened through the economic and social effects of agriculture. Because sustainable agricultural practices ultimately rest on intact ecosystem processes, upcoming shortages of water, land, and soil will increase these negative effects and emphasize the direct interest of agriculture in preserving biological diversity.

Although agricultural practices have affected nature for many centuries, until recently these effects were small in degree and temporally and spatially localized. Environmental effects worsened significantly as agricultural practices changed dramatically and rapidly after World War II (Gall & Orians 1992, Soulé & Piper 1992). Large scale, intensively managed agricultural industry largely replaced smaller farms and moved agriculture onto more marginal lands, leading to increased conflict between agriculturists and conservationists (Carroll 1990).

Modern agricultural practices affect the conservation of nature in two general ways. First, natural habitats are being converted to agricultural lands at an exponential rate, reducing and fragmenting land available for conservation, and reducing genetic resources critical to agricultural development. As prime arable land is lost to human settlement, agriculture is forced onto less and less optimal lands (Canter 1986, Corson 1990, Ehrlich & Ehrlich 1991). So far, this transition has been possible without losses in productivity due to heavy reliance on outside inputs into the agricultural system.

Secondly, agricultural practices affect the conservation of nature by the intensiveness of land use characterized by simplification, specialization, and mechanization. Management practices are built on large capital investments and continuous inputs of non-local, non-renewable inputs such as fossil fuels, fertilizers, and pesticides (de Zeeuw 1988, Plucknett 1993). These large-scale human substitutions for ecosystem services are generally unsustainable (Byrne et al. 1984, Ehrlich & Ehrlich 1991), decrease biological diversity on that land and surrounding ecosystems, and cause environmental degradation (Carroll 1990, Dahlberg 1992, Orians & Lack 1992, Reganold et al. 1990).

Large-scale, single commodity-oriented agricultural research and management strategies address problems in isolation and in series. The agricultural field is treated like an isolated laboratory rather than an integral part of an ecosystem. Landscapes are simplified (Eijsackers 1988, Gardener et al. 1991). Natural processes are unlinked and natural resources are replaced with technological alternatives (Ricklefs et al. 1984). Evaluation of production-maximization practices are assessed economically in the short-term. Farmers become trapped by the need to develop more land, make more capital investments, and add more non-renewable resources, putting themselves at higher and higher risks to environmental and social changes.

A prominent unsustainable feature of modern agricultural practices is the extensive use of fossil fuels. Heavy reliance on fossil fuels not only contributes to the loss of biological diversity, but promotes climate change. The use of fuels to clear land, the loss of tree coverage, and direct use of fossil fuels in food production, contribute significantly to the build up of CO₂ (Gilpin et al. 1992). Energy costs through fertilizer, pesticide, and water additions are rising sharply while giving diminished economic returns in many developed areas (Ehrlich & Ehrlich 1991, Pimentel et al. 1992a). Consumer demands and demographic problems associated with the large-scale nature of farming systems contribute to the energy costs of agriculture. As energy constraints are approached, population pressures could cripple agriculture unless we can develop alternative, more energy-efficient ways to produce and distribute food and learn to eat lower on the food chain (Gilpin et al. 1992).

Pesticide applications continue to dominate pest control methods (Morris et al. 1991). Approximately 2.5 billion kg of mostly broad-spectrum synthetic pesticides are used in agriculture and public health each year (Pimentel et al. 1992b). Pesticide use is costly, affects human and animal health negatively, causes environmental degradation, and destroys beneficial organisms leading to further pesticide reliance. Paoletti et al. (1992) cite evidence that pesticide residues affect beneficial invertebrates negatively in agricultural systems. Pesticides are also thought to alter the structure and function of whole ecosystems (Pimentel et al. 1992b). The toxic effects of pesticides on soil organisms, and resulting loss of soil fertility, are already troublesome to agriculture. The direct, environmental, and social costs of pesticides in the U.S. total approximately \$12 billion with a saving of approximately \$16 billion in crop value (Pimentel et al. 1992a).

Considerations of the risks associated with modern agriculture call for more research into ecological methods of pest control. Integrated pest management efforts, with strong biological control elements, are probably the best examples of the use and protection of biological diversity in modern agriculture. However, there remains much room for improvement. Though based strongly on ecological principles, IPM programs still rely heavily on reductionistic approaches to control single pests on single crops. This together with structural simplicity of the agricultural field leaves chemical control a still-common option. According to Barfield & O'Neil (1984), IPM programs must include large-scale ecological elements and processes, an understanding of mortality factors, an integrated control effort for different pests, incorporation of the dynamic nature of agroecosystems, and development of monitoring methods to meet its goals more efficiently.

Water is not valued nor managed in accordance with its ecological value. Much of the increased production capacity on agricultural lands has resulted from irrigating otherwise unproductive lands. Agriculture now uses approximately 70 percent of our world's dwindling usable water. Between 1950 and 1985 the total area irrigated nearly tripled, but economic costs have since slowed this trend (Ehrlich & Ehrlich 1991). Beyond the water resource limitations, irrigation practices increase energy demands, cause soil degradation from waterlogging and the accumulation of salts, and carry water pollution into nearby streams and lakes. Agricultural practices degrade water quality and contribute significantly to non-point pollution problems (Canter 1986, Hess 1991). Irrigation practices have led to productivity losses in approximately one-third of the world's irrigated farmland (Ehrlich and Ehrlich 1991).

Soil degradation is perhaps most directly linked back to loss of production. It is therefore best documented and best addressed by agriculturists. The management strategies that more than doubled world grain production since the 1950s have cost over 20 percent of our topsoil (Raven 1990). Currently, soil loss due to farm management practices exceeds soil formation by approximately ten-fold (Corson 1990). Soil erosion, loss of organic content, crusting, and loss of inorganic nutrients are also significant problems. Wiggins (1983) reports that soil fertility in Canada has dropped to less than one-half of its original level.

Air pollutants caused by agricultural practices arise from emissions, tillage operations, burning, wind erosion, harvesting and handling operations, pesticide applications, and vehicles (Canter 1986). These affect crop and animal production as well as human health negatively. Ozone depletion has been shown to stunt crop growth (Worldwatch Institute 1993) due to increased UV radiation. According to a recent USDA-EPA study reported by the Worldwatch Institute (1993), the U.S. currently experiences an overall annual crop harvest loss of 5-10 percent due to air pollution at a cost of \$3.5 to 7 billion each year.

The introduction and establishment of exotics can be especially problematic in highly disturbed and simplified agricultural lands. Such non-natives can threaten native fauna and flora significantly (Wilson 1988). Alien insects transmit diseases, become crop pests,

and negatively affect beneficial and other non-target invertebrate species. According to Sailer (1983) approximately 17 percent of 1500 immigrant insect species in the U.S. became pests requiring control efforts.

However, the researched and planned introduction of exotic organisms for use in biological control should not be criticized because of immigrant species. Furthermore, it is important, especially in sub-tropic, peninsular Florida, that we recognize that the term 'exotic' is relative, being both temporally and spatially scale-dependent (Frank & McCoy 1992, Noss 1990a). This greatly complicates assessing the costs of both the immigration of exotics through agricultural transport, and the encouragement of exotic species by agricultural land use strategies (Pyle et al. 1981). Preventing immigration, understanding ecological consequences, and developing eradication and control tactics for exotics will become increasingly complex and difficult challenges in land management. Entomologists will take a leading role in addressing these problems that affect natural and managed lands.

As the previous discussion suggests, we are still reaping the benefits, but starting to pay the costs of the Green Revolution. Environmental pollutants from agriculture include, heavy metals, dust, plant nutrients, pathogens, pesticides, odors, and sediments (Canter 1986). Farming practices affect soils, vegetation, fauna, water and nutrient cycles, and landscape elements leading to significant losses in biological diversity, reduced profitability, and environmental and human health threats (Paoletti 1992, Reganold et al. 1990).

Intensively managed modern agriculture has failed to create a utopian world by reductionistic approaches that neglect ecological impacts on and by the system. Energy costs and coming fossil fuel shortages, resource depletion, soil erosion, environmental contamination, and social and ecological vulnerability to environmental changes call for locally adapted, diversified agricultural practices built on ecological principles and dependent on intact natural systems. Large-scale agricultural organization, research strategies, and education efforts must be changed significantly. To meet these goals, entomologists must consider the agricultural field within the larger ecological and social context.

It is clear that we must minimize the negative environmental impacts of agriculture. Technical developments and government policy driven by reductionistic approaches and short-term perspectives cannot continue to dominate agricultural research and policy. However, the false hope of technology is alive and well as evidenced by a recent quote with regard to our ability to adjust agricultural practices to meet global climate changes. Gary Evens, the head of U.S. Department of Agriculture's Department of Global Change said, "Technological capabilities in agriculture have proven for the last 50 to 75 years to be able to keep up with any shifts and changes that have taken place" (Monastersky 1992).

AGRICULTURE-CONSERVATION CONNECTION

"The struggle to maintain biodiversity is going to be won or lost in agricultural ecosystems." (McIntyre et al. 1992)

The short-term goals of sustainable agriculture and conservation of biological diversity will necessarily become more and more opposed as population pressures increase (Robinson 1993). It is the ultimate dependence of agriculture on surrounding and distant functioning ecosystems, together with the significant environmental effects of modern agriculture that necessitates cooperation between these groups (see Aplet et al. 1992, Dahlberg 1992, Francis 1990, Paoletti 1992, Paoletti et al. 1992, Pimentel et al. 1992, Pimentel et al. 1992b, Reid & Miller 1989). However, to date most knowledge about

the interaction between natural areas and agroecosystems is incidental, disjointed and generally not used for planning and management.

Agricultural systems are dependent not only on ecosystem services from surrounding natural lands but on biological diversity in far away places. Genetic resources are critical for the development of new crops, bases for breeding resistance, increasing productivity, nutritional value, and increasing within crop versatility needed to meet climatic and future management changes facing agriculture (Ehrlich & Ehrlich 1991, Gilpin et al. 1992). Biological control programs ultimately depend on the preservation of natural areas and ecological processes in near and distant lands (Gilpin et al. 1992, Morris et al. 1991). Ecologically-based pest control programs will become even more critical as agricultural lands continue to spread and we face the negative effects of chemical control.

Nature as a Model for Sustainable Agriculture

Sustainable agriculture requires diversification for better use of ecological processes to increase resilience and reduce risks (Ewel 1991, Pimentel et al. 1992b). Nature is our best model. We must move away from maximum production to optimal production strategies that are process- rather than product-oriented. Agroecology, as defined by Stephen R. Gliessman (Soulé & Piper 1992), is the science of ecology applied to agricultural production systems for the development of sustainable agricultural practices. Natural ecosystems generally exhibit some degree of dynamic equilibrium reflecting local adaptations to abiotic and biotic elements, including efficient solar energy budgets and nutrient recycling, and dynamic plant-herbivore and host-disease associations (Soulé & Piper 1992).

Natural systems will provide models for the development of better strategies for pest management, development of better monitoring techniques, more diverse cropping systems, and low-input agricultural systems. These practices will rest on increasing biomass, plant and animal diversity, maintenance of soils and water, and reduction of wastes (de Zeeuw 1988). They require a better understanding of regional dynamics impinging on managed systems, the importance of structure in population size, fluctuations, and community dynamics of beneficials and pests. Promising examples of the potential benefits of imitating natural systems in agriculture are physical models that provide the benefits of emergent properties without detailed knowledge of how these arise or function (Soulé & Piper 1992). To date, most ecological models in agriculture extrapolate only specific natural ecological processes onto an existing production-oriented agriculture structure. This tack-on strategy offers only limited improvements and limited reduction of negative effects.

Beyond the important academic lessons in natural systems, preserved areas and their ecological processes are most critical to agriculture through connecting ecosystem and landscape-scale effects such as water filtering, biological control refuges, natural pollinators, and environmental buffer zones, corridors etc. (Dahlberg 1992, Ehrlich & Wilson 1991, Eijsackers 1988, Gilpin et al. 1992, Pimentel et al. 1992b, Soulé & Piper 1992). Agriculturists must therefore include local natural area management needs and practices. Sattaur (1987, in McNeely et al. 1990) concluded that in the hills of Nepal, approximately each hectare of farmland required 3.5 times that land area of forest to remain sustainable.

Agriculture Contributions to Conservation Biology

Just as agriculture depends on biological diversity, conservationists cannot succeed in the absence of sounder agricultural practices (Pimentel et al. 1992b, Raven 1990). Agricultural lands are the big holders of much of the world's biological diversity (Pimentel

et al. 1992b, Sutton & Tittensor 1988). These lands are the major interface between natural areas, and agricultural management practices affect surrounding natural systems (Gall & Orians 1992). Yet conservation efforts are only beginning to focus on agricultural lands (Sutton & Tittensor 1988).

Agriculture is based on applied ecological research, and its success depends on understanding, monitoring, and influencing ecological processes. Agriculturists are probably our most experienced land managers (Plucknett 1993). This wealth of knowledge has been virtually untapped by conservation biology. Although the reductionistic approaches to agriculture have led to some long-term crunchees, this approach still has many advantages and has led to important developments at genetic, population, and ecosystem levels in inquiry.

Agroecosystems differ from relatively natural systems by the addition of energy to the system, simplification, dominance of artificial selection, and production-oriented control (Odum 1984a, in Coleman & Hendrix 1988). By monitoring the relatively simplified processes in agricultural systems, we can, perhaps, better interpret adaptation and changes in community composition, structure and function related to global climate changes.

Longer and larger-scale replication problems in natural land management limit ecologists' understanding of ecosystems and landscapes (Gilpin et al. 1992). Agricultural lands vary in, 1) duration and extent of disruption of ecological structure and function, 2) plot size, and 3) surrounding land use patterns. Because agricultural expansion onto natural lands and conversion of land back to a more natural state (e.g., land set-aside projects) can often be anticipated, ecological processes can be investigated at a larger-scale than possible in natural systems (Gall & Orians 1992).

Agricultural systems also offer productive models for understanding theories and concepts important in conservation. These include island biogeography and minimum viable populations, species concepts, metapopulation structure and dynamics, delineation of major pathways of energy and materials in ecological systems, gene flow, scaling problems, disturbance, keystone species roles, impacts of land fragmentation, colonization, extinction rates, competition, genetic drift, and genetic diversity. Now is the time to use agricultural systems as laboratories and experimental plots for understanding concepts in ecology (Saunders et al. 1991). Soon agricultural lands will be further pressed to meet human nutritional needs.

Increased knowledge of the interdependence of agriculture and natural systems is critical to meet future challenges of climate and policy changes, and to create locally attuned, ecologically based, sustainable operations while reducing negative environmental impacts (Dahlberg 1992). Yet, direct studies of the importance of biological diversity on and around agricultural systems are lacking (Paoletti 1992).

Landscape Ecology

Biological diversity exists in a matrix of habitat patches including managed and relatively natural lands. They are ecologically linked and interdependent (Carroll 1990, Pimentel et al. 1992b), and together make up landscapes (Coulson & Crossley 1987). These patches are linked through the movement of materials and energy by physical and biological processes (Rice 1992, Ricklefs et al. 1984, Saunders et al. 1991). These movements are critical to the regulation of local populations, determine the area required to avoid extinction, reduce inbreeding within populations, and preserve normal organization.

Agriculture and conservation goals are linked through landscape level processes (Carroll 1990, McIntyre et al. 1992, Salwasser 1991). By studying, monitoring, and influencing the movement of energy, materials, populations, and ecological processes,

functioning ecosystems can be managed proactively (Ricklefs et al. 1984, Scott et al. 1987). As agriculture continues to expand, natural lands become increasingly fragmented, isolated, and farther apart. These effects increase the need to manage natural areas and to integrate regional land use strategies (Carroll 1990, Harris 1984, Janzen 1986). For example, farming practices can provide a source and means of successful establishment of invasive species and disease transmission onto natural lands (Carroll 1990), leading to unwanted changes in ecosystem structure and function affecting both agriculture and conservation goals.

The influence of land fragmentation on populations and processes in natural areas and the role of agricultural lands as corridors between natural areas will become more and more important areas of conservation study. The importance of this structured linkage is exemplified in Costa Rica where, although approximately 25 percent (as opposed to approximately three percent worldwide) of land has been officially preserved and managed for conservation goals, biological diversity continues to decline due largely to modern agricultural practices on surrounding lands (Pimentel et al. 1992b).

Increasing structural diversity in agroecosystems with semi-natural interfaces, such as hedgerows, wetlands, and set-asides, can provide refuges, food sources, and critical linkages among natural areas (Dennis & Fry 1992, McNeely & Norgaard 1992, Noss 1987, Paoletti et al. 1992). Increased structural heterogeneity on field margins can have beneficial or negative effects on weed and pest control (Gall & Staton 1992, Paoletti 1992, and ref. in Booji and Noorlander 1992). Development of agricultural methods to increase biological diversity without undue negative effects on production will require cooperative efforts between agriculturists and conservation biologists. Because insects are key movers of materials and energy, a better understanding of the role of insects in these land interfaces will be critical to the development of future land management.

Stress ecology, the study of human and natural disturbances on ecological systems (Odum et al. 1979, in Coleman & Hendrix 1988) has helped to interface agriculture with ecological study, and will provide important contributions to land restoration (Coleman & Hendrix 1988, Ricklefs et al. 1984). By studying how organisms persist in disturbed and simplified agricultural lands we can understand resilience and recovery better in natural systems. Such large-scale investigations are necessary for developing methods for restoring impoverished areas (Crossley et al. 1992). Land restoration efforts will become more significant as we are forced to rely on now-impoverished lands for preserving biological diversity.

Agricultural practices stand to gain many practical benefits by incorporating a landscape perspective for land management. Management strategies embedded in the regional landscape can maximize the use of natural mechanisms and save time, resources, and reduce risks of continuous intervention, while enhancing long-term resilience and stability of agricultural lands (McNeely et al. 1990, Ricklefs et al. 1984). For instance, because pesticides have far-reaching effects, the success of pesticide application is landscape-, not field-dependent (Orians & Lack 1992). Cooperation among farmers and other natural land managers is essential for effective, ecologically-based pest control strategies (Barfield & O'Neil 1984, Eijsackers 1988, Paoletti 1992).

