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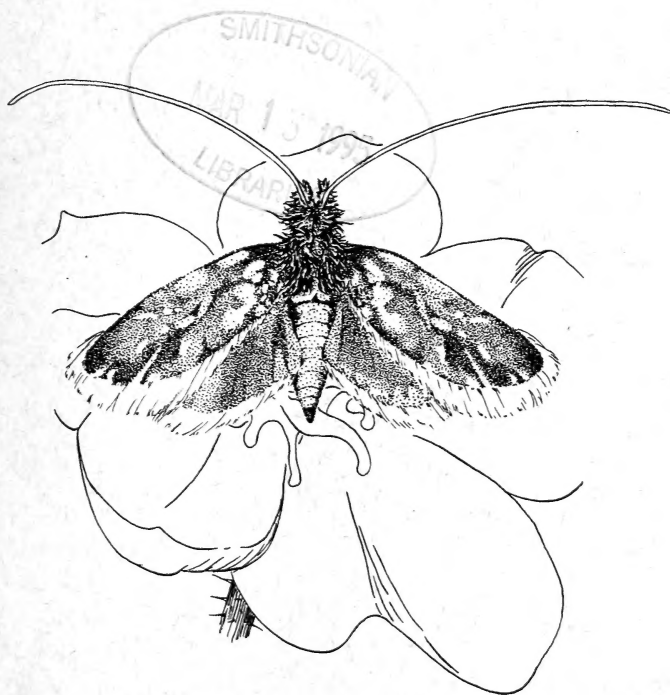
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Cover illustration: Opler's longhorn moth (*Adela oplerella* Powell) is a small, diurnal microlepidopteran in the family Incurvariidae. It occurs only in coastal central California (Marin Co., San Francisco Co., Santa Clara Co.), and it is recognized as a Category 2 candidate for listing as a threatened or endangered species. Original drawing by Larry A. Lavendel, 441 36th Avenue, Santa Cruz, CA 95062.

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PRESIDENTIAL ADDRESS 1994: STUDYING BUTTERFLY BEHAVIOR WITH A CAMERA

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My introduction to photography came early. In 1949, at age 10, I won the grand prize in a hobby show in Walnut Creek, California, with my nature display. The prize was a Kodak 126 camera and a film developing kit. My father helped me develop my photographs in our garage. A few years later when I was in the eighth grade, my dad took me to hear a talk on insect close-up photography by Dr. Ed Ross. Later, I bought his small book on insect photography (Ross 1953), but it wasn't until 1961 when I joined the army and purchased a 35 mm single lens reflex that I began to experiment with close-up photography of butterflies. Since then I have gone through a series of 5 or 6 single lens cameras, each with increasing capabilities.

My photography of butterflies took a quantum leap forward when I joined with George Krizek to write a book on butterflies of the eastern United States (Krizek & Opler 1984). George already had excellent slides of many of the eastern butterflies, especially true butterflies, but he lacked photos of many smaller species, especially skippers. I took it upon myself to fill in these gaps. About 40% of the photographs in the book were the result of my efforts. At the same time, I was conducting an intensive walking survey, recording the abundance, seasonality, and behavior of butterflies in Fairfax County, Virginia, and I often had my camera with me.

Based on countless hours of observations of butterfly behavior during my walking surveys, I acquired the patience necessary to take good photographs of unrestrained, free-living butterflies and learned when it is possible and when not to try to approach butterflies with photography in mind.

I now have a Nikon 8008S and have been amassing photographs of

western North American butterflies with which to illustrate a book in preparation by Ray Stanford and myself. I also am using my photographs to illustrate talks to school children, citizen groups, and university classes or seminars. I like the positive feedback and the "oohs" and "aahs" from the audience.

In my presidential address delivered at the 1994 annual meeting of the Lepidopterists' Society in Pine Mountain, Georgia, I presented several series of slides illustrating the kinds of behavior that one may document with a camera. I began with a series of slides of about 20 butterfly species that had taken off just as I snapped the shutter. I had saved these slides but never shown them to an audience previously. They really don't show much except the position taken by butterflies as they "push-off" from flowers.

Next I showed a series of slides to illustrate how one could document the occurrence of rare species or new records by photography. Examples shown include the first record of *Callophrys mcfarlandi* from Colorado, the first spring *Anteos maerula* seen in southern Texas, a rare sighting of *Dione moneta* in Starr County, Texas, and one of the few sightings of *Emesis tenedia* in the United States (see Figs. 1-4).

Flower visitation can be studied readily with the aid of a camera because nectaring butterflies are relatively easy to photograph. As a case study, I showed how one can document the diversity of flowers visited by a single species of butterfly. As examples, I showed a number of slides of *Battus philenor*, *Papilio multicaudatus*, and *Colias meadii* visiting a series of different flowers. One also may document the position of butterflies while they are nectaring. I also showed that one could compile a list of the number of different butterfly species visiting the same nectar plant species. As a case in point, I showed photographs of 33 different species nectaring at rabbitbrush (*Chrysothamnus nauseosus*) (see Table 1).

Some butterflies assume unusual postures when trying to nectar, and skippers in particular will exert extreme effort to obtain a good meal. I showed slides of *Atrytonopsis hianna* so deep inside the corolla of a *Penstemon* that only the tips of its wings were visible. I also showed a similarly positioned *Lerema accius* inside a *Justicia* flower.

As a case of unusual food sources, I showed a slide of several freshly

→

FIGS. 1-6. Butterfly photographs. 1, First record of *Callophrys mcfarlandi* from Colorado; 2, First spring *Anteos maerula* seen in southern Texas; 3, One of few sightings of *Emesis tenedia* in the United States; 4, Rare sighting of *Dione moneta* in Starr County, Texas; 5, *Piruna pirus* sipping moisture; 6, Mating pair of *Euphyes bimacula*, taken at the western limit of its range in Fort Collins, Larimer County, Colorado.

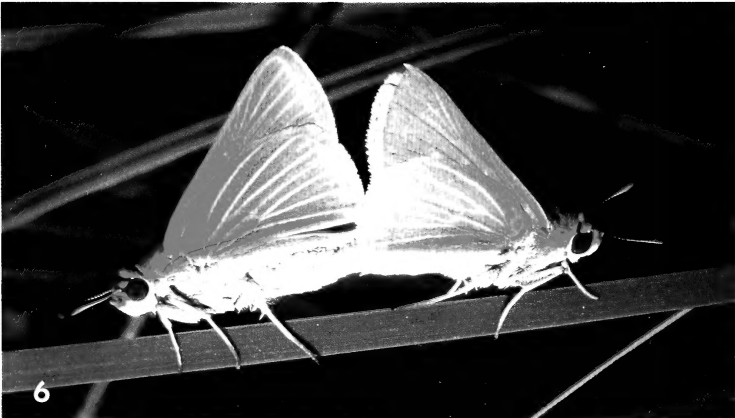
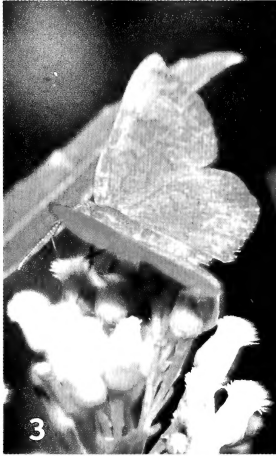
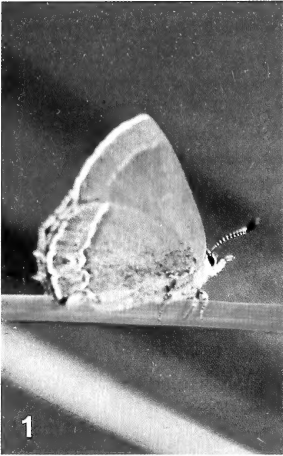


TABLE 1. Butterfly species photographed at flowers of rabbitbrush, *Chrysothamnus nauseosus*.

Family Pieridae	Family Nymphalidae (cont'd)
<i>Pontia occidentalis</i>	<i>Nymphalis antiopa</i>
<i>Colias eurytheme</i>	<i>Vanessa atalanta</i>
Family Lycaenidae	<i>Vanessa cardui</i>
<i>Lycaena helloides</i>	<i>Vanessa annabella</i>
<i>Lycaena editha</i>	<i>Vanessa virginiensis</i>
<i>Lycaena heteronea</i>	<i>Junonia coenia</i>
<i>Satyrium fuliginosum</i>	<i>Limenitis weidemeyerii</i>
<i>Satyrium titus</i>	<i>Cercyonis oetus</i>
<i>Strymon melinus</i>	<i>Cercyonis meadii</i>
<i>Leptotes marina</i>	<i>Danaus plexippus</i>
Family Nymphalidae	Family Hesperidae
<i>Euptoieta claudia</i>	<i>Pyrgus communis</i>
<i>Speyeria zerene</i>	<i>Hesperia leonardus</i>
<i>Speyeria aphrodite</i>	<i>Hesperia comma</i>
<i>Speyeria mormonia</i>	<i>Hesperia uncas</i>
<i>Speyeria edwardsii</i>	<i>Hesperia juba</i>
<i>Phyciodes campestris</i>	<i>Polites coras</i>
<i>Polygonia zephyrus</i>	<i>Polites themistocles</i>

emerged *Speyeria egleis* feeding at mammal dung. Of course we know that many butterflies will feed at dung, bird droppings, and animal carcasses.

An unusual behavior not completely explained is that of butterflies exuding moisture droplets from the tip of their abdomen, and then taking up the moisture with their proboscis. Presumably they are using the moisture to take up salts or other food sources, such as nitrogenous compounds, possibly in dried spots of animal urine. Slides illustrating this behavior showed individuals of *Piruna pirus* and *Amblyscirtes aenus* (Fig. 5).

The perching positions of males, with their anterior end elevated and the antennae at a 45 degree angle, can be documented on film. I showed slides of a few examples, including *Papilio zelicaon*, *Papilio indra*, *Feniseca tarquinius*, *Erynnis martialis*, and *Stinga morrisoni*.

Next in the sequence of behavioral steps leading to mating and reproduction, I showed slides of females being courted by males. These included *Lycaena helloides*, *Poladryas arachne*, *Chlosyne lacinia*, *Hesperia comma*, *Poanes zabulon*, and a male *Anthocharis sara* circling a female.

Mating pairs of butterflies are easy to photograph and can document which sex is the "carrier." I showed photographs of mating pairs of 26 butterfly species, the most spectacular of which was a mating pair of

Euphyes bimacula, taken at the western limit of its range in Fort Collins, Larimer County, Colorado (Fig. 6).

Photographing female butterflies is usually a difficult trick except for those species that lay batches of eggs or take a long time to insert their eggs into plant parts. I showed slides of ovipositing females of *Pieris napi*, *Celastrina argiolus*, *Celastrina* undescribed species, and *Polygonia interrogationis*. Females of *P. interrogationis* were observed to lay stacks of 3 to 5 eggs under leaves of plants adjacent to their host (Opler & Krizek 1984).

After the slides of butterflies exhibiting various behaviors leading to reproduction, I showed short sets of butterflies roosting, a possible defense display by *Ancyloxypha numitor*, and butterflies being taken as prey by various predators.

I highly recommend butterfly close-up photography not only as a way to study butterflies, but as a way to learn about their complex behavior. Butterfly photography is certainly a good way to augment either your butterfly collecting or your butterfly observations.

ACKNOWLEDGMENT

I thank my fiance Evi Buckner for allowing me to show several of her excellent photographs.

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THE BIOGEOGRAPHY AND ECOLOGY OF *EUPHYES DUKESI* (HESPERIIDAE) IN FLORIDA

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ABSTRACT. A distinctive endemic phenotype of *Euphyes dukesi* (Lindsey) was first discovered in Florida in 1971. The endemic nature of Floridian populations was only recently recognized, and the populations currently remain undescribed. Pleistocene glacial events probably contributed to the isolation of these populations from populations on the North American mainland. The species has been found in at least five types of forested wetlands in Florida. The primary hostplant is *Rhynchospora inundata* (Oakes) Fern (Cyperaceae), but *Rhynchospora miliacea* (Lam.) A. Gray (Cyperaceae) and a species of *Carex* (Cyperaceae) also are utilized. *Euphyes dukesi* is bivoltine in Florida, with adults active primarily during May-June and September-October. Adults frequent sunlit patches of hostplants within swamps and visit a variety of nectar sources. The alteration and destruction of forested wetlands threaten populations of this species. *Euphyes dukesi* has a limited distribution and is considered rare in Florida.

Additional key words: endemic, swamps, hostplants, energy resources, behavior.

Since its description, Duke's skipper, *Euphyes dukesi* (Lindsey), has remained an enigmatic and poorly understood North American member of the genus *Euphyes*. This species generally is considered rare and known from only a few widely separated localities (e.g., MacNeill 1975, Pyle 1981, Opler & Krizek 1984). In Michigan, *E. dukesi* is a state-listed threatened species (Haack 1992). Owing to this perceived rarity, a number of distributional and ecological discoveries have been documented in detail (Pliske 1957, Mather 1963, 1966, Price & Shull 1969, Irwin 1969, 1972, Covell et al. 1979). The known range of *E. dukesi* extends from Virginia, southward along the Atlantic coast to Florida, west to southeastern Texas and northward in the Mississippi drainage to Indiana, Ohio, Michigan, and southern Ontario (Opler & Krizek 1984, Holmes et al. 1991, Stanford & Opler 1993) (Fig. 1). The species is represented in Florida by a recently recognized, but undescribed endemic subspecies (Shuey 1993). Throughout its range, this species is associated primarily with the interiors of swamps, habitats that characteristically support few butterfly species. Because of this extraordinary habitat affinity, *E. dukesi* remained undiscovered until 1922 (Lindsey 1923).

In common with most other North American members of the genus, *E. dukesi* has been recorded in association only with *Carex* (Cyperaceae) sedge hostplants (Shuey 1986). In the Great Lakes region, the only reported host is *Carex lacustris* Willd., a broad-leaved species fre-

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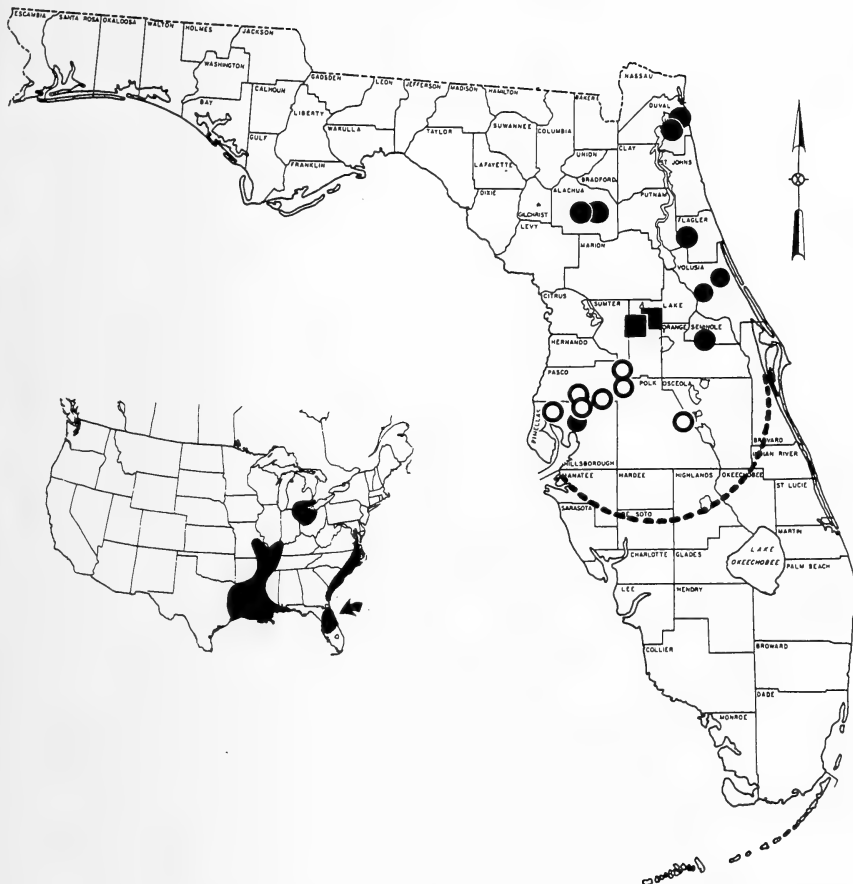


FIG. 1. Distribution of *E. dukesi* in Florida. Solid circles are historical records; open circles are populations located in central Florida 1990–1991; squares are populations discovered in 1992 by H. D. Baggett and M. C. Minno. The dotted line is the estimated southern range limit of the species. Inset map shows the generalized range of *E. dukesi* in North America (arrow indicates the range of the Floridian phenotype).

quently found within swamp forests and partially shaded drainage ditches (Pliske 1957, Shuey 1985, Iftner et al. 1992). In the Gulf States (e.g., Louisiana and Texas), *E. dukesi* has been found in association with *Carex hyalinolepis* Steud. (Irwin 1972) and *Carex lurida* Wallenb. (Rickard & Knudson 1980). *Carex lacustris* was once considered conspecific with *C. hyalinolepis* (= *C. lacustris* var. *laxiflora* Dewey). These species are very similar and it is possible that some Great Lakes populations of *E. dukesi* actually utilize *C. hyalinolepis*. The only other reported host is *Carex walteriana* Bailey which Scott (1986) listed with-

out reference. At least two additional *Carex* species are utilized in Texas (M. A. Rickard pers. comm.). Alternate common names for *E. dukesi* allude to these habitat and hostplant preferences (e.g. scarce swamp skipper [Pyle 1981] and brown sedge skipper [Scott 1986]).

For nearly twenty years following its original description, *E. dukesi* was known only from the type locality of Mobile, Alabama (Mather 1963). Although Holland (1931) predicted that *E. dukesi* would eventually be found "elsewhere along the Gulf," it was not until 1971 that the species was recorded in Florida. Until recently, the entire known Florida distribution of *E. dukesi* was limited to nine locations within six counties (Fig. 1). This species was considered very rare in Florida and records consisted of single or few individuals. In most cases, the species was encountered only once or twice at a given locality. Minno and Calhoun (in press) stress the need for surveys and ecological studies to properly determine the status of *E. dukesi* in Florida. Similar studies have led to the discovery of at least 30 populations in Ohio alone (Shuey 1985, Iftner et al. 1992). The purpose of this paper is to present the results of a detailed examination of the distribution, habitat, hostplants, and behavior of *E. dukesi* in Florida. Potential threats to Floridian populations also are identified.

BIOGEOGRAPHY

Shapiro (1971) remarked that *E. dukesi* possesses "the most extraordinary distribution of any North American butterfly," exhibiting a Coastal Plain-Great Lakes distribution pattern. He proposed that this pattern may be at least partially explained by the displacement of populations during Pleistocene glacial intervals, followed by the dispersal of the species through suitable vegetational corridors (e.g., the Mississippi and Mohawk Valleys) when the ice sheets retreated. Although Shapiro (1971) stated that *E. dukesi* is not phenotypically differentiated, the species does exhibit morphological differences to varying degrees (Mather 1963, Shuey 1994).

Remington (1968) observed that many plants and animals in peninsular Florida differ from their respective mainland populations. He identified a narrow zone of transition in northern Florida, across which little or no clinal trends exist. He attributed this to a combination of glacial and postglacial episodes, especially during the late Pleistocene. Shuey (1993) suspected that vegetational changes associated with glacial events contributed to the fragmentation and eventual divergence of peripheral populations of several species of *Euphyes*, including *E. dukesi*.

During Pleistocene glacial maxima, boreal forests penetrated far into

the southeastern United States (Webb 1990) and may have displaced populations of *E. dukesi* into refugia located in the Florida peninsula. During the Wisconsin glacial maxima (approx. 20,000 YBP), Florida's land area was much larger, extending outward to the edge of the continental shelf (Florida Plateau). At this time, swamps may have occupied bottomland and low-lying areas in northern Florida where mesic and riparian forests dominated (Webb 1990). The general climate of northern Florida appears to have remained relatively constant over the last 20,000 years (Platt & Schwartz 1990), suggesting that conditions were well suited for such refugia. Boreal forests may have acted as effective barriers, isolating populations of *E. dukesi* in Florida. Endemic populations of sand pine (*Pinus clausa* [Chapm. ex. Engelm.]) are believed to have been confined to Florida in this manner (Webb 1990). It is possible that populations of *E. dukesi* became isolated in Florida by a similar process during a glacial event prior to the Wisconsin. *Euphyes dukesi* has probably been present continuously in Florida many millennia longer than in the Great Lakes region where current populations could not have become established until after the Wisconsin glaciers had retreated (approx. 12,000 YBP). The species presumably populated present day forested wetlands during the last several thousand years in a manner consistent with island colonization.

Euphyes dukesi currently is found in Florida between the latitudes 30°20'N and 28°N, representing the southernmost populations of the species. Populations in Hillsborough County, Florida are located nearly 350 km further south than those in Texas and Alabama. Where *E. dukesi* occurs in Florida, average annual temperatures range from 18.9°C to 22.8°C (Fernald 1981). Many Florida populations are found within the Ocala Uplift physiographic district (Fig. 2) which is a highly diverse region with a relatively wide range of elevations and botanical communities (Brown et al. 1990). The remaining populations are found within the northern portion of the Eastern Flatwoods District (a low, flat region composed primarily of pine flatwoods communities), the Central Lake District (karst terrain with numerous lakes and sandhills) and the Sea Island District (pine flatwoods, dunes and salt marshes). The species probably occurs southward into the central portion of the Eastern Flatwoods District and the northern portion of the Southwestern Flatwoods District (another low, flat region dominated by pine flatwoods communities) (Figs. 1 & 2). A number of temperate species reach their southern range limit in this area (roughly 27°30'N), apparently due to decreasing habitat availability. *Euphyes dukesi* is undoubtedly absent from the Gold Coast-Florida Bay District of subtropical southern Florida. This district is low-lying and consists largely of marshes, dwarf cypress communities, and mangrove swamps (Brown et al. 1990). The

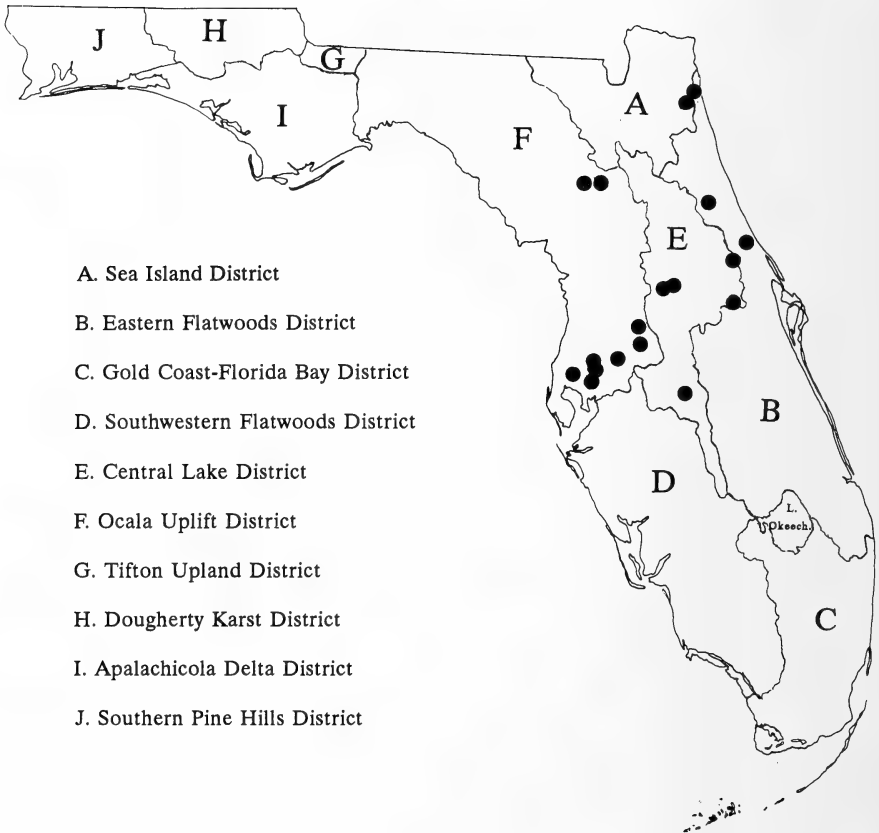


FIG. 2. Physiographic districts of Florida (adapted from Brown et al. 1990). Dots denote *E. dukeesi* populations.

ecological characteristics of forested wetlands in this region differ from those elsewhere in the State.

Populations of *E. dukeesi* almost certainly inhabit swamps within the various physiographic districts of the Florida panhandle. This portion of Florida lies only 48 km east of mainland *E. dukeesi* populations in Alabama. As a result, populations of the mainland phenotype could inhabit the western counties of the Florida panhandle and intermediate populations may extend eastward. However, if sympatric populations of these subspecies are located, with no evidence of intergradation, their taxonomic relationship should be re-evaluated. Other butterflies that share the basic distribution pattern of *E. dukeesi* in Florida include *Wallengrenia egeremet* (Scudder) (Hesperiidae), *Poanes zabulon* (Bois. & LeConte) (Hesperiidae), *Satyrium c. calanus* (Hübner) (Lycaenidae),

Incisalia henrici margaretae dos Passos (Lycaenidae), *Anthanassa texana seminole* (Skinner) (Nymphalidae), *Satyroides appalachia* (R. L. Chermock) (Satyridae), and *Cyllopsis gemma* (Hübner) (Satyridae). With the exception of *S. calanus*, these taxa are associated primarily with forested wetland habitats in Florida.

HABITAT

In August 1990, a large population of *E. dukesi* was discovered along a branch of the Big Cypress Swamp in southern Pasco County, Florida. The swamp is part of a forested wetland complex extending from central Pasco County southward into northern Hillsborough County. It supports an abundance of water ash (*Fraxinus caroliniana* Mill., Oleaceae), southern red maple (*Acer rubrum* var. *trilobum* K. Koch., Aceraceae), sweetgum (*Liquidambar styraciflua* L., Hamamelidaceae), water oak (*Quercus nigra* L., Fagaceae), cabbage palm (*Sabal palmetto* (Walt.) Lodd. ex Schultes, Arecaceae), and bald cypress (*Taxodium distichum* (L.) Rich., Taxodiaceae). Buttonbush (*Cephalanthus occidentalis* L., Rubiaceae) occurs locally throughout the swamp. Arrowroot (*Thalia geniculata* L., Marantaceae), dotted smartweed (*Polygonum punctatum* Elliot, Polygonaceae) and pickerelweed (*Pontederia cordata* L., Pontederiaceae) grow within many sunlit wet depressions. The swamp is seasonally flooded and becomes dry during the spring and autumn when precipitation levels are low. During the wet season (June–September), water levels may reach 0.5 m or more in the deeper depressions. It is within these water-filled depressions that *Rhynchospora* and *Carex* sedges form impressively large patches, sometimes dozens of square meters in size and consisting of thousands of individual plants. These sedge patches are common throughout the open understory where they grow to approximately 1 m in height and conceal many cypress aerial roots or “knees,” making travel through the swamp very treacherous (Figs. 3–4). *Euphyes dukesi* is found in close association with these sedges.

Based on this initial discovery, other forested wetlands in central Florida were surveyed in 1991 for *E. dukesi*. Swamps were selected that consisted of hardwoods with interior stands of cypress, suggesting that water levels were sufficient to support an abundance of sedges. Consequently, six additional populations of *E. dukesi* were found in Hillsborough, Pasco, Polk, and Sumter counties (Fig. 1).

Invertebrate diversity is high within swamps where *E. dukesi* occurs. Spiders are abundant, including *Nephila clavipes* (L.) (Araneidae), which constructs webs measuring 1 m or more in diameter. Large mosquitoes of the genus *Aedes* (Culicidae) are particularly troublesome. Dragonflies, such as *Epiaeschna heros* (Fab.) (Aeshnidae), patrol sunlit clear-

ings. Species of Lepidoptera inhabiting swamps with *E. dukesi* include *Callosamia securifera* (Massen) (Saturniidae), *Catocala* spp. (Noctuidae), *Oligoria maculata* (W. H. Edwards) (Hesperiidae), *Problema byssus* (W. H. Edwards) (Hesperiidae), *Wallengrenia egeremet*, *Hermemythia sosybius* (Fab.) (Satyridae), *C. gemma* and *S. appalachia*. *Calpododes ethlius* (Stoll) (Hesperiidae) frequents sunlit patches of its hostplant (*T. giniculata*) and *Papilio glaucus* (L.) (Papilionidae) is a common canopy species in many swamps dominated by hardwoods. Species of sedge moths (Glyphipterigidae) undoubtedly occur in these swamps as well. A number of vertebrates also occupy these habitats. The eastern diamondback rattlesnake (*Crotalus adamanteus* Beauvois, Viperidae) and Florida cottonmouth (*Agkistrodon piscivorus conanti* Gloyd, Viperidae) are occasionally encountered. Many species of migrating songbirds utilize the swamps as important food sources.