Multiple uses of managed lands has become less common with the growth of intensive agricultural practices due to short-term economic considerations (Gall & Orians 1992). Resource limitations and environmental degradation have revived interest in integrating land use through both time and space. Flexibility needed for future challenges to both conservation and agriculture can be enhanced by innovative multiple land use strategies (Noss 1983, 1987, Salwasser 1991). Generally, small economic losses are traded for enhanced environmental services and aesthetic value (Gall & Orians 1992).

Economic use of buffer zones around preserved areas could add versatility and resilience to local agricultural production while moderating negative effects of more intensive

agricultural practices on surrounding lands. But the potential of multiple land use is relatively unexplored. Indigenous cultures, currently relying on less intensive agricultural practices, provide unexplored lessons for multiple land use strategies.

In the U.S., large landholders such as the Bureau of Land Management, Department of Defense, Fish and Wildlife Service, Forestry Service, and Park Service are just beginning to base multiple use strategies and priorities on ecological principles. The U.S. National Forestry Management Act now incorporates biological diversity considerations through multiple land use provisions. Agro-forestry, sylvi-horticultural and sylvi-pastoral systems may provide a good start at integrating resource use and resource conservation plans (de Zeeuw 1988).

Climate

Global warming is a common problem threatening stability in both agricultural and natural ecosystems. Climatic changes could alter the abundance, distribution, and interactions among species with significant impacts on the distribution and management of agricultural and natural lands (Ehrlich & Ehrlich 1991, Gall et al. 1992, Gilpin et al. 1992). Adjustments in current practices, such as altering planting dates, changing crop varieties, and increasing irrigation, may offer little relief, especially in developing countries expected to be hit the hardest (Monastersky 1992).

According to Dahlberg (1992), the expected warming climate could drive the U.S. grain belt northward into areas where abiotic and biotic relationships differ from those to which current farming systems are fine-tuned. Land management strategies may need to be altered dramatically to meet these challenges. Agriculturists will depend on natural areas to provide alternative crops, control agents, and models for new management strategies enabling necessary large scale adjustments (Dahlberg 1992, Gilpin et al. 1992).

Changes in current agricultural practices, such as the development of less energy-intensive farming methods and increasing plant biomass on agricultural lands to absorb CO₂, can reduce the risks of climate change. Reducing deforestation rates for acquiring new agricultural lands is also important. This will, of course, increase pressures to intensify production practices on current agricultural lands. Increasing biological diversity in agricultural fields and preventing the loss of diversity in natural areas, where potential cultivars and biological control agents occur, will prove critical to agricultural resilience under changing climatic conditions (Gall & Orians 1992).

Research Needs

The ecological and practical importance of biological diversity is not well-studied by conservation biologists. We do not have an understanding of how species diversity and ecological processes translate to ecosystem dynamics and landscape heterogeneity. We know little of how natural areas benefit agriculture (Gall & Staton 1992). For example, although watersheds are claimed as important to agriculture for flood control and soil conservation, these effects have not been demonstrated clearly (Carroll 1990). We must also go beyond natural systems models aimed at minor modifications of modern agricultural practices. There is much opportunity for agriculturists to provide theoretical and empirical knowledge to conservation efforts while reaping practical benefits.

Especially important in integrating conservation and agriculture goals will be studies of how we can increase diversity at multiple levels on agricultural lands. Equally important will be investigations of how such semi-natural diversity furthers conservation goals and what kinds of diversity are profitable to agriculture. In order to make conceptual

and practical strides in these areas, we need to understand how materials and processes move between and influence agricultural and natural systems. These include adaptation, dispersal, migration, nutrient cycling, and climatic and disturbance regimes. The importance of corridors and mosaic structure in these movements must be investigated. We need a better understanding of how small- and large-scale ecological processes affect agriculture, and vice versa (Dennis & Fry 1992).

Consistent monitoring and evaluation techniques (Carroll 1990, Dourojeanni 1990) need to be developed and tested. Current differences in monitoring strategies limit cooperative efforts. Consistent methods will allow long-term monitoring and experimental manipulation of ecological variables built on process-oriented landscape management goals.

Research should be aimed at the development of long-term, landscape-level management strategies that can be adapted constantly according to monitoring results. Such adaptive environmental assessment and management approaches attempt to integrate responsibility and opportunity among agencies to cope with complex, large-scale environmental problems more effectively (Salwasser 1991). Cooperation will be critical to anticipate and respond to the challenges of climate change (Gall & Staton 1992). Such an adaptive planning strategy would rest on a hierarchical approach to understanding, monitoring and managing systems across ecologically relevant spatial and temporal scales (Noss 1990b, Rice 1992). Saunders et al. (1991) list examples of successful landscape-scale approaches to land management.

Gall & Staton (1992) outline general research needs aimed at integrating conservation and sustainable agricultural practices. These include, 1) evaluation of the ethics of agricultural practices, 2) characterization of genetic variation in crops and on agricultural lands, 3) understanding and diversifying boundary structure and function, 4) developing better water management options, 5) increasing large-scale modeling efforts, 6) investigating specific affects of agricultural practices on the surrounding area and vice versa, 7) furthering ecologically-based pest control strategies, 8) increasing studies of land management strategies of indigenous groups, 9) developing adaptive planning approaches, and 10) evaluation of international agricultural philosophy and policy for sustainability attributes. Agriculturists, and especially entomologists, stand to make major contributions in all of these efforts.

Changes in Perception

There are many optimistic opportunities for interaction between agriculture and conservation efforts. Perhaps the biggest obstacle is providing the considerable impetus needed to change reductionistic research and management strategies now in vogue in agriculture and research in general. Changes in social, political, and economic perspective will determine ultimately whether we make the necessary changes.

Public concern that modern agricultural practices negatively affect the environment, food quality, and human and animal health grew significantly in the 1960s as pesticide effects on non-target organisms were first being evaluated seriously (de Zeeuw 1988, Gall & Orians 1992). Economic benefits kept agriculturists defensive of public concerns until environmental effects began to threaten agricultural production more directly. It is not surprising that it is the most direct and evident links between agriculture and conservation where agriculturists are already cooperating with conservationists. These include the loss of soils, deterioration of water resources and water quality, the loss of genetic resources needed for crop breeding programs, and global warming. Less direct and evident interdependencies await research, policy consideration, and will ultimately depend on public pressures arising through increased environmental awareness.

In 1980 The World Conservation Strategy officially recognized that conservation can succeed only if goals are specifically tied to regional development needs. The need to

maintain essential ecological processes, to preserve genetic diversity, and to ensure the long-term preservation of natural resources as essential ingredients of sustainable development were emphasized (Green 1989, IUCN 1983, Robinson 1993).

Although ecological concerns in agriculture are probably the oldest conservation concerns addressed by practical land management, it was not until the mid-80s that the Consultative Group on International Agricultural Research (CGIAR), an informal but influential global agriculture policy and research organization, explicitly broadened its goals to include the concept of sustainability (Plucknett 1993). It was recognized that agriculture is ultimately dependent on a diverse and well-functioning earth. Through its extensive impacts on the environment, agriculturists have an obligation to contribute to conservation efforts. And, in order to develop sustainable agricultural systems, land use strategies must incorporate social, economic, and environmental impacts and these must be integrated at the landscape level.

In 1988, the Public Service Research and Dissemination Program of the University of California, Davis, conducted a workshop to address how agriculturists and conservation biologists might better work together. Sustainable agriculture and the conservation of nature were explored through research on environmentally sound land management practices. This workshop, and others that followed (see Benbrook 1991, Paoletti 1992), defined common challenges and called for cooperation between these two mutually dependent groups (Gall & Staton 1992). It was recognized that agriculture must diversify, especially at genetic and landscape levels, if it is to adapt successfully to changes in the environment and in consumer demands. It was through these workshops that agricultural objectives came to include research, policy, and management practices aimed explicitly at increasing biological diversity on agricultural lands.

However, structured interactions and unified land management efforts remain largely unexplored. In order to meet the challenge of growing human resource needs without threatening ecological integrity, we will need to integrate knowledge, share responsibility, and cooperate to find workable solutions. Success will depend on holistic, long-term, and broad-scale approaches to land use. In short, we need resource managers to become conservation biologists and conservation biologists to incorporate resource use needs.

SUSTAINABLE AGRICULTURE

“A parasite-host model for man and the biosphere is a basis for turning from exploiting the earth to taking care of it. Survival of a parasite depends on reducing virulence and establishing reward feedback that benefits the host.” (E. Odum 1992)

According to Daily & Ehrlich (1992), . . . “a sustainable process is one that can be maintained without interruption, weakening, or loss of valued qualities.” In 1980, the World Conservation Strategy popularized the term ‘sustainable development’ and stressed that development and conservation are mutually dependent (Robinson 1993). The term sustainable agriculture differs from a recent series of in-vogue approaches in agriculture, including alternative, organic, and low-input, in that it defines a goal rather than strategies. Sustainable agriculture, is by definition, vital to long-term human survivorship, and rests on any methods that minimize environmental degradation and non-renewable resource use (Benbrook 1991).

In 1991, the Technical Advisory Committee (TAC) redefined the objectives of the CGIAR to emphasize the need to achieve sustainable agriculture and to address barriers to achieving this goal. According to the TAC, sustainable agriculture requires the management of natural resources to meet human needs without degrading the environment to the point that degradation reduces the long-term potential of agriculture to remain sustainable. Conservation and management of natural resources, development of sustain-

able agricultural practices, and lessening socioeconomic pressures that affect sustainable agriculture negatively are the primary objectives (Plucknett 1993). If we include in our definition of human needs, the need for conserving biological diversity at multiple levels of organization and at multiple spatial scales, this utilitarian approach can be considered complete.

The TAC recommends research strategies that include a multidisciplinary approach, consideration of long-term objectives, and more ecologically balanced systems. Yet, to date, CGIAR's policy on the relative importance of these to product-oriented research and improving natural resource management remains unclear (Plucknett 1993). Conservation effort in agriculture has been limited primarily to the development and maintenance of plant and animal germplasm bases and associated breeding programs (Plucknett 1993). Furthermore, most international support goes to large-scale, modern approaches to agriculture (Ehrlich & Ehrlich 1991). In the U.S., the program for low-input sustainable agriculture (LISA) was implemented to reduce the use of non-renewable resources, while increasing ecological bases of agricultural practices and considering environmental consequences of agricultural practices (Reganold et al. 1990). But currently, this program seems to fall short of its goals (Hess 1991). Of the projects funded through the U.S. LISA program in 1988 and 1989, over two-thirds of all funded projects were for traditional approaches to management (Gardner et al. 1991).

Sustainable agriculture must be more ecologically and information-based with less dependence on outside non-renewable resources, especially water and energy. The maintenance of, and incorporation of, ecological processes are prerequisite to development strategies that are sustainable in the long term. We need to diversify within crop systems and across the farm landscape, managing agricultural lands according to local environmental and biological factors. Soil conservation, natural pest controls, and organic recycling will also be emphasized (Paoletti et al. 1992, Reganold et al. 1990). We cannot hope to gain the needed regional flexibility by understanding the details of local systems in the same way we have industrialized modern monocultures. We must depend on larger-scale approaches. Much work remains to be done, especially modeling natural ecosystems.

We can also learn from indigenous agricultural practices that are locally adapted (Pimentel et al. 1992b, Soulé & Piper 1992). These experienced land managers use few or no outside inputs. This has forced them to understand agro-ecological concepts critical to the development of sustainable agriculture. They also have the opportunity and the need to base their decisions of long-term costs and benefits.

Modern management strategies with sustainable elements range from small changes in established production-oriented systems to holistic ecologically-modeled process-oriented systems. Crop diversification, across time (e.g., rotation) or space (e.g., multi-cropping), can increase yields relative to monocropping, reduce soil erosion, pest and disease outbreaks, pollution, utilize nutrients and water better, and provide economic resilience (Soulé & Piper 1992). Management strategies range from simply raising two or more crops together in a field to mimicking complex ecosystem structure. The short-term costs and existing capital investments have prevented the extensive development of more complex cropping strategies. Multiple cropping is limited mostly to planting a second crop interspersed with the main one for a single purpose, such as luring pests away from the main crop (Soulé & Piper 1992).

Soil conservation is perhaps the best example of positive large-scale strides toward conservation agenda in agriculture. This is a reflection of the direct production costs of soil deterioration and soil loss. Soil quality is a reflection of physical, chemical, and biological properties that are interdependent and far-ranging. Agricultural practices that increase or prevent the loss of soil quality can simultaneously increase productivity and biological diversity.

Biological control benefits provide one of the strongest motivations for diversifying agricultural systems. The abundance, diversity, and effect of beneficial insects rest on landscape-scale ecological structure and function. Failures in biological control are usually associated with unforeseen ecological factors encountered in and around the field (Howarth 1991, Soulé & Piper 1992). The preservation or creation of natural refuges, diversification of crops, and a better understanding of the ecology of beneficials will help align pest management and conservation goals (Klingauf 1988). Yet, USDA funds for biological control research have declined (Reganold et al. 1990).

Conservation tillage not only reduces energy use for tillage, but enhances the conservation of micro-invertebrates and encourages mycorrhizal associations, while enhancing soil fertility, nutrient cycling, and water retention. The crop mulch protects the soil from wind and water erosion. However, thus far conservation tillage is less than holistic. Generally, herbicides are used for weed control increasing herbicide costs and environmental contamination (Soulé & Piper 1992). Improvements in conservation tillage will require careful monitoring and accurate timing of tillage. Increasing vegetative biomass in agricultural productions, such as with the use of cover crops, can reduce soil erosion and water runoff, and improve weed control, while providing structural benefits and increasing biological diversity in the soil (Dennis & Fry 1992, Pimentel et al. 1992b).

Of the approximately one percent of U.S. farmers practicing sustainable agriculture in 1980, most were organic farming operations. These farms are characteristically diversified, small-scale, holistic production systems. Such farming strategies represent the best examples of reducing external non-renewable inputs and increasing ecological and information bases in agriculture (Dahlberg 1992, Reganold et al. 1990). Interconnecting whole farm organic operations and actively connecting them with natural landscapes can increase resilience while providing important wildlife refuges and wildlife corridors.

Agroforestry, planting trees and food or forage crops in combination, offers common benefits to agriculture and conservation. The increased biological diversity reduces pest problems and conserves soil and water resources (Pimentel et al. 1992b). Depending on the intensity of extraction and management, these systems can maintain considerably more biological diversity than monocultures while enhancing ecological bases of management practices (Ewel 1986, Pimentel et al. 1992b).

Improved pasture management is another opportunity for simultaneously enhancing livestock production while conserving biological diversity and lessening environmental degradation, especially soil erosion and water pollution. Reducing the use of feed grains and increasing forage rations could help diversify farming systems (Gardener et al. 1991). Livestock manure use in agriculture could be better managed to increase biomass and biological diversity on agricultural lands and reduce water pollution downstream. According to Safley et al. (1983) only about six percent of manure is used. Yet the total amount of nutrients available in manure produced by livestock each year in the U.S. is almost equal to the amount applied as external commercial fertilizers (Pimentel et al. 1992b).

In developed countries, a growing awareness by the general public for food safety and environmental problems caused by modern agricultural practices has been a strong impetus for better aligning agriculture and conservation. However, attaining sustainability in agriculture will require further shifts in farmer and consumer environmental awareness. Wants must be separated from needs and the advantages of diverse diets and alternative food crops must be stressed. Extension programs need to be revitalized to better inform the public and farmers of conservation concerns of agriculture. Farmer networks need to be strengthened and better informed of research in agriculture and conservation. On-farm research should be promoted better to develop regionally attuned and coordinated efforts, involve farmer expertise better, and improve experimental validity (Soulé & Piper 1992). Entomologists can do much to influence consumers' views of insects and their damage, and the assessment of cosmetic considerations.

As resources dwindle and the human population continues growing exponentially, we must incorporate non-monetary factors, such as resource depletion and environmental degradation, and longer term views of costs and benefits into our accounting (Nash 1991, Soulé & Piper 1992). Odum (1992) lists the need to bridge together human and natural goods and services and short-term economically-driven and long-term sustainable management as one of the great concepts in ecology.

The costs of research and development of more ecologically-sound agricultural practices cannot be allowed to fall into the hands of farmers alone. It is the broad-ranging and long-term connections of agriculture, environmental health and safety, and social well-being that ties conservation and agriculture. Finding common ground will require increased support for research, new policy, and more and better public education.

Barriers to Progress

As early as the 1940s Aldo Leopold was calling for long-term, ecologically-based views of land management (Noss 1991), yet such strategies are only beginning to be developed. Various barriers must be overcome if we are to address sustainable agriculture and conservation problems effectively with limited resources and time. These barriers are institutional, social, and economic factors that limit interaction and cooperation in developing long-term, broad-based, ecological approaches and solutions. They include reductionistic approaches to problem solving in science, university, government policy, and granting agency structures, promotion requirements, lack of support for farmers, and lack of a value base for ecological services (Benbrook 1991, Soulé & Piper 1992).

Simply bringing together multiple disciplines will not overcome these obstacles. Future solutions will rest on the need for multiple disciplines to speak the same language, operate on the conceptual framework, and agree on goals and limitations. We will also need increased funding for collecting empirical data, development of models, and progress in ecological theory. Rice (1992) provides an hierarchical conceptual framework to overcome some conceptual and terminological problems in an effort to facilitate integration of agriculture and conservation biology. This approach examines common biological diversity attributes in agriculture and natural areas across multiple time and spatial scales, and focuses on common and divergent methods of these two groups in understanding, impacting, and managing this diversity.

The single crop, production maximization approach grew out of a period of abundant land, natural resources, and young methods. Problems are approached in series and solutions often create further problems. These approaches are no longer appropriate as we move into a period characterized by dwindling land and natural resources and limited technological advancement possibilities (Soulé & Piper 1992). Yet our current approaches are driven by inertia inhibiting change and innovation. Past payoffs of reductionistic, short-term approaches in modern agriculture bias current funding, hindering the development of ecologically-based management practices. Research and management strategies need to be revamped to function better in a stable rather than growth environment.