Freshwater forested wetlands, or swamps, can be defined as ecosystems that support trees where soils are periodically flooded or saturated by fresh water for significant periods of time during the life cycle of the trees (Lugo 1984). These ecosystems comprise ten percent of Florida's land area (Ewel 1990) and have been classified by a variety of methods (e.g., Penfound 1952, Cowardin et al. 1979). Wharton et al. (1977) classified Florida swamps into 26 types, but *E. dukesi* has been found in association with only a few of these. Many *E. dukesi* populations in Florida are found in blackwater creek swamps (blackwater floodplain forests). These swamps occupy the floodplains of streams, are dominated by bottomland hardwoods, and are seasonally flooded (Wharton et al. 1977). The population of *E. dukesi* in southern Pasco County (the largest known population in Florida) occurs in a swamp that can loosely be defined as a mixed hardwood swamp (K. C. Ewel pers. comm.). A similar nearby swamp has been characterized as a mixed hardwood bald cypress forest (Rochow 1983) and a mixed-hardwood and cypress floodplain (Rochow 1985). The wetter portion of the swamp is floristically comparable to blackwater creek swamps but no distinct stream channel is present. The upper zones of the swamp are similar to hydric hammock subsystems in which oaks (*Quercus* spp.) and cabbage palmetto (*S. palmetto*) predominate.

Smaller populations of *E. dukesi* have been found in association with stillwater swamps. Most of these swamps are seasonally flooded and derive water from rainwater and shallow ground water (Wharton et al. 1977, Ewel 1990). A small number of *E. dukesi*, including larvae and pupae, have recently been found in association with *R. inundata* in stillwater lake fringe swamps of north-central Florida (M. C. Minno pers. comm.). These swamps are found adjacent to lakes, are dominated by bald cypress, and have fluctuating water levels (Wharton et al. 1977). *Euphyes dukesi* has rarely been found in stillwater swamps that possess



FIG. 3. Habitat of *E. dukesi* near Cypress Creek Swamp, Pasco Co., FL (note extensive understory of sedges).

an upperstory consisting almost entirely of bald cypress. Many cypress swamps contain deep water interiors, restricting sedges to small clumps on raised areas (such as around tree bases). Other such swamps are very dense, without sedge understories, or are more open and provide insufficient shade for *E. dukesi*.

One male and one female *E. dukesi* were found at the edge of a bay swamp (bayhead) in eastern Polk County. Stillwater bay swamps are dominated by bay trees [*Persea* spp., Lauraceae; *Gordonia lasianthus* (L.) Ellis, Theaceae; and *Magnolia virginiana* L., Magnoliaceae] and are constantly wet (Wharton et al. 1977). These swamps are usually very dense and provide little habitat for *E. dukesi*. However, the sedges at the collection site grow along the sunlit margin of the swamp and *E. dukesi* was flying where little shade is available. This atypical open habitat is reminiscent of a Louisiana population of *E. dukesi* discussed by Irwin (1972) and some other populations in the lower Mississippi drainage.

Using the classification of Cowardin et al. (1979), all Florida swamps in which *E. dukesi* is known to occur can be described as of the Palustrine System, Forested Wetland Class, and of the Subclasses Broad-leaved Deciduous (mixed hardwood swamps and creek swamps), Narrow-leaved Deciduous (cypress swamps and lake fringe swamps), and



FIG. 4. Sunlit patch of *R. inundata* growing in the interior of a mixed hardwood swamp (Pasco Co., FL).

Broad-leaved Evergreen (bay swamps). *E. dukesi* will undoubtedly be discovered in other types of swamps as well.

Based on these habitat observations, as well as observations of adult energy resources and behavior described below, "appropriate" swamp habitat for *E. dukesi* in Florida exhibits four basic characteristics: (1) an upperstory usually dominated by broadleaf deciduous trees, (2) a broken canopy allowing scattered sunlight penetration into the interior of the swamp, (3) an open understory with an abundance of sedges (ideally, some patches of sedges are sunlit for several hours each day), and (4) the presence of sunlit nectar sources within the interior of the swamp and/or directly adjacent to the exterior of the swamp (these flowers must be available during the months when *E. dukesi* adults are expected to occur). In addition, large swamps, and swamps that are located near other similar swamps, are more likely to support populations of *E. dukesi* than swamps that are small and isolated.

HOSTPLANTS

Throughout Florida, *E. dukesi* populations are associated primarily with beaked-rush sedge, *Rhynchospora inundata* (Oakes) Fern (Cy-

peraceae), rather than *Carex* sedges as expected. In 1990, several waxy pupae and pupal exuviae of *E. dukesi* were found in loose silken shelters on *R. inundata* in Pasco County. Although *R. inundata* is apparently the primary host, pupae were also found on *Rhynchospora miliacea* (Lam.) A. Gray (Cyperaceae) and a species of *Carex*. Furthermore, females were observed ovipositing on *R. inundata* and *R. miliacea*. These *Rhynchospora* hostplants are widespread and common throughout Florida (Gale 1944, Wunderlin 1982, Clewell 1985, Dressler et al. 1987).

Although the *Carex* utilized by *E. dukesi* in Florida remains unidentified, it is probably *C. lupulina* Muhl. ex. Schkuhr. (Cyperaceae) which is widespread at the site. Larvae produced by *E. dukesi* females captured at the site were lab reared on *C. lupulina* (M. C. Minno pers. comm.). *Rhynchospora miliacea* and *C. lupulina* grow throughout the swamp, but in smaller clumps and less abundantly than *R. inundata*. This is the first time that *E. dukesi* has been known to utilize more than one hostplant at a single location. In central Florida, *E. dukesi* has been seen ovipositing single ova near the midrib on the upperside of sedge blades. This is contrary to the observations of Pliske (1957) who noted oviposition on the underside of blades in Michigan populations.

All seven reported hostplants of *E. dukesi* are found throughout much of the eastern United States and may be fed upon in many areas. *Carex lacustris* is the only host not known to occur in Florida (Godfrey & Wooten 1979). At least 39 species of *Rhynchospora* and 52 species of *Carex* are found in the southeastern United States (Godfrey & Wooten 1979) and it is likely that *E. dukesi* exploits a number of additional sedges. *Euphyes dukesi* does not appear to be restricted to broad-leaved sedges. Blade widths of known hosts range from as little as 2–5 mm (*C. walteriana*) to 1 cm (*Rhynchospora* spp.).

Rhynchospora inundata also serves as a hostplant of *S. appalachia* in many Florida swamps (Brown 1973). Both *E. dukesi* and *S. appalachia* are swamp-dwelling sedge feeders and have been recorded in many of the same forested wetlands throughout their ranges, including Florida. However, *S. appalachia* is more widespread and apparently enjoys a broader range of ecological requirements than *E. dukesi*. In Florida, *S. appalachia* is found in a number of swamps where *E. dukesi* is not known to occur.

It is also notable that *Arotis derasa* (Herrich-Schäffer) (Hesperiidae), a closely related Brazilian species formerly considered a member of *Euphyes*, also occurs in forested habitats and utilizes *Rhynchospora* as a hostplant (Mielke 1972). *Arotis* is probably a sister genus to *Euphyes* (Shuey 1987) and the similarity of habitats and hostplants may be due to "shared" ancestral ecological requirements (J. A. Shuey pers. comm.).

PHENOLOGY

Great Lakes populations of *E. dukesi* are univoltine, with adults flying primarily from late June through mid-August (Shull 1987, Holmes et al. 1991, Iftner et al. 1992). From Kentucky and Virginia southward, *E. dukesi* is bivoltine, flying primarily from mid-May through June and mid-August through early October (Covell et al. 1979, Nielsen 1982, Opler & Krizek 1984). Despite the comments by several authors (e.g., Opler & Krizek 1984, Scott 1986, Opler & Malikul 1992) that *E. dukesi* probably produces three broods in the extreme southern portion of its range, historical capture dates in Florida suggested only two broods. Extreme dates for each brood were 29 May (1979)–6 June (1979) and 14 September (1977)–8 October (1978). Only one record fell outside these dates; a single specimen (the first from Florida), collected in July 1971.

The population of *E. dukesi* in southern Pasco County was studied to determine the total number of broods and length of each flight period. Adults emerge nearly simultaneously and can become common within two or three days. In 1991, the first freshly emerged adults were observed on 11 May and the species was encountered at the site on a weekly basis until 8 June when only several worn females were found. None were observed on 30 April or 15 June, thus the first brood flight period lasted for approximately one month. The timing of the first brood can vary, apparently due to differences in precipitation. In 1993, when spring precipitation levels were below that of 1991, adults were not observed until 21 May and were still present after 16 June. Extreme dates for the first brood at this site are 9 May(1992)–16 June(1993). The second brood is comparable in length; extreme dates at this site (not including a single unusual record from 18 August 1990) are 13 September(1990)–13 October(1990). There is no evidence of a third brood in Florida (Fig. 5). The species is probably bivoltine in Texas as well, but the broods appear to be extended (M. A. Rickard pers. comm.). B. Mather (pers. comm.) suspected that capture dates in Mississippi “meant more than two broods—or if only two then rather long flight periods.” Most other members of the genus *Euphyes*, including *E. dion* (W. H. Edwards), *E. bayensis* Shuey, *E. berryi* (Bell), and *E. bimacula* (Grote & Robinson), are generally believed to be bivoltine in the Deep South (Opler & Malikul 1992). Like these congeners, *E. dukesi* probably does not produce three broods anywhere within its range. Records that allude to a third brood are probably referable to the anomalous emergence of first and second brood individuals, extended flight periods and/or differences in brood timing between populations. Although adults of *E. dukesi* may potentially be encountered in Florida over a six month

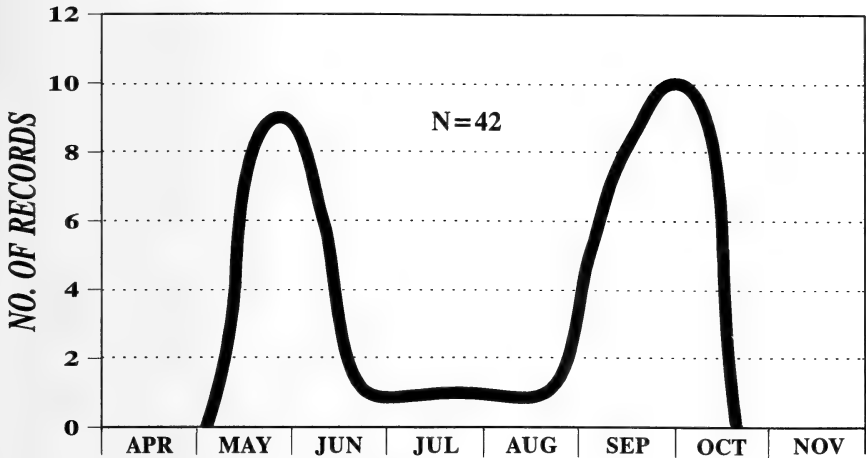


FIG. 5. Temporal distribution of *E. dukesi* in Florida (based on data from 1971–1993; record-any number of adults captured at a given locality on a given day).

period, they should be expected only during a month in spring and again during a month in autumn. The flight periods roughly coincide with the onset and termination of the wet-season.

ADULT BEHAVIOR

Most habitat descriptions for *E. dukesi* are inaccurate and misleading, often given simply as “shaded swamps.” Clark and Clark (1951) stated that the species is found in deep swamps, “seldom venturing out of the shade.” Opler and Krizek (1984) also remarked that *E. dukesi* is “found in the shade of wooded swamps.” However, adults are rarely encountered in densely shaded portions of swamps. Rather, they are most often observed around patches of hostplants that are at least partially sunlit. This is true in the Great Lakes region as well as in Florida (pers. observation, see habitat photo in Iftner et al. 1992; plate 4, row 3).

The dark ground color, contrasting wing surfaces and bobbing flight combine to give Floridian *E. dukesi* the appearance of giant *Ancyloxypha numitor* (Fab.) (Hesperiidae) or large, swamp-inhabiting *Poanes massasoit* (Scudder) (Hesperiidae). Adults usually fly just above the sedges, rarely exceeding 1.5 m in height. Males patrol through and around the sedges in search of females, but do not appear to be territorial. When males encounter one another, they quickly resume patrolling without altercation. If receptive females are not located within a patch of sedge, patrolling males will rapidly fly to another patch and continue their search. Females are less active than males and usually must be flushed from the sedges unless they are visiting nectar sources



FIG. 6. Female *E. dukesi* resting among shaded *R. inundata* blades.

or ovipositing. When ovipositing, females concentrate activity around sedge plants growing singly or in small clumps along the more shaded perimeter of sedge patches (Fig. 6). Both sexes have been seen flying through adjacent upland forests, and one female was observed visiting flowers along the edge of a large pasture over one hundred m from the nearest swamp. Females probably disperse widely in search of hostplants and may rapidly colonize nearby swamps when hostplants become available. Adults are most active within the humid interior of swamps when the weather is warm and sunny. However, as with many other swamp or forest inhabiting Lepidoptera, they also are active in warm overcast weather, even during brief thunder showers. Both sexes of *E. dukesi* have been observed dorsal basking (Fig. 7) on dew-laden sedge leaves as early as 0800 h (EDT) (when sunlight first begins to penetrate the wooded habitat). Under optimum weather conditions adults become active by 0830 h and may continue to fly or remain at sunlit nectar sources until roughly 1800 h.

ADULT ENERGY RESOURCES

There is typically a lack of flowers growing in swamp environments, thus few adult energy resources have been documented for *E. dukesi*



FIG. 7. Male *E. dukesi* dorsal basking on sunlit sedge blade.

(see Opler & Krizek 1984, Iftner et al. 1992). Frequently visited nectar sources are sunlit, including those of the interior of swamps. In central Florida, adults of the first brood have been observed visiting *C. occidentalis*, *P. cordata*, and *Cirsium* sp. (Asteraceae). Those of the second brood visit *P. cordata*, *P. punctatum*, and *Bidens alba* (L.) DC. (Asteraceae). All known nectar sources in Florida are white or purple. This color preference has also been noted in Ohio (Iftner et al. 1992). *Cirsium* sp. and *B. alba* occur outside the swamp environment and attract *E. dukesi* into more open habitats. Nectar source visitation in open situations also has been observed in Great Lakes populations (Price 1970, Shuey 1985, Iftner et al. 1992). Closely related Neotropical species of *Arotis* also leave their forested habitats to obtain nectar (Mielke 1972).

Individuals of *E. dukesi* visit flowers that occur from near ground level (*B. alba*) to at least 2.5 m in height (*C. occidentalis*). Adults are quite docile when feeding and often can be approached closely or even touched. When feeding, they do not engage in sexual behavior. Males and females have been observed simultaneously visiting the same blooms of *P. cordata* and *C. occidentalis* without interaction.

THREATS AND STATUS IN FLORIDA

It is unlikely that avocational collecting could negatively impact populations of *E. dukesi*. There is a general bias by most lepidopterists

against entering wet, mosquito-infested environments. As Niering (1985) aptly stated, these habitats are often viewed as "dark, mysterious, forbidding places, to be avoided at all costs." This undoubtedly has contributed to the enigmatic reputation of *E. dukesi*. This species is very localized and often inhabits only a small area within a given swamp, increasing the likelihood that a population will be overlooked. In addition, there is little or no commercial value associated with this species. By far, the most serious threats to *E. dukesi* in Florida are the alteration and destruction of forested wetlands.

Since the late eighteenth century, Florida has lost over half of its wetlands, mostly through conversion to agriculture and development. In only ten years, between the mid-1970's and mid-1980's, over 640,000 ha of wetlands were destroyed (Yokel 1992). For example, construction of Rodman Reservoir (Oklawaha Lake) in Putnam County resulted in the elimination of nearly 4000 ha of floodplain forest along the Oklawaha River (Lugo & Brown 1984). Although laws currently exist to conserve and manage wetlands in Florida, they have been inadequately implemented and enforced (Yokel 1992). At least one population of *E. dukesi* in Florida is thought to have been extirpated as a direct result of the destruction of swamp habitat. The fragmentation and isolation of remaining forested wetlands can greatly reduce the ability of female *E. dukesi* to locate other swamps and establish new populations.

The direct destruction of forested wetlands is not the only danger to populations of *E. dukesi* in Florida. The cutting of a large number of bald cypress or other trees from a swamp could lead to a pronounced increase in sunlight penetration and the possible elimination of a local *E. dukesi* population. The drainage of swamps can result in the loss of sedges necessary to support populations of *E. dukesi*. Rochow (1985) provided evidence that intensive deep underground water pumping also may adversely affect nearby forested wetland vegetation. Such pumping in the Cypress Creek Well Field in central Pasco County (near a large population of *E. dukesi*) appears to have lowered the water table and resulted in a drastic reduction in the amount of *R. inundata* and *R. miliacea* over a five year period (Rochow 1983). The channelization of streams can also lower the water table and similarly eliminate sedges from associated floodplain swamps. Road construction through floodplain swamps can effectively prevent natural drainage, thereby raising water levels and flooding out populations of sedges (Wharton et al. 1977). Populations of *E. dukesi* also could disappear due to extended natural drought or flooding conditions. The ecological characteristics of forested wetlands are largely determined by hydroperiod (length of time the soils are annually saturated) (Ewel 1990). Therefore, any changes in the fluctuation of water within a swamp could potentially alter the habitat beyond the threshold of acceptability to *E. dukesi*.

Despite these risks, some Florida populations of *E. dukesi* are relatively secure. Several populations occur in the Green Swamp of central Florida. This region encompasses 2234 km² and serves as the headwaters of five rivers. Approximately 80 percent of this total wetland area is forested (Brown 1984). The Green Swamp is one of Florida's most important groundwater recharge areas and is managed by the State of Florida as an Area of Critical Concern. Many forested wetlands in this region serve as important nesting areas for wading birds. Loss of wetland habitats in this region will probably be minimal.

Swamp habitats support a number of rare and poorly known organisms in Florida. The vulnerability of these ecosystems underscores the urgency in understanding these species. Because of the strict ecological requirements and limited number of known *E. dukesi* populations in Florida, the endemic peninsular phenotype is still considered rare, despite the discovery of additional populations (Minno & Calhoun in press). Many habitats that appear acceptable have not yielded *E. dukesi*, emphasizing our incomplete understanding of the ecological requirements of this species. Appropriate swamp habitats should be examined for the presence of *E. dukesi*. Known populations should be closely monitored and, if necessary, managed to ensure the continued survival of this interesting Florida wetland inhabitant.

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**JERAPOWELLIA BURNSORUM, A NEW GENUS
AND SPECIES OF MOTH FROM THE SOUTHWESTERN
UNITED STATES (TORTRICIDAE: OLETHREUTINAE)**

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ABSTRACT. *Jerapowellia*, new genus, is proposed for *J. burnsorum*, new species, which is described from 36 male and 3 female specimens captured in New Mexico and Arizona. Diagnostic character states of *Jerapowellia* are lack of male valvul costal hook, a state shared with *Rhyacionia*, and presence of spinelike setae on the uncus, a character state apparently unique in Eucosmini. Capture dates range from 26 March to 27 May. As in *Rhyacionia*, males are strongly attracted to carbon acetate baits with double bonding in the ninth position.

Additional key words: Eucosmini, *Rhyacionia*, pheromone trapping, Arizona, New Mexico.

Males of the taxon described here have appeared in large numbers in traps baited with synthetic attractants to detect *Rhyacionia* species (Stevens et al. 1985, C. R. Ward pers. comm.). It rarely has been collected by other means, perhaps because of early-season adult flight which precedes most collecting activity.

In the following description, **boldface roman type** signifies character states diagnostic of subfamily Olethreutinae, **boldface italic type** signifies those diagnostic of tribe Eucosmini, and *plain italic type* signifies those diagnostic for the genus. Terminology and classification follow Horak (1991) and Horak and Brown (1991). The letter n preceded by a number indicates number of specimens underlying an observation. Forewing length measurement excludes tegula but includes fringe. Wing venation was studied with permanent preparations (3 n) and temporary ones prepared by wetting wings with xylol (5 n).

***Jerapowellia* W. E. Miller, new genus**

Figs. 1-5

New genus near *Rhyacionia*, Stevens et al. (1985).

Male and female (39 n). Head. Antennal length 0.5 times forewing length, **one ring of scales per flagellar segment**, basal segment unmodified. Labial palpus ascending, scaling of second segment spreading, third segment porrect, length of second segment 2.5 times length of third segment. Proboscis length 0.5-0.75 times length of labial palpus. Scaling of front and crown dense, bushy. Thorax. Smooth-scaled, metathoracic legs unmodified. Forewing (Figs. 1, 2). Smooth-scaled, slightly broader toward termen, lacking costal fold, costa slightly and uniformly curved from base to apex, apex acute, termen convex, dorsum slightly

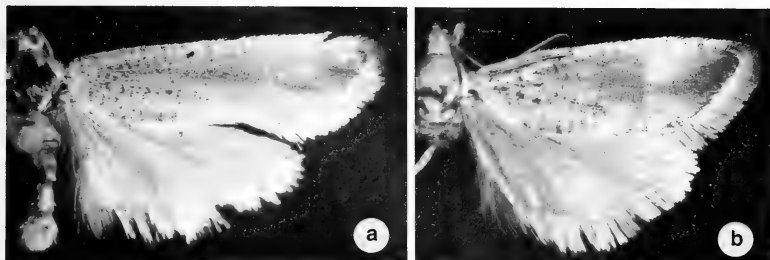


FIG. 1. Wings of *Jerapowellia burnsorum*. a, Male paratype from Albuquerque, New Mexico, forewing length 11.0 mm; b, Female paratype from near Kingman, Arizona, forewing length 8.5 mm.

curved. Twelve veins present, all separate except M_2 and M_3 which are connate; R_1 arising at middle of cell, R_2 arising nearer R_3 than to R_1 , CuA_2 arising at distal 0.67 of cell; internal veins of cell obscure or nearly obscure. Hindwing (Figs. 1, 2). Termen straight, **cubital vein with pecten on upper side**, R_s and M_1 connate, **M_3 and CuA_1 stalked**, anal margin unmodified, lacking melanic sex scaling. Abdomen. Lacking paired ventrolateral papilliform scale pockets and lateral or dorsal hair tufts. Male genitalia (Figs. 3a, b; 9 n). *Uncus* with between 15 and 20 large spinelike setae on each inner lateral surface, bilobed in outline, prominent, well sclerotized, with base forming paired lateral finely and sparsely setose lobes that project ventrally; socii absent if not consisting of the foregoing lobes; **valva with large unsclerotized area basally**, inner face well sclerotized, *lacking costal hook*, lacking clasper, cucullus barely delineated by slight neck constriction; **transtilla absent, gnathos reduced; aedeagus fused with anellus narrowly at base**, lacking cornuti; anellar ring around base of aedeagus narrow, laterally lobed. Female genitalia (Fig. 4; 3 n). **Sterigma not connected with anterior apophyses**, lamella antevaginalis rudimentary; lamella postvaginalis elongate, emarginate posteriorly, evenly sclerotized, neither setose nor microtrichiate, overlapping sternite, separated from sternite by sutures; ostium bursae small; **sclerotized ring present near ductus seminalis**, corpus bursae with two short, conical, unequal sized signa. Attractants. Males respond strongly to carbon acetate baits with double bonding in the ninth position, but at one Arizona locality they unexpectedly responded to one with double bonding in the eighth and tenth positions (Stevens et al. 1985, C. R. Ward pers. comm.).

Type species. *Jerapowellia burnsorum*, new species.

Etymology. *Jerapowellia* is of feminine gender and a patronym honoring the distinguished lepidopterist and tortricidologist Jerry A. Powell, one of the collectors of the new taxon.

Discussion. The hallmarks of *Jerapowellia* are the absence of a costal hook on the male valva, and presence of the prominent uncus with spinelike setae on inner lateral surfaces. The first of these character states is shared only with *Rhyacionia* among Nearctic Eucosmini, and the second with no known genus of Eucosmini in the Nearctic or Palearctic (Heinrich 1923, Kuznetsov 1987). *Jerapowellia* keys to *Rhyacionia* in Heinrich's (1923) key to Nearctic genera of Eucosmini, and to *Gravitarmata* in Kuznetsov's (1987) key to Palearctic genera of Eucosmini. *Jerapowellia* differs from *Rhyacionia* and *Gravitarmata* most importantly in having the spinelike setae on the uncus, and in lacking cornuti. Attraction to carbon acetates with double bonding in the ninth position as observed for *Jerapowellia* is the mode predominating in *Rhyacionia*; it occurs to some extent in other Eucosmini, and is least common in Olethreutini and Grapholitini (Roelofs & Brown 1982).

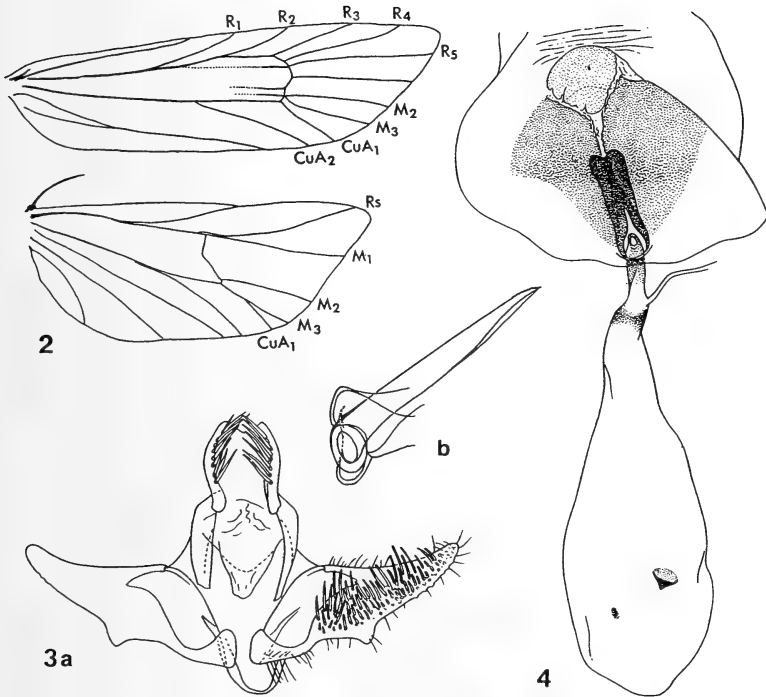
***Jerapowellia burnsororum* W. E. Miller, new species**

Figs. 1-5

Character states in the generic description apply as well as the following.

Male. Length of forewing 7.5-11.5 mm, averaging 9.3 mm (36 n). Head. Length of second segment of labial palpus 1.25 times eye diameter, length of antennal pecten subequal to flagellomere length; labial palpus, front, crown, and antenna clothed with a mixture of brownish white-tipped scales and pure white scales. Thorax. Scaling similar to that of head, but paler; pro- and mesothoracic legs clothed with brownish white-tipped scales and pure white scales, metathoracic legs with shining white scales. Forewing (Fig. 1). Length 3.1-4.1 times middle width. Fasciae and costal strigulae absent, scaling of upper side mostly shining reddish rust tinged with purple in center, costal and dorsal margins yellowish; costa, dorsum, and basal 0.5 speckled with brownish black; fringe at termen shining reddish rust, grayish elsewhere. Scaling of under side gray, paler toward edges. Hindwing (Fig. 1). Scaling of upper and under sides light gray, fringe paler. Abdomen. Dorsal scaling shining tan, ventral scaling white. Genitalia (Figs. 3a, b; 9 n). Length of aedeagus 0.4-0.5 times valval length, gradually tapering distally, distal 0.33 open ventrally, asperities present apically. Valval inner surface with spinelike setae of variable length, cucullus tapering distally to a rounded point, with a rudimentary pollex.

Female. Exterior as described for male, except forewing length 8.5-9.5 mm, averaging 9.2 mm (3 n). Genitalia (Fig. 4; 3 n). Anterior apophyses longer than posterior apophyses. Ostium bursae located at



FIGS. 2-4. Structures of *Jerapowellia burnsororum*. 2, Wing venation; 3, Male genitalia; a, Valvae and associated structures, drawn from genit. prep JAP 3841; b, Aedeagus, drawn from genit. prep. RLB 966; 4, Female genitalia, drawn from genit. prep. JAP 3688.

anterior end of sternite 7, ductus bursae short, a sclerotized bulging structure at posterior end of sternite 7.

Types. Holotype male: [Turkey Park, 8500 ft (2590 m), ponderosa pine zone] 12 km W Portal, Arizona, Apr. 77, Hopk. U.S. 36912-B, R. Stevens collector, genit. prep. JAP 4188, in Essig Museum of Entomology, University of California, Berkeley.

Paratypes. Females: Emory Pass, 8200 ft [2500 m], Black Range, Grant & Sierra Cos., New Mexico, V.27.59, J. M. & S. N. Burns collectors, genit. prep. JAP 3688; Hualapai Mts., 6500 ft [1980 m], 10 mi [16 km] SE Kingman, Mohave Co., Arizona, IV.11.59, J. M. & S. N. Burns collectors, genit. prep. JAP 3915; Hualapai Mt. Park, Mohave Co., Arizona, 6100 ft [1860 m], IV.11/12.86, [J. A.] Powell & [J. W.] Brown collectors, genit. prep. WEM 195933.

Males: Same data as preceding except genit. prep. WEM 195931; Sitgreaves Nat. For., Chevelon R[anger] D[istrict] [Arizona], IV.25.74, D. T. Jennings collector, genit. prep. JAP 3841; 4 specimens, same

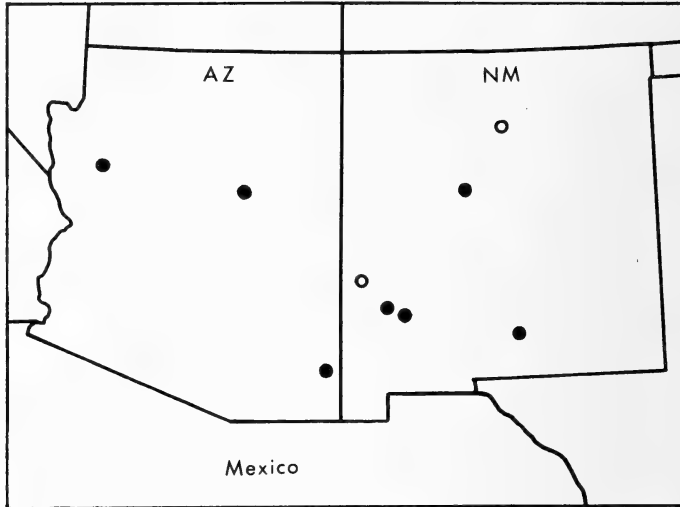


FIG. 5. Distribution of *Jerapowellia burnsororum* specimen records. Solid circles represent specimens examined in this study, open circles unexamined specimens reported by Stevens et al. (1985).

locality as holotype, Apr. and May 77, wing prep. WEM 2610931; 2 specimens, 25 km N Silver City, New Mexico, Hopk. U.S. 36911-B, R. Stevens collector, genit. prep. JAP 4185, wing prep. WEM 2510931; Hualapai, E9 [Arizona], genit. prep. RLB 966; Lincoln N [ational F[orest], 22 km N Ruidoso, New Mexico, Apr. 77, Hopk. U.S. 36910-B, R. Stevens collector; 25 specimens, all Albuquerque, Bernalillo Co., New Mexico, various local sites and dates in 1991 and 1992, mostly the latter, C. R. Ward or B. Stech collectors, genit. preps. WEM 912922, 195932, 912921, 812923, and wing prep. WEM 2410931.

Paratypes are deposited in the Essig Museum of Entomology, University of California, Berkeley, California; New Mexico State University, Las Cruces, New Mexico; University of New Mexico, Albuquerque, New Mexico; University of Arizona, Tucson, Arizona; National Museum of Natural History, Washington, D.C.; American Museum of Natural History, New York, New York; Canadian National Collection, Ottawa, Ontario; The Natural History Museum, London, England; Mississippi Entomological Museum, Mississippi State, Mississippi; and University of Minnesota, St. Paul, Minnesota.

Etymology. The name *burnsororum* is a patronym honoring the earliest known collectors of the species, John M. and Sarah N. Burns, the first renowned for literary as well as lepidopterological accomplishments.

Discussion. The species is sexually monomorphic. The illustrated

sexes (Fig. 1) depict the minor variation in color pattern among individuals, and the range of broad to narrow forewings, respectively, between small and large adults of either sex. The lamella postvaginalis varies in length by approximately 2.3 to 4.0 times its width (3 n). The type series includes specimens (9 n) from four *Pinus ponderosa* Laws. (Pinaceae) trap localities of Stevens et al. (1980, 1985).

Geographical range. *Jerapowellia burnisorum* is known from New Mexico and Arizona (Fig. 5). The dispersed collection localities in these States suggest the species also may occur in neighboring areas of Texas, California, Nevada, other contiguous States, and Mexico.

Biology. The flight period is early and long, capture dates extending from 26 March to 27 May (29 n). The period is perhaps protracted by wide topographic occurrence, elevations of capture ranging between approximately 300 and 2600 m.

The larval food plant is unknown, but moths have been trapped in pine stands (Stevens et al. 1985, C. R. Ward pers. comm.), and forewing color is typical of many Lepidoptera that feed on *Pinus*. Mapped collection localities (Fig. 5) compared with geographic ranges of pines (Critchfield & Little 1966) show that several species of *Pinus* occur at one or a few collection points, and that one pine, *P. ponderosa*, probably occurs at all of them.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *GIGANTOFALCA* FROM ARGENTINA (LYCAENIDAE)

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ABSTRACT. Striking structural characters diagnostic for the hairstreak genus *Gigantofalca* are illustrated through a comparison of *G. calilegua*, n. sp., (northern Argentine tropical forest), to a superficially similar, sympatric noncongener *Calystryma phryne*. *Gigantofalca* species, unique in morphological characters of both sexes, show little external sexual dimorphism and are most often mistaken for large females of *Calystryma*. *Gigantofalca* currently contains three described species whose combined distribution suggests members might occur throughout tropical forest regions of South America. Hairstreak butterflies show remarkable diversity and endemism in Andean tropical forest remnants south of the Tropic of Capricorn.

Additional key words: Temperate South America, austral South America, neotropics, endemism, refugia.

Of the twenty genera of Eumaeini treated by Johnson (1991) in the large "*Calycopis/Calystryma* grade," species of *Gigantofalca* (Johnson 1991:16) possess the most striking morphological structures, including unique sculpturing of the genital apparatus and terminal tergites into unusual (sometimes asymmetrical) configurations. However, aside from their relatively large size (forewing alar expanse up to 15 mm) and brown dorsal wing color in both sexes (some *Calycopis/Calystryma* grade show blue), little distinguishes *Gigantofalca* species externally from other sympatric and synchronic members of the grade, particularly brown *Calystryma*.

Specimens of *Gigantofalca* appear to have been overlooked because of initial misdetermination of gender, a problem also reported by Bálint (1993) in Neotropical polyommata lycaenids. The discovery of the two previously described species, *G. stacya* Johnson (Amazon basin, Brazil) and *G. duida* Johnson (Duida Plateau, Venezuela) (Johnson 1991), resulted simply from random dissections of brown *Calystryma*-like individuals during museum based research.

The recent capture of a new *Gigantofalca* species in Parque Nacional Calilegua of northern Argentina is important for several reasons: 1) generic characters of *Gigantofalca* are re-emphasized by the discovery of a southern Neotropical congener; 2) typical of *Gigantofalca* elsewhere, the new Argentine species is sympatric with a common non-congeneric "look-alike" (in this case *Calystryma phryne* Johnson, Eisele & MacPherson) and distinction of these taxa may facilitate recognition of *Gigantofalca* elsewhere; 3) diversity and endemism in tropical Lepidoptera near the temperate latitudes of the Neotropical Realm have

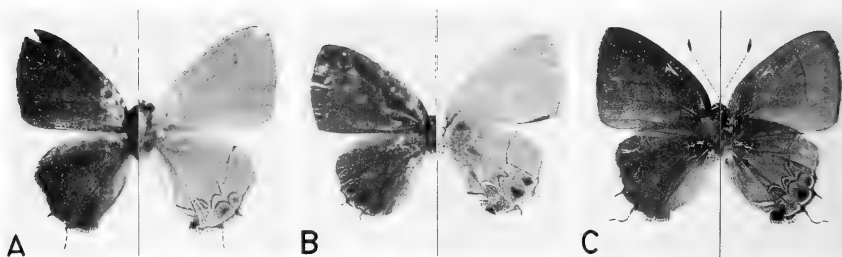


FIG. 1. Side by side comparison of upper (left) and under (right) surfaces of *Gigantofalca calilegua* holotype male (A), and *Calystryma phryne* holotype male (B) and recently collected female (C), same data as *C. calilegua* holotype.

not been widely recognized by biologists as Neotropical “refugia” or “centers of endemism.”

Taxonomic Descriptions

Terminology follows Johnson (1991): DFW/DFW = dorsal fore- and hindwings; VFW/VHW = ventral fore- and hindwings; band(s) (the VFW, VHW tripartite band(s) basally colored, distally black and white) are referred to by basal color only. Geographic terms enclosed in quotation marks follow Encyclopedia Britannica (1972).

Subfamily Theclinae

Tribe Eumaeini (sensu Eliot 1973)

Infratribe Calycopina (sensu Johnson & Kroenlein 1993b)

Genus *GIGANTOFALCA* Johnson 1991:16, figs. 8, 33–35

Diagnosis. Externally similar to myriad Neotropical taxa that are brown above and brown beneath and have a pronounced W-shaped element in anal area of the VHW disjunct from the rest of band at cell M3 (Fig 1). *Generic Characters* (Fig. 2): Terminal abdominal segments of males and females elaborately sculptured in tergum and sternum. Male genitalia with falces elaborately sculptured and as large or larger than valvae; valvae with highly sculptured terminoventral components, including elements additional to the paired valval lobes typical of the tribe. Female genital plate greatly sculptured and terminolaterally spinescent (elongate pronglike elements asymmetrical in all known species).

Sympatric Noncongeners (based on *Calystryma*, Fig 4.): Terminal abdominal modification limited to an angulate plate along the tergite dorsum (AB, a); male genitalia with simple arched falces (shorter than valvae) (CD, g); valvae, labibes, and saccus of generally even contour and tapered shape (h). Female genitalia with elements of genital plate

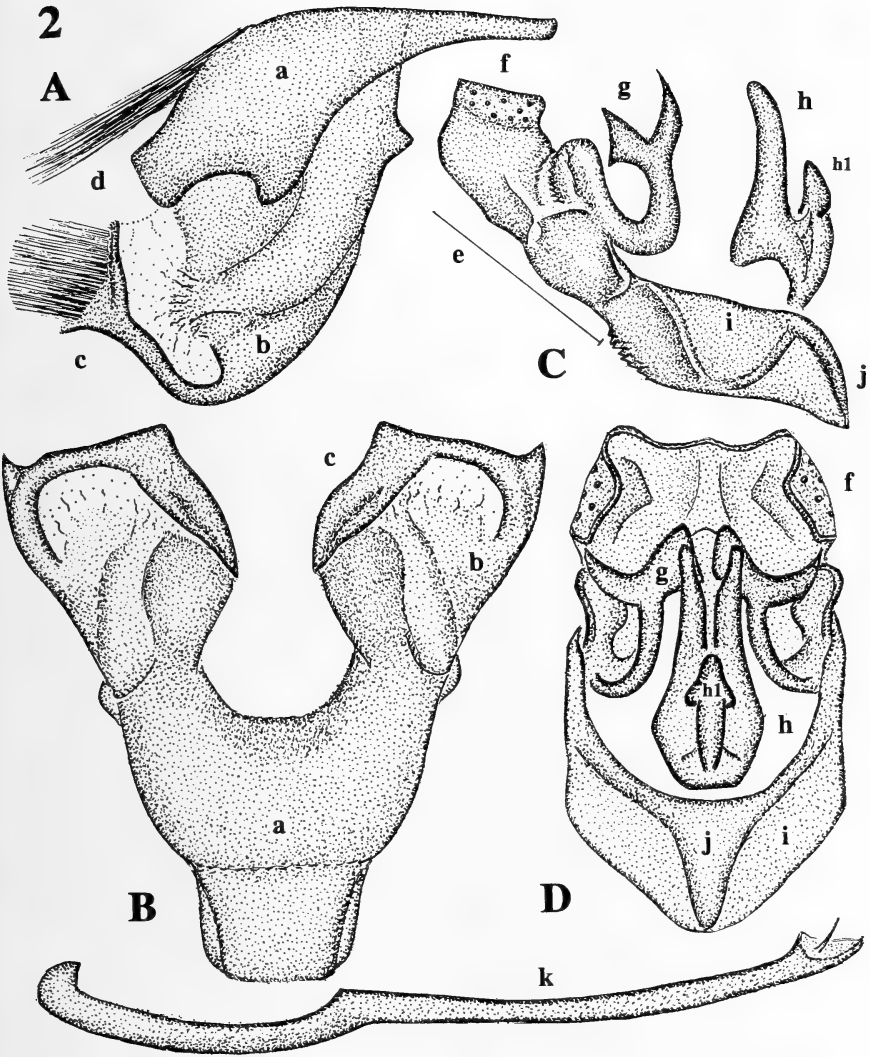


FIG. 2. Morphology of *Gigantofalca* exemplified by *G. calilegua* (lettered for cross reference to *Calystryma phryne*, Fig. 4). A, Tergal/sternal structures, lateral view; B, Tergal/sternal structures, dorsal view; C, Genitalia, lateral view; D, Genitalia, ventral view. Small case a-k, cross reference notations, **bold** indicating elements of generic character for *Gigantofalca*. a, Modified terminal tergite (d, spicules [shown only in A]); b, Modified terminal sternite (e, apodemial lobe and spicules [latter shown only in A]); e, Length and attachment (cross-line) of brush organs; f, Labibes; g, Falces; h, Valvae (h1, knob-ended spike, an "additional component" in this species, *sensu* Eliot 1973); i, Vinculum; j, Saccus; k, Aedeagus, lateral view.

symmetrical, less spinescent than in *Gigantofalca* (*Calystryma* with four short terminolateral teeth).

***Gigantofalca calilegua* K. Johnson, new species**

Figs. 1A, 2

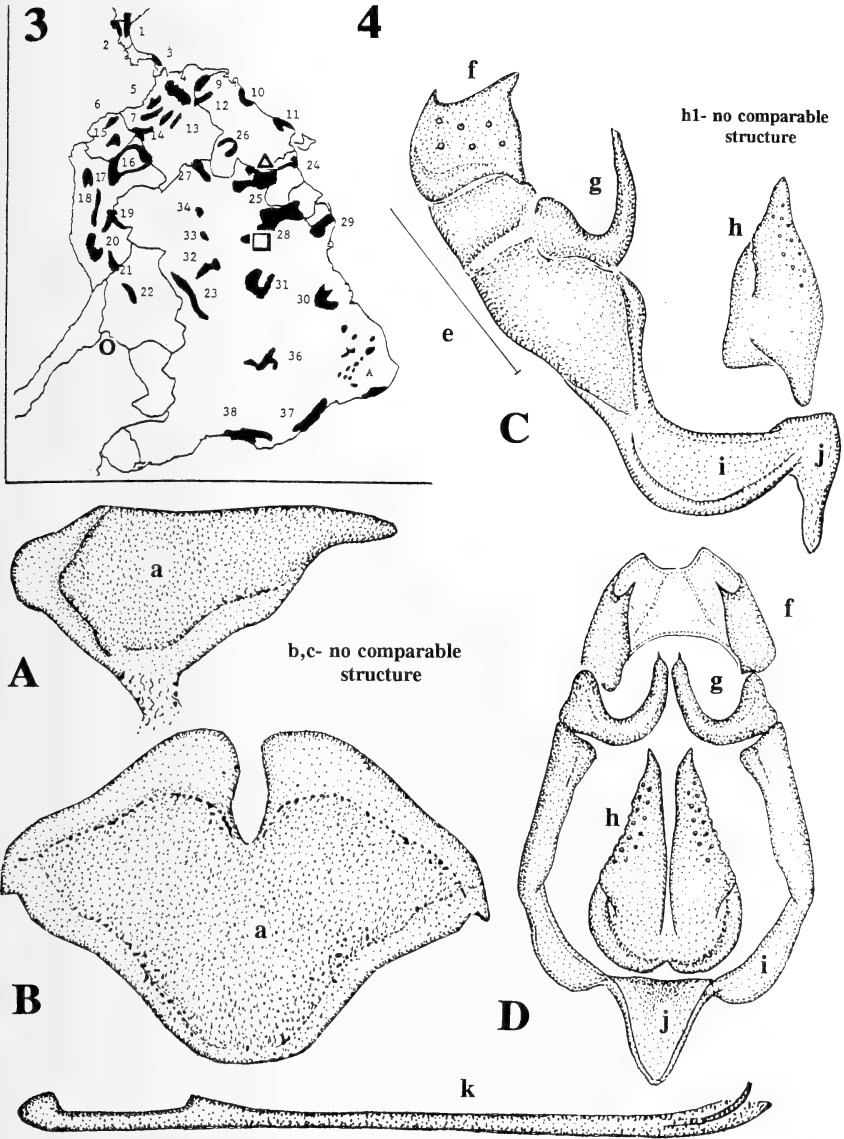
Diagnosis. Differs from common co-occurring *Calystryma phryne* (Figs. 1B, 1C, 3) by generic characters, blackish DFW/DHW coloration, and slightly less lavish VHW limbal coloration. Differs from *Gigantofalca stacya* and *G. duida* by aforementioned DFW/DHW coloration (congeners warm brown) and the following unique structural characters (Fig. 2): sternite eight with elongate posterior apodeme terminating in an upturned spatulate lobe covered with spicules (c); male genitalia with falces terminally bifurcate (g) and valvae with ventrocentral, terminally protruding, knob-ended spike (h1).

Description. *Male:* Forewing length 14.0 mm ($n = 1$). DFW and DHW blackish brown, androconial patch absent; HW margin with short tail at vein CuA1, longer tail at CuA2. VFW and VHW gray-beige; FW with deep red postmedial band, extending from costa to cell CuA2; HW with deep red medial band extending from costa, interrupted at cell M3 into pronounced W-shaped element extending to anal margin; limbal area with dull red-orange orbs (cells M3 and CuA1) and suffusive blue-gray (cell CuA2); anal tuft black at base.

Male Morphology and Genitalia (Fig. 2): Terminal abdominal segments with elaborate sclerotinal sculpturing ["subchordate incised posterior cavity" of Field 1967a, b = "sipc" of Johnson 1991]; tergite eight extending anterior beneath sixth abdominal segment, terminating posterior with lateral lobes and elongate spicules at a central notch (AB, ad); sternite eight with elongate posterior apodeme terminating with a spiculate spatula-shaped lobe (AB, c). Genitalia (CD) with vinculum ventrally robust and angulate (f-j), saccus broadly attached to vinculum along the entire anterior margin (i, j); valvae with paired lobed tapered caudally in dorsal element, ventrum with ventrocentral, terminally protruding, knob-ended spike (h1); falces with widely bifurcate terminal lobes (g); aedeagus robust with straight shaft, length exceeding rest of genitalia by about one-fifth, caecum comprising about one-third aedeagal length (k).

Type. Holotype male, ARGENTINA, Jujuy Province, Parque Nacional Calilegua, upland on vehicle track at 5-6 km W of Rt. 34 Park entrance, in hot humid forest break, 1200 hrs, 14 February 1991, swarming with many other butterflies in bright sun after morning rain (see Remarks), K. Johnson and D. Kroenlein, deposited in AMNH.

Remarks. *Affinities of the New Species:* The genitalia and terminal tergite structure of *C. calilegua* easily distinguish it from *Calystryma*



FIGS. 3-4. Distribution map and genital morphology. **3**, Centers of endemicism (cd) generalized by Johnson (1981) showing known occurrences of *Gigantofalca* species; open triangle = *G. duida* (Roraima ce), open square = *G. stacya* (Manaus ce), open circle = *G. calilegua* (ce not recognized); nearest centers are Bolivian "Yungas" (#22) and SE Brazilian centers (#37 and 38). **4**, Morphology of *Calystryma phryne* sympatric and synchronic with *G. calilegua* (lettered for cross reference to latter) Major differences: **b**, **c**, (denoting no structures comparable to sternal elements of *G. calilegua*); **f**, Labibes prolonged; **g**, Falces small, nonbifurcate; **h**, Valvae simple, tapered (**h1** denoting no structure comparable to knob-ended spike of *G. calilegua*); **i**, **j**, Vinculum/saccus bifurcate; **k**, Aedeagus straight.

species. However, compared to locally sympatric *C. phryne*, *G. calilegua* differs externally only by the darker DFW and DHW color and less lavish limbal markings (Fig. 1). Described in 1988, *C. phryne* initially was poorly known but since has been collected in numbers in "eastern slope" upland mesic forest (Jujuy and Salta Provinces); it has an undescribed sister taxon in the xeric "western slope" Monte biome, in Cafayate, Salta Province (Hayward 1965, Johnson et al. 1988).

Genital morphology of *G. calilegua* (Fig. 2) also immediately identifies it as a *Gigantofalca* species, unique in many characters, but most like the northern Duida Plateau *G. duida* (Roraima center of endemism, Brazil). The new species and *G. duida* share a wide anterior sternite, but that of *G. calilegua* is far less elaborate in *G. duida* and lacks a spatulate terminus (Johnson 1991: fig. 8). Type series of the three described species comprise all that is known of *Gigantofalca*.

Biogeography of the Type Locality: Calilegua Park (Fig. 3) (spelling conformed to Rand McNally & Company 1992) was set aside only recently as a national park, postdating most Argentine literature on the nation's park system (APN 1987). The area rises abruptly approximately 2500 m above lowland "Chaco" outlying (at 50 km) the main body of the eastern Andean slope in Jujuy Province. Currently, the park is crossed by a single dirt track (off Argentine Rt. 34 near Libertador General San Martín), and its tropical forests are largely undisturbed. Recent collections of Lepidoptera in Calilegua Park (1991–1992 AMNH expeditions) include many tropical butterflies previously unrecorded from Argentina and numerous others requiring taxonomic description (Johnson 1992a, 1992b, 1993; Johnson, Eisele & MacPherson 1992, 1994; Johnson & Kroenlein 1993a, 1993b; Johnson & Sourakov 1993). Diversity and apparent local endemism of tropical Lepidoptera in Calilegua Park deserves mention because of the park's Andean location south of the Tropic of Capricorn. From this latitude southward, tropical and subtropical forest occurs only in remnants—scattered from Jujuy Province to the "frost-free island" of Tucuman and northern Catamarca provinces (APN 1987)—far to the south and west of areas of South America usually noted for endemism in tropical forest butterflies (Fig. 3). These centers of endemism, or the admixture of taxa listed for Argentina by Hayward (1973), do not suggest occurrence of tropical genera like *Gigantofalca* in northwestern Argentina. The recent descriptions of numerous tropical forest Theclinae from Calilegua Park (and other northwestern Argentine tropical forests) suggest that earlier characterizations of low tropical diversity in this region were influenced by sampling error (Ackery 1984 [following Hayward 1973]) or restriction of study to particular taxonomic groups (Brown 1976, among other "refugia" literature).

Etymology. A proper noun, used in apposition to denote the type locality.

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A NEW PANAMANIAN CLEARWING MOTH (SESIIDAE: SESIINAE)

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ABSTRACT. A new species of Sesiidae from Panama, *Carmenta foraseminis* Eichlin, is described and illustrated. Host plant information and collecting localities are provided. A complex of related species, *C. guyanensis* (Le Cerf), *C. theobromae* (Busck), and *C. surinamensis* (Möschler), is discussed. The name *corporalis* (Meyrick) is synonymized under *surinamensis*.

Additional key words: types, genitalia, Lecythidaceae, Fabaceae, Sterculiaceae.

I am describing the following species to make the name available for a subsequent paper in this same issue (see Harms & Aiello 1995: 43). These researchers forwarded to me for identification a series of specimens they reared from seeds of *Gustavia superba* (H.B.K.) Berg (Lecythidaceae) from Barro Colorado Island, Panama. The thrust of their report is to document the apparent unusual behavior of seed boring by larvae of clearwing moths (Sesiidae).

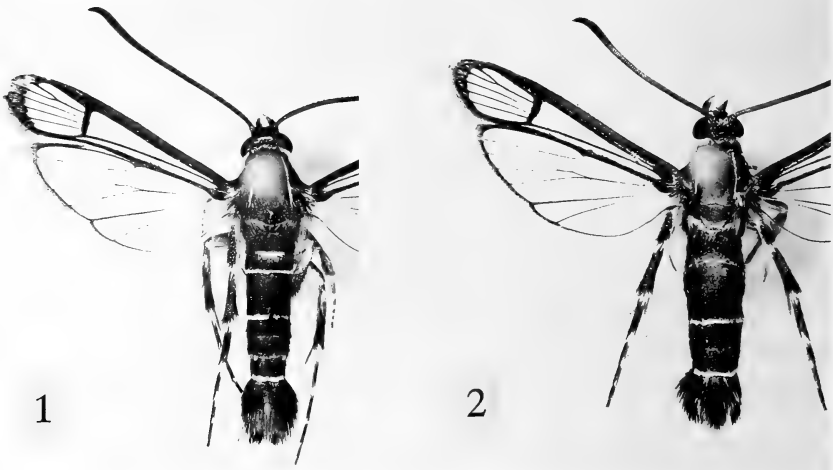
From material accumulated for ongoing revisionary studies of the clearwing moths of the Western Hemisphere (Eichlin 1986, 1989, Eichlin & Duckworth 1988), I discovered several more specimens of the unknown borer from this same and other localities and some on different hosts. Also, upon further examination, I learned that the undescribed species is but one of a complex of similar appearing species, separable mainly on the basis of male genitalic features.

Carmenta foraseminis Eichlin, new species

(Figs. 1-4)

Male (Fig. 1). Head with vertex brown-black; front brown-black medially, white laterally; occipital fringe dorsally brown-black, laterally white; antenna brown-black, usually with pale yellow on apical third; labial palpus smooth and somewhat flattened ventrally, mostly brown-black laterally, often with some white or pale yellow at base of second segment, white ventrally, perhaps with a hint of pale yellow. Thorax brown-black, yellow patch beneath wing, narrow yellow, subdorsal, longitudinal stripe, yellow on dorsoanterior half of metathorax. Abdomen brown-black, dorsally with narrow yellow bands on segments 2, 4, 6, and 7, or on all segments for some specimens (Venezuela); ventrally strongly banded pale yellow or white on 4-7, variously on other segments. Legs brown-black, white on forecoxa, white on tibial tufts and at joints of tarsi. Forewing with narrow margins and discal spot brown-black; ventrally with some pale yellow powdering. Hindwing hyaline, no discal spot. Wing length of both sexes 8-9 mm. Genitalia as in Fig. 3, with gnathose/tegumen area somewhat complex; crista sacculi structure complex; saccus elongate, nearly half as long as ventral margin of valvae; socii elongate.

Female (Fig. 2). Same as male, except less white ventrally on palpus and forecoxa;



FIGS. 1-2. Adults of *Carmenta foraseminis*. 1, Holotype male (wing length 8 mm); 2, Allotype female (wing length 8.5 mm).

abdomen dorsally with narrow yellow bands on segments 2, 4, and 6, ventrally with wide pale yellow to white bands on 4-6. Genitalia as in Fig. 4.

Types. *Holotype* ♂ (NMNH): PANAMA: Is. Barro Colorado, emerged 14-19 Jul. 1993, from *Gustavia* seeds, Kyle Harms.