Current reward systems in academia are based on individual achievements, on quantity rather than quality of the work, and on the ability to attract grant money. Rewards for publishing positive results in a relatively short time biases projects toward clear cut, non-risky research efforts. Group efforts are de-valued as are less-flashy, more difficult and, often, more important projects (Noss 1990a). The peer-review system also promotes status-quo efforts and hinders innovative approaches. Soulé and Piper (1992) note that new journals often arise out of new innovative ideas that aren't accepted in established journals.

Private interest granting agencies generally promote non-ecologically based methods in agriculture. This is evident in biological control efforts where companies promote

biotechnology approaches over more ecologically-based approaches to pest control (Benbrook 1991). Government agencies also show biases in their support. According to Soulé & Piper (1992), the USDA supported biotechnology approaches to the problem of nitrogen fixation over more ecologically-based proposals partly because these approaches have the potential to produce profitable products. Even in the LISA program, specifically set up to promote sustainable agriculture, more innovative projects that demand large shifts in current agroecosystem structure are not well funded (Gardner et al. 1991).

Project funding, institutional organization, graduate education, and extension and farmer education all need major revision if we are to meet agriculture's goals of sustainability (Barfield & O'Neil 1984). Yet land grant university departments have generally become more isolated and specialized (Norgaard 1992). Isolation narrows perspective and reduces options. We need ways to promote and reward long-term studies, and to reward researchers involved in such projects. According to Soulé and Piper (1992), 17 land-grant universities have sustainable agricultural research programs. Although most sustainable agricultural programs involve interdisciplinary study graduate programs, these usually fall short of truly integrating information and experience needed to develop holistic problem solving skills.

U.S. agricultural policy, research funding and institutional structure rest on economic interests and on the political power these interests instill. The use of commercially available non-renewable resources to produce commercial agricultural products is promoted. The use of less economically valued information and ecologically-based processes needed to create sustainable agricultural systems are neglected (Norgaard 1992).

The lack of an accounting for the ecological foundation on which economic and political structures ultimately rest is a major obstacle to integrating agriculture and conservation goals and land use strategies (McNeely & Norgaard 1992). Farms are viewed as enterprises rather than ecological systems. Capital investment debts tie modern farmers to old philosophies and methods (Gilpin et al. 1992). Farmers are discouraged from developing or participating in holistic approaches to agriculture by federal farm programs that make shifting practices economically unprofitable (Reganold et al. 1990). Government support agencies are set up to address special interests. We need new approaches to address more diffuse, collective interests that agriculturists and conservationists face (Norgaard 1992). Ultimately these barriers will be overcome only with increased public awareness and social support for merging conservation concerns and farming management practices (Gilpin et al. 1992).

Until recently global and U.S. agricultural policy has both neglected agriculture's direct dependence on the environment and contributed to the loss of biological diversity (Dahlberg 1992, Pimentel 1992b). Energy dependence, industrialization, specialization, and reductionistic approaches have put agricultural systems at considerable ecological and environmental risk (Gall & Orians 1992, Soulé & Piper 1992). Increased research efforts will fall short of the goals of sustainable development unless these changes are fortified with policy promoting environmental responsibility.

Present, often out of date, policies will likely lead to dire consequences economically, socially, and perhaps even further threaten the environment. Most current programs attempt to minimize risks or counter negative effects when risks are realized. These provide agriculturists with information, services, and economic buffers (Dahlberg 1992). Such tack-on approaches are often not well researched, too late, ineffective, and contribute to other problems. Some public policies even penalize farmers for resource preservation and environmental protection efforts (Benbrook 1991). Policy changes have amounted to a series of modifications of agricultural practices to address more and more dire environmental degradation.

Policy development that ties conservation and agricultural goals is in its infancy. Future policies will grow out of interdisciplinary research, better methods to tie ecology and economics, and especially increased environmental awareness by the general public,

farmers, and policy makers. We need innovative ways to incorporate long-term and far-reaching environmental costs and benefits effectively in our economic and social policies.

As population pressures continue to put additional pressure on agriculture and the environment, environmental policy will come to put bigger and bigger constraints on agricultural methods. The Clean Air Act, Clean Water Act, Endangered Species Act, and National Environmental Policy Act already influence farm production. Recent changes in the Coastal Zone Management Act are aimed at controlling non-point pollution sources (Organization for Economic Co-operation and Development 1993). This legislation mandates increased scrutiny of current agricultural practices. Future environmental legislation could further threaten productivity as the general public becomes better informed of the environmental consequences of current agricultural practices. To avoid this, agricultural policy must become more integrated and proactive.

Probably the most successful conservation policy in agriculture is the Conservation Reserve Program, a part of the Food Security Act of 1985, designed to address soil degradation. This program ties conservation and agricultural goals directly at the level of landscape structure and function. Farmers are encouraged to place marginal crop lands into wildlife reserves (Gall et al. 1992). Beyond soil conservation, this program has contributed to the reversal of land fragmentation, creation of wildlife habitat, with positive effects on regional processes, and enhanced aesthetics (Dunn et al. 1993). Energy and water conservation policies and programs need to be addressed better in agricultural policy as has soil conservation (Dahlberg 1992). Policies promoting ecological approaches to low-input sustainable farming methods could efficiently address water, energy, soil, and pollution problems simultaneously.

The 1990 Farm Bill extended the 1985 Conservation Reserve Program and further incorporates environmental objectives into farm policy and contributes to long-term conservation goals (Hess 1991). It specifically addressed the need to increase biological diversity and to provide wildlife habitat in the Wetlands Protection Provisions, Conservation Reserve Program requirements, and Water Quality Incentives Program. These programs have at least potential to benefit farmers economically by reducing inputs of non-local non-renewable resources such as pesticides and fertilizers and by increasing non-agricultural value of their lands (Kinsinger 1991).

Pimentel et al. (1992b) recommend several government agricultural policies to encourage development of sustainable agricultural practices. They point to the need to focus on biological control of pests, promote protection of organisms that maintain ecosystem quality, and encourage protection of biological diversity upon which sustainable agriculture ultimately rests. Creative incentives for compliance with conservation goals must be combined with farmer education programs.

Although such policy development should be commended, we must go beyond sustainable development aims in policy if agriculturists are to take full responsibility for their role in the conservation of biological diversity. We need agriculturists to participate more in general environmental policy, especially the design of conservation policy, and to participate in inter-agency land management responsibilities (for European examples, see Organization for Economic Co-Operation and Development 1993). In a step in that direction, the current proposal to create a National Biological Diversity Conservation and Environmental Research Act includes the Agricultural Research Service on its governing board (Blockstein 1988). As conservationists and agriculturists move together in their aims, the study of insects will become more and more critical, yet, to date, there has been little input by entomologists in the creation of such legislation.

EDUCATION

“. . . a lot more than better science is required to maintain biodiversity and land health. We need a new ethic, and an ethic put into action.” (R. F. Noss 1991)

Environmental education remains the most important and timely challenge in conservation. Public education efforts lag behind changes in philosophy in the conservation movement. Public support continues to rest on emotional rather than intellectual motives. But we cannot hug genes or landscapes (Noss 1991). Fewer than 10 percent of Americans are considered ecologically literate (Kellert 1980a, in Noss 1991). Rather than investing in education of the complexities of ecology, charismatic species are often used as ploys for ecosystem preservation. This is potentially devastating to conservation efforts. Once the species is gone, there is no reason to save the ecosystem.

Public apathy toward invertebrate and ecosystem conservation stems from limitations of current species-oriented public relations programs by conservationists, biased environmental education programs, limitations of reductionistic science, political and economic constraints, and a lack of input by entomologists in conservation and environmental education (Thomas 1978). We must provide the general public with a more sophisticated awareness of ecological concepts and the costs and risks of modern agriculture (Gardner et al. 1991).

Hale (1991) lists 50 of the most important ecological concepts according to professional ecologists [from Cherrett (1989)]. These range from genetic to landscape ecology and include abiotic and biotic processes stressing population ecology and community dynamics. Entomology offers a unique opportunity to teach these concepts and connections that are necessary for informed decision-making (Pyle et al. 1981).

Insects are ubiquitous, diverse, versatile, easy to observe, easy to rear, and intimately tied to plants. Entomology includes the study of most of the world's biological diversity and addresses some of the most crucial of practical problems facing humans. Such a mix of basic and applied objectives provides an unparalleled opportunity to develop an ecologically-based value system needed for simultaneously attaining conservation and sustainable agriculture goals. This need has been largely avoided in science and, so far, neglected in conservation education.

But there are some drawbacks to focusing on insects. Many adults and, soon enough, their children and students associate insects with bad experiences. A lack of information usually leads to negative biases. For example, of 1117 adults surveyed in Arizona, over half disliked or were afraid of arthropods (Byrne et al. 1984). These biases arise partly because the general public is unduly focused on pest insects, as are entomologists. These researchers also found that women are more likely to feel negatively toward insects. Women not only teach their biases to their children, but make unhealthy personal decisions and support policies that reflect those biases. Women in entomology can provide role models for young women and children that will help to alleviate these biases.

In the Arizona study, education level was correlated with positive views of insects, suggesting that exposure to general biological principles translated to specific positive emotional responses. This finding supports the use of entomology to teach general ecological principles. Positive attitudes towards insects are likely to lead to improved environmental decisions. For example, Levenson (1978, in Byrne et al. 1984) found that positive attitudes towards insects were associated with support for non-chemical pest control strategies.

Experiential learning helps to connect resource entities to the larger systems which they influence, and from which they arise, and upon which they ultimately depend. Yet local information and hands-on experiences are rare in most environmental and, especially conservation, education. In the U.S. children and adults are usually taught about tigers and panda bears and rain forests. These teaching strategies encourage separation of information and emotional motivation to act. Meanwhile there is little understanding of how local systems function and provide for human needs.

In an effort to remedy this shortcoming in environmental education, the Ecological Society of America formed a group called Ecologists for Education in Local Natural History. This organization encourages professional ecologists to contribute to teaching

local natural history by 1) developing field guides and new instructional materials, 2) adapting and updating materials currently used, 3) helping in teacher training workshops, 4) helping to set up fellowships to promote local environmental education, and 5) providing avenues to enhance communication (Feinsinger 1987). Because the key models available to teach these lessons are insects and insect-plant interactions, entomologists have tremendous potential to assist in these important efforts.

Encouraged by Feinsinger's plea, a group of ecologists from the University of Florida recently developed a local field guide to the schoolyards in north central Florida entitled, *Handbook to Schoolyard Plants and Animals of North Central Florida* (Feinsinger 1987). This exemplary publication was followed by an activity guide and teacher training workshops. The local schoolyard natural history lessons are accessible and hands-on. These publications will become models for the development of other localized ecological lessons.

University programs, characterized by reductionistic, technologically-based science, generally do not provide students with skills and perspectives necessary for developing holistic approaches to land management (Dahlberg 1987). The limitations of this narrow approach to environmental problems is exemplified by tack-on remedies (Raloff 1993), and the unrealistic hope that technology will continue to solve agricultural problems (Monastersky 1992).

Agriculture provides a productive, but relatively unexplored, model for integrating diverse subject areas through the study of current human issues. All science, including social and economic science can be integrated through sustainable agriculture programs. We also need to further develop interdisciplinary opportunities and inter-department communication in sustainable agriculture programs if we want to build innovative policy, programs, and research goals. Entomologists have much to offer such efforts.

Agriculture and Environmental Education

Most Americans know very little about agriculture and its significance to their lives and to their environment. In 1988 the Committee on Agricultural Education in Secondary Schools provided recommendations for changes in agriculture education. Educational programs directed at agriculture students, such as 4-H and Future Farmers of America, were revamped. But this reorganization was directed primarily at providing skills and experiences appropriate for agro-business. The committee also stressed that agricultural literacy, including economic, social, and environmental significance, should be a part of general education and can be an effective vehicle to develop ecological literacy. Although the treatise of agricultural subjects includes natural resource management, the 1988 recommendations do not specifically tie natural resource preservation, ecology, and conservation with agricultural education. Entomologists have a responsibility to contribute to demonstrating this connection.

In 1981 the USDA initiated 'Ag in the Classroom,' an agriculture education program directed at elementary school students. This program provides information and resources to encourage agricultural study. It includes in-service training programs designed to integrate food and fiber production subject matter into school curriculum (Committee on Agricultural Education in Secondary Schools 1988). Although limited by funding and support, the Ag in the Classroom program could become an effective vehicle for conveying conservation issues in agriculture. An obvious route to teach this connection would be through the study of insects.

In 1989, the Entomological Society of America Standing Committee on Education and Training (ETC) began an outreach program designed to demonstrate how insects can be used to teach diverse subject areas (Akre & Hansen 1992). These programs are accessed through the National Science Teachers Association. The ETC encourages entomologists to develop programs that can be incorporated into the outreach effort. This is a great opportunity to provide teachers with information and materials that demon-

strate the need for cooperation between agriculture and conservation. The ETC also provides contacts who are willing to assist teachers to better utilize insects in teaching. Professional entomologists can also contribute by assisting the Committee of Youth Science Development of the ESA to promote the value of entomology to students and the general public (Knutson 1989).

At the university level, Orr (1991) promotes the integration of agriculture and liberal arts colleges to combine abstract and practical intelligence necessary for the future of agriculture and conservation. In the early 1900s, approximately one-third of the U.S. population lived on farms. That percent is now only about 2.2 (Committee on Agricultural Education in Secondary Schools 1988). This dramatic demographic shift was accompanied by a loss of motivation to protect biological diversity. Tangible, relevant ecological lessons offered by small, diverse farms were lost. Orr encourages the use of college farms as interdisciplinary laboratories, a substitute for childhood farm experiences, a resource to help revitalize rural life, and a site for preserving biological diversity. College farms provide unique learning centers based on holistic, experiential, interactive approaches to problem solving. Such alternative learning experiences should encourage the development of sustainable agricultural practices and integrating conservation concerns in agriculture.

Farmers also need better information about sustainable agriculture and the need for integrating conservation and agricultural interests. Only with a broadened perspective including long-term ecological costs and benefits of agricultural practices can farmers, ranchers, and foresters accurately assess profitability (Reganold et al. 1990). The severe on-farm health problem associated with pesticide use is a grave example of the consequences of too little information (Pimentel et al. 1992a, Soulé & Piper 1992). Networks that promote information gathering, assessing and sharing among farmers should be encouraged and supported in agriculture.

The Florida Entomological Society and the Entomological Society of America have long stressed the importance of communicating the relevance of entomology to the general public. However, until recently efforts have lagged behind this philosophy (Price 1991). And even today, educational efforts remain outdated and narrow in view. A noteworthy exception is a tremendously successful summer teacher education course recently developed by Don Hall, of the University of Florida. This course focuses on local insect natural history, and provides an impressive example of the potential that entomologists have to contribute to environmental education. The primary objectives are to enhance awareness and appreciation of insects through hands-on experiences and to broaden opportunities to teach biology, ecology, and natural history using insects. Teachers that attend the course then provide further teacher training programs providing an effective pyramid of information transfer.

The designation of national and state insects could do much to promote entomology and broaden education and research opportunities. I am happy that the ESA is supporting the monarch butterfly to become our national insect. I think the monarch is a good choice for this title because the monarch is well-known, widely distributed, accessible, regularly crosses national boundaries, demonstrates the problem of species-oriented conservation, and, perhaps most importantly, its beauty can open awareness to less attractive invertebrates. But truly the species doesn't matter, a national insect would do much to promote public awareness of more enlightened views of conservation biology and I encourage your support.

The dire need for cooperation among agriculturists and conservationists has heightened our capacity and our responsibility to educate the public about insects. By increasing our attention on insect natural history and conservation concerns, entomologists can help to change the current negative views of entomology as a narrow applied science addressing ugly, unwanted pests. Entomology can be seen as a broad-based, relevant, exciting, and interactive experience. To accomplish this transformation we

cannot leave any educational opportunity unexplored, but we will do best to focus on young children, as they are the most open.

ENTOMOLOGISTS' ROLES

Entomologists "seem strangely unstirred as a group by the biological diversity problem." (T. Lovejoy, from Knutson 1989)

Current goals of agriculture and conservation are unattainable unless entomologists move beyond current myopic views of the role of entomology in research, management, and education. We cannot depend only on the valuable lessons from applied entomology to meet these goals. Yet we cannot afford to cut further into the limited support for applied research. The needed boost in support for expanding entomological research goals will come from educating the public and policy makers of the ecological significance of insects.

Raven (1990) estimates that only about five percent of arthropods have been named, and we have significant information on probably less than one percent of those. If we are to conserve biological diversity we need to better understand this group taxonomically, ecologically, and evolutionarily. Without better estimates of the total number of species, estimates of extinction rates remain elusive, and the problems of conservation, therefore, ambiguous. Discrepancies in species number estimates come largely from our lack of understanding the composition, structure and function of ecosystems (Gaston 1991, Paoletti et al. 1992). A better understanding of feeding habits, relative abundance, and size versus number of insects would strengthen our estimates of biological diversity (Helliwell 1982, McNeely et al. 1990). The study of insects will also contribute to our understanding to how human activities translate to extinctions in this and other groups. We need input from insect taxonomists, biogeographers, and insect ecologists to provide such information to policy makers and conservation biologists.

Worldwide, studies of insects aimed at conservation goals are severely lacking relative to the diversity of species and their ecological significance. This reflects difficulties related to the abundance, diversity, and paucity of methods, together with a striking negligence by researchers. This lack of information is most apparent in the tropics, where most biological diversity rests and the least aggressive research occurs. These constraints are probably the most critical barrier to global conservation goals. Entomologists are needed to correct this incongruence (Wilson 1988).

In the U.S., the Endangered Species Act, with its problems, will remain a prominent effort in conservation biology. Proportionately more and more candidate species will be insects (Bean 1993). Successful listing and development of recovery plans rest on our understanding abundance, distribution, habitat needs, and vulnerability to human impacts. This policy will become practically stifled without significant input from entomologists.

Pyle (1976) suggests several areas of research needed to address conservation concerns for insects. These include autecological studies of threatened species, biogeographic surveys of native species, increased investigations of genetics and population biology, and population regulation factors. Pyle encourages involvement of entomologists with the Office of Endangered Species for better use of limited funds to address insect conservation.