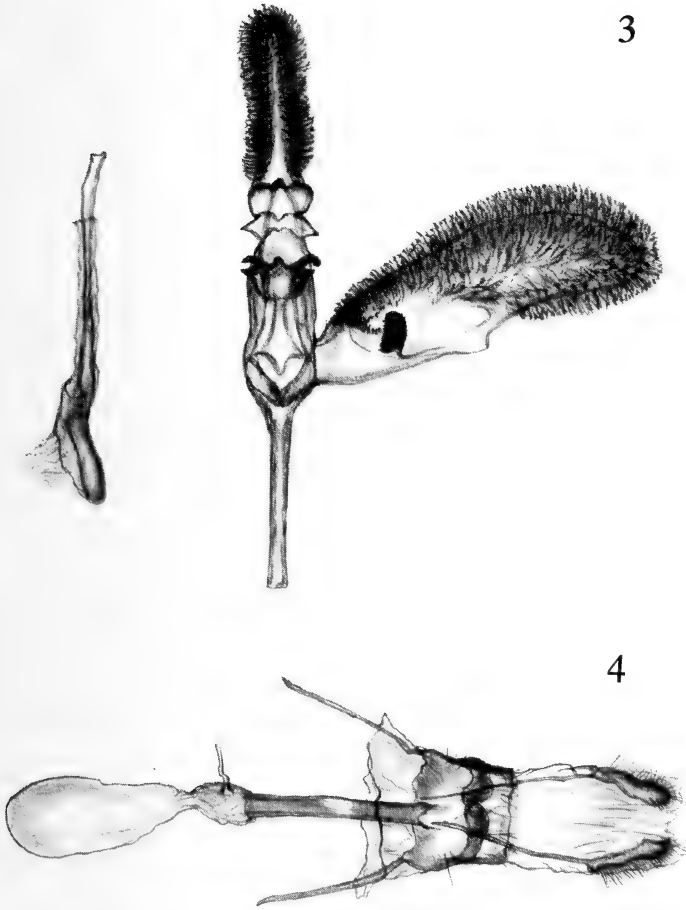
Allotype ♀ (NMNH): same data as holotype, except emerged 8 Aug. 1993.

Paratypes (59): 4 ♂♂, 1 ♀ (NMNH): Same data as holotype. 1 ♀ (NMNH): PANAMA: Is. Barro Colorado, emerged 11 Jul. 1993 from *Gustavia* seeds, col 26 Jun., Kyle Harms. 1 ♀ (NMNH): PANAMA: Arraijan, flew inside car, 12 Aug. 1984, A. Aiello. 1 ♂, 1 ♀ (CDFA): same data as holotype, except CDFG genitalia slides #856 and #857 (respectively) by S. A. Kinnee. 3 ♀♀ (AMNH): T. Hallinan, Balboa, C. Z., Panama, 26 Jun. 1914; A.C. 5690. 1 ♂ (AMNH): T. Hallinan, Culebra, C. Z., Panama, 4 Mar. 1914; A.C. 5690; genitalia slide #854 by S. A. Kinnee. 1 ♀ (AMNH): Balboa, C. Z., 11 Nov. 1914; A.C. 5690. 1 ♂, 1 ♀ (CDFA): Boca d Pauarando, Sambu Vy., S. Darien, Pan., H. Pittier; ex. seeds of *Eschweilera* sp., H. Pittier, ♂—genitalia slide #855 by S. A. Kinnee. 10 ♂♂, 6 ♀♀ (NMNH, CAS): Z-2143, seeds of membrillo, *Gustavia angustifolia*; Chinilla River, C. Z., 8 Jun. 1923, J. Zetek. 5 ♂♂, 14 ♀♀ (NMNH, LACM, CDFA): Z-3176, Barro Colorado, Canal Zone, on *Gustavia superba*, Zetek, collector. 7 ♂♂, 1 ♀ (NMNH, CDFA): AV cacao pod, A. P. Trocones, 5 May 1938 (6 ♂♂—emerged June 4, 9(2), 15, 21, 22, 24), Municipio Ureña, Estado de Tachira, Venez., C. H. Ballou; and San Felipe, Venez., C. H. Ballou (1 ♂, 1 ♀—emerged 24 May 1938).

Host plants. *Gustavia angustifolia* Benth., *G. superba*, *Eschweilera* sp. (all Lecythidaceae), and *Theobroma cacao* L. (Sterculiaceae) (see this issue—Harms & Aiello 1995:43).

Distribution. Panama, Colombia, Venezuela, and probably Brazil (see Discussion below).

Etymology. The specific name *foraseminis* is derived from the Latin *foro* (to bore) and *seminis* (seed). The name refers to the seed boring behavior of the larvae.



FIGS. 3-4. Genitalia of *Carmenta foraseminis*. 3, Male (aedeagus detached); 4, Female.

Discussion. Five female specimens—labeled Bahia, Brazil, May 1931, reared from seeds of *Gustavia augusta*—may be *C. foraseminis*. However, males are necessary to precisely identify related species. The female genitalia are like those of a similar species, *C. guyanensis* (Le Cerf), of which I have identified male specimens labeled Huytanahan, Rio Purus, Brazil, December 1921. Additional localities for *C. guyanensis* are in French Guiana, Bolivia, and Peru, but no host plants are recorded.

Also included in this complex of similar species is *C. surinamensis* (Möschler, 1878), a borer in seeds of certain legumes (Harms & Aiello 1995). This research revealed that *C. corporalis* (Meyrick, 1930), de-

scribed from Taperinha, Brazil, is a synonym of *C. surinamensis* (Möschler) [**new synonymy**]. The species *C. surinamensis* is now known from Brazil, Surinam, Guyana, Trinidad, Panama, and Costa Rica.

Another species of this complex, *C. theobromae* (Busck), from Colombia and Venezuela, was obtained from young plants and pods of cacao. During continuing studies of neotropical Sesiidae, I expect to discover additional species belonging in this group.

ACKNOWLEDGMENTS

I thank Kyle Harms (Princeton University) and Annette Aiello (Smithsonian Tropical Research Institute, Panama) for bringing the unknown species to my attention and for supplying specimens and data. The following persons and institutions provided specimens used in this report: F. H. Rindge, American Museum of Natural History (AMNH); P. H. Arnaud, Jr., California Academy of Science (CAS); J. P. Donahue, Los Angeles County Museum of Natural History (LACM); D. R. Davis, National Museum of Natural History, Washington, D.C. (NMNH); collection of V. O. Becker, Brazil. Special thanks to Scott Kinnee, California Department of Food and Agriculture (CDFA), Sacramento, for various technical assistance.

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SEED-BORING BY TROPICAL CLEARWING MOTHS (SESIIDAE): ABERRANT BEHAVIOR OR WIDESPREAD HABIT?

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ABSTRACT. The seed-boring behavior of clearwing moths is discussed, in particular that of *Carmentia foraseminis* Eichlin reared from seeds of *Gustavia superba* (Lecythidaceae) in Panama. Larval food plant and distribution data for a complex of similar species are provided.

Additional key words: *Carmentia foraseminis*, *Gustavia superba*, Barro Colorado Island, life history, seed-predation.

It is well known that larvae of the clearwing moth family Sesiidae are borers in tree trunks, branches, and roots (Scoble 1992). They also attack shrubs, vines, and herbaceous plants, and occasionally feed in galls (Scoble 1992). A number of important pest species decrease plant vigor and inflict serious vegetative damage on commercially grown crops (King & Saunders 1984, Holloway, Bradley & Carter 1987, Scoble 1992).

The vast majority of sesiid larval food plants reported in the literature are for temperate species, and Eichlin and Duckworth (1988) present a list of these for North American clearwing borers. Scant information exists concerning the natural history of tropical sesiids; it has been assumed that their habits are similar to those of temperate species. What follows is a discussion of the seed-feeding behavior of a clearwing moth from Panama.

Larvae of a sesiid were found feeding within the fruits and seeds of *Gustavia superba* (H.B.K.) Berg (Lecythidaceae) that were collected on the ground during June and July 1993, on Barro Colorado Island, Panama. Reared adults were sent for identification to Thomas Eichlin, Insect Biosystematics Laboratory, California Department of Food and Agriculture, Sacramento. He determined that the species is new to science. He, therefore, provides the original description of the species (*Carmentia foraseminis* Eichlin) in this issue of the Journal (Eichlin 1995: 39).

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On Barro Colorado Island, the fruits of *G. superba* mature during the wet season, primarily June, July, and August (Croat 1978, S. Joseph Wright unpublished data). Fruits are multi-seeded and are either cauliflorous or ramiflorous. Although they may be intact when they fall, many are damaged by primates while still on the tree (Oppenheimer 1968, Hladik & Hladik 1969). When collected from the ground, many fruits show damage made by terrestrial mammals (Sork 1987). Most fruits on the ground contain at least some seeds that have been damaged by *C. foraseminis* larvae.

On 26 June 1993, the damaged seeds from two *G. superba* fruits were placed in a plastic container; adult sesiids were reared from them. The first moth emerged from one of the seeds on 11 July. The pupal exuviae was left protruding from the larval tunnel.

An intact fruit of *G. superba* was collected from the forest floor and brought back to the laboratory on 15 July. By 20 August, nine adult *C. foraseminis* (Fig. 1) had eclosed from this fruit, all leaving their pupal exuviae projecting from their tunnels (Fig. 2). Five more adults emerged from the same fruit between 21 August and 8 September.

Additionally, 128 seeds (all showing at least minor tunneling damage) were removed from intact fruit and from fruit partially eaten by vertebrate frugivores and seed-predators. All were placed in an arthropod cage. Thirteen adult *C. foraseminis* emerged from these seeds over the course of 20 days.

Carmenita foraseminis larvae can subsist on either isolated seeds or seeds within fruits of *G. superba*. Because nearly all pupal exuviae were found projecting from seeds or fruits, it seems unlikely that the larvae ever pupate elsewhere, in contrast to some members of the family that pupate in the soil (Scoble 1992).

Given that many, perhaps most, fruits and seeds are eaten by ground-foraging mammals (e.g., agoutis, squirrels, and peccaries) soon after falling (Sork 1987), it is curious that adult moths emerged as many as six weeks after falling to the ground. One would expect that individuals remaining in fallen fruit soon would be eaten or buried by mammals. Perhaps the majority of adults emerge before fruit fall; however, if the majority of infested fruits drop before sesiid emergence, seed-eating mammals may have a large impact on the population dynamics of these insects.

In the species description, Eichlin (1995) reports on *C. foraseminis* reared from seeds of *G. angustifolia* Benth., *G. superba*, and a species of *Eschweilera* (Lecythidaceae), all from Panama, as well as from pods of cacao (*Theobroma cacao* L., Sterculiaceae), from Colombia and Venezuela. He also states that he has seen four females of an unidentified species, reared from seeds of *G. angusta* L. in Bahia, Brazil. These



FIG. 1. *Carmenta foraseminis* adults. Male paratype (top), emerged mid July 1993; female allotype (bottom), emerged 8 August 1993.

could be either *C. foraseminis* or *C. guyanensis* (Le Cerf), but males are necessary for positive identification.

According to Eichlin (1995), *C. foraseminis* belongs to a complex of similar appearing species (including *C. guyanensis*, *C. surinamensis* (Möschler), and *C. theobromae* (Busck)), differentiated mostly on the basis of male genitalic structures.

Though not published, seed-infestation by sesiid larvae has been observed by others. Nicholas D. Smythe (pers. comm.) reared a strikingly similar sesiid from the extremely hard seeds of *Prioria copaifera* Griseb. (Fabaceae). His two specimens are deposited in the collection of the Smithsonian Tropical Research Institute (STRI), Panama. Eichlin, who is conducting a systematic revision of Western Hemisphere Sesiidae, reports (pers. comm.) on two additional Panamanian specimens of this same sesiid (in the National Museum of Natural History) that were reared in 1929 also from the seeds of *P. copaifera*. He identified the species as *Carmenta surinamensis*. In addition to feeding on seeds of *P. copaifera* in Panama, *C. surinamensis* is known to feed also on seeds of *Pentaclethra* sp. and *Mora* sp. (both Fabaceae) (Eichlin, pers. comm.) in Costa Rica and Trinidad, West Indies. Originally described from Surinam, this moth now is known from Brazil (Eichlin 1995), Guyana, and Panama. Hartshorn (1983) reports that in Costa Rica he has found what appear to be sesiid larvae feeding on the cotyledons of *Pentaclethra macroloba*, but that they do not seem to hinder germination.

August Busck (1910) described *C. theobromae* of this complex from Colombia and Venezuela: "Bred by Mr. P. L. Guppy from dry pods of Cacao." Another similar species, known from French Guiana, Brazil, Bolivia, and Peru, is *Carmenta guyanensis*, whose larval food plant is unknown. More species belonging to this complex are likely to be discovered, according to Eichlin. Perhaps most, or all, of these will prove to be seed or pod-boring as well.

Eichlin and Duckworth (1988) list more than 165 larval food plant records for 82 North American sesiids, representing 16 sesiid genera. The larval food plants represent 82 genera in 34 plant families. Fifty-two sesiid species (63%) are reported from single larval food plant species. Of the remaining 30 species, only eight are on more than one plant family, and 22 are on one to five plant genera (in each case on a single family). *Synanthedon scitula* (Harris) is exceptional, having been reported on 17 plant genera in nine families. These observations suggest that while North American sesiids have radiated onto a wide array of larval food plants, most species are not particularly polyphagous.

Although records for the few sesiids reared so far from tropical fruits involve only eight plant species in three families, *C. foraseminis* has been reared from fruits of two of those plant families. These limited data raise several questions. Is fruit and seed feeding a widespread habit among tropical sesiids or is it limited to a few species or genera? Do tropical sesiids feed on plant groups different from those of their temperate relatives? Are they more generalized in their choices of larval food plant species than are temperate species? To put it another way,



FIG. 2. *Gustavia superba* fruit from which *Carmenta foraseminis* have emerged, leaving their pupal exuviae projecting from their tunnels. The bent over individual just below the pedicel is in the process of eclosion.

is our knowledge of tropical sesiids meager because we've been looking in the wrong places, or is it for lack of trying? We urge others to join the search for answers to these questions. Those wishing to augment our knowledge of tropical sesiid life histories would do well to rear insects from a wide variety of fruits, particularly large ones. Tropical leguminous plants, with their great proliferation and diversity of species, might be a productive group on which to search for seed-boring sesiids. Perhaps plant species related to those utilized by temperate region sesiids should be targeted also.

A total of 10 reared *C. foraseminis* adults have been distributed among the collections of STRI, the Museo de Invertebrados 'G.B. Fairchild' of the University of Panama (MIUP), the NMNH, and Thomas D. Eichlin (CDFA).

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THE BIOLOGY AND DISTRIBUTION OF
HEMILEUCA ELECTRA (SATURNIIDAE) POPULATIONS IN
THE UNITED STATES AND MEXICO, WITH
DESCRIPTIONS OF TWO NEW SUBSPECIES

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ABSTRACT. Analysis of adult phenotypes indicates that distinctive populations of *Hemileuca electra* usually are restricted to well defined desert plant communities. This has resulted in *Hemileuca electra clio* being separated taxonomically from the Mojave Desert population and the formal recognition of unique populations from the Sonora Desert of Baja California, Mexico. We describe two populations as new subspecies, *Hemileuca electra mojavensis* and *H. electra rubra*, and discuss other populations in southern California and Mexico. The known range of *H. electra* has been extended to include southwest Utah, southern Nevada, portions of Arizona, California, and south into Baja California and Baja California Sur, Mexico. Flat-top buckwheat (*Eriogonum fasciculatum*) is the only larval hostplant in the United States, but in Mexico other hosts are used.

Additional key words: *rubra*, *mojavensis*, Lower Colorado Desert, Vizcaino Desert, Mojave Desert.

Hemileuca electra Wright is a day-flying saturniid moth that occurs over a vast area, from southwestern Utah to Baja California Sur, Mexico (Fig. 1). The nominate form was described from the California coastal chaparral plant community, but populations occur in the Mojave Desert and in three distinct subdivisions of the Sonoran Desert. Desert communities are expansive, often leading the casual observer to believe they are homogenous. However, there is a great deal of complexity in desert plant communities brought on by elevation, edaphic, and climatic factors. When populations are subject to differing natural selection in discontinuous or different habitats, unique phenotypes may develop if gene exchange is sufficiently restricted. Colonization of a new area may be accomplished by a few individuals, or a single female moth resulting in a limited initial gene pool (founder effect). With time, variability of the population may increase, but certain characteristics present in the parent population may be irrevocably lost, or selected against, resulting in unique biological or phenotypic traits. As a result, many distinctive populations may be assigned to one species, and the sum total of these populations and their attributes define the species. As presented in this paper, local populations also may experience unique biotic and abiotic conditions that result in changes in behavior, the time of egg hatch and

eclosion of adults, and hostplant preferences. Under such circumstances, the taxonomic status of a population may be difficult to assess based only on museum specimens.

It has been our observation that among North American *Hemileuca*, the more extensive their range in mosaic environments, the more likely it is for them to express a wide range of variability in all life stages. In reviewing *Hemileuca electra* populations, we found that some phenotypes are part of a cline that extends over many km, while another population exhibits such sharp discontinuity that species status was considered. The criteria we used to judge the status of *Hemileuca* species and subspecies is presented in the methods section.

The *H. electra* populations examined include: (1) nominate *H. electra* from coastal chaparral plant community of southern California, south to the area of San Quintin, Baja California, Mexico; (2) *Hemileuca electra clio* Barnes & McDunnough, a dark phenotype from the Arizona Upland plant community of Arizona; (3) the Mojave Desert population that extends across portions of southern Utah, Nevada, and California, characterized by its distinctly white forewings; (4) a Colorado Desert population extending from Riverside County, California, south into the deserts of Baja California, Mexico, characterized by its smaller size and mottled forewings; (5) a Vizcaino Desert population extending from south of El Rosario to approximately Rosarito in Baja California, Mexico, characterized by its large size and red coloration; (6) a population in Baja California Sur, Mexico, with a wide range of phenotypes, but with an overall appearance somewhat similar to that found in coastal and desert southern California populations 600 km to the north. Brown (1982) defined and described in detail the above plant communities.

METHODS

Adult specimens from each population were collected from August to November in traps baited with pheromone-emitting virgin females as described in Collins and Tuskes (1979), or netted as they approached females placed in screen cages. Quantitative characters were measured on field collected males. In order to secure additional females, larvae were collected during February and March and reared to maturity. Specimens also were borrowed from Mike Smith, Pat Savage, David Hawks, Guy Bruyca, and the Natural History Museum of Los Angeles County.

Six quantitative characters and eleven qualitative characters were scored on each adult. Quantitative characters included: (1) forewing (FW) length as measured from the apex to wing base; (2) diameter of the FW discal spot; (3) width of white FW medial patch between veins Cu1 and Cu2; (4) diameter of hindwing (HW) discal spot; (5) width of

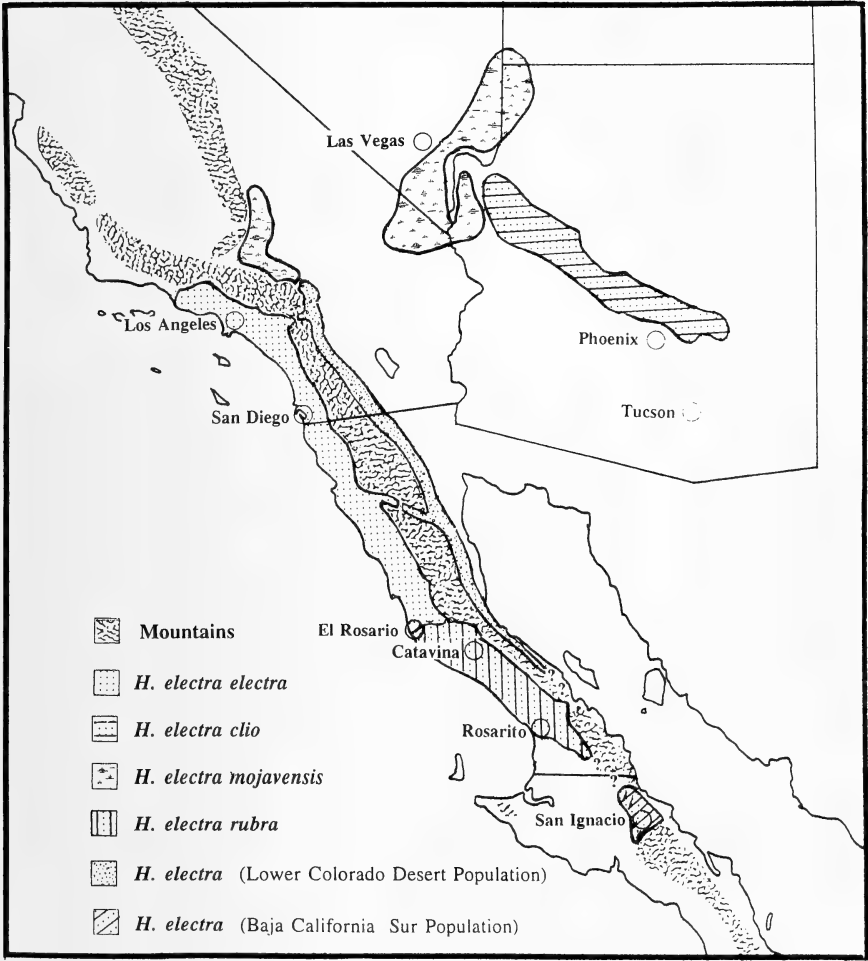


FIG. 1. Distribution of *Hemileuca electra* populations in the United States and Mexico.

black HW margin between veins m2 and m3; and (6) FW length to width ratio (higher values indicate narrower wings). Qualitative characters included: (7) black FW submarginal line touching discal spot; (8) presence of red scaling on antemedial area and/or inner FW margin or costal area; (9) color of male HW anal area (red or black); (10) color of ventral abdominal surface (black & white or black & red/pink); (11) color of the thorax (black & white or black & red); (12) color of the thoracic collar (white or red/pink); (13) transparency of wings [Wings were considered transparent if a data label could be read through the wing, translucent if the data on the label could be seen but not read,

and opaque if it could not be seen though the wing.]; (14) base of FW black and white or black only; (15) presence or absence of white marking between submarginal line and wing margin; (16) presence or absence of pupil in HW eye spot; and (17) color of the tegula (black & white or black & red).

When possible, 20 males and 10 females from each location were scored. The quantitative data were analyzed with a One-Way ANOVA, a correlation matrix and t-test, and discriminant analysis. Discriminant analysis was applied only to males, as too few females were available for a meaningful analysis. Nominate *H. electra* was used as the reference population. Data for multiple locations within each population are presented individually in order to better characterize variation. Qualitative characters were scored and summarized as percent occurrence.

Although there is no definition of how distinctive a population must be to warrant subspecies status, we set our criteria as follows. The population must be geographically and phenotypically distinct, and genetically compatible with other populations. Ideally, the characters that define the population would represent an adaptation to a unique environment. Although this aspect is difficult to evaluate, as a principle it involves life history traits, genetic compatibility, and the environment the population occupies, and places less emphasis on what is sometimes trivial phenotypic variation.

RESULTS

Of the 17 characters used to evaluate each specimen, characters 14–17 did not contribute significantly to distinguishing populations statistically, and thus these data are not presented or discussed. Other characters (2 & 4) were not statistically significant when all locations within a range were pooled, but in some instances individual locations differed significantly; these were included because of the trends they exhibit. Table 1 presents data for nominate *H. electra*, *H. electra rubra*, the blend zone populations, and the populations in Baja California Sur, Mexico. The information is based on 248 males from 12 locations. The forewing length of *rubra* and Baja California Sur population is significantly larger than that of nominate *H. electra* ($p > 0.01$), and the black hindwing margin of *rubra* is smaller ($p > 0.05$). Differences in qualitative characters between *H. electra electra* and *H. electra rubra* are striking. Other than size, the Baja California Sur population has similarities to nominate *H. electra* and the Lower Colorado Desert population. The intermediate character of blend zone males to the north (El Rosario) and south (Rosarito) of the *H. electra rubra* populations are characterized in Table 1.

Table 2 compares data for females from various *H. electra* popula-

tions. The average forewing lengths of female *clio* and *rubra* are significantly ($p > 0.05$) larger than that of nominate *H. electra*. The white forewing medial areas of *clio* and nominate *H. electra* are smaller than those of *rubra* and *mojavensis* ($p > 0.05$). The hindwing black margins of *mojavensis* and *rubra* are narrower than in other populations ($p > 0.05$), as is the hindwing discal spot of *mojavensis*. Too few females from the Lower Colorado Desert population were available to include this population in the statistical analysis. Differences in qualitative characters also are shown. Table 3 compares data for nominate *H. electra* males with *H. electra clio*, *H. electra mojavensis*, and the Lower Colorado Desert population, and is based on 267 specimens from 12 locations. The forewing length, hindwing discal spot, and margin width of *H. electra clio* are significantly ($p > 0.05$) larger than nominate *H. electra*. Southern populations of *H. electra mojavensis* are larger than nominate *H. electra* ($p > 0.05$), but others from the northern part of the range are not. The width of the white medial forewing area is larger ($p > 0.05$) in Mojave and Lower Colorado Desert populations than in nominate *H. electra*. Populations in Arizona from east of Davis Dam towards the type locality of *H. electra clio*, exhibit a reduction in size of the white forewing medial area and a tendency toward larger hindwing margins and discal spots than *mojavensis* populations. The Lower Colorado Desert population from Riverside and San Diego counties is most similar to the Mojave Desert population, but the white forewing medial area is significantly smaller.

Discriminant analysis separated *H. electra electra*, *H. electra clio*, and *H. electra mojavensis*. Ninety-three percent of the variance was accounted for by hindwing margin width, forewing length, hindwing eye spot diameter, and width of medial white forewing area. The Lower Colorado Desert population was placed by the analysis mid-way between *H. electra electra* and *H. electra mojavensis*, with some points overlapping nominate *H. electra* and *mojavensis*.

***Hemileuca electra* Populations**

Adult *H. electra* are attractive red, black, and white day-flying moths. Since adults lack functional mouth parts and thus do not feed, they are short-lived compared to most butterflies. Comstock and Dammers (1939) described the immature stages and biology of *Hemileuca electra*. Additional biological and distributional information has been published by Tuskes (1984) and Stone and Smith (1990). All *H. electra* populations have one generation per year. Depending on the population, the adult flight period may begin as early as July or as late as September. Adults emerge in the morning and depending on the temperature, the male flight begins between 0730 and 1000 h. Although mating occurs in the

TABLE 1. Comparison of male *Hemiteuca electra rubra* and Baja California populations with *H. electra electra*.

Males	FW* length	FW* discal	FW white patch	FW discal	HW margin	FW/HW ratio	Discal touch	Base FW red	HW anal black	V-Abd B&W	Collar white	Thorax B&W	Sam- ple Size
<i>H. electra electra</i>													
Motte Reserve	25.0	4.5	2.6	2.7	2.3	2.3	96%	0%	87%	100%	100%	100%	30
Riverside Co., CA	0.8	0.2	0.3	0.4	0.3	<0.1							
San Pasqual	25.0	4.5	1.7	2.3	2.1	2.4	90%	0%	80%	100%	100%	100%	30
San Diego Co., CA	0.9	0.4	0.9	0.4	0.3	<0.1							
El Secorro	25.3	4.1	3.2	2.3	1.8	2.4	60%	0%	75%	100%	95%	100%	20
Baja Cal., Mexico	1.0	0.4	0.6	0.3	0.2	0.1							
<i>H. electra/rubra</i> hybrid zone													
El Rosario	25.5	3.9	2.9	2.3	1.8	2.5	47%	15%	20%	67%	7%	35%	30
Baja Cal., Mexico	0.7	0.5	0.9	0.5	0.2	0.8							
<i>H. electra rubra</i>													
Pt. Canoas	26.3	3.5	3.3	1.8	1.3	2.6	53%	100%	10%	0%	0%	10%	30
Baja Cal., Mexico	1.3	0.5	0.8	0.3	0.2	<0.1							
El Progreso	29.5	4.1	4.5	2.4	1.7	2.6	14%	100%	0%	0%	0%	0%	7
Baja Cal., Mexico	0.8	0.3	0.7	0.4	0.4	<0.1							
Catavania	29.1	3.9	4.6	2.0	1.3	2.5	0%	100%	0%	0%	0%	0%	15
Baja Cal., Mexico	1.2	0.5	1.9	0.2	0.3	0.1							
Chapala	28.7	4.3	4.2	2.5	1.4	2.6	24%	100%	0%	0%	0%	0%	20
Baja Cal., Mexico	1.1	0.3	0.5	0.2	0.3	0.1							
P. St. Rosalita	28.1	4.1	3.6	2.1	1.6	2.5	46%	100%	0%	33%	0%	0%	12
Baja Cal., Mexico	1.0	0.8	1.0	0.3	0.2	0.9							
Baja California Sur, blend population													
10 km N Rosarito	29.0	4.1	4.2	2.1	1.5	2.6	10%	58%	0%	35%	3%	10%	20
Baja Cal., Mexico	1.0	0.3	0.6	0.3	0.3	0.1							
15 km S Rosarito	28.1	4.1	4.0	2.3	1.8	2.5	29%	21%	21%	71%	11%	36%	14
Baja Cal., Mexico	1.4	0.6	0.8	0.3	0.3	<0.1							
Baja California Sur, Mexico population													
Mesquiteal	27.6	4.5	3.5	2.7	2.4	2.4	60%	0%	50%	98%	95%	100%	20
Baja Cal. Sur, Mexico	1.3	0.6	1.0	0.4	0.4								

* Measurements in mm. FW = forewing, HW = hindwing, V-Abd = ventral abdominal surface, B&W = black and white. See methods for full definition of characters.

TABLE 2. Comparison of female *Hemileuca electra* from various populations.

Females	FW* length	FW discal	FW white patch	HW discal	HW margin	FW/HW ratio
<i>H. electra electra</i>	29.6 1.3	4.6 0.5	1.7 0.8	2.8 0.3	3.1 0.4	2.2 <0.1
<i>H. electra rubra</i>	33.0 1.1	4.5 0.2	5.5 1.3	2.4 0.2	2.4 0.5	2.3 <0.1
<i>H. electra mojavenensis</i>	30.5 1.3	4.1 0.5	6.6 1.9	1.9 0.3	2.3 0.7	2.2 <0.1
Lower Colorado Desert population	31.5 1.6	4.4 0.3	4.2 1.2	2.2 0.4	3.4 0.6	2.2 <0.1
<i>H. electra clio</i>	31.9 1.3	5.3 0.8	1.4 1.7	4.0 0.7	3.5 0.5	2.2 <0.1

	Discal touch	Base FW red	V-Abd B&W	Collar white	Thorax B&W	Sample size
<i>H. electra electra</i>	80%	0%	100%	100%	100%	12
<i>H. electra rubra</i>	20%	100%	0%	0%	0%	5
<i>H. electra mojavenensis</i>	0%	60%	100%	100%	0%	13
Lower Colorado Desert population	100%	0%	100%	33%	33%	3
<i>H. electra clio</i>	80%	0%	100%	100%	10%	9

* Measurements in mm. FW = forewing, HW = hindwing, V-Abd = ventral abdominal surface, B&W = black and white. See methods for full definition of characters.

morning, we observed females ovipositing from the afternoon to at least early evening; females have been collected occasionally at lights. The eggs are laid in rings or clusters that hatch between December and March. The early instar larvae are black and feed gregariously, while late instar larvae feed singly; the spines of these larvae are urticating. Pupation occurs in the soil or under surface debris; the pupal stage may last up to three years.

Hemileuca electra electra (Figs 2 & 16) inhabits the coastal chaparral plant communities of southern California (San Diego, Orange, Los Angeles, western Riverside, and southwestern San Bernardino counties) to just south of San Quintin, Baja California, Mexico (Fig. 1). Populations are found from sea level to approximately 1000 m. As a result, the mountain ranges that separate the chaparral and desert communities (San Gabriel, San Bernardino, San Jacinto, and Laguna mountains) define the northern and eastern limits of the population. A great deal of habitat has been lost to development, from the Los Angeles basin south to Laguna Beach, and we do not know the status of *H. electra* in this portion of its range. The only hostplant utilized by the

larvae is flat top buckwheat (*Eriogonum fasciculatum* Benth.; Polygonaceae). Females are similar to males in appearance but are larger, have more rounded and more densely scaled wings, and lack the black scaling on the anal portion of the hindwing that is common among males (Figs. 2 & 16). Table 1 characterizes males from three locations, and Table 2 characterizes females from southern California.

The flight season extends from July to December, with most records from mid-September and early October. During August and September we frequently observe flight activity during the morning and afternoon, with few or no males active during the hottest part of the day. As the days shorten and cool (October–December), flight continues throughout the day.

The average number of eggs per ring is 49 (standard deviation (SD) of 15.2, $n=76$ rings), with an average individual egg weight of 1.7 mg (SD 0.7 mg). The gray-green eggs hatch between late December and early March. The mature fifth instar larva has a brown ground color and three lateral cream to light yellow lines that extend nearly the length of the larva. Pupation occurs during April and May.

Hemileuca electra clio Barnes & McDunnough (Figs. 3–5 & 19–21) was described in a brief fashion from specimens collected at Kingman, Mohave Co., Arizona. Ferguson (1971) illustrated the lectotype and syntype and expressed concern regarding the lack of material and status of this subspecies. The melanic tendencies of *H. electra clio* were discussed by Ferguson, but a non-melanic topotype similar to the phenotype found in the Mojave Desert of California was illustrated, suggesting a variable population. As a result, a wide variety of phenotypes came to be called *H. electra clio*. Adults were characterized as being larger than nominate *H. electra*, and generally thought to have either predominately white or black forewings.

Collecting efforts during the past 20 years by Guy Bruyey, David Hawks, Mike Smith, Pat Savage, and the authors, resulted in a better understanding of the distribution and biology of this population. The type locality is at the western edge of this subspecies' range and borders the blend zone with the Mojave Desert population of *H. electra* (Fig. 1). Of 26 males collected at the type locality by Pat Savage, 20 were melanic or had melanic tendencies, and only 6 had clear white markings on the forewing. Since the name *clio* already was associated with the slightly melanic syntype and melanic tendencies have been mentioned in the literature, we applied the name *clio* to melanic populations from Kingman east to at least Pinal and Gila counties, Arizona. Most specimens are very dark; it is common for 40–60% of the hindwing and 70–100% of the dorsal forewing to be black. Females are characterized in Table 2 and males in Table 3.

TABLE 3. Comparison of male *Hemileuca electra chto* and *H. electra mojavensis* populations with *H. electra electra*.

Males	FW* length	FW discal	FW white patch	HW discal	HW margin	FW/HW ratio	Discal touch	Base FW red	HW anal black	V-Abd B&W	Collar white	Thorax B&W	Sample size
<i>H. electra electra</i>													
Motte Reserve	25.0	4.5	2.6	2.7	2.3	2.3	96%	0%	87%	100%	100%	100%	30
Riverside Co., CA	0.8	0.2	0.3	0.4	0.3	<0.1							
San Pasqual	25.0	4.5	1.7	2.3	2.1	2.4	90%	0%	80%	100%	100%	100%	30
San Diego Co., CA	0.9	0.4	0.9	0.4	0.3	<0.1							
Lower Colorado Desert population													
Mt. View/Springs	26.8	4.6	4.5	2.0	2.1	2.4	30%	0%	3%	100%	100%	93%	30
San Diego Co., CA	0.8	0.7	0.8	0.4	0.4	<0.1							
White Water Canyon	26.0	4.3	4.6	2.4	2.0	2.3	40%	0%	0%	100%	100%	30%	15
Riverside Co., CA	1.0	0.4	0.7	0.2	0.2	0.1							
E. Ensenada	26.4	4.5	3.9	2.5	2.2	2.5	21%	0%	0%	0%	93%	100%	15
Baja Cal., Mexico	1.2	0.5	1.0	0.3	0.3	0.1							
<i>H. electra mojavensis</i>													
LA & SB counties, CA	27.4	4.5	6.4	2.0	1.6	2.3	0%	30%	0%	100%	94%	90%	30
	1.0	0.4	1.0	0.3	0.2	<0.1							
Washington Co., UT	25.1	3.7	6.7	1.8	1.4	2.3	0%	100%	0%	100%	100%	70%	10
	1.3	0.3	0.7	0.1	0.1	0.1							
Newberry Mts.	25.9	4.0	4.7	2.2	1.7	2.3	10%	60%	0%	100%	60%	30%	15
Clark Co., NV	0.8	0.5	0.9	0.2	0.2	0.1							
E. Davis Dam	26.3	4.2	3.9	2.3	1.9	2.3	20%	40%	0%	100%	50%	50%	20
Mohave Co., AZ	0.8	0.4	0.6	0.3	0.3	0.1							
Hualapai Mts.	26.6	4.5	2.7	3.2	2.3	2.3	50%	40%	0%	100%	80%	60%	12
Mohave Co., AZ	0.8	0.5	1.1	0.3	0.2	0.1							
<i>H. electra chto</i>													
Kingman	27.0	4.3	3.0	2.9	2.3	2.4	50%	10%	0%	90%	80%	40%	30
Mohave Co., AZ	1.0	0.4	1.1	0.3	0.4	<0.1							
Superior	28.2	5.2	1.8	3.5	3.0	2.3	76%	10%	0%	100%	60%	13%	30
Pinal Co., AZ	0.7	0.5	1.3	0.4	0.4	<0.1							

*Measurements in mm. FW = forewing, HW = hindwing, V-Abd = ventral abdominal surface, B&W = black and white. See methods for full definition of characters.

Hemileuca electra clio is restricted to Arizona and occurs in the Arizona Upland plant community as defined by Brown (1982). It has been collected in Mohave, Yavapai, Maricopa, Gila, and Pinal counties (Fig. 1). Nearly all specimens exhibit melanic tendencies, and many have little or no white markings on the forewing. With the exception of the red on the basal part of the hindwing, some *clio* superficially resemble *Hemileuca juno* (Packard). Most specimens have been collected from mid-September to mid-October. The significance of the dark adult phenotype is unknown; it may allow better thermoregulation during the fall and/or may help the adult blend into the rocky surroundings.

The larval hostplant is flat-top buckwheat. The eggs are larger (avg. 2.7 mg., SD 0.2) and are laid in smaller clusters (avg. 31 eggs, SD 7.2, n=10 rings) than those of *H. electra electra*. Mature larvae often have darker dorsal scoli, and the intersegmental area is usually black; among nominate *H. electra* the intersegmental area is often a brick red, and dorsal scoli are black and yellow.

***Hemileuca electra mojavensis* Tuskes & McElfresh,**
new subspecies
 (Figs. 8–10 & 17–18)

Holotype: Male (Fig. 10). HEAD: Eyes brown. Frontal, vertex and clypeal scales red. Antennae plumose, black and bipectinate. THORAX: Dorsally clothed with elongated black, red, and white scales. Thoracic color white and light pink. Legs black and red. ABDOMEN: Dorsal surface red, with tuft of red scales at tip. Ventral surface black, intersegmental area white, causing a banded pattern. FOREWING: Length from apex to base, 29 mm. Costa, antemedial area, and outer margin black. Black discal spot with white pupil. Medial area with white scales. Ventral surface with red and black costal and antemedial areas. Pattern similar to dorsal surface but with red scales present in antemedial area. HINDWING: Length 21 mm. Ground color red. Anal margin with long red scales, outer margins black. Discal spot solid and black. Ventral surface similar to dorsal surface.

Allotype: Female (Fig. 22). HEAD: Eyes brown. Frontal, vertex and clypeal scales red. Antennae bipectinate, reddish-brown. THORAX: Dorsally clothed with elongated red scales, tegula white. Legs black and red. ABDOMEN: Dorsal surface red. Ventral surface black, intersegmental area white, causing a banded pattern. FOREWING: Length from apex to base, 31 mm. Costa and outer margin black. Antemedial area black, white, and pink. Black discal spot with white pupil. Medial area with white scales. Ventral surface of FW with costa, outer margin, and discal spot black, remainder of wing red. HINDWING: Anal margin with long red scales, outer margins black. HW discal spot solid and black. Ventral surface of HW similar to dorsal surface.

Types: **Holotype.** Male, 1.5 km west of Phelan, San Bernardino Co., California, 28 Sept. 1973, P. Tuskes. **Allotype.** Female, 1.5 km N. of Barnwell, New York Mts., San Bernardino Co., California. 26 Sept. 1981, P. Tuskes. **Paratypes.** California, San Bernardino Co., 3 males, same data as holotype; 48 males, 11 females, N. base of Ord Mt., E. of Hesperia, 23–26 Sept. 1989, G. Bruyey, D. Hawks, & S. McElfresh, 10 males, same location, 26 Sept. 1994, S. McElfresh & P. Tuskes; 3 males Coxey Rd., S. of Apple Valley, 3 Oct. 1987, M. Smith. Nevada, Clark Co., 1 female, Hwy 161, 5 km. W. Jean, 5 Sept. 1987, M. Smith; 4 males, Newberry Mts., nr X-Mass Tree Pass, 29 Sept. 1987, P. Savage. Utah, Washington Co., 5 males, Hwy 91, nr Shivwits, 20 Sept. 1987, P. Savage, 1 male,

same location, eclosed 5 Aug. 1987, M. Smith. The holotype, allotype, and paratypes are deposited in the collection of the Natural History Museum of Los Angeles County.

Etymology. This distinctive population is named based on its distribution in the Mojave Desert of the southwestern United States. In California, the Spanish spelling of Mojave has been retained, while in Arizona, Mohave County has an English spelling. Since most of the Mojave Desert is in California, as is the type locality for this subspecies, we also use the Spanish spelling.

Paratype variation. The antemedial area of either sex may be solid black, or black with one or on occasion two white patches. In a small percentage of the population, the black scaling of the antemedial area may extend to the discal spot. The thoracic collar varies from white to pink. Average forewing length: males 27.4; females 30.5 mm.

Diagnosis. Adults of *H. electra mojavensis* are characterized by the extensive white medial forewing which clearly isolates the discal spot from the black margin and extends as a solid band from near the apex to the inner wing margin. On the hindwing, the black margin is narrower than that of the nominate form, and the anal area of the wing has no black scaling. Further, *mojavensis* is larger than nominate *H. electra*, exhibits little sexual dimorphism other than size, and the wings are heavily scaled and not translucent. It is distinguished from *H. electra clio* by its predominately white forewing, orange hindwing, and narrow black hindwing margin. Melanic tendencies are often associated with *clio* and the hindwing is red and black (Figs. 3–5 & 19–21). Tables 2 & 3 summarize many additional differences between *mojavensis*, *clio*, and nominate *H. electra*.

Distribution. *Hemileuca electra mojavensis* occurs primarily in the moderate elevations of the Mojave deserts of California, Arizona, Nevada, and Utah (Fig. 1). Utah, Washington Co., Hwy 91, near Shivwits at Apex Mine Rd. Nevada, Clark County, Hwy 161, 5 km NNW of Jean; Railroad Pass, SE of Henderson; Spring Mts., Calico Basin; and X-mass Tree Pass, Newberry Mts. Arizona, Mohave Co., Hwy 68, 10.7 miles east of Davis Dam, Black Mts. California records are so numerous that only geographic areas are given: San Bernardino Co., Hackberry Mts., New York Mts., Providence Mts., Ord Mt., Granite Mts., Lucerne Valley, Morongo Valley, Apple Valley, and Pioneertown; Los Angeles Co., Phelan, Pearblossom, and Little Rock. Kern Co., Red Rock Canyon off Hwy 14.

Discussion. The habitat of *H. electra mojavensis* differs from that of *H. electra clio*, in that the Mojave Desert usually lacks summer rains and is hotter and drier than the Arizona Uplands plant community of *H. electra clio*. The averaged combined winter and summer temperature for the Mojave is 20.2°C, followed by the Lower Colorado at

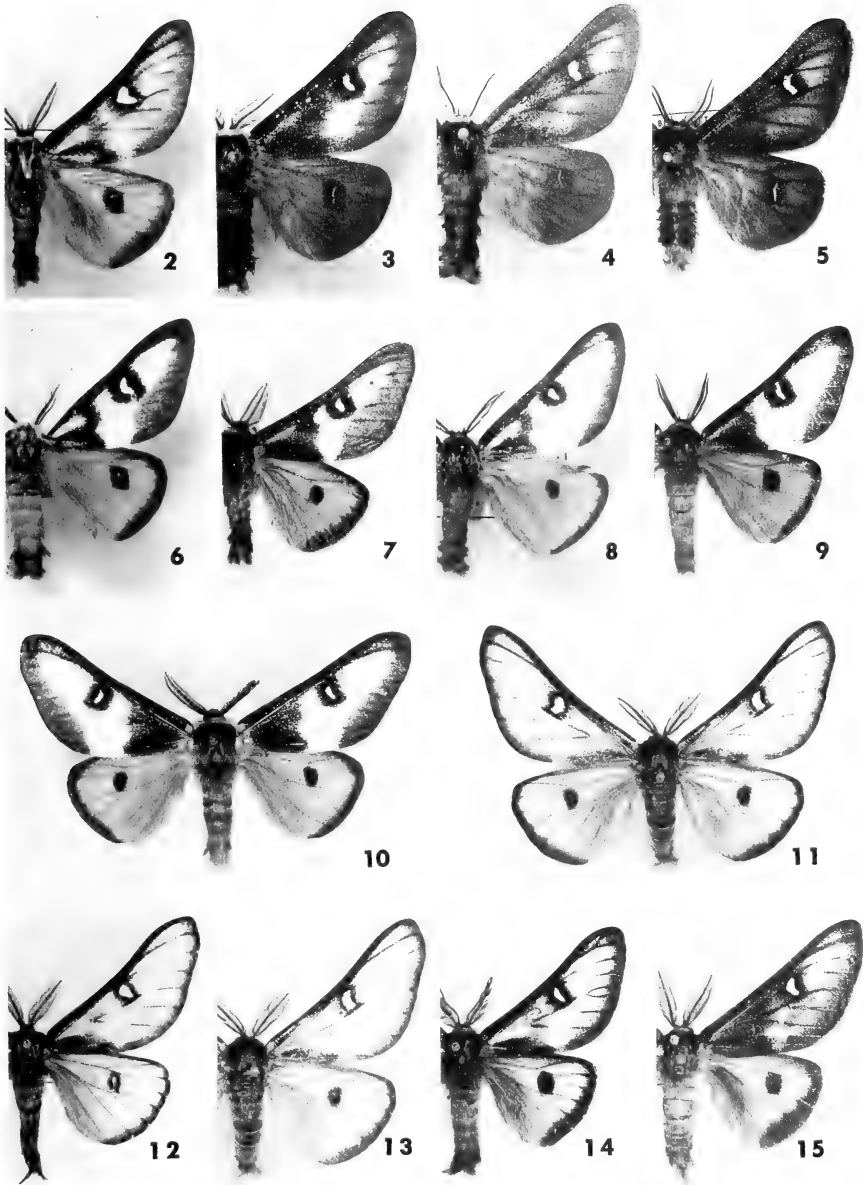
18.2°C, and the Arizona Upland at 17.7°C. The light forewing coloration may be important in thermoregulation. Other Mojave Desert *Hemileuca* have primarily white fore- and hindwings. On the eastern edge of its range there is a narrow transitional band between the Mojave Desert and the Arizona Upland plant communities where intermediate *H. electra* phenotypes occur. The best known area is between Oatman and Kingman in Mohave County, Arizona, a distance of about 45 km. Kingman (the type locality of *clio*) is on the eastern edge of the blend zone, thus, it is not surprising that topotypes exhibit a wide range of phenotypes that contributed to earlier confusion.

Nearly all adult records are from mid-September to late October. We have collected adults as early as 0800 h and as late as 1730 h. Females are more likely to be found flying in the afternoon and on occasion have been collected at lights. The adults typically fly within 2 m of the ground.

The clusters of eggs contain an average of 16 (SD 3.2, n=11 rings) large gray eggs. The larvae of *mojavensis* feed on *Eriogonum fasciculatum* var. *polifolium* (Watson). On occasion we have found larvae on *E. wrightii* Torr., but have not observed them feeding. Early instar larvae are found in late February or early March, and pupation occurs in April. Mature larvae tend to have a dark gray-black ground color, the intersegmental area is black, and the three lateral abdominal lines are nearly white. Thus, *mojavensis* larvae look quite similar to those of *H. electra clio*. There are five larval instars. The adult phenotype remains consistent regardless of where field collected eggs or larvae are reared.

A cross between a coastal San Diego female *H. electra electra* and a male *H. electra mojavensis* produced F₁ males similar to *mojavensis*, but larger and with more black on the forewing. The F₁ females were very large, and although the forewing was similar in markings to that of *mojavensis*, all were melanic. One female was very melanic and appeared to lack ova (Tuskes 1984). A second batch of larvae produced an F₁ generation that were similar to *mojavensis*. Tuskes (1984) provided biological information and a distribution map for this subspecies, but at the time it was not distinguished from *H. electra clio*. He also identified the Lower Colorado Desert *electra* population as related to, but different from, what herein is described as *H. electra mojavensis*.

Western Lower Colorado Desert population (Figs. 6-7 & 17-18). Based on discriminant analysis, this population was separate from, but has similarities with, both nominate *H. electra* and *H. electra mojavensis*. Although distinctive, it was not named because additional field work in Mexico would be required to understand its relationship to the population in Baja California Sur, the Vizcaino population, and the



FIGS. 2-15. Male *Hemileuca electra*. 2. Nominate *H. electra*, San Diego, Co. CA. 3.-5. *H. electra chio*, Pinal and Gila Co., AZ. 6. & 7. Lower Colorado Desert population, San Diego and Imperial Co., CA. 8. & 9. *H. electra mojavnensis* paratypes, San Bernardino Co., CA. 10. *H. electra mojavnensis*, holotype, San Bernardino Co., CA. 11. *H. electra rubra* holotype, Catavina, Baja CA, Mexico. 12. *H. electra rubra* paratypes, nr Chapala, Baja CA, Mexico. 13. *H. electra rubra* paratypes, nr El Progreso, Baja CA, Mexico. 14. & 15. Baja California Sur population, nr Mezquital, Mexico.

nominate form. This population differs from nominate *H. electra* in its slightly larger size, the presence of more white on the forewing, an absence of black on the anal portion of the hindwing, and the heavily scaled opaque wings (Table 3). Of 46 males examined from the desert of east San Diego and Imperial counties, and Baja California, Mexico, the black forewing margin extends to the discal spot or within 1 mm of the discal spot in 94%, and only one male was similar to *mojavensis*.

The geographic boundaries of this population are well-defined, and it appears to be isolated from nominate *H. electra* by the mountain ranges that separate the coastal chaparral from the desert plant communities. These mountains range from 1500 to 3000 m in elevation. Most nominate *H. electra* populations occur below 1000 m. There is possible reproductive interaction between nominate *H. electra* and the Colorado Desert population in a few of the lower passes that occur in Riverside County, California, and in the Valle de la Trinidad area, a pass between the Sierra de Juarez and Sierra San Pedro Martir of Baja California, Mexico. The Colorado Desert population occurs south of *H. electra mojavensis* and east of nominate *H. electra* (Fig. 1).

This population inhabits the desert slopes of the San Jacinto Mountains in Riverside County, south along identical habitat approximately 270 km to the Sierra San Pedro Martir in Baja California, Mexico. As with *mojavensis*, it is not found in the low desert flat lands, but rather along the edge of the mountain ranges where the desert variety of flat-top buckwheat, *E. fasciculatum* var. *polifolium*, is found. This distribution pattern corresponds with the western limits of the Lower Colorado Desert, a subdivision of the Sonoran Desert. The Lower Colorado Desert is warmer than the Mojave Desert during the winter, and is considered to be a subtropical desert, whereas the Mojave is a warm temperate desert (Brown 1982).

Specific collecting locations in California include: Riverside Co., 10 km SW of Oasis, Chino Canyon, White Water Canyon, and Eagle Mts. near Big Wash. San Diego Co., Scissors Crossing, Sentenac Canyon, Mason Valley, Desert View Tower, Jacumba, and 5 km E. of Manzanita. Imperial Co., Mountain Springs. Baja California, Mexico, Hwy 3, 150 km, and 130 km E. of Ensenada. At 55 km east of Ensenada, black scaling begins to appear on the anal area of the male hindwing, and the black hindwing margin becomes wider; both are characters associated with nominate *H. electra*.

The ova of this population are light beige and slightly larger than those of nominate coastal *H. electra*. The average number of eggs per cluster is 19 (SD 3.2, n=14 rings). Plants of *E. fasciculatum* var. *polifolium* are generally much smaller than coastal *E. fasciculatum* var. *fasciculatum*, and often not as dense. Fewer ova per cluster may be

an adaptation to the smaller hostplant. A large number of gregarious larvae on a small plant may preclude any from surviving. The eggs and larvae are similar in appearance to those of *mojavensis*.

***Hemileuca electra rubra* McElfresh & Tuskes, new subspecies**
(Figs. 11-13 & 24-25)

Holotype: Male (Fig. 11). HEAD: Eyes brown. Frontal, vertex, and clypeal scales red. Antennae plumose, bipectinate, black. THORAX: Dorsally clothed with elongated red scales, tegula red with some black scaling. Thoracic collar red. Legs red and black. ABDOMEN: Dorsal surface red, with tuft of red scales at tip. Ventral surface black, intersegmental area red, causing a banded pattern. FOREWING: Length 30.2 mm. Costa and outer margin black. Discal spot black with light yellow pupil. Antemedial area red, faint antemedial black line. Inner margin red. Remainder of wing transparent with occasional red or black scales. Ventral surface pattern similar to dorsal, but costa red, and red scales on inner margin more prevalent. HINDWING: Length 20 mm. Anal margin with long red scales, thin (<1.5 mm) black outer margins. Discal spot black with small white pupil. Remainder of wing transparent. Ventral similar to dorsal surface but with sparse red scaling more noticeable.

Allotype: Female (Fig. 24). HEAD: Eyes brown. Frontal, vertex, and clypeal scales red. Antennae bipectinate, red. THORAX: Dorsally clothed with elongated red scales; tegula red. Thoracic collar red. Legs red and black. ABDOMEN: Dorsal surface red, ventral surface with red and black banding. FOREWING: Length 33.5 mm. Costa red and black. Margin black, submargin red, curved postmedial line black. Discal spot black with light yellow pupil. Faint black antemedial line. Remainder of wing red. Ventral surface pattern similar to dorsal, but the antemedial and postmarginal lines absent. HINDWING: Length 25 mm. Anal margin with long red scales, thin (<1.5 mm) black margins. Discal spot black with small light yellow pupil. Remainder of wing red. Ventral wing surface similar to dorsal.

Types. **Holotype:** Catavina, Baja California, Mexico, 13 Oct. 1988, P. & A. Tuskes, S. McElfresh, M. Collins. **Allotype:** Hwy 1 (PK 169.3), 5.3 km NNW of Catavina, elevation 607 m, Baja California, Mexico, 14 Sept. 1984, J.P. & K.E. Donahue. **Paratypes:** Baja California, Mexico. 10 males, same data as holotype. 2 females, same data as allotype. 1 male, 7 km N. El Progreso, 8 Oct. 1988, Tuskes. 4 males, 5 females (reared), 5 km N. El Progreso, Sept./Oct. 1989, Tuskes. 2 males, 1 female, 4 km W. of Punta Prieta, 9 Oct. 1988, Tuskes, McElfresh & Collins. 12 males, 3 km E. Santa Rosalillita, 13 Oct. 1988, Tuskes & McElfresh. 10 males, 4 km S. of Chapala, 9 Oct. 1988, Tuskes, McElfresh & Collins. 3 males, 6 females (reared), 4 km S. of Chapala, 8-23 Oct. 1989, Tuskes. 25 males, 10 km NE. Puerto Canoas, 11 Oct. 1987, S. McElfresh & D. Hawks. The holotype, allotype, and paratypes are deposited in the collection of the Natural History Museum of Los Angeles County.

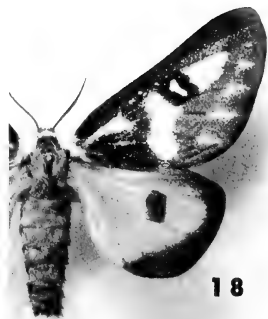
Paratype variation. Specimens from near the Pacific coast (Puerto Canoas, Santa Rosalillita) tend to be smaller and the thorax slightly darker than material from more inland populations. On an individual basis, the width and intensity of black maculation is variable in both sexes. The hindwing discal spot does not always have a white/light yellow pupil, but may appear as a black dot. Males: Tegula red or red and black. Inner forewing margin varies from red and black to white and black, or may contain all three colors. Newly emerged specimens have sparse white scaling in the medial portion of the forewing, but scales are less noticeable in specimens that have flown. Females: Medial



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17



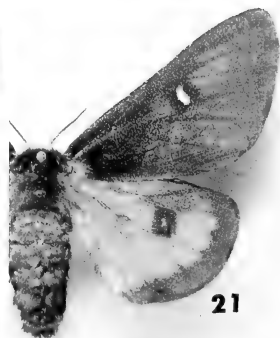
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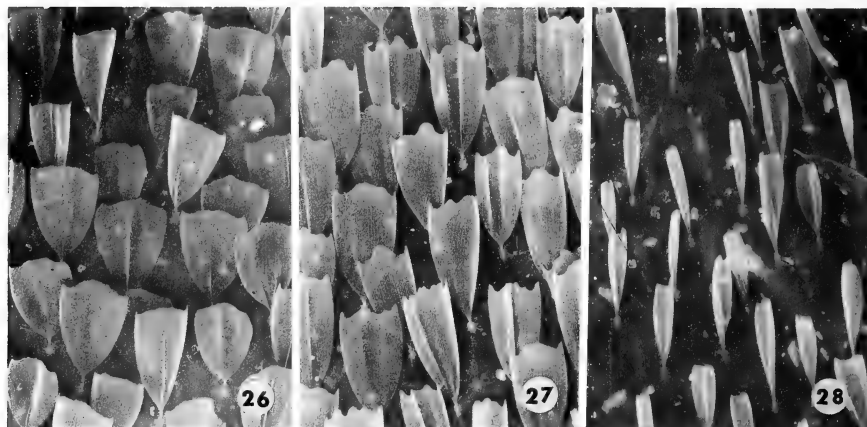
forewing area red or pink; one of seven wild females has white scaling in the medial area. On the forewing, black may extend from the margin to the postmedial line eliminating the red submarginal area; the black may be slightly reduced resulting in isolated red wedges between these two lines; or as in the allotype these two lines may be clearly separated by a red submarginal area.