Due to their small size, short life cycles, habitat specialization, and relatively small ranges, insects offer probably the best models for furthering theory and methodology in conservation biology. Problems to which entomologists can offer significant contributions include the species concept, speciation, extinction, inbreeding, importance of genetic variation, competitive exclusion, population regulating factors, island biogeography, the ecological impacts of land fragmentation, the role of corridors, the ecology of exotics, and climatic effects on population dynamics and distribution. By studying these systems

and comparing them with vertebrate models, we can strengthen management strategies currently based on vertebrate studies.

Research in insect ecology will help us to preserve ecological processes and habitat structure. By studying insect population dynamics at several spatial and temporal scales, we can improve land acquisition decisions, land management, land restoration, and landscape linkages. These will, in turn, provide models for predicting insect population dynamics in agricultural operations. Conservation-oriented research, especially in the tropics, promises practical information on ways that insects can be used for biological control, pollination, environmental monitors, food, medical products, and as tools in research and education (Samways 1988).

Finally, I encourage entomologists to contribute to the development of field-oriented, interdisciplinary programs in entomology, and to participate in interdisciplinary endeavors aimed at addressing long-term agricultural and environmental problems. I also encourage increased efforts by The Florida Entomological Society to provide support, technical advice, information exchange programs, linkages with other groups, and to encourage conservation-oriented research at their annual meetings and in their journal.

DISCUSSION

"Our large brains may have originated 'for' some set of necessary skills. . . , but these skills do not exhaust the limits of what such a complex machine can do. . . Built for one thing, it can also do others, and in this flexibility lies both the messiness and the hope of our lives." (S. J. Gould 1980, p. 57-58, in Williams 1992)

Conservationists have recognized the need to focus on larger-scale approaches to addressing the loss of biological diversity as they begin to value ecological processes beyond habitat protection for endangered species. They await input for defining biological diversity, development of viable monitoring and management strategies, and public support to achieve these goals. Because of the importance of insects in species diversity and ecological roles, entomologists have perhaps the greatest potential and responsibility to contribute to conservation goals simultaneously and cost effectively through theoretical, methodological and educational contributions.

In the next 10 years world population will increase by more than one billion people (Raven 1990). We simply cannot continue our present per capita rate of co-opting most of the net terrestrial primary productivity (Ehrlich & Ehrlich 1991). Non-renewable resource depletion and waste build up stifle the earth's ability to absorb further stresses by humans. Entire ecosystem composition, structure and function are threatened, with support characteristics breaking down.

We need more than an Endangered Species Act and small modifications in agricultural practices. We cannot afford to continue the time consuming and cost ineffective efforts aimed at a handful of species that we're unlikely to be able to save. We would better spend our time investigating how natural systems work, why are they resilient, how they recover from stress, how to best monitor them, how to lessen human-induced stresses, and how to mimic these in agricultural production systems. Successful land management strategies will hinge on long-term studies of invertebrates and their associations. Agriculturists, and perhaps most importantly entomologists, should be key players in such efforts.

The future of agriculture depends on broader perspectives spatially and temporally, cooperation, resource conservation, and holistic, ecologically-based approaches, with increases in information and decreases in non-renewable resource use (Francis 1990). Entomologists must aim toward the development of innovative agricultural practices that can address growing human population needs with rapidly dwindling natural re-

sources. The impacts of pesticides and exotics on non-pest species, the development of more diversified crop systems, better management of forest systems, and the implementation of multiple land use strategies will be important areas of study.

Environmental education remains the most timely challenge in conservation. It is not well-appreciated that humans are not generally prepared to handle long-term and large-scale problems that now face agriculture and conservation. Although our large brains provide the capacity to think in the abstract and model complex problems, our nervous system was shaped by short-term reinforcement and punishment (Ehrlich 1988). It is because of this important shortcoming that Ehrlich & Wilson (1991) warn of hard choices ahead, suggesting that nations will have to make choices between saving their natural heritage and maintaining the economic well-being of their citizens. Assuming that in the long run the latter depends on the former, we must make great strides in education to prepare for coming changes.

A better understanding of the role of invertebrates in natural systems and increased public awareness and appreciation of this group are critical for future development and management strategies that can no longer depend on human emotional responses to a few cuddly critters. In order to educate the general public to what are often less than intuitive ecological concepts, we must rely on factually-based, locally accessible information. Experience-based lessons in local natural history and ecology can accomplish these goals most effectively by focusing on invertebrates.

In order to meet these challenges, we entomologists need to address our responsibility to the 99 percent of insect species, and 90 percent of all biological species, that are not considered pests (Wilson 1987). In order to maximize this possibility, which I'm advocating as a moral responsibility, we must 1) open our journals to conservation-oriented research, 2) encourage structured interactions with conservation biologists, 3) spend relatively more time studying the roles of insects in natural systems, 4) contribute to the development of ecologically-based agricultural management strategies, and to the selection, design and management of protected areas, 5) contribute to conservation policy development, and 6) educate the general public of the direct and indirect values of insects.

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BEHAVIOR IN BUTTERFLIES AS A MEANS OF
CONSERVATION: COMPARISON OF INSULAR AND
CONTINENTAL FAUNA

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ABSTRACT

Behavior is one of the major components affecting the survival of butterfly species. Certain physiological requirements, such as regulation of body temperature, search for nutrients and partitioning of other resources must be met, but the ability to meet them can be enhanced through behavior. Insular and continental butterfly species may display similar perching and flight behavior based on familial relationships. Reduction in species diversity and population numbers can most often be attributed to variation in climate and weather patterns and changes in land use, especially those changes that result in habitat fragmentation or loss. Chemical pesticides and possible extirpation of species through predation and over-collection are secondary causes of reductions in most cases. Through the critical examination of butterfly behavior in both insular and continental species, we can derive a more complete picture of the requirements necessary to sustain populations and can further enhance conservation and management efforts.

Key Words: Behavior, butterflies, West Indies.

RESUMEN

El comportamiento es uno de los componentes mayores que afecta la supervivencia de las especies de mariposas. Ciertos requerimientos fisiológicos, tales como la regulación de la temperatura del cuerpo, la búsqueda de nutrientes, y el demarcamiento de otros recursos, tienen que ser satisfechos, pero la capacidad de satisfacerlos puede ser aumentada por el comportamiento. Especies insulares y continentales de mariposas pueden mostrar comportamiento semejante de postura y vuelo basado en las relaciones familiares. La reducción en diversidad en las especies y en los números de población puede ser atribuida más frecuentemente a la variación en patrones de clima y tiempo y en los cambios del uso de la tierra, especialmente aquellos cambios los cuales resultan en la fragmentación o la pérdida de hábitat. La plaguicidas y posiblemente la extirpación de especies por la predación y el coleccionamiento excesivo son causas secundarias de las reducciones en la mayoría de los casos. Por la examinación crítica del comportamiento de mariposas tanto en las especies insulares como en las continentales, podemos derivar un imagen más completa de los requerimientos necesarios para sostener las poblaciones y así aumentar los esfuerzos para la conservación y el manejo.

The success of an individual organism, whether a butterfly or single-celled protozoan, is measured by its ability to survive and reproduce. Butterfly behavior, which can be determined through observations of diverse sets of activities, is an integral component of survivorship and reproduction. Physiological requirements, such as the regulation of body temperature must be met, but are generally associated with body size. Butterfly behaviors, such as flight and perching, are important and may vary within the habitat during different parts of the day. Males and females may have different behaviors, but they have common needs for nutrients, partition resources (e.g., nectar), roosting sites,

and the ability to effectively elude predators. Any species' reproductive success depends upon the ability of the sexes to locate one another and the ability of the offspring to thrive. Sophisticated mating behaviors and specialized communication resources may enter into the courtship ritual. Other behaviors are used to ward off predators. These may vary depending on predator density and the species' susceptibility to predation. Behavior is the common thread throughout all of these multifaceted activities and, therefore, plays an integral role in the survival and reproduction of butterfly species. The purpose of this paper is to: (1) examine the biological requirements of some butterfly species for survival, (2) propose possible reasons for population declines and/or diversity of some species, (3) discuss some of the similarities and differences in inter- and intrafamilial butterfly behavior within continental and insular faunas as they relate to survival, and (4) suggest how knowledge of butterfly behavior can be used to conserve and preserve their faunal diversity.

I shall restrict this discussion to the New World. The insular butterfly fauna, therefore, will be that of the West Indies, especially the Lesser Antilles. Observations on behavior and habitat are based on personal experience, unless otherwise listed.

BIOLOGICAL REQUIREMENTS

Butterflies, like other organisms, have certain biological needs to maintain their populations. They need a habitat, or place to reside, that not only provides sufficient area for shelter, but which also provides areas for perching during the morning for thermoregulation and for roosting sites during the night. Other sheltered areas should be available for those species that diapause during times of severe climatic changes, such as drought. An adequate food supply should be readily accessible that not only includes sufficient nectar sources to sustain adults, but also the appropriate host-plants for the larvae to complete their life cycle. Adult butterflies can afford to be generalists on various nectar sources, but the immature stages cannot. Finally, but not least of all, individuals within established populations must be able to locate mates to perpetuate the species. Hopefully, there is sufficient genetic diversity to maintain a constant population.

POPULATION DECLINES

With few exceptions, population sizes of butterfly species fluctuate over time. In some cases, however, population levels may continue to decline for extended periods of time. Based on the requirements cited previously and field observations, the potential causes for population declines may include: climate, changes in land use, habitat fragmentation or loss, pesticides and other control methods, insect collectors and predators.

Changes in climate that influence butterfly populations can have dramatic affects. Such examples would include the recent floods in the midwest and hurricanes Andrew and Hugo. The latter hurricane passed through the northern Lesser Antilles in 1989, causing devastating effects on insect populations, as well as human inhabitants. On the island of Nevis, no birds and few butterflies were noted during the following year. Gradually both groups have recolonized the islands, but increased numbers of agricultural animals, particularly goats, continue to outcompete butterflies and other insect herbivores for existing plant resources. Butterflies, which were common, such as the sulfur butterflies, *Eurema* (Pieridae), are few in number. The reason changes in insular climate and weather patterns have such pronounced effects is that the normal ecological balance is altered markedly with the loss of available niches and suitable food supplies.

Changes in land use and habitat fragmentation that cause loss of habitats can be very detrimental. There is a definite correlation between habitat loss and plant and

Lepidoptera diversity (Erhardt & Thomas 1991). Unfortunately, all butterflies are affected by habitat loss. Although some species can adapt to a certain degree to habitat fragmentation, other populations cannot. Sedentary butterflies, particularly those of precinctive (=endemic as defined by Frank & McCoy 1990) species which have small, isolated populations and a limited geographic range, can be eliminated overnight. For example, on a small stretch of land in the middle of Anegada Island, the easternmost of the British Virgin Islands, two new species, *Calisto anegadensis* Smith, Miller & McKenzie (Satyridae) and *Copeodes eoa* Smith, Miller & McKenzie (Hesperiidae), were described from an isolated tussock grass patch (Smith et al. 1991). This area was once designated for a new golf course which, had it been developed, would more than likely have meant the end of both species. Neither species has been located on any of the other Virgin Islands.

Some butterflies can also have limited habitat requirements on continents, and the lack of breadth may adversely affect the species. Such was the case in California where the only available habitat for an unlisted lycaenid subspecies, *Glaucoopsyche lygdamas palosverdesensis* E. M. Perkins & J. Emmel, was bulldozed overnight to build a tennis court. Butterfly populations react rapidly to such changes in their environment. It is obvious that both continental and insular butterfly populations can be affected by the loss or fragmentation of habitats. As the forests, especially the rain forests, are depleted, the diversity of the butterfly fauna will also be markedly reduced.

Chemical pesticides and other control measures can alter population numbers. A good example involves the butterfly fauna on the larger Lesser Antillean islands, such as Antigua, which have been cultivated with sugarcane since the middle of the 17th century. On Antigua, agricultural practices coupled with the loss of native host plants has probably contributed to a decline in the species diversity.

Insect overcollection and predators can affect insect populations. Although it has not been documented that any butterfly species has been extirpated due to overcollection, it could adversely affect some species that have a very tenuous hold on their existence due to small population sizes. Common sense dictates that collectors should exercise extreme caution in taking samples since inappropriate actions could further reduce already small, isolated populations to critical levels.

On the other hand, natural predators play an integral role in the biological control of prey species. Occasionally, populations of predators may fluctuate markedly and competition for prey species may have the unavoidable affect of reducing populations to critical levels. Given sufficient time, adequate food and other resources, populations of these prey species will recover.

Each of these potential causes, or combinations thereof, can cause a decline in population, or complete extirpation of a butterfly species. However, the major problem most frequently encountered appears to be the loss of habitat. Increased knowledge of flight, mate location, and nutrient search behaviors obviously are crucial to conservation and management of butterflies and their fragmented habitats.

CONTINENTAL VERSUS INSULAR BUTTERFLY POPULATIONS

Butterflies are probably the most studied and researched group of insects. The West Indian butterfly fauna is noted for its precinctive species, and the number of recorded taxa has increased from 312 to 330 within the last eight years (Smith et al. 1994). However, the continental fauna is even greater in size. Approximately 1,000 taxa are recorded from North America north of Mexico (Miller & Brown 1981), and several times as many species can be found in the Neotropical areas. For example, 1,500 to 2,000 species have been found in a single rain forest in Brazil (Emmel & Austin 1990, Austin et al. 1993). However, the number of species depends on various factors, particularly the available habitat area, especially for insular faunas (see MacArthur & Wilson 1967).

Insular populations of normally common dispersalist species, such as *Danaus plexippus* (L.), may not be present on every island each year and the individual number of species on the wing during a given flight period may change with seasonal rains.

On individual West Indian islands, there are generally fewer large-bodied species (e.g., Papilionidae, Heliconiidae, and Nymphalidae) as compared to the number on continents. The inverse is true of the smaller-bodied species (e.g., Lycaenidae and Hesperidae). On Puerto Rico and the Virgin Islands (Fig. 1), for example, usually one or two

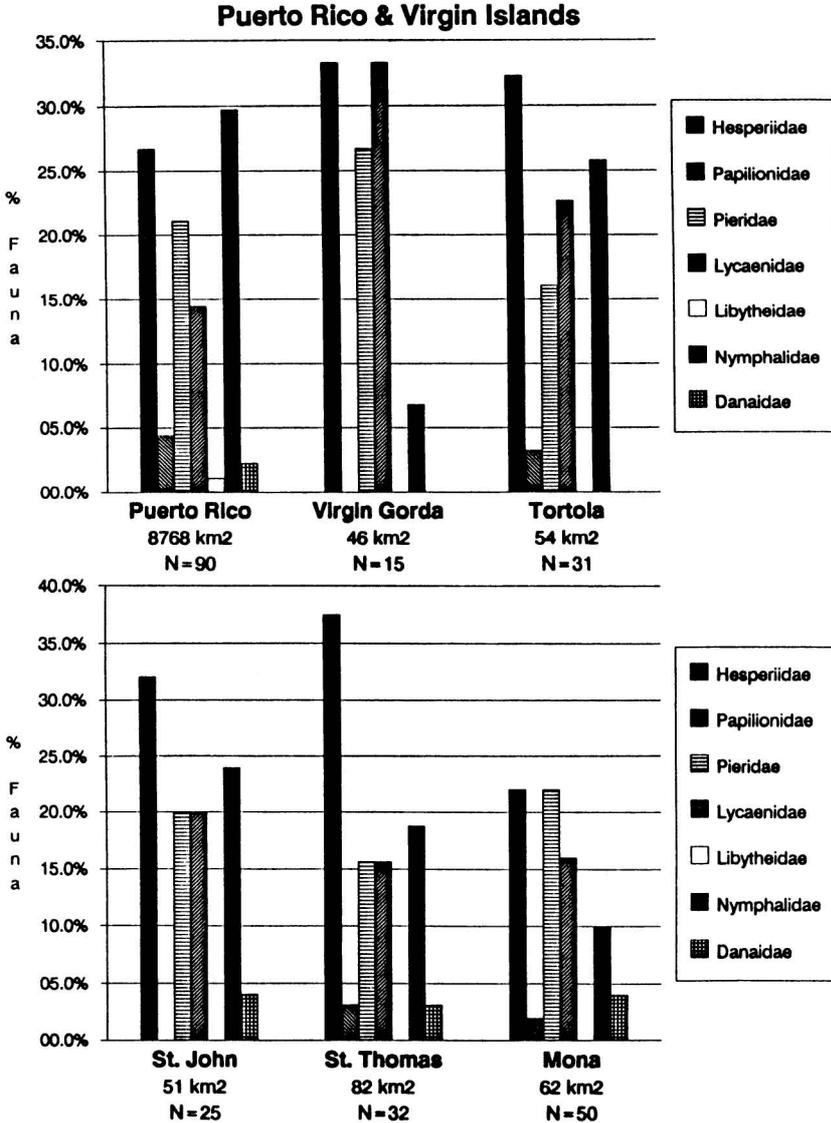


Fig. 1. Comparison of the butterfly species recorded by family on Puerto Rico and the Virgin Islands.

species of swallowtail butterflies (Papilionidae) are recorded from each island, while in central Florida eight species of swallowtail butterflies can be found. The genus *Eurema* (Pieridae), with its relatively smaller wing expanse, has more than 20 species recognized in the West Indies, but only 16 species have been recorded from all of North America.

BUTTERFLY BEHAVIOR

Flight is the most conspicuous behavior in butterflies, and the type of flight, frequency of movement, and flight pattern are usually categorized by familial association. The recognized categories are: (1) sedentary (Satyridae), (2) strong flying but relatively sedentary (Nymphalidae, and particularly the Heliconiidae), and (3) more highly mobile and dispersalist species (some Hesperidae, Lycaenidae, Nymphalidae and Danaidae, particularly *Vanessa cardui* (L.) and *Danaus plexippus* (L.)).

Some of the primary differences associated with flight involve the search for available nutrients and perching behavior. *Heliconius* (Heliconiidae) are relatively sedentary butterflies, fluttering lazily about an inflorescence, and sometimes perched hanging downward while taking nectar. In contrast, the swallowtails (Papilionidae), which have a much larger body size, can often be observed perched on a leaf trying to thermoregulate in early morning sun. During the day, these insects, which are very strong fliers, continue to flutter their hindwings while taking nectar, often moving rapidly from one flower to the next. This darting and rapid flight of the swallowtail butterflies, while foraging briefly for nectar, usually is in response to predators, most frequently well-educated birds.

Other behaviors are associated with the search for available nutrients. Some butterflies, such as the satyrid genus *Euptychia*, a complex group associated with monocots as larvae, may be seen perching and probing along the base of an immature grass inflorescence seeking the sticky nectar. Although Satyridae are sedentary fliers and normally located in more sheltered habitats, those of the genus *Euptychia* may be found in the more open grassy areas during the rainy season in Costa Rica and other neotropical countries.

Feeding behaviors within taxa can vary between continental and insular populations. For example, the lycaenid *Pseudolycaena marsyas cybele* (Godman & Salvin) (Fig. 4-5) is precinctive to St. Vincent, while the nominate continental subspecies, *P. m. marsyas* (L.) is widely distributed throughout Mexico and Central America (Fig. 2-3). The adults

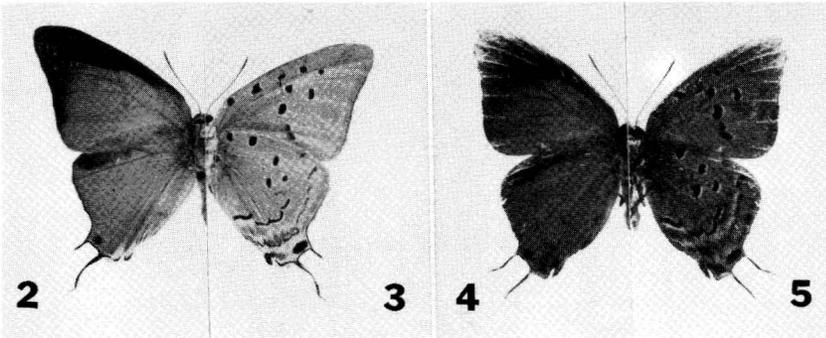


Fig. 2-5. Feeding behavior can vary within taxa such as the continental butterfly *Pseudolycaena m. marsyas* (2, upper, 3, under surfaces) and its Lesser Antillean relative *Pseudolycaena m. marsyas cybele* (4, upper, 5, under surfaces).

of the continental subspecies prefer to feed on *Senecio* (L.) spp. with their wings upright or, occasionally, spread out, while at the same time crawling around on the inflorescence. In contrast the St. Vincent subspecies prefers nectar from plants that are most frequently encountered on that island (*Cordia* and *Croton*). The adults of this latter subspecies glide along paths with no established flight or territorial pattern, perch on inflorescences with their wings held upright, and then walk, or more specifically, wobble back and forth along the inflorescence, probing the base of each nectary. The unmistakable coerulean blue upper wing surface is evident only briefly during flight. This behavior may be a successful defense strategy against birds or other predators.

Flight behavior may be correlated with, or in direct response to, the butterflies' habitat, and the number of microhabitats within the habitat are significant for faunal diversity. The continental rain forest with its altitudinal gradients and structural variety provide numerous microhabitats for butterfly species. For example, females of *Morpho menelaus* (L.) frequent the understory, occasionally perching on tree stumps, while males fly along partially open clearings or high in the canopy. Other adults of the satyrid genera *Callitaera* Butler, *Haetera* Fabricius, and *Pierella* Herrich-Schaeffer fly rapidly through ground cover of various aroids and lianas searching for mates and available nectar sources (Fig. 6-9). Their cryptic appearance and rapid, somewhat tumbling flight, obviously affords some protection from predators.

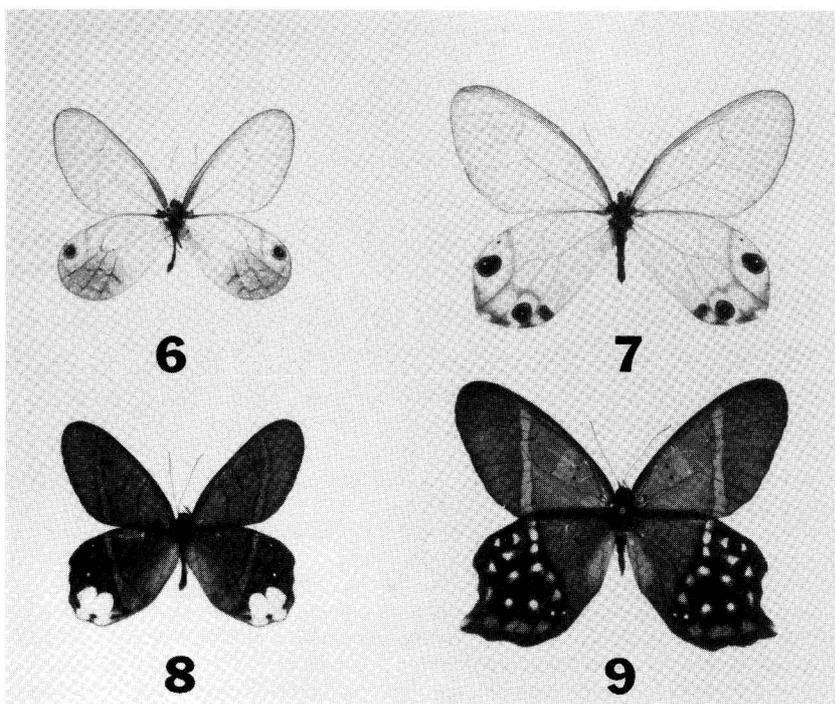


Fig. 6-9. Neotropical satyrid butterflies, such as (6) *Callitaera pireta* (Cramer), (7) *Haetera piera* (L.), (8) *Pierella astochye lucia* Weymer, and (9) *Pierella hyalinus dracontis* (Hübner) (9), are afforded some protection from predators through their cryp-

Most islands have restricted land areas with limited resources, and more pronounced seasonal changes than continents. Here, the emergence patterns are modified and reduced to coincide with or following seasonal rains. Also, the habitats tend to dry out quickly, leaving butterflies with limited resources and flight periods.

The skipper butterflies (Hesperiidae) are noted for their fast, rapid flight in both continental and insular faunas. In the West Indies, these butterflies can be observed flying in and out of low vegetation along roadsides, along sunlit dappled forest paths, or around the forest edge. Their flight pattern is usually associated with an established territory. Generally, skippers fly slowly with a standard wingbeat pattern, about 24-36 cm above the ground. Normally, they fly about 12 cm above the vegetation along the roadsides. In deeper woods or forests, they often spend considerable time perched on flowers or leaves, punctuated by brief periods of flight. Skippers in Florida exhibit similar behavior in the summer. After mid-day they spend time searching for mates and flying in and out of the denser vegetation, usually 12-28 cm above the ground or vegetation. Often these dark butterflies fly into brushy vegetation, perch a while, and then resume their patrolling flight pattern within their established territory, searching for a mate or nectar sources.

AVOIDANCE BEHAVIOR

In both continental and insular species, butterfly flight avoidance behavior is changed markedly in response to the presence of birds and other predators. The swallowtail genus *Battus* ranges throughout North, Central and South America, and the Lesser Antilles. Two species, *B. philenor* (L.) and *B. polydamas* (L.) are represented in central Florida. In the Lesser Antilles, there are several markedly different precinctive subspecies of *B. polydamas*: *B. p. neodamas* (Lucas) from Guadeloupe, *B. p. dominicus* (Rothschild & Jordan) from Dominica, and *B. p. xenodamas* (Hübner) from Martinique (Fig. 10-12). This species is the only swallowtail distributed in the Lesser Antilles, and it is a notably strong flier. There is little interchange or migration of the subspecies between islands, however, despite inter-island distances of less than 25 km in some cases. Like other swallowtails, these butterflies do not spend much time taking nectar in the presence of predatory birds.

The importance of flight avoidance behavior in large versus small butterflies is more evident in the Pieridae. Adults of the larger pierids, such as *Phoebis sennae* (L.) (Fig. 15) and *P. philea* (L.) (Fig. 16) and even *Ascia monuste* (L.) (Fig. 13), fly rapidly with darting movements in the presence of birds in both insular and continental populations. In similar habitats, the smaller pierids, such as *Eurema elathea* (Cramer) (Fig. 14) spend most of their time flying with a constant wingbeat frequency no more than 24-28 cm above the ground. These species are not usually the preferred prey for predators associated with their particular type of habitat.

Wing markings that aid in predator avoidance are particularly evident in continental butterfly fauna. Disruptive coloration patterns accentuate the potential distastefulness associated with chemical defenses in butterflies aligned in Mullerian and Batesian mimicry complexes (Brower 1984). These groups share the same habitat and often are difficult to identify in flight. Similar wing and color patterns are found in a wide range of lepidopteran families from Ithomiidae through Papilionidae, Arctiidae, and Castniidae. They are also evident in the tiger-striped complex from Central America: *Lycorea cleobea atergatis* (Doubleday) (Fig. 17), *Mechanitis lysimnia dorysus* Bates (Fig. 18), *Heliconius ismenius telchinia* (Doubleday) (Fig. 19), and *Chetone angulosa* (Walker) (Fig. 20).

Sophisticated mimicry complexes are not present in the insular fauna, but some butterflies have developed rather interesting social aggregations which may be considered primitive mimicry complexes. For example, four precinctive *Libytheana* Michener

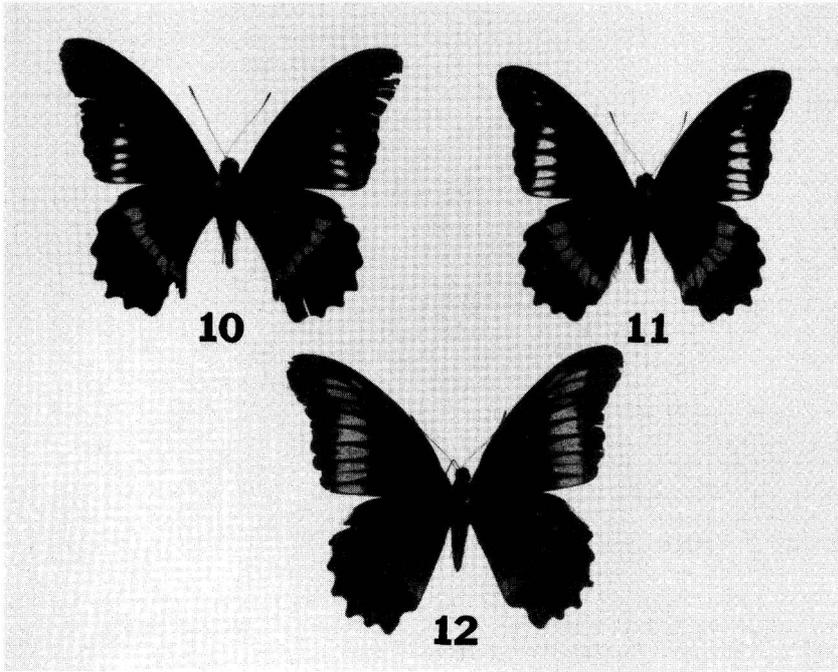


Fig. 10-12. Subspecies of *Battus polydamas* recorded from selected islands in the Lesser Antilles have similar feeding and predator avoidance behaviors: (10) *B. p. neodamas* (Guadeloupe), (11) *B. p. dominicus* (Dominica), and (12) *B. p. xenodamas* (Martinique).

("snout" butterflies) are recorded from the West Indies. These butterflies are noted for their elongated labial palpi. Unlike their continental relatives, the populations are quite small, and solitary individuals are observed infrequently. These species are restricted to drier vegetative areas of the islands. On Dominica, in the Lesser Antilles, it is not uncommon to see *Libytheana fulvescens* (Lathy) (Fig. 21-22) in flight with *Dryas iulia dominicana* (Hall) (Fig. 23-24), *Memphis dominicana* (Godman & Salvin) (Fig. 25-26), and *Vanessa cardui* (Fig. 27-28). This social aggregation is usually observed as the butterflies fly along wooded paths in a queue, with a rippling and darting flight pattern. *Memphis dominicana* and *D. dominicana* are more gregarious as adults than the other two species and can be observed interacting frequently. Although the wing expanse and the under-surface patterns are remarkably different, the color patterns displayed by all of these butterflies blend readily into the xeric underbrush. Populations of bird predators observed in this area are higher than in inland, moist habitats, and perhaps these butterflies find safety in numbers.

Other elaborate avoidance behavior includes the use of warning coloration, for example, the large eyespots so prominently displayed on the under hindwings of the continental owl butterflies (*Caligo* Hübner). These butterflies, with a wing expanse of 6-8 cm, are crepuscular and are often seen along forest paths. They usually perch upside down on twigs, tree trunks or other similar haunts, and when disturbed, they display the

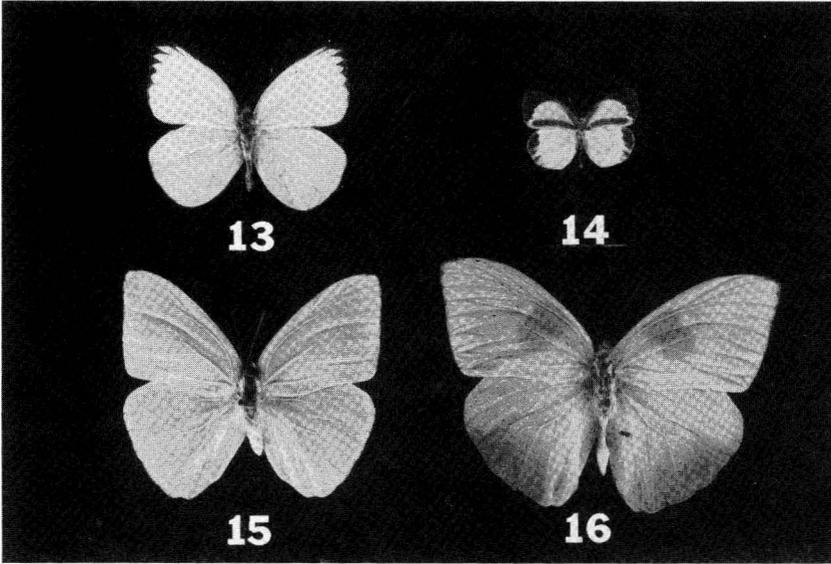


Fig. 13-16. Birds and other predators generally prefer larger-bodied butterflies, such as (15) *Phoebis sennae* and (16) *P. philea*, as opposed to smaller-bodied butterflies, such as (13) *Ascia monuste*, or (14) *Eurema elathea*.

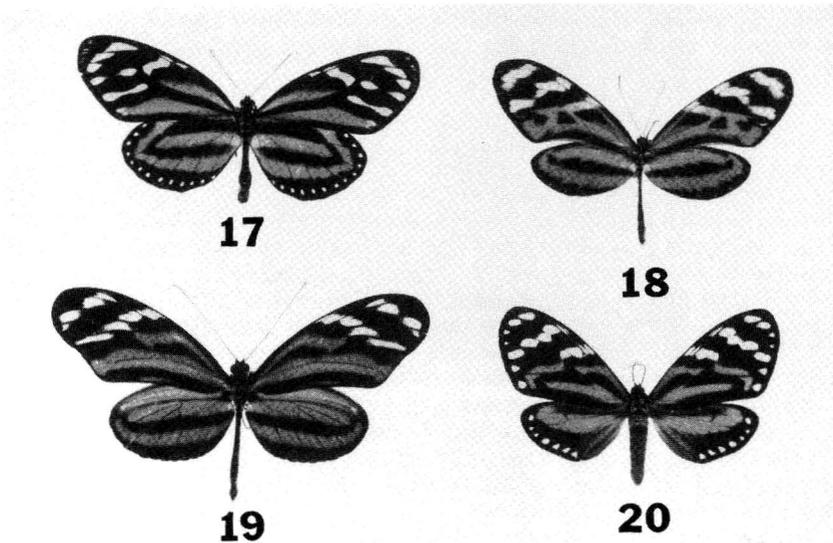


Fig. 17-20. Disruptive wing coloration patterns accentuate the potential distastefulness in this Mullerian mimicry complex: (17) *Lycorea cleobea atergatis*, (18) *Mechanitis lysimnia dorysus*, (19) *Heliconius ismenius telchinia*, and (20) *Chetone angulosa*.

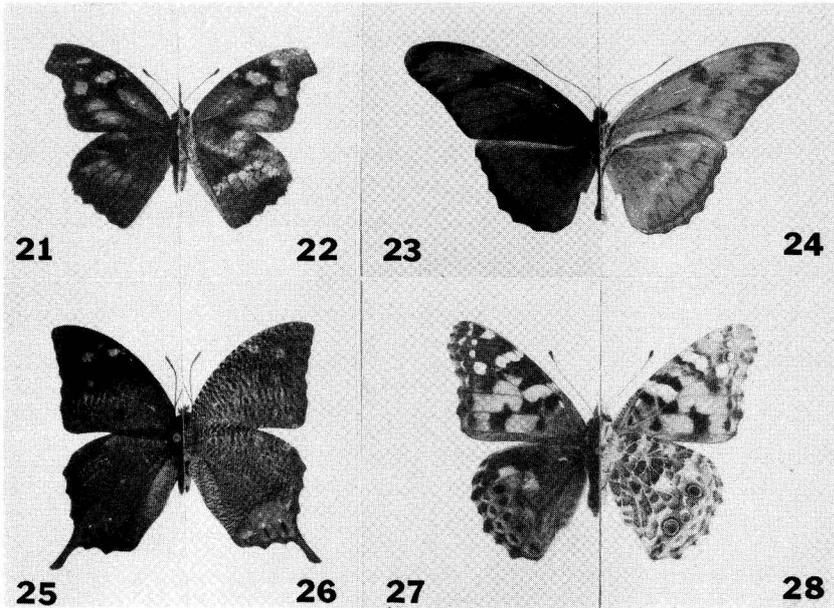


Fig. 21-28. Insular social aggregation and mimicry complex from Dominica, Lesser Antilles: *Libytheana fulvescens* (21, upper and 22, under surfaces), *Dryas iulia dominicana* (23, upper and 24, under surfaces), *Memphis dominicana* (25, upper and 26, under surfaces), and *Vanessa cardui* (27, upper and 28, under surfaces).

ominous eyes on their wings. In the West Indies, some butterfly species, such as the precinctive, diurnal satyrid genus *Calisto* Hübner, possess small eyespots, but these butterflies are not powerful fliers. Thus, the combination of the small eyespots and rather delicate flight behavior are not very effective in warding off predators.