Diagnosis. A comparison of characters between *rubra* and nominate *H. electra* is summarized in Tables 1 and 2. In addition to those already mentioned, other important diagnostic characters of *rubra* males are: the thorax, collar and usually the tegula are predominately red; the ventral abdominal surface is pink and/or red; the black hindwing marginal band is narrow and the anal area of the wing is free of prominent black scales. Females: the forewing is opaque and the dorsal surface is usually pink/red, and black, the antemedial area is usually red. Only 1 of 7 wild females had a white forewing medial area. The thorax and frequently the tegula are red. Among both sexes of nominate *H. electra*, the forewing, thorax, tegula, and ventral abdominal surface is black and white, while the thoracic collar is white (Tables 1 & 2).

Distribution. This subspecies occurs only in the northwest section of the Vizcaino Desert, a subdivision of the Sonoran Desert habitat of Baja California, Mexico. The distribution is from just north of El Progreso, south to Rosario, a distance of 220 km, and from the Pacific coast east to the edge of the arid central gulf habitat (Fig. 1). The Vizcaino subdivision is characterized by a unique plant community associated with arid conditions. The average precipitation of 27 stations is 9.9 cm/yr, with a range of 4.8 to 15 cm/yr (Brown 1982). Some of the unique vegetation includes elephant tree or torote (*Bursera microphylla* A. Gray; Burseraceae), elephant tree or copalquin (*Pachycormus discolor* (Benth.); Anacardiaceae), cardon (*Pachycereus pringlei* (S. Wats.); Cactaceae), and boojum or cirio (*Idria columnaris* Kell.; Fouquieriaceae).

Discussion. The most distinctive and largest specimens of *H. electra rubra* come from the central peninsular area between El Progreso and Chapala. Males from these locations have nearly transparent forewings with a slight reddish cast. The forewing averages 13% longer than that

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FIGS. 16–25. Female *Hemileuca electra*. 16. Nominate *electra*, San Diego, Co. CA. 17. & 18. Lower Colorado Desert population, San Diego and Imperial Co., CA. 19.–21. *H. electra clio*, Pinal and Gila Co., AZ. 22. *H. electra mojavenensis*, allotype, New York Mts., San Bernardino Co., CA. 23. *H. electra mojavenensis* paratypes, San Bernardino Co., CA. 24. *H. electra rubra* allotype, nr Catavina, Baja CA, Mexico. 25. *H. electra rubra* paratypes, nr Chapala, Baja CA, Mexico. [With the exception of female *H. electra mojavenensis*, most populations have white or red scaling between the forewing postmedial line and wing margin. Although there is individual variation, females of *H. electra mojavenensis*, and *H. electra rubra* have narrower black hindwing margins.]



FIGS. 26-28. Electron micrographs of male *H. electra* medial dorsal forewing. 26. *H. electra clio*. 27. *H. electra electra*. 28. *H. electra rubra*.

of nominate *H. electra*, but some individuals are as much as 30% larger. The relative difference in size is about the same as the difference between *H. hera* (Harr.) and *H. hera magnifica* (Rotger). Specimens from near the Pacific Ocean tend to be smaller and have some black on the thorax, but the wings are still quite transparent.

Electron micrographs of male forewings show that the scales of *rubra* are less dense and more curled than those of *H. electra electra* (Figs. 26-28). Differences in scale density and the laterally curled, somewhat conical shape are the primary reasons for the transparent appearance of the wings. The loss of scales with age contributes to the appearance, but it is not the primary cause as reared specimens which have not flown still exhibit this character.

Females of *rubra* express phenotypic variation related to environmental conditions experienced during the larval and pupal stages. Fourth and fifth instar larvae collected in Baja that emerged in the fall produce the striking red/orange to pink wild phenotype. In captivity, pupae that hold over and emerge the following year produced females with a great deal of black smudging on the pink forewing. When reared from ova or as field collected 1st and 2nd instar larvae, the females had a reddish antemedial area and red along the inner forewing margin, but the remainder of the forewing was black and light pink or white. The forewings of these females are similar to those from the Lower Colorado Desert population but differ by the presence of the red to red-orange ground color. Rearing conditions only affected the forewing pigments of females and had no influence on other *rubra* characters.

The phenotype of the male does not appear to be influenced by rearing conditions.

Well-defined transitional populations have been identified at both the northern and southern boundaries. The northern transitional population is a step cline that occurs primarily from El Rosario south approximately 25 km. At El Progreso, 50 km south of El Rosario, the phenotype is that of *rubra*. Specimens from the blend zone differ from nominate *H. electra*, exhibiting decreases in the size of the fore- and hindwing discal spot, the hindwing margin, and black scaling on the hindwing anal area. There are corresponding increases in wing length, width of the white forewing medial area, frequency of red thoracic collar, and transparency of the wings (Table 1). We have only three females from this area and all have pink/red forewings. This blend zone corresponds with the transitional area between the California Coastal Chaparral and Sonoran Desert plant communities (Fig. 1). Males from 32 to 50 km west of Bahia de Los Angeles have sparse black scaling on the anal area of the hindwing, but otherwise are typical for *rubra*.

South of El Rosarito specimens exhibit transitional characters found in the more southern population. About 50% of these specimens have sparse black scaling on the anal area of the hindwing, increased black scaling on the thorax, red or white thoracic collars, and less transparent wings. All of these characters are found commonly in the Baja California Sur *H. electra* populations. Material from the northern and southern transitional populations was not included in the paratype series.

Hybrid crosses between nominate *H. electra* from San Diego and *H. electra rubra* from El Progreso and Lake Chapala provide further evidence for the genetic divergence of this population. During 1988 and 1989 six crosses were made with the following results. Over 97% of the eggs hatched, and if the female was from San Diego the ova hatched in January or February; if the female was from Mexico the ova hatched in December. All larvae developed rapidly with little mortality. In the prepupal stage, mortality exceeded 85%. Of those that pupated, over 30% were deformed and died during the summer. Of the normal pupae, approximately half failed to emerge and died after 2 years. Only 5–6% emerged as adults. Some males and most females had wing deformities on the left side, and only 2 of 6 females had eggs in their abdomen. As a control, nominate *H. electra* and *H. electra rubra* colonies from El Progreso and Lake Chapala were reared at the same time. These had approximately 90% survival with no notable deformities among the adults. Last instar larvae collected from the hybrid zone produced 3 females; 2 had wing deformities and none contained eggs. Thus, both laboratory hybrid females and those from

the hybrid zone display deformities and had significantly reduced fecundity.

Crosses between female nominate *H. electra* and male *rubra* resulted in F_1 females that were similar to nominate *H. electra*, but half had red collars. The F_1 males, likewise, were similar to *rubra*, but the wings were not as transparent. When the reciprocal cross was made, the F_1 females were more similar in appearance to *rubra*. The males had red thoracic collars, but the hindwing had distinctive black scaling in the anal area, a character common to nominate *H. electra* males. A comparison of these findings with the intermediate population near El Rosario, Mexico, suggests a great deal of similarity. The narrow hybrid zone may be maintained by the close proximity of contrasting selective forces found in the California coastal chaparral and Sonoran Desert, and the degree of genetic incompatibility between these two populations. The rapidity by which one phenotype and biological pattern is replaced by another, and its close association to floral shifts is striking.

The apparent lack of genetic compatibility with nominate *H. electra*, the utilization of additional hostplants, and the unique adult morphology and phenotype are strong arguments that *rubra* is a distinct species. We have described it as a subspecies because the relationship between *rubra* and the Lower Colorado and Baja California Sur populations in Mexico require further study to determine the extent of their compatibility.

First instar larvae have been collected from December though mid February. The large number of 4th and 5th instar larvae observed in early-February 1988 (perhaps 70%) suggests that most eggs hatched in December, which is earlier than nominate *H. electra*. Although we have found prepupal larvae in early February, most larvae pupate during March. Larvae from late emerging eggs pupate in April.

South of Lake Chapala mature larvae usually are found during the day at the base of the main stem, or on the ground under flat-top buckwheat. Feeding patterns suggest that some mature larvae wander from plant to plant, even when the host is not depleted, perhaps to avoid parasitoids. By searching for fresh frass on the ground under the hostplant it was easy to locate mature larvae.

The only known larval hostplant for nominate *H. electra* is flat-top buckwheat. But observations in Baja California indicate that other host plants are also utilized by *rubra*. In 1982, McElfresh and Bruyca found 30 mature larvae near Catavina feeding on tamarisk (*Tamarix* sp.; Tamaricaceae), an imported desert tree. In the fall of 1987, hundreds of males were observed near Punta de los Canoas, and in early-February of 1988, a mature larva was found about 42 km west of Bahia de Los

Angeles. The fact that no *Eriogonum* could be found at either location suggests other host plants must be utilized.

While camping west of Punta Prieta during February 1988, we found second through last instar larvae commonly feeding on flat-top buckwheat and boojum tree, and two hatched egg rings were located on stems at the base of boojum. In addition, perhaps two dozen mature larvae were feeding on *Pachycormus discolor*, and one on ocotillo (*Fouquieria splendens* Engelm.; Fouquieriaceae). In October 1988, six egg rings were found on boojum 3 km north of El Progreso. All rings were on the south side of the plant and within 1.5 m of the ground. A search of the buckwheat at this same location did not reveal additional egg rings. Though mature larvae tend to wander and appear to be oligophagus, it does not mean that either ocotillo or elephant tree are suitable hosts for early instar larvae. Often, early instar larvae do not survive on alternate plants that support mature larvae (Tuskes 1984).

The eggs of *rubra* are beige and average 2 mg each, while those of nominate *H. electra* are gray-green and weigh slightly less. Egg rings deposited on boojum averaged 104 eggs (SD 6.4, n=6 rings), nearly three times more eggs per ring than the same species deposits on buckwheat (avg 44, SD 4.5, n=6 rings). Boojum trees represent a massive vertical but dispersed larval resource when compared to the more frequent and horizontally dispersed buckwheat. The increase in eggs per ring minimizes the number of oviposition flights a female must make. The shift in the number of eggs per ring may be induced by hostplant chemistry detected by the female during oviposition. Mature larvae of *rubra* have a blackish ground color, the lateral lines tend to be white, and the intersegmental areas are black to dark brown. As might be expected, larvae from the blend zone have intermediate phenotypes.

Based on topography, it is likely that an *H. electra* population occurs in the low coastal mountains southwest of Scammon's Lagoon. Ralph Wells (pers. comm.) observed *H. electra* larvae on Cedros Island located northwest of Scammon's Lagoon, but was not able to rear them.

Baja California Sur, Mexico population (Figs. 14–15). From the area of San Ignacio, Baja California Sur, to just east of Mezquitil, there is a population that superficially resembles material from the Lower Colorado Desert population and nominate *H. electra*. Most, but not all, have a white thoracic collar and black thorax with no reddish tendencies. The wings are black and white but translucent instead of opaque. Specimens are larger than nominate *H. electra*, but have black scaling on the anal hindwing area in 50% of the males. Black scaling on the anal portion of the hindwing is a character usually found only in nominate *H. electra*. Further, a few specimens have nearly melanic fore-

wings (only a trace on the hindwing), not unlike *H. electra clio*. This extensive variation is found in our small series of 24 males.

The habitat of this population is best described as scrub thorn which receives summer rains. Neither boojum nor flat-top buckwheat is present, although elephant tree and ocotillo are common. We have not found a larva or identified the most probable larval hostplant for this population. The population may extend further south, but possibly only on the Pacific Ocean side of the mountains. Extensive collecting with caged females and traps from Santa Rosalia to the mountains southwest of Loreto in 1990 and 1991 failed to produce adults.

To the north, a narrow blend zone between this population and *rubra* occurs south of Rosarito. In 1991 we collected at El Arco, in the mountains between Rosarito and San Ignacio, but did not find adults. We believe moths are present, but the quality of the dirt road did not allow us to go beyond El Arco, even with 4-wheel drive vehicles.

CONCLUSION

Hemileuca electra electra and *H. electra rubra* occur on the Pacific Ocean side of the coastal mountains, in relatively continuous habitat. *Hemileuca electra clio*, *H. electra mojavenensis*, and the Lower Colorado Desert populations often occur in isolated habitat, and as might be expected, exhibit greater phenotypic variation. The extensive phenotypic and life history variation probably represents adaptations to the environment, making it difficult to speculate on the origin and ancestral phenotype of this species. Based on adult maculation, male genitalia, and larval morphology, *H. electra* is most closely related to *H. juno*. *Hemileuca juno* occurs in southern Arizona, New Mexico, extreme western Texas, and adjacent portions of Sonora, Mexico, where the larvae feed on woody legumes. Of the various *H. electra* populations, adult *H. electra clio* most closely resemble those of *H. juno*. Whether this similarity is the result of close ancestral relationships or convergence is not known.

Although larvae of all populations in the United States feed on flat-top buckwheat, populations in Baja California, Mexico, are polyphagous. The southernmost population also exhibits phenotypic characters found in nearly all other *H. electra* populations. We considered the possibility that the *electra-juno* ancestor evolved in mainland Mexico and possibly dispersed by island-hopping across the gulf during more favorable times, and became what we now recognize as *H. electra*. Polyphagous feeding behavior is often interpreted as ancestral, and the occurrence of *H. electra* on Cedros Island suggests island-hopping is possible for this species. This scenario is not supported, based on the

biogeographic pattern of other saturniids that have colonized the peninsula of Baja California (e.g., *Eupackardia*, *Rothschildia*, *Hyalophora*, *Agapema*, *Saturnia*, *Sphingicampa*, and other *Hemileuca*), and its morphological relationship to *Hemileuca* outside of the *H. tricolor* complex. The southern population of *H. electra* may be one of the most recent, and not yet well-adapted to an environment that includes dependable summer rains and a new array of hostplants.

Hemileuca electra has spread successfully throughout desert plant communities because of its genetic flexibility and adaptability. *Hemileuca electra* has adapted to the various plant communities with subtle changes in seasonal and daily flight patterns, and unique adult phenotype. The number of eggs per cluster varies depending upon the larval hostplant and population, and the eggs of desert populations are larger and lighter in coloration which may allow them to reflect solar energy and reduce water loss. The utilization of new larval hostplants in Mexico requires a change in the selection of oviposition sites, the actual process of oviposition, and of course the ability to identify the hostplant. Larval feeding behavior must change to minimize predation and parasitization, and optimize thermoregulation on a hostplant such as boojum. The variability within the populations that define *H. electra* has contributed to its success in the harsh desert and semi-desert environment from Utah to Mexico.

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BIOLOGY OF *PROSERPINUS CLARKIAE* (SPHINGIDAE)

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ABSTRACT. *Proserpinus clarkiae* (Boisduval) is a small, green, diurnal sphingid ranging widely through western North America. *Proserpinus clarkiae* larvae were reared from ova of field collected adults and the life history is herein described for the first time. *Clarkia unguiculata* (Lindley) (Onagraceae) is a larval host for *P. clarkiae*. In captivity, larvae may be reared on *Clarkia unguiculata*, *C. concinna* (Fischer & C. Meyer), and *Fuchsia* sp. (Onagraceae). Instars 1 through 4 are predominantly green with pink or fuchsia markings and are cryptic on the host. The final instar has radically different color and markings from earlier stages, as in related species and genera, and appears cryptic against senescing grasses and annual plants among which it must search for foodplants. Pupation occurs at the soil surface under solid objects

Additional key words: *Clarkia unguiculata*, *Euproserpinus*, Onagraceae, crypsis, pheromone.

Proserpinus Hübner is a predominantly North American genus that includes seven species, as currently delineated, with one species restricted to the Palearctic Region (Hodges 1971). The early stages have not been described for any American species. Partial life history descriptions have been published for *P. terlootii* (Henry Edwards) (last instar and pupa) (Comstock 1948); *P. flavofasciata* (Walker) and *P. juanita* (Strecker) (last two instars of each (Hodges 1971); and *P. gaurae* (J. E. Smith) (last instar and pupa) (Hodges 1971). The paucity of life history information is likely the result of the rarity of most *Proserpinus* species.

Proserpinus clarkiae (Boisduval) (Figs. 1-2) is a small, green, diurnal sphingid ranging widely through western North America (Hodges 1971). It is univoltine, with adults in spring or early summer depending on elevation and latitude. In California, *P. clarkiae* is abundant at localities in the far north and rare in the south. The purpose of this paper is to present the biology of this species and describe the early stages while comparing immature characters with those of related species.

METHODS

On 20 March 1988, I collected four adult female *Proserpinus clarkiae* in Gates Canyon, Solano Co., California, between 1350 and 1530 h. One female was placed in a 1000 ml beaker lined with a damp paper towel. The top of the beaker was closed, but not sealed, with a loose sheet of clear glass. The beaker was kept indoors where it was 1/3 to 1/2 illuminated by direct sunlight. When condensation appeared on the underside of the glass sheet, the glass was turned over. Oviposition onto the paper occurred only during periods of high activity, while the moth was in flight, predominantly between 1100 and 1600 h. Ova were laid



FIGS. 1-2. Adult *Proserpinus clarkiae*. 1. Male, 2. Female. Scale bar = 1.0 cm.

singly; ninety-two ova were produced by one moth between 21 and 22 March; oviposition ceased after 22 March. During subsequent years other females were induced to oviposit under the same conditions. The ova were stored in a dry beaker under indoor conditions at room temperature (15–21°C). Larvae were reared indoors and offered various plants in the Onagraceae. Late stage larvae were kept in a terrarium over two inches of sand with dry grass and plant debris on the surface; or over two inches of silty soil with stones and clay pots sunk slightly into the soil surface.

Preserved specimens (in alcohol) of ova (n=4), and first (n=7), third (n=1), fourth (n=4), and fifth instar (n=1) larvae are deposited in the collection of the Essig Museum of Entomology, University of California, Berkeley.

LIFE HISTORY

Ova (Fig. 3). Lime green, smooth, chorion transparent; round, oblong, slightly compressed laterally; mean = 1.14×0.89 mm, range = 1.1×0.93 to 1.19×0.85 mm (n=7). A day before eclosion, ova are predominantly yellowish, and the yellow larvae visible through the chorion, with remnant green yolk laterally.

Larva: First instar (Fig. 4). Head: Yellowish green, width 0.63 mm (n=7). Body: Thoracic legs yellowish green. Ground color light green. Spiracles light green. Prolegs light green. Minute club-shaped scoli clear. Dorsolateral scoli on thoracic and abdominal segments 1 through 7 in longitudinal pairs (each scoli centered on anterior and posterior halves of segments). Anal horn absent, replaced by pair of scoli. Three longitudinal pairs of scoli along dorsolateral lines of terminal segment, caudal of anal scoli. Single, reduced, lateral scoli on abdominal segments, double on thoracic segments. A ventrolateral series of scoli in oblique pairs on abdominal segments. Anal shield dark green to pink. Mean length at eclosion 3.08 mm, range 3.02 to 3.17 mm (n=10).

Second instar. Head: Yellowish green, width 0.7 to 0.8 mm. Body: Thoracic legs yellowish green. Ground color green to yellowish green, caudal end slightly darker in some. Spiracles green. Faint pale green dorsolateral line along length of body to tip of terminal segment. Prolegs green to yellowish green. Anal prolegs dark green to slight pinkish. Anal shield pink to fuchsia. Anal horn absent. Late stadium length 11 to 12 mm.

Third instar. Head: Green, width 1.5 to 1.6 mm. **Body:** Thoracic legs pinkish. Ground color green. Whitish panicula profuse over body, each bearing a microscopic, clear seta from its center. Spiracles green. Dorsolateral band pale green. Prolegs green or pink to fuchsia. Anal prolegs fuchsia. Caudal end of terminal segment pinkish. Anal shield pink to fuchsia. Anal horn absent. Larvae variable in the amount of pink markings, if any. Late stadium length 14 to 18 mm.

Fourth instar (Figs. 5, 6). **Head:** Green to pink, width 2.2 to 2.6 mm. **Body:** Thoracic legs green to pink. Ground color green. Spiracles pink. Whitish panicula profuse over body, each with a microscopic clear seta. Dorsolateral stripe whitish, margined dorsally by dark green. Ventrolateral surface green, sometimes tinged pink. Ventral surface green or pinkish. Caudal end of terminal segment fuchsia. Anal prolegs and anal button fuchsia. Anal horn absent. Color variable, with the extent of pink shading on the ventral to ventrolateral surface, prolegs and head, grading from all green to all pink to fuchsia. Late stadium length 23 to 30 mm.

Fifth instar (Figs. 7, 8). **Head:** Light reddish brown, width 3.5 to 3.7 mm. **Body:** Coloration radically different from that of earlier instars, brownish pink to fuchsia. Panicula profuse over body, black dorsally, whitish ventrally, all bearing microscopic black setae from their centers. Prothoracic shield and thoracic legs reddish brown. Spiracles light gray. Dorsal surface dorsal of the dorsolateral line black to grayish black. Lone pinacula create a small cream dot just dorsal to the dorsolateral line, on the posterior margin of abdominal segments 1 through 7. A field of straw-cream laterally from dorsolateral line through ventrolateral line. Intersegmental area of thoracic and abdominal segments, ventrad of dorsolateral line, pinkish tinged with cream. Spiracles surrounded by oblong grayish black blotches extending obliquely (anterodorsal to posteroventral) over lateral surfaces of segments, surrounded by the lateral straw-cream color. In some specimens the oblique blotches form a heavy, continuous lateral band of interconnected oblique bars the length of the body, with a comparatively thin dorsolateral line and a broken, straw colored ventrolateral line. Large oblique oval spots of jet black surround abdominal spiracles 1 through 8, contained entirely within the oblique blotches. Ventral surface and prolegs brownish pink.



FIGS. 3-11. Early stages of *Proserpinus clarkiae*. **3.** Ova. Scale bar = 1.0 mm; **4.** First instar larva, lateral view. Scale bar = 1.0 mm; **5.** Fourth instar larva, lateral view; **6.** Dorsal view. Scale bar = 1.0 cm; **7.** Last (fifth) instar larva, lateral view; **8.** Dorsal view. Scale bar = 1.0 cm; **9.** Pupae: top, dorsal view; center, ventral view; bottom, lateral view. Scale bar = 1.0 cm; **10.** Cremaster, ventral view (note bifurcate tip). Scale bar = 1.0 mm; **11.** Right dorsolateral view of pupa, abdominal segments 2 and 3 showing pitting. Scale bar = 1.0 mm.

Anal button ringed in black, straw-cream with a dark reddish brown dot at the center. Anal horn absent. Early stadium length 26 to 33 mm, late stadium length 55 to 60 mm.

Pupa (Figs. 9-11). Length ranges from 20 to 26 mm, mean = 24 mm (n=7), width to 7 mm. Chestnut brown, tending darker brown caudally, with dark brown metathoracic protuberances on the dorsum. Cremaster conical, tapering to a sharp, bifurcated point (Fig. 10), contrasting sharply with the highly flattened structure described by Comstock (1948) for *P. terlootii*. Surface smooth; anterior half of each abdominal segment heavily pitted (Fig. 11).

RESULTS AND DISCUSSION

Eclosion commenced nine or ten days after oviposition. Upon eclosion, larvae fed on the chorion. First instar larvae ate only small portions of fresh, young *Oenothera hookeri* (Torrey & A. Gray) (Onagraceae) leaves, and high mortality was experienced. Artificially overcrowded larvae pinching each other with their mandibles, and reduced feeding on *O. hookeri* contributed to mortality. *Clarkia unguiculata* (Lindley) (Onagraceae) was accepted readily by larvae of all stages. I reared larvae to maturity on *Fuchsia* sp. (Onagraceae) obtained at a nursery. In addition, *Clarkia concinna* (Fischer & C. Meyers) was readily accepted by fourth and fifth instar larvae.

Boisduval (1852) assumed that *P. clarkiae* fed on Onagraceae based on the Old World *Proserpinus proserpina* (Pallas), whose habits were well known at his time. "We have given to this species the name of *clarkiae* by analogy, for we believe we can assure in advance that it nourishes itself of a plant of the Oenotherae family."

Species of *Proserpinus* and the related sphingid genera *Euproserpinus* Grote and Robinson and *Arctonotus* Boisduval are Onagraceae-feeders (Comstock & Dammers 1935, Comstock 1948, Hodges 1972, McFarland 1966, Tuskes & Emmel 1981), so the prediction that *P. clarkiae* should be found on plants of this family seemed warranted.

During the spring of 1988, Daniel Rubinoff, Lee Shoemaker, and I conducted extensive searches of dense stands of the annual *C. unguiculata* at Gates Canyon. On 9 April, Shoemaker located a second instar larva, and on 30 April, one each of fourth and fifth instar larvae of *P. clarkiae* were located by Rubinoff on *C. unguiculata*. I later discovered two *P. clarkiae* pupae in the Bohart Museum of Entomology at the University of California, Davis, bearing the labels: (1) "Marin Co., Fairfax, Food *Clarkia*, June 1940, Bred;" and (2) "Sonoma Co., Spring Mt., Food *Clarkia*, June 1940, Bred, J. S. Buckett collection."

I observed female *P. clarkiae* exhibiting oviposition behavior on an unidentified *Clarkia* species at Dardanelle, Tuolumne County, on 16 June 1991, and 10 miles east of McCloud, Siskiyou County, California, on 19 June 1988, but have not seen ova in the field.

Early instar larvae are cryptic on *Clarkia* foodplants, which often have fuchsia colored stems and petioles. Third and fourth instar larvae also strongly resemble the *Clarkia* fruiting bodies (which are present during larval development) in size, color, and shape. The fifth instar larva bears no resemblance to any part of the foodplant. At this stage of development, the larvae are quite large, and under normal circumstances, may consume several entire plants of most *Clarkia* species (because they are small), and may have to travel between plants. The broken pattern and straw colors of the fifth instar may serve as a form

of crypsis against the drying annuals and grasses among which the larva must search for foodplants. The late stage development of this insect, at most localities, coincides with the drying out of the grasses and annuals.

This drastic change in larval color and markings at late instar development appears to be characteristic of *Proserpinus* as well as *Euproserpinus* (Comstock & Dammers 1935, Tuskes & Emmel 1981) and *Arctonotus*. As in *P. clarkiae*, the penultimate larvae of *P. flavofasciata* and *P. juanita* are green with pale dorsolateral lines (Heitzman & Heitzman 1987, Hodges 1971). The mature larvae of these, as well as *P. gaurae* and *P. proserpina*, are marked like *P. clarkiae*, with the intricate pattern of blotches and lines of contrasting color. *Proserpinus proserpina* is depicted by Chinery (1989), with dark grey or brown dorsum, cream lateral field, prolegs, and venter, oblique black blotches surrounding the spiracles, and a caudal button of black, ringed in cream. I suspect that early instars *P. proserpina* are green with the dorsolateral line, but I haven't yet found confirmation of this in the literature. *Proserpinus gaurae* has oblique blotches of red, surrounded by white on a yellow-green field, and a "dark" ventral surface (Hodges 1971). *Proserpinus juanita* has a "brick red" ground color and white or cream dorsolateral and oblique lateral lines (Hodges 1971), and black lateral blotches in a cream field, with dark brownish prolegs and ventral aspect (Heitzman & Heitzman 1987; as depicted in a photograph), and black anal button surrounded with a white ring. *Proserpinus flavofasciata* is predominantly brown with black spots, with white and black bands (one each) surrounding the black caudal button (Hodges 1971). Preultimate instars of *P. terlootii* have not been described, but green with a light dorsolateral stripe is to be expected. *Proserpinus terlootii* may differ from its congeners by having a late stage similar to earlier stages, being predominantly green (Comstock 1948) and having the dark lateral blotches reduced to a small size. Still, a dorsal profusion of orange pinacula ("minute round spots," Comstock 1948) could give the larva a brownish color. Due to small foodplant size at some localities, late instar *Euproserpinus phaeton* (Grote & Robinson) may outgrow their hosts much like *P. clarkiae*. McFarland (1966) noted larvae of *E. phaeton* to be cryptic on the desert floor, against the debris of mature and senescing annuals. However, where *E. phaeton* does not outgrow its foodplant, late instar larval coloration remains cryptic and disruptive, such as on mature prostrate mats of *Camissonia bistorta* (Nutt. ex T.&G.).

In captivity, pupation occurred six or seven weeks after eclosion. When mature larvae were maintained on two inches of sand with a surface layer of dry weeds and grass, pupation was aborted, and larvae

wandered over the surface of the sand until they died (presumably from desiccation). Pupation occurred in a cell against the under surface of stones, bricks, and clay pots resting on silty soil. The higher humidity presented by silt capped with solid objects may have been the critical factor for successful pupation and pupal survival. Larvae may be able to detect higher soil humidity near and under solid objects on the surface, and such cues may initiate burrowing. No attempts at burrowing were observed over the dry (and dusty) sand. Humidity may also be important to successful emergence as is the case for *E. phaeton* (McFarland 1966).

Insects reared from Del Puerto Canyon (1990) emerged in the spring of the following year. Emergence dates ($n=5$) ranged from 24 March to 3 April 1991. As with *P. terlootii* (Comstock 1948) and *E. phaeton* (Comstock 1938), some *P. clarkiae* pupae survived into a second year, suggesting the possibility of emergence delay until spring of a subsequent year.

Adults emerged between 0700 and 1300 h ($n=4$). Although adult *P. clarkiae* are as small as adult *E. phaeton*, they do not expand their wings upon emergence in the same manner as *E. phaeton* (McFarland 1966), where wing expansion is hydraulically forced up against gravity. *Proserpinus clarkiae* expands its wings in the manner of most moths, by allowing the wings to hang below the elevated and inclined body, while the insect clings to a near-vertical or overhanging substrate.

In the late morning of 29 March 1991, a resting female, having emerged about two hours earlier, extruded its papillae anales and maintained this posture for over an hour (until disturbed). This observation, along with the sexually dimorphic adult antennae (male antennae are larger and setose) (Figs. 1, 2), suggests probable pheromonal mate attraction in *P. clarkiae*. Males of *P. flavofasciata* appear to be attracted to pheromones (Reed et al. 1987).

Adult flight occurs between 1000 and 1700 h. Highest activity occurs in the afternoon between 1400 and 1600 h. Adults use a wide range of nectar sources, including *Clarkia* species (Onagraceae), *Vicia* species (Fabaceae), *Ribes aureum* (Pursh) (Grossulariaceae), *Cirsium* species (Asteraceae), *Eriodictyon californica* (Hook & Arn.) (Hydrophyllaceae), *Dichelostemma capitatum* (Salisb.) (Liliaceae), *Asclepias cordifolia* (Benth.) (Asclepiadaceae), *Salvia columbariae* (Benth.) (Lamiaceae) (all my observations), and *Stachys* species (Lamiaceae) (J. Powell pers. comm.).

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GENERAL NOTES

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A "MICROBIAL COST" OF BUTTERFLY-ANT MUTUALISMS (LYCAENIDAE)

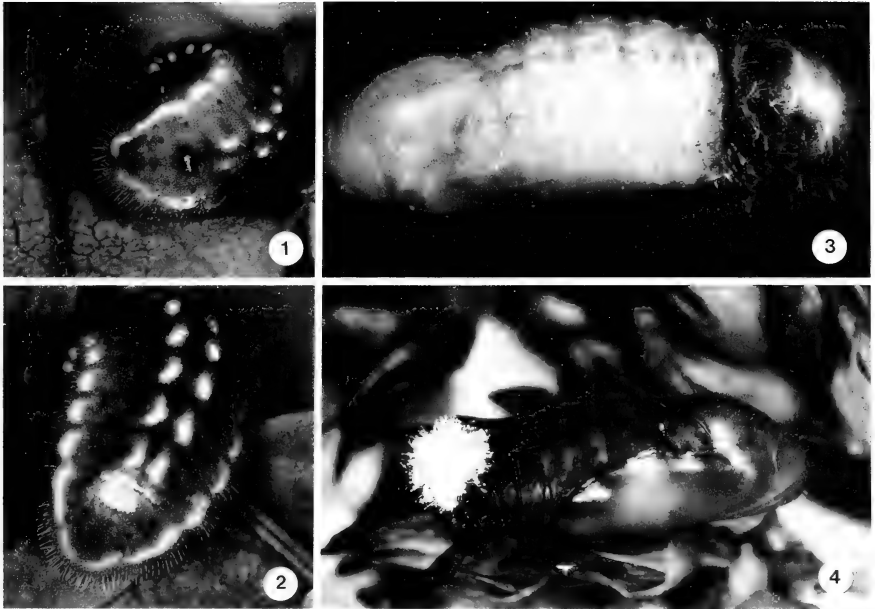
Additional key words: *Polyommatus*, Formicidae, myrmecophily, dorsal nectary organ, fungal infection.

The larvae of a large number of species in the Lycaenidae and Riodinidae associate with ants (Fiedler 1991). These associations, termed myrmecophily, are mediated by secretions of specialized epidermal glands, so-called myrmecophilous organs (Cottrell 1984). Vibratory communication between caterpillars and ants also may be involved (DeVries 1991). In certain cases, such as the well known Palearctic genus *Maculinea* van Eecke, larvae enter the host ants' nest at some stage of their development, where they prey on ant brood or solicit trophallactic feeding from their hosts (Thomas et al. 1989). Such ant-butterfly interactions bear traits of parasitism. In contrast, the majority of Lycaenidae associate with ants outside ant nests on their hostplants (Fiedler 1991). These caterpillars attract ants with the help of nutritive secretions from two types of glands. The dorsal nectary organ (DNO), located mediodorsally on the seventh abdominal segment, secretes droplets of a clear liquid containing carbohydrates and/or amino acids (Maschwitz et al. 1975, Pierce 1983, 1989). In addition, numerous minute hair-derived glands called pore cupola organs (PCOs) deliver secretions attractive to ants, probably amino acids in certain cases (Pierce 1983). Taken together, these secretions may constitute a substantial food resource for ants (Pierce et al. 1987, Fiedler & Maschwitz 1988). The ants, in turn, may protect the caterpillars against natural enemies (Pierce & Eastal 1986, Pierce et al. 1987). Hence, butterfly-ant interactions of this latter type are mutualistic trophobioses (but see Peterson 1993).

Mutualistic interactions between different species generally are accompanied by trade-offs between costs and benefits for both partners. The delicate and complex balance between costs and benefits is decisive for the ecological outcome and evolutionary stability of any such interspecific association. In lycaenid butterfly larvae, the production of energy-rich secretions may pose a severe developmental cost (Pierce et al. 1987, Baylis & Pierce 1992; but see Fiedler & Hölldobler 1992, Wagner 1993, Fiedler & Saam 1994). Furthermore, parasitoids may be attracted by the ant-guard (Nash 1989) or by the DNO secretions (Schurian et al. 1993). We here report on another type of cost associated with myrmecophily—fungal infections that invade the larvae via the DNO.

In summer 1992, we reared larvae and pupae of 3 myrmecophilous European lycaenid species in association with ants to investigate possible developmental costs of myrmecophily (Fiedler & Saam 1994). All larvae were reared from eggs laid by field-caught females. Caterpillars were kept individually in closed translucent plastic vials (125 ml) from the third instar onwards. The vials were lined with moist filter paper and were placed in an environmental chamber (25°C, L:D cycle 16:8 h). Food in excess (freshly cut plant material from a natural habitat) was provided daily, larval faeces were removed daily, and each caterpillar was transferred into a clean plastic vial with new filter paper every day. Hence, although the rearing conditions may have been more humid than in a natural environment, care was taken to reduce the risk of larval infections (see Schurian 1989, Fiedler & Saam 1994, for further details on the rearing method).

Most of the caterpillars were reared in association with worker ants taken from laboratory colonies of 3 different ant species (see below). One or more forager ants (depending on the treatment, see Fiedler & Saam 1994) were carefully placed in the rearing vial with a brush. The ants rapidly associated with the larvae and tended them constantly. The ants were moved daily into the fresh clean vials together with "their" caterpillar



FIGS. 1-4. Infected larvae and pupae. 1, Fourth (= final) instar caterpillar of *Polyommatus (Lysandra) bellargus*, with fungal infection at the DNO. White sporangia start to protrude from the glandular opening; 2, Advanced stage of fungal disease in *P. bellargus*. The whitish fungus covers an increasing portion of the dorsum of A7; 3, Freshly molted pupa of *P. (Lysandra) coridon*. The cast cuticle of the fourth instar larva is colonized by a fungus in the region of the former DNO. The pupa survived after removal of the cast skin (courtesy M. Treidtel); 4, Pupa of *Polyommatus icarus* with well developed fungus sporangia at the location of the larval DNO.

and remained with this caterpillar until pupation. In a few cases when ants died prior to pupation, these were replaced by nestmates to ensure a constant tending level.

Fungal infections starting at the DNO occurred in two facultatively myrmecophilous species: *Polyommatus icarus* (Rottemburg) reared on *Medicago sativa* L. (Fabaceae) inflorescences, and *P. (Lysandra) bellargus* (Rottemburg) reared on *Coronilla varia* L. (Fabaceae) leaves. The first external sign of infection was a dark discoloring at the DNO. One or two days later, the first whitish fruit bodies of the mold became visible (Fig. 1), and in the following 2-3 days the fungus extended widely around the DNO (Fig. 2). In total, three of 105 individuals of *P. bellargus* and 6 of 133 *P. icarus* caterpillars died from such infections in the final larval instar. In one *P. icarus* individual, the lethal fungus developed in the freshly molted pupa exactly at the location of the larval DNO (Fig. 4).

Polyommatus icarus and *P. bellargus* generally were quite susceptible to larval infections, which accounted for a mortality of 29 individuals (27.6%) in *P. bellargus* and 26 individuals (19.5%) in *P. icarus*, respectively (Chi^2 1 df = 2.16, $p = 0.14$). In a third, facultatively myrmecophilous species, *Plebeius (Aricia) agestis* (Denis & Schiffermüller) reared on *Geranium molle* L. (Geraniaceae) foliage, fungal infections at the DNO have not been observed, and the overall susceptibility of larvae to infectious diseases was significantly lower (3 out of 118 caterpillars, 2.5%, under identical rearing conditions; Chi^2 1 df = 22.98; $p < 0.0001$ for comparison *agestis* versus *bellargus/icarus*).

Surprisingly, all 9 caterpillars that died from a DNO-based fungal infection during summer 1992 had been kept in continuous association with ants throughout the third and fourth instar. The 3 caterpillars of *P. bellargus* had been associated with 5 *Lasius flavus* (Fabricius) workers, with 2 *Lasius flavus*, or with 2 *Lasius niger* (Linnaeus) ants, respectively. Out of the 6 *P. icarus* caterpillars, one had been kept with 5 *L. flavus* ants, one with 2 *L. flavus*, and two each with either 2 *L. niger* ants or 1 *Myrmica rubra* (Linnaeus) worker. Therefore, DNO-based fungal infections could develop irrespective of the species or number of tending ants. However, due to the small absolute number of such infections, their apparent restriction to ant-tended caterpillars was not significant statistically (Fisher's exact test, $p > 0.32$ for individual *Polyommatus* species, $p = 0.14$ for both species combined).

In 1991, a few cases of DNO-based fungal infections were observed in another European species, *Polyommatus (Lysandra) coridon* (Poda). As in the aforementioned lycaenids, *P. coridon* larvae are facultative myrmecophiles. In this case, however, the experimental caterpillars were collected in the field as third and fourth instars after hibernation, and then were kept without ants in the laboratory (rearing conditions as above). Infections developed in the fourth instar and usually killed the caterpillars. In one exceptional case, the infection broke out in the prepupal phase of the fourth instar (Fig. 3). This caterpillar successfully molted, and after removal of the fungus-covered exuvia, the pupa survived and eventually produced a healthy butterfly.

In his revision of the *Lysandra* group of the genus *Polyommatus*, Schurian (1989: 24) speculated that ant attendance could decrease the caterpillars' risk of suffering from bacterial or fungal infections, since certain secretions of ants (in particular from the metapleural gland) are well known for their antimicrobial properties (e.g., Hölldobler & Wilson 1990). We found no support for such a "hygienic effect" of ants on caterpillars. In the 1992 experiments, overall mortality rates due to larval infections were not different between ant-tended larvae (all ant treatments combined) and non-tended controls (χ^2 1 df < 0.11 , $p > 0.74$ for *P. bellargus* and *P. icarus*).

In the case of DNO-based infections, remnants of the energy-rich secretions may have contaminated the cuticle and setae around the DNO, thereby facilitating the establishment of pathogenic fungi. Alternatively, the fungi could have germinated inside the glandular reservoirs of the DNO. In any case, the presence of a DNO with its opening into the larval body offers an additional opportunity for pathogenic fungi to attack lycaenid caterpillars. Although we have no data on the incidence of such infections under natural conditions, our observations indicate that this is another potential cost factor associated with myrmecophily, which previously has received little attention.

In the extensive literature on myrmecophilous Lycaenidae, there are scattered reports that the larvae of certain myrmecophilous lycaenids may suffer from infections if deprived of their host ants in captivity. However, most of these records lack quantitative data or illustrations, and all refer to obligatory myrmecophiles that produce large amounts of secretions and totally depend on their host ants for survival. Reported examples include 4 species in the predominantly African tribe Aphnaeini, namely *Aphnaeus hutchinsoni* Trimen, *Spindasis natalensis* (Westwood), *Chloroselas pseudozeritis* (Trimen), *Poecilmitis lycegenes* (Trimen), (Jackson 1937, Clark & Dickson 1971), as well as *Hypolycaena erylus* (Godart) and *Arhopala pseudocentaurus* (Doubleday) (Jacobson 1912, Norman 1949). Our findings in 3 European species of the genus *Polyommatus* show that infections at the myrmecophilous organs also occur in facultative myrmecophiles, and even if tending ants are present. Such larvae produce much smaller amounts of DNO secretions, less than 15 μ l per lifetime in the case of *P. icarus* (Burghardt & Fiedler unpublished data); they associate unspecifically with a variety of ant taxa; and they do not depend on the presence of ants for survival. Facultative myrmecophiles account for the species majority of the family Lycaenidae (Fiedler 1991). Clearly, the selective importance of infectious diseases in lycaenid caterpillars and possible trade-offs with myrmecophily are a rewarding area for further studies in the laboratory as well as in the field.

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LATENT POLYPHENISM AND DIRECT DEVELOPMENT IN *PIERIS VIRGINIENSIS* (PIERIDAE)

Additional key words: diapause, hostplant, Brassicaceae.

In many pierids, seasonal polyphenism in wing pattern is coupled with diapause (Oliver 1970, Shapiro 1976), which is facultatively inhibited by rearing larvae under long-day photoperiods and warm temperatures (*P. rapae* L., Barker et al. 1963; *P. napi* L., Lees and Archer 1981; *P. napi oleracea* Harris, Oliver 1970). Populations of *Pieris napi* may contain individuals with varying response to natural photoperiod (Shapiro 1976), as well as individuals whose diapause lasts for several years (Shapiro 1979). Unexpected environmental stress such as unseasonably cold weather can induce more individuals to enter carryover diapause, ensuring the population's survival during extreme but short-lived environmental changes (Shapiro 1979). Yet another pierid diapause pattern is one in which all members of the population diapause and the insect is univoltine.

Pieris virginiensis Edwards is a monophagous species that uses an ephemeral, vernal hostplant, toothwort, *Cardamine diphylla* (Michx.) A. Wood (= *Dentaria diphylla* Michx.). Matching the restricted growing season of its host, *P. virginiensis* is a univoltine species that enters diapause when reared at summer photoperiods that inhibit diapause in *P. napi oleracea* (Shapiro 1971). Facultative diapause has been observed in several *P. virginiensis* populations, however. Forbes (1960) refers to a rare second brood of *P. virginiensis* occurring in Massachusetts and West Virginia, but does not give specific localities. Bowden (1971) reared 3 non-diapausing offspring from a stock of *P. virginiensis* sent to him by S. A. Hessel presumably from Washington (Litchfield Co.), Connecticut.

Shapiro (1971) obtained direct-developing *P. virginiensis* by subjecting the larvae to continuous light at 25°C. While the normal adult phenotype of *P. virginiensis* resembles a smokey version of the heavily veined vernal form of *P. n. oleracea*, Shapiro found that non-diapausing *P. virginiensis* adults were indistinguishable from the summer form of *P. n. oleracea*, a phenotypic similarity also noted by Forbes (1960). Shapiro concluded that the mechanism for phenotypic polyphenism was still intact but latent in *P. virginiensis*. We report here on a population of *P. virginiensis* producing direct-developing individuals whose offspring we have crossed in the laboratory.

Pieris virginiensis occurs together with *P. n. oleracea* in beech-maple-hemlock woods near Lee, Massachusetts (Berkshire Co.). Large stands of toothwort are present in early spring and are followed by garlic mustard, *Alliaria petiolata* (Bieb.) Cavara & Grande (= *A. officinalis* Andr.), as the season progresses. By mid-July the toothwort population has senesced; only garlic mustard remains in abundance along with small stands of watercress, *Rorippa nasturtium-aquaticum* (L.) Hayek (= *Nasturtium officinale* R. Br.), and cuckoo-flower, *Cardamine pratensis* L. Together these crucifers could support a sizable summer brood of either species. Courant et al. (1994) present evidence of incipient host range expansion of *P. n. oleracea* to garlic mustard, but there is no evidence that *P. virginiensis* is able to exploit garlic mustard successfully (Bowden 1971, our unpublished data) although they oviposit on it in the field (Roger W. Pease, Jr. personal communication, Courant et al. 1994, Porter 1994).

On 7 May 1993 we collected from this site seven female *P. virginiensis* which laid

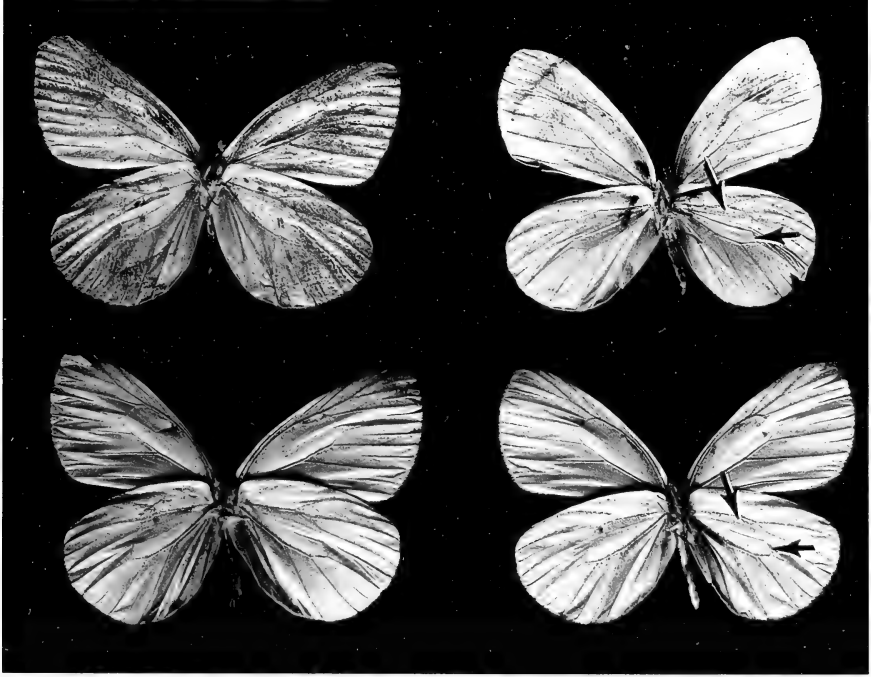


FIG. 1. Ventral view of direct-developing lab-reared offspring from field-caught females of *P. virginiensis* and *P. n. oleracea* near Lee (Berkshire Co.) Massachusetts. Top row from left: *P. virginiensis* ♂, *P. virginiensis* ♀. Bottom row from left: *P. n. oleracea* ♂, *P. n. oleracea* ♀. All were reared under long day conditions (16L:8D; 27°C day:19°C night) and eclosed within 10 days after pupation. Arrows show where LHW color was sampled in the discal cell near the origins of veins Rs and M₃.

eggs in our laboratory. Eggs hatched 11–20 May and larvae were reared as one combined brood under long-day laboratory conditions (16L:8D, 27°:19°C) on a variety of crucifers. On 21 May 1993 the larvae began to pupate. We noted two pupal colors, brownish white as described by Edwards (1888), and green which included a phenotype closely resembling non-diapausing *P. n. oleracea*, as well as intermediates between brown and green. The pupae were kept in our laboratory (room temperature: 22–26°C) with the intent to later chill them to break diapause.

Of the approximately 80 *P. virginiensis* pupae, 8 male and 8 female adults emerged between 1–21 June 1993, eclosing from green or intermediate pupae, although not all green or intermediate pupae developed directly. Possibly these 16 were siblings, because the offspring of all 7 wild-caught females were reared together. Like the non-diapausing *P. virginiensis* observed by Shapiro (1971) and Forbes (1960), the first generation of lab-reared offspring resembled the pale yellow summer form of *P. n. oleracea*, except the ground color of the wing was very white (Fig. 1). Melanic markings varied on the costal margin of the forewing and on the outer edge of the hindwing, but wings lacked the characteristic vernal melanic markings along the veins.

Three matings were observed among these 16 direct-developing *P. virginiensis* adults. One female died soon after mating without laying eggs. Eggs from the other mated females were reared separately under the above long-day conditions. The second lab-reared generation had higher than normal larval mortality in the first three instars; of 36

TABLE 1. Diapause and direct development in a second lab-reared generation of *P. virginiensis*. Shown are the diapausing and non-diapausing male and female offspring from 2 females that developed without diapause under long-day laboratory conditions. Females A and B were mated to direct-developing males which were also from the first generation of lab-reared offspring from wild-caught *P. virginiensis* mothers.

	Diapausing	Non-diapausing	Lost/died	Total number
Female A				
♂	1	1	1	3
♀	0	4	1	5
Female B				
♂	1	2	2	5
♀	1	6	0	7
Totals				
♂	2	3	3	8
♀	1	10	1	12

third instar larvae, only 20 pupated (12 ♂ and 8 ♀). The same variation in pupal colors was noted. Both matings produced direct-developing and diapausing individuals (Table 1).

To quantify HW ground color, we took pictures of the LHW underside of lab-reared (summer phenotype) *P. n. oleracea* (9 ♂, 9 ♀) and direct-developing *P. virginiensis* (14 ♂, 11 ♀ from 2 lab-reared generations) using a video camera recorder (SONY CCD-TR81) with incandescent lighting (standardized using Kodak R-27 gray card). We input these pictures into a Macintosh computer and Adobe Photoshop 2.5 (Adobe Systems, Mountain View, CA). Two ground color samples were taken from the discal cell (Fig. 1) and characterized for red, green, and blue color components for which higher numerical values correspond to whiter hues. The color sample values from each specimen were averaged. Because these values were not normally distributed, they were compared using a one-tailed Mann-Whitney test (Zar 1984). All three color components in *P. virginiensis* are equal to or higher than their counterparts in the *P. n. oleracea* sample (Mann-Whitney $U'_{[18,25]} = 340$ for red [$p = 0.0023$]; $U'_{[18,25]} = 311.5$ for green [$p = 0.033$]; $U'_{[18,25]} = 337.5$ for blue [$p = 0.0056$]).

Non-diapausing individuals of *P. virginiensis* may occur for two reasons. First, the facultative diapause expressed in members of the *napi* group may be latent in *P. virginiensis* (Shapiro 1971). This explanation is consistent with observations that other populations of *P. virginiensis* contain direct-developing individuals (Bowden 1971, Forbes 1960). Lack of a suitable summer hostplant would limit the success of non-diapausing *P. virginiensis* in Connecticut. However, the site at Lee, Massachusetts, contains small stands of watercress, an acceptable hostplant for *P. virginiensis* (Bowden 1971, our unpublished data) that may permit flight season expansion similar to that observed by Shapiro (1975) in a Sierra Nevada population of formerly univoltine but now partially bivoltine *P. napi microstriata* Comstock.

A second explanation for direct-developing *P. virginiensis* is hybridization with *P. n. oleracea*. These two species occur in sympatry in Lee, Massachusetts; the middle of the *P. virginiensis* brood in early May coincides with the first emergence of *P. n. oleracea*. An interspecific mating (*oleracea* ♂ × *virginiensis* ♀) was observed near this site, but was infertile (Chew 1980). Hybridization experiments with these species, however, have produced viable offspring (Bowden 1971). Lorković (1986) also reports a successful interspecific hybridization, but does not report on offspring survival. Introgression of "facultative diapause" alleles into *P. virginiensis* by hybridization is problematic because the F_1 hybrid, which would emerge in June, cannot backcross with *P. virginiensis* after the *P. virginiensis* flight season ends in mid-May. However, our direct-developing *P. virginiensis* offspring could be F_1 hybrids. Where *P. virginiensis* and *P. n. oleracea* are

sympatric, a second brood of *P. virginensis*, or an F₁ brood, might easily be missed because it closely resembles *P. n. oleracea* summer phenotype.

Considerable evidence suggests that expression of lepidopteran diapause is under genetic control (Shapiro 1976, Danks 1987), although Powell (1987) did not find convincing evidence for genetically fixed expression of prolonged diapause in his review of some 90 lepidopteran species. We have demonstrated that crosses of direct-developing *P. virginensis* yield both direct-developing and diapausing individuals. Our small numbers and relatively high mortality/loss rate in the second lab-reared generation make it difficult to determine transmission genetics and further investigation is needed.

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MELANISM HAS NOT EVOLVED IN JAPANESE
BISTON BETULARIA (GEOMETRIDAE)

Additional key words: peppered moth, form "carbonaria."

No example of natural selection in Lepidoptera is more widely recognized than industrial melanism in *Biston betularia* (L.) (Geometridae). In Britain, the common name for the species is the peppered moth because the typical, pale adult is covered with white scales mottled with black splotches. It was the only form known until 1848 when the first melanic variant was discovered near Manchester, England. By the turn of the century about 98% of Manchester *B. betularia* populations were melanic, or "carbonaria" as the jet-black morph came to be known. Similar changes were recorded in the vicinities of other industrial cities throughout Britain. The primary reason for the rise in frequency of the carbonaria form was its enhanced crypsis in polluted woodlands blackened by industrial soot. Against the darker backgrounds, paler morphs were more conspicuous to predators. Because the replacements of paler forms by melanic variants coincided with the industrialization of various regions, the phenomenon was dubbed industrial melanism. For the most comprehensive review of the early history of industrial melanism in *Biston betularia* and other lepidopteran species, see Kettlewell (1973).

Just over a century after the first melanic *B. betularia* was reported, the British government legislated the Clean Air Acts to enforce smokeless zones. Since that time Sir Cyril Clarke has documented a dramatic decline in the frequency of carbonaria from 93% to 23% between 1959 through 1993 on the Wirral Peninsula, just south of Liverpool (Clarke et al. 1985, 1993, 1994). For many years, gray foliose lichens encrusting the boughs and trunks of trees were thought, without any direct evidence, to afford hiding places for the pale form; however, the major reversals in morph frequencies recorded in recent years have occurred in the virtual absence of such lichens (Grant & Howlett 1988), indicating that the role of lichens in the natural history of *B. betularia* has been exaggerated. What seems certain, in any case, is that habitat modifications resulting from industrial practices and related human activities continue to affect the evolution of this species.

B. betularia is a Holarctic species, widely distributed across the higher latitudes or at higher elevations. What were once regarded as separate species have been reclassified as geographic races or subspecies (Rindge 1975, Clarke et al. 1993). The North American subspecies, *Biston betularia cognataria*, is also polymorphic in some populations for a typical form and a melanic variant called "swettaria." American typicals, called pepper-and-salt geometers, are generally darker than British typicals, closer in appearance to intermediate "insularia" forms (Kettlewell 1973). "Swettaria" is indistinguishable from British "carbonaria," and is likewise inherited as a dominant allele at a single locus (West 1977). Although swettaria is rare or uncommon in most *cognataria* populations, it has been recorded at very high frequencies near some industrial regions (Owen 1961, 1962, Sargent 1974, West 1977).

Biston betularia also lives in Japan where its subspecific name is *parva* and its common name is *Oo-shimofuri-eda-shaku*, meaning frosted, branch-measuring moth. In paleness, Japanese *parva* lies between typical American *cognataria* and British typicals. Published accounts of the whereabouts and "whenabouts" of *parva* are sketchy, however, as it has not attracted much attention in Japan.