CONCLUSION

Decline in butterfly populations is often the direct result of loss of, fragmentation of, or changes in the habitat. Changes in climate, the use of pesticides, overcollection and natural predation are secondary causes. Behavioral observations on the butterflies are needed to give accurate information on nutrient, habitat, and other biological requirements necessary for attempts at conservation. Despite contrasts in habitats and niches, insular and continental representatives of butterfly families often display similar behavioral patterns, some of which may be more elaborate in one geographic area than another. The study of butterfly behavior with respect to resource and habitat partitioning can be used to enhance conservation and management efforts. In addition, the management of the available habitats should include enhancement of resources in non-critical areas.

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INDOOR AND OUTDOOR FORAGING LOCATIONS OF
PHARAOH ANTS (HYMENOPTERA: FORMICIDAE) AND
CONTROL STRATEGIES USING BAIT STATIONS

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ABSTRACT

While Pharaoh ants, *Monomorium pharaonis* (L.), are generally considered indoor pests, we observed these ants foraging at 51.7% of outdoor monitoring sites located on exterior wall surfaces of apartment buildings in contrast to 11.6% of indoor sites. The number of ants per infested monitoring site did not vary significantly with counts averaging from 46 to 118. Commercial bait stations containing a delayed action toxicant placed solely on the exterior walls of buildings, or outdoors, provided a 94% reduction in Pharaoh ant numbers within 1 week in contrast to a 9% reduction in untreated buildings. This was similar to the reductions from buildings treated with bait stations placed both indoors and outdoors. While a total of 3 ants were found indoors in treated apartments, indoor counts from untreated buildings also were low. Initial outdoor ant counts were 2 to 20 times higher than indoor counts, and the significant population reductions were attributed to a reduction in counts from outdoor sites.

Key Words: *Monomorium pharaonis*, pest control, toxic baits, urban pest ants, household insects, Florida.

RESUMEN

Anunque generalmente se considera que las hormigas faraónas, *Monomorium pharaonis* (L.), son plagas de puertas adentro, observamos estas hormigas en 51.7% de los sitios de monitoreo de puertas afuera sobre las superficies de paredes del exterior de edificios de apartamentos, en contraste con 11.6% de los sitios de puertas adentro. El número de hormigas por sitio de monitoreo infestado no varió significativamente, el rango de conteos siendo 46-118. Las estaciones de cebo de acción toxica retardada de preparación comercial colocadas en las paredes exteriores de los edificios, y proveyeron una reducción en números de hormigas faraónas a 94% dentro en una semana, en contraste a una reducción de 9% en edificios sin tratamiento. Eso fue similar a las reducciones en edificios tratados con estaciones de cebo colocadas afuera y adentro. Aunque un total de 3 hormigas fueron encontradas dentro de apartamentos tratados, conteos dentro de edificios no tratados tambien fueron bajos. Conteos iniciales de hormigas puertas afuera fueron entre 2-20 veces más altos que los conteos adentro, y las reducciones significantes de poblaciones se atribuyeron a una reducción en conteos de los sitios externos.

Pharaoh ants, *Monomorium pharaonis* (L.), are a major indoor pest throughout the world, often occurring in hospitals, food establishments, office buildings, and apartment complexes (Edwards 1986, Smith 1965). The use of baits impregnated with delayed action toxicants or insect growth regulators is an important strategy for the control of ants. It promotes the dissemination of the active ingredient to an entire colony (Lofgren

1986) and can reduce pesticide exposure in sensitive areas such as hospitals or food preparation areas (Edwards 1986). For Pharaoh ant control, Edwards (1986) recommended that baits be placed at foraging sites, nest locations, and adjoining areas. Labels on commercial ant baits generally suggest that stations be placed indoors, near foraging trails and possible nest sites. Bieman & Wojcik (1990) suggested the treatment of the periphery of buildings because structure-invading ants may live outdoors. Thus, the determination of nest and foraging sites is important to the success of baiting strategies for Pharaoh ant control.

In temperate areas, Pharaoh ants usually establish nests indoors (Sudd 1962, Smith 1965). In the tropics, or in areas where warm temperatures are maintained, such as refuse dumps, outdoor nests can be established (Kohn & Vlček 1986). While nest locations were not reported, Haack (1991) reported that Pharaoh ants foraged on the exterior periphery of houses in Texas during the spring and summer, when temperatures were warm and outdoor food sources were available.

In this study we document the foraging of Pharaoh ants outdoors in Florida, and compare the efficacy of placing commercial bait stations on exterior building surfaces, or outdoors, versus outdoors and indoors to control Pharaoh ants.

MATERIALS AND METHODS

The study site was an apartment complex located in Alachua County, near Gainesville, Florida. A total of 12 single story buildings consisting of either 4 one-bedroom apartments (approximately 176 m² interior area per building) or 4 two-bedroom apartments (approximately 248 m² interior area per building) were used. Populations of Pharaoh ants were estimated by placing white index cards (7.5 x 6.5 cm) baited with peanut butter (approximately 1 g) at 6 locations inside and 6 locations outside each apartment. Interior card placements were in the living room on the window sill; in the kitchen on the sink counter, and on the floor near the dishwasher; in the bathroom on the basin counter, and on the floor behind the toilet; and, in the bedroom on the window sill. Exterior locations included the bottom of the front door; the top and diagonally opposite bottom of the courtyard gate; and, on top of the courtyard wall at the intersection of the courtyard and apartment walls. The remaining locations were selected from the following areas: the water spigot; the wall/air conditioning hose junction; the electric meters; and cracks in the wall where ants were observed. Exterior cards were placed on vertical surfaces with double-sided adhesive foam mounting tape. Cards were set in place between 0930 to 1200 hours EDST and were checked approximately 2 h later. Pharaoh ants were counted on both sides of each card and then shaken off at the same location from which they were collected. The presence of red imported fire ants, *Solenopsis invicta* Buren, on the baited cards also was noted. The normal pest control service was suspended for the duration of the study.

A survey was conducted on 15 September 1992 to characterize foraging locations from all buildings. Indoor and outdoor temperatures at the beginning of the survey were 27.2 and 28.6 °C, respectively. The percentage of infested cards per building and the number of ants per infested card between indoor and outdoor locations were compared by *t*-tests. In addition, the percentage of cards with ants was determined for each sampling location. The mean number of ants per infested card also was compared among locations by Ryan-Einot-Gabriel-Welsch multiple range test (SAS Institute Inc. 1988). Outdoor locations that had only 1 infested card were combined into a single category designated as "other". The bathroom basin and toilet locations also were combined to obtain homogeneous variances.

To determine the effectiveness between outdoor only and indoor plus outdoor placements of toxic bait stations in reducing Pharaoh ant populations, commercial bait stations

were assigned to the 12 buildings following a completely randomized design. Treatments consisted of Maxforce® Pharaoh Ant Killer bait stations (The Clorox Co., Oakland, California) placed indoors and outdoors; Maxforce® bait stations placed only outdoors; Pro-Control™ bait stations (Micro-Gen Equip. Corp., San Antonio, Texas) placed indoors and outdoors; and an untreated control. A total of 3 buildings were used per treatment. The Maxforce® and Pro-Control™ baits contained the delayed action toxicants hydramethylnon (0.9%) and sulfluramid (0.5%), respectively. The Pro-Control™ treatment served as a standard because its active ingredient differed from the Maxforce® treatments. Pretreatment populations were determined from the survey used in the foraging study reported above. Commercial bait stations were positioned adjacent to the bait card locations on the same day as the pretreatment survey, immediately after counts were made. For the outdoor treatments 24 bait stations were used for each building, and for the indoor plus outdoor treatments 42 to 48 stations per building were used. Bait stations were left without replacement for the duration of the study. Post-treatment populations were monitored weekly for 4 weeks (21 September through 14 October 1992) following the same procedure as the pretreatment survey. Outdoor temperatures during the population monitoring ranged from 19.4 to 33.1°C.

Pretreatment Pharaoh ant counts were either transformed to $\log_{10}(X + 1)$ to obtain homogeneous variances, or ranked, and then compared by analyses of variance. The average percent reduction in counts from the pretreatment to post-treatment counts per card per building was evaluated by analyses of variance and Tukey's HSD tests (SAS Institute Inc. 1988) for each sample date. The arcsine transformation was performed on percentages prior to analyses.

RESULTS

Pharaoh ants were present on 51.7% (± 5.0 SEM) of the cards placed outdoors for each building, which was significantly greater ($P < 0.0001$; $t = 6.693$; $df = 22$) than the 11.6% (± 3.3 SEM) of the cards located indoors that were infested. The average number of ants per infested card per building did not vary significantly ($P = 0.725$; $t = 0.356$; $df = 20$) between outdoor (82.9 ± 15.0 SEM) and indoor (75.1 ± 15.8 SEM) locations. Infested cards were located most frequently ($> 10\%$) on the courtyard wall, the top of the courtyard gate, the water spigot, and the front door (Table 1). The average number of ants per card did not vary significantly among infested locations (Table 1).

Red imported fire ants were present on 8.6% (± 1.1 SEM) of the outdoor cards per building over the duration of the study. The bottom of the courtyard gate accounted for 48.7% of the cards with fire ants, followed by the bottom of the front door with 12.6%. None of the indoor locations had fire ants.

All treated buildings had significantly greater ($P < 0.05$) reductions in Pharaoh ant populations than the control over the 4-week period when populations were based on bait cards located both indoors and outdoors (Table 2). Differences between the outdoor only and the indoor plus outdoor commercial bait station applications were not significant (Table 2). Differences between the Maxforce® and Pro-Control™ bait stations were not significant (Table 2).

Pretreatment Pharaoh ant populations inside the apartments were from one-half to one-twentieth the level found outdoors. Ants were not detected inside any of the treated buildings following the placement of the commercial bait stations for the first 3 weeks and 3 ants were found in the fourth week. However, the reductions were not statistically different from the reductions reported for the control buildings on the first, second, and fourth weeks post-treatment. In the third week post-treatment, the control buildings had an 11.1% reduction in population, which was significantly less than the treated

TABLE 1. FREQUENCY AND AVERAGE NUMBER OF PHARAOH ANTS PER CARD AMONG LOCATIONS WHERE PHARAOH ANTS WERE PRESENT.

Card Location	Indoors vs. Outdoors	% of Cards with Ants ¹	Avg. No. Ants/Card ²
Courtyard Wall	Outdoor	18.6	118.1
Courtyard Gate (Top)	Outdoors	14.4	57.0
Water Spigot	Outdoors	12.6	88.5
Front Door	Outdoors	10.2	100.6
Bedroom Window (Int ³)	Indoors	9.6	60.6
Air Conditioner	Outdoors	9.0	110.3
Bedroom Window (Ext ⁴)	Outdoors	7.2	116.8
Living Room Window	Indoors	6.6	93.6
Other	Outdoors	5.4	46.3
Courtyard Gate (Bot ⁵)	Outdoors	3.6	73.3
Toilet + Basin	Indoors	3.0	64.0

¹Percentages based on a total of 167 infested cards.

²Averages were not significantly different ($P>0.05$) by Ryan-Einot-Gabriel-Welsch Multiple Range Test.

³Int, interior side of window.

⁴Ext, exterior side of the window.

⁵Bot, bottom of the gate.

buildings (Table 3). Post-treatment Pharaoh ant counts were more prevalent on the outdoor bait cards. Percent reductions on the outside of treated buildings were significantly greater than the controls for all post-treatment sample dates (Table 4). There was a gradual decline in ant populations from control buildings throughout the study (Tables 2 and 4). This resulted in diminishing differences in percent reductions between treated and control buildings.

TABLE 2. AVERAGE PERCENT REDUCTION IN PHARAOH ANT COUNTS OBTAINED INSIDE AND OUTSIDE OF APARTMENT BUILDINGS ONE TO FOUR WEEKS FOLLOWING PLACEMENT OF COMMERCIAL BAIT STATIONS INDOORS AND OUTDOORS, OR OUTDOORS ONLY. STUDY WAS CONDUCTED 15 SEPT. THROUGH 14 OCT. 1992, NEAR GAINESVILLE, FLORIDA.

Treatment (placement)	Week 0	Average Percent Reduction Inside & Outside ¹			
		Week 1	Avg. Count ² Week 2	Week 3	Week 4
Maxforce (out only)	29.5	93.7 a	98.7 a	99.6 a	100 a
Maxforce (in & out)	24.3	99.6 a	98.9 a	99.8 a	99.8 a
Pro-Control (in & out)	35.0	99.8 a	99.0 a	99.9 a	100 a
Control (untreated)	22.8	8.5 b	27.0 b	43.6 b	71.3 b

¹Averages followed by the same letter in each column are not significantly different ($P>0.05$) by Tukey's HSD test on arcsine transformed data. Untransformed percentages are presented.

²Average number of ants per card per building. Number of cards per building ranged from 35 to 48. Pretreatment counts are not significantly different ($F=0.97$; $df=3,8$; $P=0.45$) by analysis of variance on $\log_{10}(X+1)$ data.

TABLE 3. AVERAGE PERCENT REDUCTION IN PHARAOH ANT COUNTS OBTAINED INSIDE OF APARTMENT BUILDINGS ONE TO FOUR WEEKS FOLLOWING PLACEMENT OF COMMERCIAL BAIT STATIONS INDOORS AND OUTDOORS, OR OUTDOORS ONLY. STUDY WAS CONDUCTED 15 SEPT. THROUGH 14 OCT. 1992, NEAR GAINESVILLE, FLORIDA.

Treatment (placement)	Average Percent Reduction Inside ¹				
	Week 0	Week 1	Avg. Count ²		Week 4
		Week 2	Week 3		
Maxforce (out only)	3.2	100 a	100 a	100 a	100 a
Maxforce (in & out)	15.1	100 a	100 a	100 a	99.7 a
Pro-Control (in & out)	6.3	100 a	100 a	100 a	100 a
Control (untreated)	8.5	70.9 a	80.5 a	11.1 b	100 a

¹Averages followed by the same letter in each column are not significantly different ($P>0.05$) by Tukey's HSD test on arcsine transformed data. Untransformed percentages are presented.

²Average number of ants per card per building. Number of cards per building ranged from 18 to 24. Pretreatment counts are not significantly different ($F=1.13$; $df=3,8$; $P=0.39$) by analysis of variance.

DISCUSSION

In our study, Pharaoh ant foraging was more prevalent outdoors than indoors as evidenced by the higher number of infested, outdoor monitoring sites. The most frequented indoor locations were at the windows, which suggested that even indoor foraging tended toward outside locations. Foraging at windows has been attributed to the presence

TABLE 4. AVERAGE PERCENT REDUCTION IN PHARAOH ANT COUNTS OBTAINED OUTSIDE OF APARTMENT BUILDINGS ONE TO FOUR WEEKS FOLLOWING PLACEMENT OF COMMERCIAL BAIT STATIONS INDOORS AND OUTDOORS, OR OUTDOORS ONLY. STUDY WAS CONDUCTED 15 SEPT. THROUGH 14 OCT. 1992, NEAR GAINESVILLE, FLORIDA.

Treatment (placement)	Average Percent Reduction Outside ¹				
	Week 0	Week 1	Avg. Count ²		Week 4
		Week 2	Week 3		
Maxforce (out only)	60.6	92.6 a	98.4 a	99.5 a	100 a
Maxforce (in & out)	33.6	99.3 a	98.1 a	99.7 a	99.9 a
Pro-Control (in & out)	62.8	99.8 a	99.1 a	99.9 a	100 a
Control (untreated)	37.3	1.5 b	20.8 b	55.9 b	63.8 b

¹Averages followed by the same letter in each column are not significantly different ($P>0.05$) by Tukey's HSD test on arcsine transformed data. Untransformed percentages are presented.

²Average number of ants per card per building. Number of cards per building ranged from 17 to 24. Pretreatment counts are not significantly different ($F=0.58$; $df=3,8$; $P=0.64$) by analysis of variance on ranked data.

of dead insects which are often found on window sills and which serve as an important food source for Pharaoh ants (Sudd 1962). Selectively placing bait stations at potential foraging sites on the outside of buildings should increase the probability of Pharaoh ants encountering and feeding on baits when they are actively foraging outdoors.

Pharaoh ants were not found on any of the cards that had fire ants and they were probably excluded from these cards because of the aggressive foraging behavior of fire ants (Banks & Williams 1989, Baroni-Urbani & Kanno 1974). In addition, they may have been prevented from foraging at bait stations if fire ants were foraging at the same location. Because fire ants were found predominantly at monitoring sites located near the ground, it might be advantageous to place bait stations at higher locations.

The significant reductions in Pharaoh ant populations based on all monitoring sites can be attributed to the significant reductions in ants sampled on the outside of treated buildings. The gradual increase in percent reductions from control buildings throughout the study may have reflected a seasonal decrease in foraging activity as temperatures became cooler. Kohn & Vlček (1986) reported the disappearance of Pharaoh ant colonies near the surface of refuse dumps at the onset of cooler weather in Czechoslovakia.

Indoor monitoring sites in treated buildings did not reveal reductions in Pharaoh ant populations that were consistently greater than controls because indoor counts in the controls were low. These counts averaged 4.1 (± 5.9 SD) ants per monitoring card per building over the 4 week post-treatment sampling. Percent reductions in the controls for the first, second and fourth weeks post-treatment averaged 83.8% (± 14.8 SD) in comparison to the 100% (± 0.1 SD) reduction in treated buildings. On the third week post-treatment, when indoor population reductions in the treated buildings were significant, cool temperatures (26.6 °C falling to 20.9 °C) may have favored greater foraging activity indoors in the controls. Despite the relatively low number of ants found indoors, a majority of the Pharaoh ant trails originated from soffit areas. This suggested that the ants were nesting within the buildings with the outside foraging activity being indicative of a structural infestation.

Placing commercial bait stations indoors and outdoors was shown to be effective in controlling Pharaoh ants in houses in Texas (Haack 1991). In that study, stations were placed where ants were foraging, resulting in an average of one station being used every 9.3 to 13.9 m² of interior floor space and 1 station every 3 to 6.1 linear meters along the exterior perimeter of each house. We have shown that selectively placing 24 stations at potential foraging sites on exterior locations of buildings, which had perimeters of 79.3 meters (one station per 3.3 linear meters), was sufficient to provide substantial population reductions outdoors within 1 week. These reductions were comparable to buildings with stations placed both indoors (one station per 7.4 to 10.3 m²) and outdoors (one station per 3.3 linear meters). Thus, the selective placement of bait stations only on the outside of buildings can serve as an effective control strategy when Pharaoh ants are actively foraging on the exterior of buildings. By eliminating interior treatments under these circumstances, this strategy may result in lower application costs, and reduce pesticide exposure in the indoor environment.

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POPULATION LEVELS OF *LEPTODICTYA TABIDA*
(HEMIPTERA: TINGIDAE) IN FLORIDA SUGARCANE

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ABSTRACT

Three sugarcane (*Saccharum* spp.) fields in southern Florida were sampled to assess population densities of the sugarcane lace bug (*Leptodictya tabida* Herrich-Schaeffer) on leaves during 1990 - 1992. The study began several months after the bug was first discovered in Florida. A mean of 6.3 (SEM=0.51) bugs (all life stages) per leaf was observed over the entire study. Average densities per field per sample date ranged up to 74 bugs (all stages) per leaf. The bug was present from late spring through winter but exhibited a propensity for 2 annual peaks in density, one during late spring/early

summer before summer rains and one during the fall after summer rains. Bug populations were very low from late March to May. A general decline in densities of the bug occurred during the study. No parasites, predators or pathogens of the bug were observed. In a laboratory trial, adults and nymphs survived 3-h exposures to 0° and -5°C, indicating short periods of cold weather may have little impact on population levels of the bug. Among 14 sugarcane varieties, 'CP73-1547' was relatively resistant to the bug while 'CP81-1254' was relatively susceptible based on bug densities per leaf.

Key Words: Sugarcane lace bug, sugarcane, population levels, temperature, varietal resistance.

RESUMEN

Se muestrearon mensualmente tres campos de caña durante 15 a 27 meses para determinar la densidad de poblaciones del chinche de encaje de la caña de azúcar desde 1990 a 1992. Este estudio comenzó varios meses después que este insecto fue descubierto en la Florida. Se observó un promedio de 6.3 (patrón de error=0.51) chinches de encaje (todas las etapas de vida) por hoja. El promedio de densidad por campo por fecha de muestreo fue tan alto como 74 chinches de encaje (todas las etapas) por hoja. Los huevos fueron más abundantes en las hojas superiores, mientras que las ninfas fueron más abundantes en las hojas inferiores. Generalmente, el chinche de encaje estaba presente en caña desde tarde en la primavera y durante el invierno, pero demostró una propensión de 2 apogeos de densidad, uno durante tarde en la primavera o principios del verano antes de las lluvias de verano, y el otro durante el otoño después de las lluvias del verano. Los chinches de encaje usualmente no se detectaron durante los finales de Marzo-Mayo. Durante este estudio ocurrió una reducción general en la densidad de este insecto, posiblemente porque las condiciones ambientales eran las menos ideales para este insecto. No se observaron parásitos, depredadores, o patógenos del chinche de encaje. En una prueba de laboratorio, adultos y ninfas del insecto sobrevivieron 3 horas expuestos a 0 y a -5°C, lo que indica que periodos cortos de frío pudieran tener poco efecto contra los niveles de población de este insecto. Entre 14 variedades de caña de azúcar, 'CP73-1547' fue relativamente resistente mientras que 'CP81-1254' fue relativamente susceptible a este insecto basado en la densidad por hoja.

The sugarcane lace bug, *Leptodictya tabida* (Herrich-Schaeffer), was first reported in Florida during 1990 (Hall 1991). Infestations were already widespread in sugarcane (*Saccharum* spp.) across southern Florida when the bug was discovered. Feeding damage to leaves was often extensive in heavily infested fields. Yield reductions may have occurred in fields where extensive damage occurred, but no quantitative assessments have been made on the economic impact of *L. tabida*. No parasitoids, predators or pathogens of the bug were observed in surveys conducted after the initial discovery of the bug during 1990 (Hall 1991). An unsuccessful attempt was made during May 1991 to import a mymarid parasitoid, *Erythmelus* sp., into Florida from Venezuela for control of eggs of *L. tabida* (Nguyen & Hall 1991). Varietal resistance to the bug has been noted in Hawaii (Chang 1985), and it was more abundant in one commercial variety of sugarcane in Florida than another (Hall 1991).

No research has been conducted to quantify population densities or to assess population dynamics of *L. tabida* in sugarcane in southern Florida. Quantitative information on population levels of the bug would be valuable in determining its economic importance and in assessing management strategies. Such information would serve as a base for future comparisons in evaluating the pest status of the bug and in justifying additional

attempts to import natural enemies. Natural control factors in Florida could render the bug a relatively unimportant pest in sugarcane, as was the case with the sugarcane delphacid, *Perkinsiella saccharicida* Kirkaldy (Sosa et al. 1986, Bennett et al. 1990).

Reported here are data on population levels of *L. tabida* in southern Florida. Three sugarcane fields were sampled for 15 to 27 months to investigate population dynamics of the bug and to survey for natural enemies. Survival of *L. tabida* exposed to cold temperatures was investigated in a laboratory trial. A sugarcane variety trial was sampled to determine if infestation levels of the bug differed among 14 varieties.

MATERIALS AND METHODS

Field Surveys

Three commercial sugarcane fields in Palm Beach County were sampled monthly. Two fields were 16 ha and one was 2 ha in size, and each field contained the commercial variety 'CL61-620'. None of the fields received any insecticide treatments during the study. A field located about 11.3 km southeast of Clewiston was sampled October 1990 through December 1992. This field contained a plant-cane crop when sampling was initiated in 1990, a 1st-ratoon crop in 1991 and a 2nd-ratoon crop in 1992. The field was harvested twice during the study, on 24 February 1991, and 19 March 1992. A 2nd field located about 12.0 km south of South Bay was sampled November 1990 through January 1992. This field contained a plant-cane crop in 1990 and a 1st-ratoon crop in 1991; the field was harvested on 29 March 1991. A 3rd field located about 0.8 km southeast of Lake Harbor was sampled May 1991 through December 1992. This field contained a plant-cane crop in 1991 and a 1st-ratoon crop in 1992; the field was harvested on 11 March 1992. Data on rainfall in the vicinity of each field and on air temperatures in the vicinity of one field were collected from weather stations located 1.0 to 4.7 km from each field.

Six locations were sampled in each of the 3 fields. The locations were selected so that they were widely separated within each field and generally no closer than 50 m to any edge of the field. The same locations were sampled throughout the study. At each location, 2 mature leaves were removed from each of 5 stalks spaced 1.5 m apart along a row; one leaf was the upper-most mature leaf (i.e., just below the whorl) and one was the 5th upper-most leaf (or the lowest mature leaf if fewer than 5 mature leaves were present). A total of 60 leaves was therefore collected from each field on each sample date. Scissors were used to gently cut the leaves from the stalks without disturbing bugs. The leaves were placed into individual plastic bags and transported in a cooler to a laboratory where the number of live adults, nymphs and intact (not hatched) eggs per leaf were counted. Bugs which crawled off leaves onto the inside of a bag were counted and included in the total count per leaf. Means ($\bar{x} \pm \text{SEM}$) were calculated. Each leaf and the bugs on each leaf were also visually examined for parasitoids, predators and pathogens.

Eggs on leaves from 2 of the fields were screened for parasitoids each time the fields were sampled by excising pieces of leaves with eggs, placing them into ¼ dram glass shell vials and plugging the vial with tissue. The vials were placed into a small rack inside a clear plastic box, and a lid (not air-tight) was placed onto the box. A small beaker of water was placed inside the box to maintain high humidity. The boxes were held in an air-conditioned laboratory at approximately 25.5° C, and the vials in each box were periodically examined under a microscope over 6 to 8 weeks for emerged egg parasitoids.

Cold Temperature Study

Field-collected adults and nymphs collected during December 1991 were held for 3 h at 0° or -5 °C. Five petri dishes, each containing 10 adults, and 5 dishes, each containing 10 nymphs, were placed into a temperature cabinet set at 0 °C (± 1 °C). Simultaneously, 1 petri dish containing 10 adults and 1 dish containing 10 nymphs were each placed on a laboratory bench as controls. After 3 h, the petri dishes were removed from the temperature cabinet and placed on the laboratory bench; 2 h later, the number of live bugs in each dish was counted. The temperature study was then repeated at -5 °C using a second group of bugs. Percent survival of adult and nymph bugs after each of the 3-h cold treatments was determined.

Varietal Resistance

Small plots of 14 sugarcane varieties in a yield trial in Palm Beach County were sampled for *L. tibida* during August 1991. Each variety was planted in a single 15-m row, 5 replications per variety. The 5th mature leaf below the whorl on each of 5 stalks per plot was sampled for bugs. The numbers of adults, nymphs and eggs per leaf were counted. An LSD statistical test ($P=0.05$) was conducted to compare bug levels among the sugarcane varieties (PROC GLM, MEANS LSD, SAS Institute 1987).

RESULTS AND DISCUSSION

Field Surveys

A mean of 6.3 bugs (all life stages) per leaf was observed across all samples taken in the 3 sugarcane fields. Overall mean densities observed were 0.3 adults, 1.6 nymphs and 4.5 eggs per leaf (Table 1). Individual counts on leaves ranged up to 75, 175, 295 or 323 adults, nymphs, eggs or all stages, respectively. Up to 177 adults and nymphs were observed together on a single leaf. Among the 3 fields sampled, bugs were most abundant at the South Bay field. Means (\pm SEM) over all samples at this field were 1.6(0.58) adults, 2.2(0.52) nymphs, 12.6(2.15) eggs, or 15.8(2.39) bugs (all stages) per leaf. The highest mean densities observed on individual sample dates were 23.4 (8.8) adults, 33.0 (10.9) nymphs, or 42.4 (20.1) eggs per leaf.

Over all samples, a mean of 7.0 bugs (all stages) per leaf was observed on upper leaves and a mean of 5.6 bugs on lower leaves (Table 1). Our observations indicated that nymphs remained on the same leaf throughout development and adults moved up to younger leaves to oviposit.

Densities of *L. tibida* in the Clewiston (Fig. 1) and South Bay (Fig. 2) fields declined during January 1991 and did not increase again until July 1991. However, moderate

TABLE 1. MEANS (\bar{x}) AND STANDARD ERRORS (SEM) FOR THE NUMBER OF *L. TABIDA* PER LEAF ON THE UPPER VERSUS LOWER LEAF SAMPLED ON SUGARCANE STALKS.

Lace Bug Stage	Upper Leaf \bar{x} (SEM)	Lower Leaf \bar{x} (SEM)	Overall \bar{x} (SEM)
Adults	0.3(0.07)	0.2(0.09)	0.3(0.06)
Nymphs	1.1(0.21)	2.0(0.32)	1.6(0.19)
Eggs	5.7(0.69)	3.4(0.47)	4.5(0.42)
Overall	7.0(0.81)	5.6(0.64)	6.3(0.51)

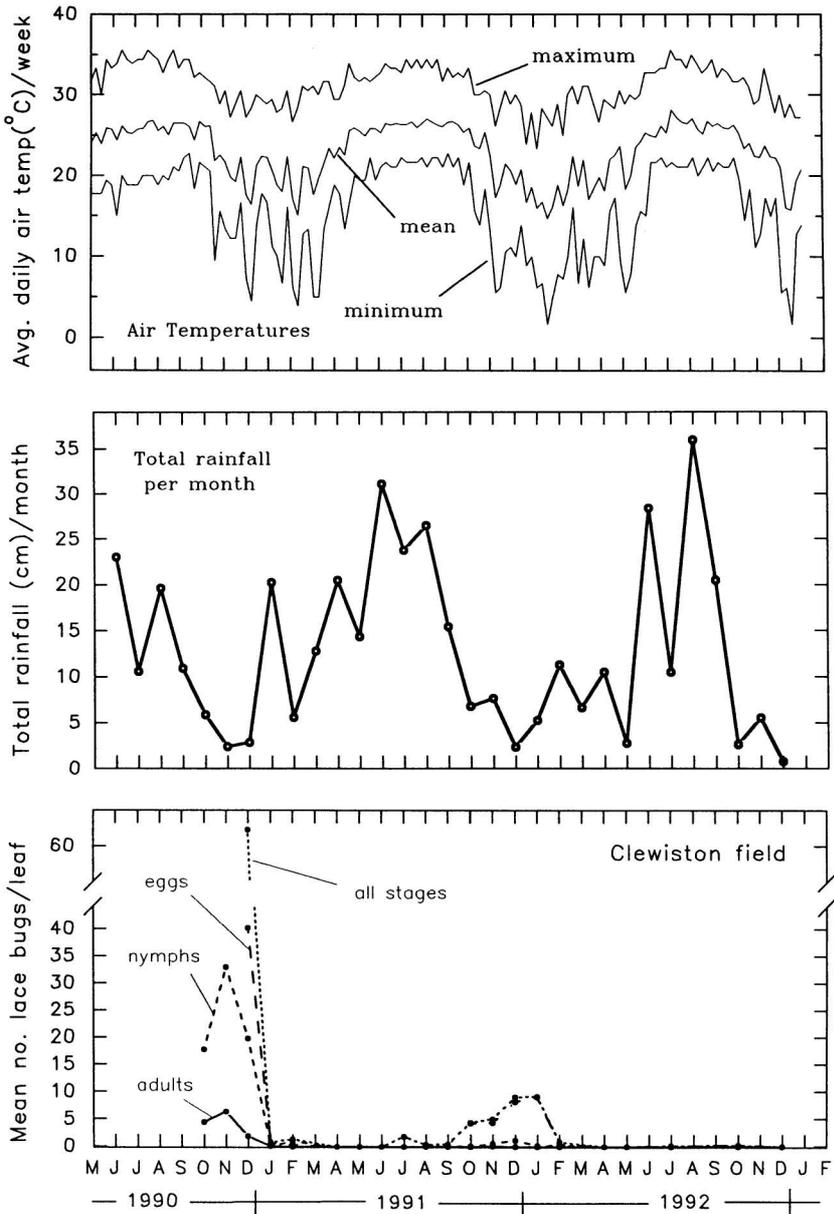


Fig. 1. Average daily temperatures per week (mean, maximum and minimum, °C); rainfall (monthly, cm); and population levels of *L. tabida* on sugarcane leaves near Clewiston, Florida during October 1990 - December 1992. Sampling for eggs was not initiated until December 1990.

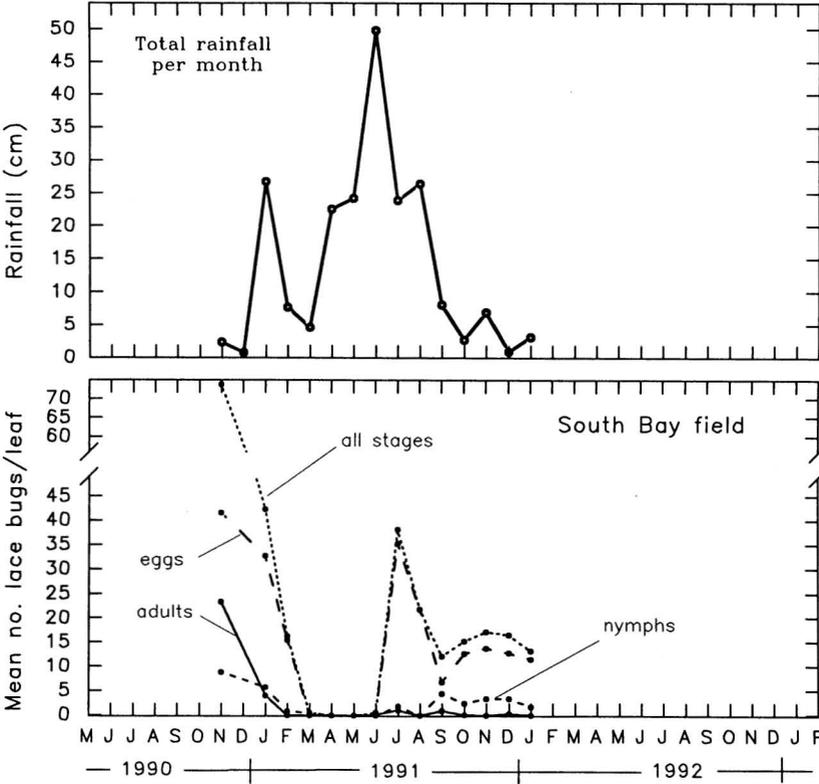


Fig. 2. Rainfall (monthly, cm) and population levels of *L. tabida* on sugarcane leaves near South Bay, Florida during November 1990 - January 1992.

levels of the bug were already present when sampling was initiated during May 1991 at the Lake Harbor field (Fig. 3). Data from 1991 indicated bugs exhibited 2 peaks in population levels, during June-July and during October-January. However, low densities of the bug may persist from late spring/early summer until winter (Fig. 2). Few or no bugs were detected in any of the fields from late March through May. Harvesting during the winter may reduce population levels of the bug, but the data from our study indicated that densities naturally declined before harvest in late winter. Crop development in conjunction with environmental conditions may influence an increase in population levels of the bug during late spring/early summer. According to Box & Guagliumi (1953), *L. tabida* in Venezuela is common on the underside of foliage from 6 months of age onward.

Although moderate densities of the bug were present during January 1992 at the Clewiston field, no more than an average of 1 bug (all life stages) per leaf was observed on any sample date over the rest of the year (Fig. 1). Bugs were detected during July and again during October-December at the Lake Harbor field during 1992, but the levels observed during 1992 were lower than during 1991 (Fig. 3). In fact, overall population densities in each of the 3 fields generally declined over the course of the study. Based on visual examinations of the data, the general decline in lace bug densities that occurred

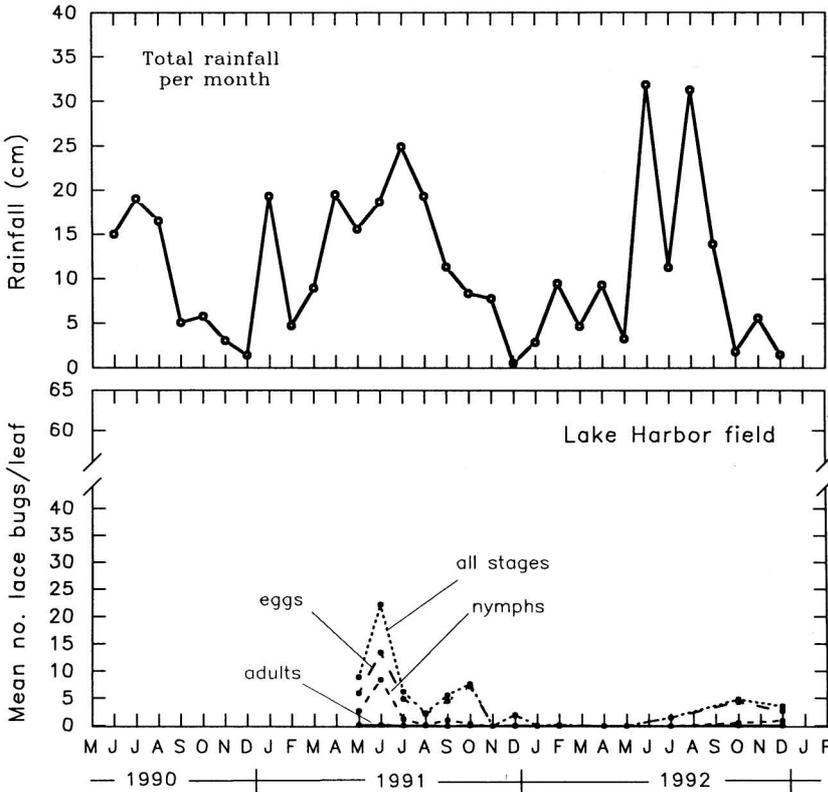


Fig. 3. Rainfall (monthly, cm) and population levels of *L. tabida* on sugarcane leaves near Lake Harbor, Florida during May 1991 - December 1992.

during 1990-1991 did not appear to be directly related to any changes in rainfall (Figs. 1,2,3) or air temperatures (Fig. 1).

No parasitoids, predators or pathogens of *L. tabida* were observed during the study. No parasitoids were recovered from eggs held in the laboratory. Eggs were often found together in small clusters on leaves, sometimes only a few clusters per leaf and sometimes many. In screening for egg parasitoids, vials into which the small portions of leaves with egg clusters were placed each finally contained from 3 to 21 eggs (\bar{x} =8.8 eggs, SD =5.7). Nymphs emerged in only about half of the vials. In vials in which nymphs emerged, an average of 55% (SEM =16.5) of the eggs hatched. Our holding procedures may not have been optimal for egg development and eclosion, especially if the eggs were collected shortly after oviposition. Given the above deficiency, further searches for egg parasitoids of *L. tabida* in Florida may be warranted. No parasitoids of nymphs or adults have been reported in other geographical regions (e.g., see Chang 1985, Nguyen & Hall 1991), nor did we observe any signs of parasitism of these life stages on leaves we examined. However, we did not hold any adults or nymphs to positively determine that no parasitoids were present. There was no evidence that the general decline that occurred in bug densities during the field survey was a result of any biological control.

TABLE 2. POPULATION DENSITIES OF *L. TABIDA* ON 14 DIFFERENT SUGARCANE VARIETIES.

Variety	\bar{x} per Leaf ^a	
	Adults & Nymphs	Eggs
CP81-1302	3.8c	23.4bc
CP73-1547	5.2c	11.8c
CL73-239	13.0bc	20.8bc
CP82-1210	17.2bc	28.6bc
CP82-1592	18.4abc	48.2abc
CP80-1743	20.8abc	39.2abc
CP70-1133	22.0abc	23.4bc
CL61-620	23.0abc	34.2abc
CP78-2114	32.4abc	44.8abc
CP72-2086	34.4abc	22.4bc
CP80-1827	35.8abc	56.8ab
CL59-1052	39.4abc	46.0abc
CP81-1254	48.6ab	71.8a
CP82-1172	57.8a	43.8abc
LSD	39.9	37.9

^aMeans in the same column followed by the same letter are not significantly different ($P=0.05$), LSD test.

Cold Temperature Study

None of the lace bug adults or nymphs died due to 3 hours of exposure to either 0 °C or -5 °C. The occasional cold weather that typically occurs within the sugarcane region in southern Florida during the winter may have little impact on population levels of the lace bug.

Varietal Resistance

The population density of *L. tabida* adults and nymphs among the 14 sugarcane varieties ranged from 3.8 to 57.8 per leaf (Table 2). Densities of eggs ranged from 11.8 to 71.8 per leaf. Significant differences were found among some varieties with respect to bug infestation levels. The varieties 'CP81-1302' and 'CP73-1547' were infested by fewer adults and nymphs than the varieties 'CP81-1254' and 'CP82-1172'. Fewer eggs of the bug were observed on 'CP73-1547' than on 'CP80-1827' or 'CP81-1254'. The data indicated 'CP73-1547' is more resistant to the bug than 'CP81-1254'. The variety 'CL61-620', which was sampled under the field study, appeared to be intermediate with respect to infestation levels of the bug. Plant resistance to *L. tabida* could be a factor influencing population levels of the bug in sugarcane in southern Florida.

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OBSERVATIONS ON THE MATING BEHAVIOR OF
MALE *STICTIA HEROS* (HYMENOPTERA: SPHECIDAE)

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ABSTRACT

Males of the neotropical sand wasp *Stictia heros* (Fabr.) displayed territorial behavior in female nesting areas, presumably to gain access to newly eclosed virgin females. Males hovered above a fixed point of the beach and defended small areas (1 m²) with rapid flights at all intruders. Observations of marked individuals revealed that males defend the same site for at least several days. Unlike head and abdominal temperatures, the thoracic temperature of males varied independently of ambient temperature, indicating active thermoregulation of the flight muscles. Differences between our results and those of Larsson (1989) are discussed.

Key Words: Reproduction, wasps, territoriality.

RESUMEN

Los machos de la avispa perforadora del suelo neotropical *Stictia heros* (Fabr.) mostró comportamiento territorial en áreas de nidos de hembras, presumiblemente para lograr acceso a hembras vírgenes nuevamente emergidas. Los machos revolotearon arriba de puntos fijos en la playa y defendieron áreas pequeñas (1 m²) con vuelos rápidos a todos los intrusos. Observaciones de individuos marcados revelaron que los machos defienden el mismo sitio por varios días. Contrario a las temperaturas abdominales y de la cabeza, la temperatura torácica de los machos variaba independientemente de la temperatura ambiental, indicando termoregulación activa de los músculos de vuelo. Se discuten algunas diferencias entre nuestros resultados y los de Larsson (1989).

Sand wasps typically occupy hot, sunny habitats where thermoregulatory constraints might be expected to influence their activity pattern and behavior. Indeed, several studies (e.g., Willmer 1985, Larsson 1990) have described the effects of high ambient temperature (T_{am}) on the nesting and provisioning behavior of female sand wasps. In comparison, little attention has been given to body temperature regulation and its effects on behavior in male sand wasps. In one of the few studies addressing this subject, O'Neill & O'Neill (1988) found males of the beewolf *Philanthus psyche* Dunning modified their territorial behavior in response to high T_{am} by changing perch locations from the ground to plants and shortening perching duration at any one site.

Recently, Larsson (1989) described alternative mating tactics among males of the sand wasp *Stictia heros* (Fabr.) and proposed that changes in ambient temperature affected the display of these tactics. Specifically, Larsson (1989) reported that between approximately 0700-1045 hours *S. heros* males patrolled emergence and nesting areas by making looping, circular flights over large areas (75 m²) of the beach. While displaying patrolling behavior, males were apparently not aggressive at all or only weakly so. At about 1045 hours, however, males were observed to switch from patrolling to territorial behavior. When adopting territorial behavior, males hovered at fixed positions above the beach and vigorously defended areas of about 25 m² against all intruders. Males remained territorial until the end of their daily flight period at approximately 1145 hours.

Larsson (1989) proposed that by switching behaviors males were able to reduce their thoracic heat load and thereby remain active despite rising ambient temperatures. As support for this suggestion, Larsson (1989) measured thoracic temperatures (T_{th}) of patrolling and territorial males and found that the average thoracic temperature excess ($T_{th} - T_{am}$) did not differ significantly between these groups even though territoriality was exhibited under higher T_{am} (33-34 °C) than patrolling (28-32 °C).

Here, we provide some additional behavioral observations for *S. heros* males as well as more complete data on body temperature regulation. As will be shown, the information presented here does not support the notion that thermoregulatory constraints influence the mating tactics exhibited by *S. heros* males.

MATERIALS AND METHODS

Data were collected between 30 January to 4 February, 1987, at Playa Naranjo and between 26 February to 4 March, 1987, at Playa Tamarindo in Provincia Guanacaste, Costa Rica. Larsson (1989) also used Playa Naranjo for his study, which was conducted from 3-8 January, 1989. At Naranjo, we established a small plot (4 m x 4 m) on the beach, marked all males found within this area, and made hourly censuses of the plot between 0600-1800 hours on two different days. Males were uniquely marked with a small dot of enamel paint on thorax; marks were applied directly to unanesthetized males held in an aerial net. Using a mercury thermometer, we also measured T_{am} at 30 cm above the sand (the height at which males typically fly) at hourly intervals on the two census days. At Tamarindo, we established three plots (each 5 m x 5 m) and on one day censused males hourly between 0600-1800 hours. T_{am} was measured as described above.

At Tamarindo, we also obtained temperature measurements of the thorax, abdomen (T_{ab}), and head (T_{he}) for individual males. Temperatures were measured with a 0.03 mm copper-constantan thermocouple threaded into a 30-gauge (0.3 mm diam) hypodermic needle with the thermocouple junction mounted in the orifice. Temperatures were read to within 0.1 °C using a Bailey Bat-12 thermocouple thermometer. Males were captured in flight with an aerial net and then quickly positioned within the netting (without touching the wasp), and the needle probe was inserted into the center of the thorax and abdomen (the order was alternated between successive males). Head temperature was

then recorded for about half of the individuals. All 3 temperatures were read within 8-10 s of capture. T_{am} was then measured at the point of capture.

RESULTS

The timing of male activity differed slightly between the two study sites. At Naranjo, 4-5 males were always present in the plot during censuses conducted between 0900-1300 hours on both census days, while no males were seen at any other time of the day. T_{am} increased from approximately 33 °C to 38 °C during the period of male activity, and the maximum T_{am} recorded was 39.5 at 1400 hours. Males were active somewhat earlier at Tamarindo. An average of 5 males were present per plot during censuses conducted between 0800-1100 hours (range: 3-6 males per plot per census), and males were absent during all other censuses. T_{am} increased from approximately 31 °C to 38 °C during the period of male activity and peaked at 40.1 °C at 1400 hours. At both sites, females were engaged in nest building and provisioning throughout the day.

Though active at slightly different times, males at both localities exhibited territorial behavior exclusively. Males in both populations hovered about 30 cm above a fixed point of the beach and defended small areas (about 1 m²) via rapid flights at all intruders. Males were in nearly continuous flight and landed infrequently for brief (2-5 s) intervals. Casual observations also revealed that males periodically left their territory (and the beach) for periods of 10-30 min; these territories remained vacant during the owner's absence. Upon being chased, intruders invariably left the immediate area, and no instances of escalated aggression, such as grappling, were observed. At least over periods of several days, territory holders appeared to be highly site-faithful. At Naranjo, we marked a total of 5 males in the study plot (all on the first day of observations), and all of them defended their original territory for the remainder of the study period (i.e., for the next 4 days).

Males of *S. heros* appeared to maintain relatively constant T_{th} at different T_{am} . Simple linear regression revealed that T_{th} varied independently of T_{am} ($t=0.7$; $P < 0.5$; Fig. 1) and ranged only between 39.6 °C and 44.0 °C (mean=41.6 °C). In contrast, both T_{ab} ($t=13.6$; $P < 0.0001$) and T_{he} ($t=5.9$; $P < 0.0001$) increased with increasing T_{am} (Fig. 1) and did so at rates similar to one another ($t=0.9$; $P < 0.5$) and to unity ($T_{ab} - t=0.1$; $P < 0.9$; $T_{he} - t=0.6$; $P < 0.9$). As these results imply, $T_{th}-T_{am}$ was inversely related to T_{am} ($t=5.6$; $P < 0.001$, while both $T_{ab}-T_{am}$ ($t=1.2$; $P < 0.20$) and $T_{he}-T_{am}$ ($t=0.6$; $P < 0.90$) varied independently of T_{am} .

One mating was observed during our study at Tamarindo at 0830 hours. A tight cluster of 10-15 males formed quickly on the sand, and intense fighting continued for approximately 10 s. The mating pair then broke free from the group and immediately flew inland away from the beach. Several males pursued the mating pair for at least 30-40 m at which point they were lost from view.

DISCUSSION

The behavior of male *S. heros* in the populations we studied was similar to that described for males of *S. signata* (L.) (Post 1981) and *S. vivida* (Handlirsch) (Evans 1966). In all of these species, males hover over small areas (1-7 m²) in female nesting areas and defend their territory by chasing, butting, or grappling with intruders. Moreover, males of these species appear to exhibit high site fidelity and may defend the same territory for days or weeks. Alternate, non-territorial mating tactics have not been reported for either *S. signata* or *S. vivida*. In contrast, *S. carolina* (Fabr.) males patrol large areas within nesting aggregations and do not exhibit aggressive behavior (Evans 1966, Evans & O'Neill 1988).

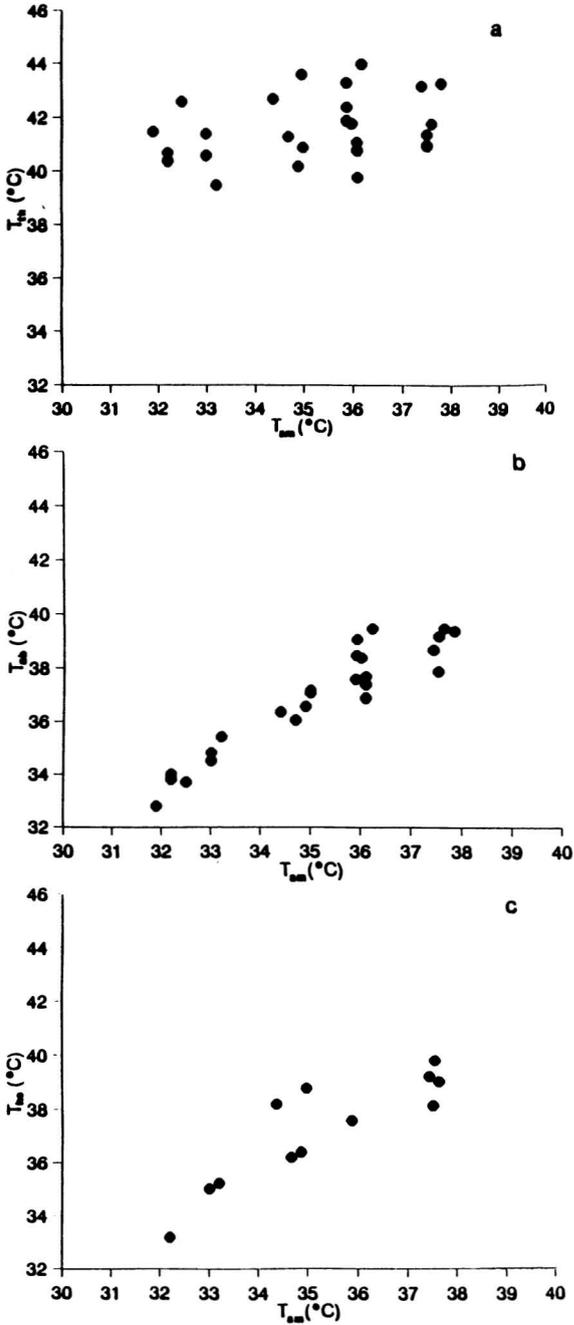


Fig. 1. Relationships between T_{amb} and T_{th} (a), T_{ab} (b), and T_{he} (c) per male of *S. heros*. Regression equations: $T_{th} - Y = 38.1 + 0.10(X)$, $r^2 = 0.05$, $n = 25$; $T_{ab} - Y = 1.6 + 1.0(X)$, $r^2 = 0.89$, $n = 25$; $T_{he} - Y = 6.3 + 0.87(X)$, $r^2 = 0.59$, $n = 14$.

The observation by Larsson (1989) that *S. heros* males in his study population displayed both territorial and patrolling tactics indicates greater plasticity in male behavior than previously recognized for the genus. At present, however, it is not known what factors affect the expression of non-territorial behavior in *S. heros*. However, two results from our study call into question Larsson's (1989) proposal that thermoregulatory constraints were responsible for the behavioral shift he noted from patrolling in the early morning to territoriality near the end of the activity period. Most importantly, we observed male territoriality over a wide range of T_{am} , including early morning when thermoregulatory constraints were probably negligible. It thus appears unlikely that territoriality represents a temperature-specific mating tactic. In addition, unlike Larsson (1989), who found that T_{th} of males increased with increasing T_{am} , we observed that T_{th} was relatively constant over a wide range of T_{am} . Therefore, at least over the thermal range considered, our data do not indicate that *S. heros* males encountered serious difficulty in regulating T_{th} . Though T_{ab} and T_{he} both increased with increasing T_{am} , they were lower than T_{th} over all T_{am} and presumably did not constrain male behavior.

Alternatively, it is possible that male density affects the expression of non-territorial mating tactics, such as patrolling, in *S. heros*. Male density was approximately five times higher in the populations we studied than in Larsson's (1989) population (20 males per 100 m² vs. 4 males per 100 m², respectively). Perhaps when population size is low, males increase their searching areas to compensate for the low density of emerging females; in this situation, the defense of a small area may result in extremely low encounter rates with receptive females. Note this scenario differs from that described for other insects (e.g., Alexander 1961, Borgia 1980), where the expression of territorial behavior is inversely related to male density.

In conclusion, insufficient data for *Stictia* species exist to characterize intrapopulation variation in male mating behavior. Larsson's (1989) observations on *S. heros* are intriguing, since they reveal previously undetected plasticity in mate searching tactics. However, additional data are required to describe more completely the nature and occurrence of different mating tactics and to identify the factors underlying their expression.

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