Inoue (1982) and R. Sato (pers. comm.) report that the species can be collected in the middle and northeastern part of Honshu during early July to the middle of August, and in Hokkaido from the middle of July until late August. Collectors include it in their reports, but the numbers recorded are conspicuously small (e.g., Kurata 1965 [n = 1]; H. Sato et al. 1985 [n = 3]). In other published lists, it is conspicuously absent [n = 0] (e.g., Kurata 1969, H. Sato & Fukuda 1985, H. Sato et al. 1986). By contrast, the Wirral census of British *B. betularia* has averaged 500 specimens per year over the past 35 years in one location (Clarke et al. 1994). Clearly, Japanese *Biston betularia* has not been the focus of similar scrutiny. Here we report our attempts to survey populations of *B. betularia*

TABLE 1. The numbers of *Biston betularia* trapped at various locations in Japan.

Date ¹	Location	Latitude	Altitude (m)	No. of moths	Method ²	Collector ³
1988						
6/4-13	Setagaya Tokyo	35°37'	40	0	a	
6/14-29	Takao, Tokyo	35°39'	300	0	a	
7/3-7	Aizu-arakai, Fukushima	37°09'	400	0	a	
7/13-15	Ohizumi, Yamanashi	35°53'	1000	0	a	
Mid-July	Yuzawa, Niigata	36°36'	1000	16	a, b	Rikio Sato
7/22-8/5	Mikasa, Hokkaido	43°24'	200	0	a	
8/5	Sapporo, Hokkaido	43°13'	15	1	c	Masahito Kimura
8/6	Tomuraushi, Hokkaido	43°20'	600	0	a	
8/8-11	Mikasa, Hokkaido	43°24'	200	0	a	
8/6-16	Minami-aiki, Nagano	36°02'	1300	67	b	Masamitsu Wada
8/15-17	Takao, Tokyo	35°39'	300	0	a	
9/1-7	Shiga, Nagano	36°42'	1600	1	a	
1992						
7/4	Kawakami, Nagano	35°56'	1400	2	a, b	
7/20-24	Sugadaira, Nagano	36°32'	1600	107	a, b	
7/28	Mt. Odaido, Iwate	39°44'	1000	3	b, c	Nobuo Doi
8/1	Mt. Hiromori, Akita	40°22'	300	5	a, b	Masayuki Tanaka
Early Aug.	Namiai, Nagano	35°34'	1000	2	c	Michio Ihara
1993						
7/15-17	Sugadaira, Nagano	36°32'	1600	103	a, b	

¹ One trapping night spans two dates; dates listed indicate the evening traps were started, not the following morning.

² a = MV Robinson trap, b = black light & sheet method, c = fluorescent lamp.

³ Collections by other than authors are listed.

parva from rural and urban/industrial vicinities to determine whether or not industrial melanism has also occurred in Japan.

We used two kinds of light traps to sample moth populations: a) Robinson funnel traps (Robinson 1952) with mercury vapor lamps (100 or 160 watt) and b) fluorescent black lights (20 watt) used to illuminate sheets of stretched white cloth or plastic 2-mm mesh.

Table 1 lists all of the trapping sites and the total numbers of *B. betularia* taken during the time intervals shown. The species was absent in our moth catches taken in mixed deciduous stands in the Tokyo area, but it was present in rural habitats geographically distant from industrial centers. The largest samples were collected at three localities: 1) Yuzawa, Niigata, 2) Minami-aiki, Nagano, 3) Sugadaira, Nagano. Straight lines between these collection points are only 50 to 90 km long, but direct passage is thwarted by complicated ranges of mountains higher than 2000 m. The sites in Yuzawa and Minami-aiki are surrounded by forests abundant in *Larix kaempferi* (Lambert) (Pinaceae) and some *Betula platyphylla* Sukatchev (Betulaceae). In Sugadaira, collections were made in the center of a cattle field where *Betula ermanii* Chamisso and *B. platyphylla* birch trees are maintained. *Larix kaempferi* and *B. ermanii*, both of which are listed as host plants of *Biston betularia parva* by Inoue (1982), are likely major food sources for the populations we sampled.

Sample size differences at the various locations likely result from combinations of factors, including weather conditions and, especially, seasonal timing. *Biston betularia* flies at different times during the summer in different parts of its distribution. On the Wirral, for example, Sir Cyril Clarke routinely operates his trap each year from 1 June through 31 July (Clarke et al. 1994), but the best time to collect this species lasts only about two weeks beginning around the middle of June. A few are flying as early as late May, but by August the breeding season for *B. betularia* is over on the Wirral, although there is

an abundance of other moth species still flying. August, on the other hand, is a good month for trapping *B. betularia cognataria* in the mountains of Virginia (West 1977, Grant & Howlett 1988) where the species is bivoltine. Yet, *cognataria* have never been reported just a few hundred miles away in eastern Virginia. Thus, over short geographic, altitudinal, and temporal distances, the species may be present or absent in collections. Once a specimen is caught at a location, we can be certain that it occurs there, but its absence proves nothing unless traps are run at the same location throughout an entire season, and preferably over several years.

To our knowledge (through previous experience from trapping in England, the Green and White Mountains of Vermont and New Hampshire, New York's Adirondacks, Michigan's Upper Peninsula, as well as the Appalachian Mountains and Coastal Plain of Virginia), the species does not thrive where summers are long and hot. At the same latitudes, however, it may be common at higher elevations where cooler temperatures prevail. *Biston betularia* is reportedly capable of feeding on 30 widely different genera of host plants (Tietz 1972), many of which are common where this moth species apparently is not; therefore we would not suggest that its distribution is solely restricted to the availability of potential host plants.

Different wave lengths of light are variously effective in trapping different moth species (Robinson 1952). We considered the possibility that the paucity of *B. betularia* in our traps during the 1988 season might have resulted from the wrong wave length emitted by the Toshiba 100 watt MV bulbs used by us for the first time that year, even though the traps caught hundreds to thousands of moths of numerous other species each night. The following year, however, the same bulbs were used successfully to trap *B. betularia* elsewhere, thus eliminating wave length as the explanation for the absence of this species in the traps at certain locations.

In all, we examined 307 specimens of this species during the course of our study. No melanics were found at any location. We cannot conclude that melanic variants are entirely absent in Japanese *B. betularia*, but it seems reasonable to conclude that such forms are not common. This conclusion is reinforced by H. Inoue (pers. comm.) who indicated that to his knowledge no one has ever reported collecting a melanic variant of *B. betularia* in Japan. As Owen (1962) has observed, rare forms often are over-represented in museum collections simply because they are rare. All things taken together strongly argue that color polymorphism does not exist in *B. betularia* populations anywhere in Japan. This does not preclude that rare variants arise by recurrent mutation, but considerably larger sample sizes are necessary to assess mutation rates.

Based on this study and from the collective experience of other workers in Japan, it appears that this species and Japanese industry are allopatric, i.e., heavy industry is mainly concentrated along the coast, and *B. betularia* lives in the central mountains and farther north. In our judgment, Japanese industry has not blackened the surrounding countryside as did British industry during its prime. Hence, even if *B. betularia* populations do occur near Japanese industrial centers, it is unlikely that a carbonaria-like form arising by mutation would enjoy the same advantage as it once did in Britain.

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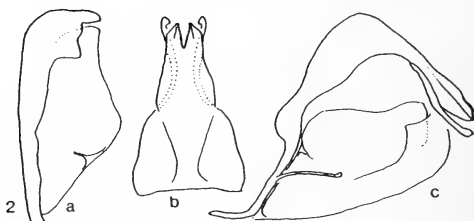
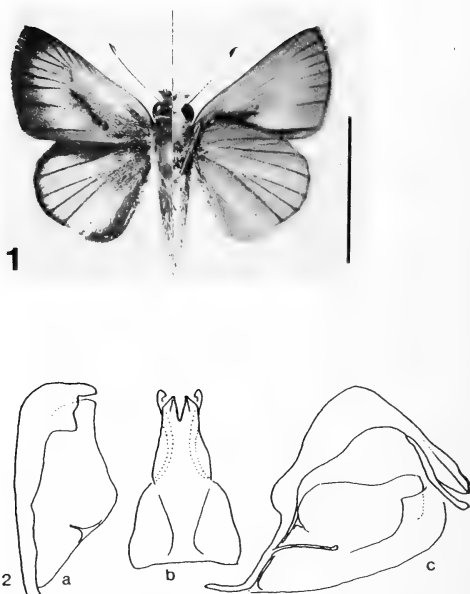
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FIRST RECORDS OF *PARACHORANTHUS MAGDALIA* (HESPERIIDAE)
FROM THE BAHAMAS, AND EXTENSION OF THE BAHAMIAN
RANGE OF *BATTUS DEVILLIERS* (PAPILIONIDAE)

Additional key words: West Indies, Cuba, dispersal, colonization, biogeography.

The addition of butterfly species to faunal lists in the Bahamas and elsewhere in the West Indies may reflect discovery of long-established but overlooked populations, chance interception of newly arrived vagrants, or discovery of new colonies they have established. Species that are not on the wing throughout the year may readily be missed on islands



FIGS. 1-2. *Parachoranthus magdalia*. 1, Male: left upperside, right underside. Nicholl's Town, North Andros, scale line: 10 mm; 2, Genitalia: a, left valva, inner aspect (setae on outer surface omitted); b, dorsal view of genital capsule; c, lateral view of genital capsule with left valva removed.

surveyed during brief and sporadic visits, and the probability that small numbers of vagrants will be recorded is very low, unless they achieve at least temporary colonizing success. Against this background, we note and discuss two recent Bahamian records of biogeographical interest in the context of inter-island dispersal and colonization, and provide further data on Cuban-Bahamian faunal links.

Parachoranthus magdalia (Herrich-Schäffer) (Hesperiidae) has been considered a Cuban endemic species, unknown from the Isle of Pines but widely distributed and locally abundant on the main island. It occurs from the lowlands to the mountains, most frequently in open, grassy habitats, but also along shady forest tracks. Its life history is unknown, but grasses presumably serve as larval foodplants. Between 12 and 28 August 1993, six males were collected (DK) near Nicholl's Town, at the northeastern tip of Andros Island. They were found in two small natural clearings (100 m²) in mature hammock forest with trees to 10 m, generally flying swiftly and perching on broad leaves. Nectaring was not observed, and the butterfly was not seen on nearby disturbed, open land. All specimens collected were fresh. The butterflies were sparsely distributed; generally only a single specimen was seen on each visit to the locality in the morning, and perhaps another in the afternoon. Seven more males, most in fresh condition, were collected when the locality was revisited on 17-18 October 1993. No females were found; in Cuban sites when *P. magdalia* is abundant this sex is reclusive, and males greatly predominate in random samples.

The Andros specimens (Fig. 1) are identical in wing pattern to series of males from Soroa, Pinar del Río, and other Cuban localities. They do not differ appreciably in size (Andros: mean forewing length 10.36 mm, $n = 13$, range 9.7-11.0 mm; Cuba: 10.40 mm, $n = 20$, range 9.5-11.2 mm). The genitalia of Andros specimens (Fig. 2) and Cuban specimens are identical.

Battus devilliers (Godart) (Papilionidae) has been known previously as widely distributed throughout Cuba, perhaps more frequent in the west, recently found on the Isle of Pines, and elsewhere known only from southern, central, and northern localities on Andros Island. On 27 June 1993, the authors, with Neil Davies, recorded a worn female of *B. devilliers* near the north-west end of Lake Cunningham, in the north-central region of New Providence Island. Ten days later, other specimens were seen in this locality by Leonard C. Smith, and on 5 August newly emerged adults were recorded by DK in a recently cut-over area of scrub 200 m from the original site. On 20 September we revisited the area and counted 30 specimens in 45 minutes, some fresh and others worn, and added two further sight records the following day at localities up to 5 km to the east. On 3 October it was equally common. The records are concentrated in a disturbed area where young secondary forest was cleared early in 1993 and by summer was covered by low plants, including *Leucaena leucocephala* (Lam.) (Fabaceae), *Stachytarpheta jamaicensis* (L.) (Verbenaceae), *Bidens alba* (L.) (Asteraceae), and species of *Lantana* (Verbenaceae). The butterflies often enter the cleared land from the forest, generally flying swiftly, but making brief nectaring visits to *Stachytarpheta*, *Lantana camara*, and *Bourreria ovata* trees at the cut edge of the forest.

New Providence and Andros islands differ greatly in size, in their terrain, and in the history of documentation of their butterfly faunas. The former is relatively small (207 km²), populous, and increasingly damaged by development, and was the first Bahamian island for which lists of butterflies were compiled (Sharpe 1900). Andros is much larger (5960 km²), largely covered by pineland in the east. Mature pines were logged extensively about 20 years ago, but the forest is now recovering. The west is fringed with mangrove and includes vast areas of temporarily flooded sawgrass prairie with scattered pine associations, and the small human population is gawped in communities only along the east coast. Much of the island remains virtually inaccessible, and butterflies have been sampled from only a small proportion of the total area of the island. Much of our knowledge of the butterfly fauna is based on the work of Clench (1977) and later records of Harvey and Peacock (1989). These differences may be considered in assessing the two new records.

The arrival of *B. devilliers* on New Providence is perhaps less surprising than the virtual absence of its relative *B. polydamas* from the island. Although the latter was recorded by Sharpe in a collection made at the end of the last century, and West (1966) found it along the north coast in 1945, it seems to have disappeared subsequently, and the senior author recorded it only once during the past thirty years. Other than in the extreme south, *B. polydamas* is distributed widely in the Bahamas, and was abundant on North Andros in August 1993, only 40 km to the west. Its decline and present rarity on New Providence cannot be attributed to lack of larval foodplants: Correl and Corell (1982) record *Aristolochia passiflorifolia* (A. Rich. in Sagra) (Aristolochiaceae) and/or *A. pentandra* (Jacq.) from all the larger Bahamian islands except Cat Island, Great and Little Inagua, and the Turks and Caicos Islands (where *B. polydamas* has been recorded by St. Leger (1991) only as a rare vagrant); both plants are present on Andros and New Providence. The area where *B. devilliers* was first found was visited regularly in the past by DK, and while a very small population may have been maintained for some time, an abundance such as that seen in September and October 1993 could not have gone undetected. If the first record in June was a chance interception of a founder vagrant, then the subsequent population build-up was remarkably rapid. Whenever the initial colonization occurred, it is possible that the absence of larval competition from another *Battus* contributed to the present success of *B. devilliers*.

We can be less confident that *Parachoranthus magdalia* is a recent arrival on Andros than for *B. devilliers* on New Providence. In addition to Clench's stays between 1973 and 1976, field work on the island has been carried out by several visitors including the authors and others, but only for short periods, and it seems to us more probable that this skipper is a long-established but overlooked resident. It is not inconspicuous, but small colonies could have escaped notice among the scattered sites sampled on Andros in the past. Furthermore, one of us (DSS) noted great variation in abundance in Cuban localities, from one year to the next, further stressing the role of chance in recording or missing a resident species. It remains possible that the fresh *P. magdalia* collected were the progeny

of recent immigrants, but they were found in the region of Andros furthest (350 km) from Cuba, almost twice the distance between the southernmost point of Andros and the north Cuban coast.

The recognition of *P. magdalia* on North Andros may stimulate search for it in other localities, perhaps leading to further information on its distribution on the island. Moreover, studies on Cuban and Bahamian populations at the level of molecular genetics might well contribute information on the history of its presence outside its island of origin. Vagrancy with colonization potential, realized or otherwise, is a notable feature of West Indian butterfly faunas; moreover, several instances of faunal exchange between southern Florida and the islands have been recorded in recent decades (Smith et al. 1994). Continued monitoring of *B. devilliers* on New Providence offers an opportunity to follow the fate of a vagrant, in this instance presumably from Andros, that has achieved conspicuous initial success as a colonist.

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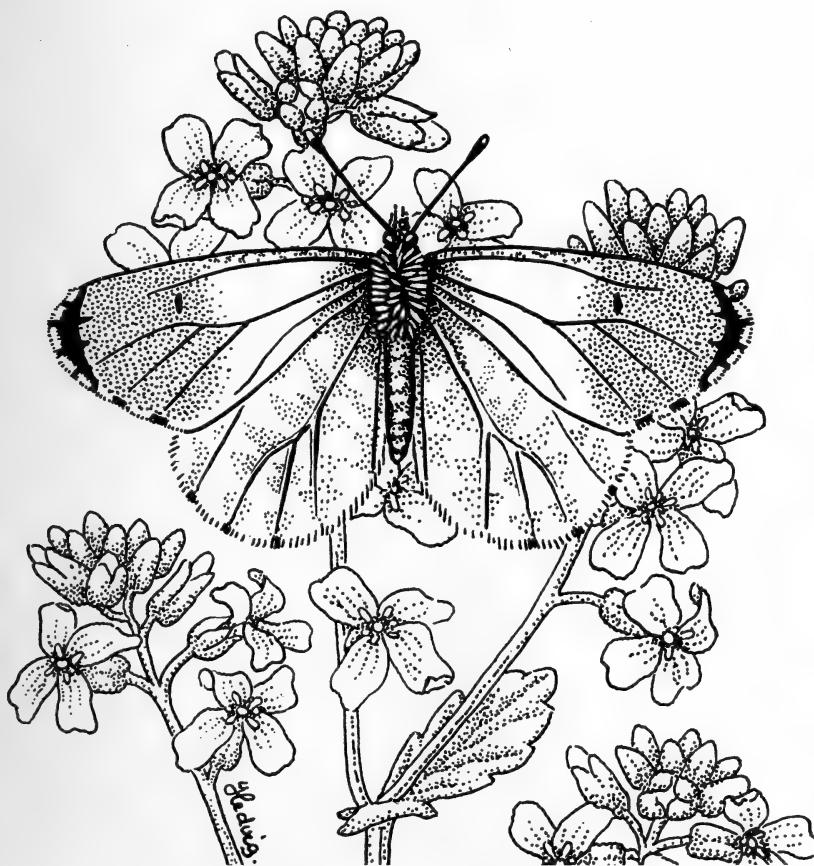
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Cover illustration: The European orange-tip, *Anthocharis cardamines* (Pieridae), sitting on *Barbarea vulgare* (Brassicaceae). Original drawing by Hedvig Wright Ostern, Torsarudstuppen 25, 3430 Spikkestad, Norway.

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RARE LEPIDOPTERA AT MOUNT PIPER, VICTORIA—THE ROLE OF A THREATENED BUTTERFLY COMMUNITY IN ADVANCING UNDERSTANDING OF INSECT CONSERVATION

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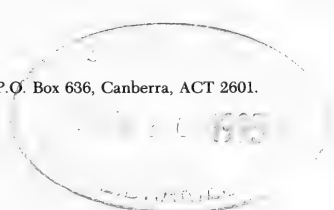
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ABSTRACT. Mount Piper, Victoria, Australia, is the site of a unique assemblage of diurnal Lepidoptera, designated formally as a "Threatened Community." The problems of evaluating status and defining the biology of rare butterflies hilltopping there are exemplified and discussed on the basis of surveys from 1991-1993. Management steps needed to sustain the community are outlined.

Additional key words: Lycaenidae, hilltopping, status evaluation, survey, legal protection.

Protective legislation for species and communities and practical conservation management are complementary activities in sustaining natural biodiversity in many parts of the world. Recent legislation in Victoria, Australia, is providing for new and holistic emphases on conservation of the State's biota, because it includes provision for protection of "threatened communities" and for control of "threatening processes," as well as merely prohibiting the capture of nominated taxa. The Flora and Fauna Guarantee Act 1988 aims to "guarantee that all taxa of flora and fauna and ecological communities in Victoria can survive, flourish, and retain their potential for evolutionary development in the wild." This paper is a preliminary account of the Act in operation, and the consequent development of a practical conservation strategy for a threatened community designated "Butterfly Community No. 1," at Mount Piper (32°12'S, 145°0'E), 80 km north of Melbourne in central Victoria (Fig. 1).

¹ Current address: Australian National Conservation Agency, P.O. Box 636, Canberra, ACT 2601.



The community is characterized and designated by the presence of several rare Lycaenidae, and the vegetation and ants associated with these. In particular, Mount Piper is the site of the only known co-occurrence in Victoria of two rare lycaenid butterflies, *Acrodipsas myrmecophila* (Waterhouse & Lyell) and *A. brisbanensis cyrilus* (Anderson & Spry). The "threatened community" is based on the biotic association rather than the site; i.e., if additional sites in the State were found to harbor these two species, those automatically would come under the same protection as Mount Piper. The two *Acrodipsas* species are listed as protected taxa under schedule 2 of the Act, and they and the community are listed because they are considered to be "significantly prone to future threats that are likely to result in their extinction, primarily because of their restricted occurrence and sensitivity to environmental conditions."

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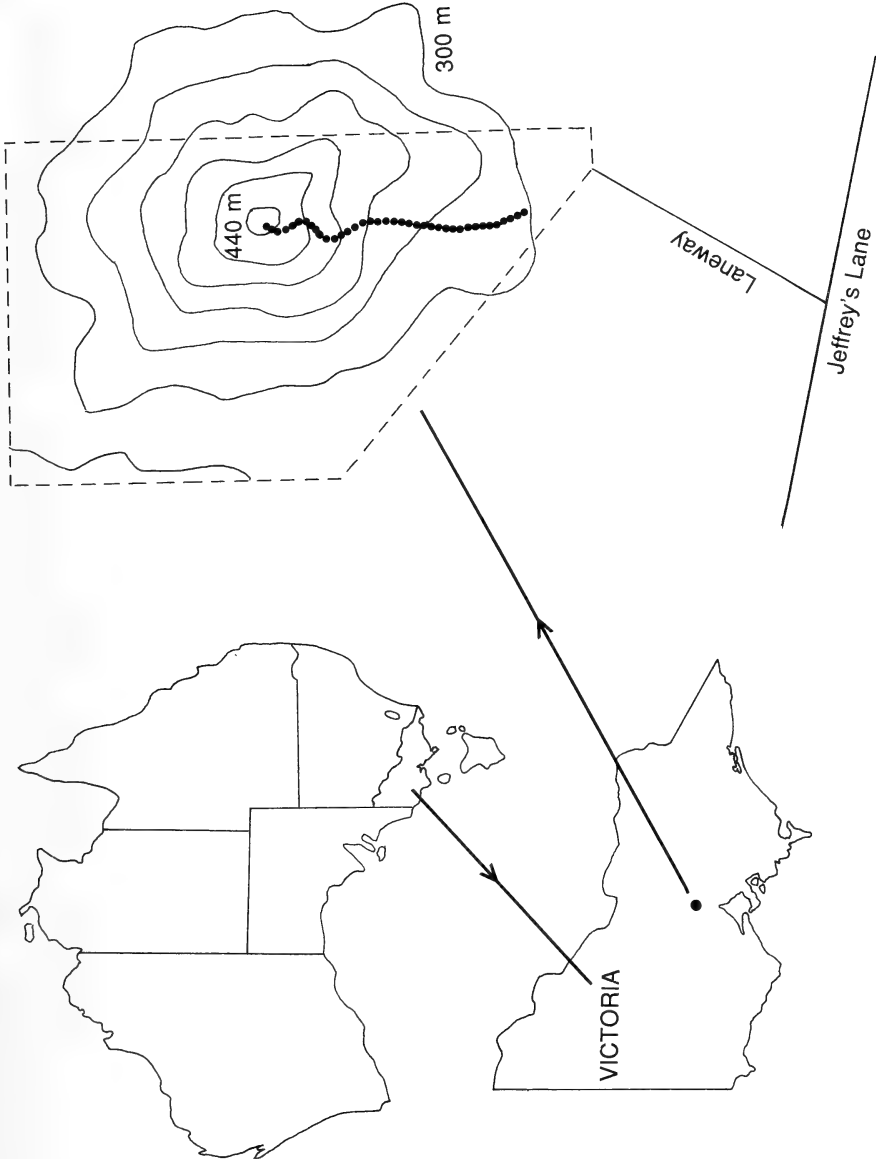
- (1) the status of any taxon nominated must be investigated to determine whether listing is justifiable and, if so
- (2) an "Action Statement" setting out the management and conservation needs must be prepared and, in due course, implemented. This implementation is currently under way for Butterfly Community No. 1.

This paper summarizes the significance of Mount Piper as a site for rare diurnal Lepidoptera and reviews information accumulated during two years of systematic survey of these insects and the associated ants on and around the mountain (Britton & New 1992, 1993, Jelinek et al. 1994). The difficulties of studying extremely rare species for which little biological information is available are emphasized.

MOUNT PIPER

Mount Piper is an isolated volcanic plug rising to 456 m from the surrounding plains. It is an island of natural vegetation surrounded predominantly by land cleared for pasture, habitat inhospitable to many native insects and other biota, and is typical of the small remnant habitats common in much of the intensively-settled parts of Australia. It has been a favored butterfly collecting locality for several decades because of the propensity of a number of desirable species to hilltop

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 FIG. 1. Location of Mount Piper in Victoria. Contour lines are 30 m intervals; walking track to summit indicated. Dashed line is boundary of current Education Reserve.



around the summit. However, its local prominence has led to the development of the summit for transmission and survey purposes, a vehicle track that led almost to the summit, tree felling to establish sight-lines from the trigonometrical station, and the construction of communication towers and a radio shed just below the summit. Easy general access led to despoliation through selective timber cutting, firewood collecting, the presence of grazing stock (such as cattle and goats), activities of feral animals (such as rabbits), a more general vehicle access, and the establishment of non-native grasses and other introduced weeds. During the 1940s, timber from Mount Piper was used to fire the local Broadford paper mill, and mining for antimony and gold occurred on the mountain. There have been recent moves to re-establish mining activities and to explore further for minerals in the area. Mount Piper is an important scenic area to the local community, and is figured on the logo of the local town, Broadford.

DEVELOPMENT OF CONSERVATION CONCERN

The community was nominated for listing under the Flora and Fauna Guarantee on 23 October 1989, and recommended finally for listing on 22 May 1991. The recommendation recognized that the assemblage of flora and fauna present included several rare or extremely rare butterflies, and that the community was threatened by habitat damage including fire, land clearance, and damage by feral and other grazing animals. The Scientific Advisory Committee noted also that significant butterfly species were threatened by overcollection, and that proposals for gold-mining (and resulting dust, vibration, and vegetation clearance) would lead to serious damage to the community and its butterfly fauna if they were pursued. At this time, much of Mount Piper (nearly 56 ha) was included in an Education Reserve for the Study of the Natural Environment established in 1980.

The Action Statement (Jelinek 1991) set out a preliminary appraisal of the management issues needed to prevent extinction of the community. Earlier management actions included the eradication of feral goats (1990) and removal of the radio mast, shed, and associated structures (1990). Intended management, in addition to the restriction on taking flora and fauna provided by the act, was deemed to necessitate a number of steps, namely (1) research and monitoring of the rare butterflies, (2) survey of other sites where the community might occur, (3) identification of the critical habitat, (4) protective zoning of the area by the Shire of Broadford, (5) implementing an education and awareness program in the local community—including encouraging sympathetic management of private land adjoining the community, (6) eradicating exotic weeds and rabbits, (7) revegetating disturbed areas and tracks,

(8) implementing a fire management program and (9) providing informative displays for visitors to the reserve.

These parameters and others were assembled into a research strategy which could help to ensure that management of the community—especially the rare lycaenids—could be pursued from a basis of sound knowledge (Jelinek 1992).

The major initial steps were to define and assess the abundance of the fauna of diurnal Lepidoptera at Mount Piper and the biology and resource needs of significant species, and to determine whether those species occurred also on other (putatively similar) hills in central Victoria. This work was commenced in the 1991–92 and 1992–93 seasons. Transect counts and hilltop surveys were made for adult diurnal Lepidoptera throughout the main flight seasons (November–March inclusive), with the frequency depending on weather: 51 visits were made over the two periods. All aspects and altitudes of the mountain were included in surveys, in addition to the surrounding lowland and roadside corridor vegetation along Jeffrey's Lane and the Laneway into Mount Piper (Fig. 1). Ants were collected by pit-fall trapping and direct searches and sweeping of vegetation.

THE BUTTERFLY COMMUNITY

Most species of butterflies encountered are recognizable by sight, but others, including hilltopping lycaenids, were captured to assure accurate identification. Twenty species were recorded in 1991–92, and 32 in the more extensive survey of 1992–93. Thirty-seven species of butterflies (including previous records) are now known from Mount Piper and its immediate vicinity. These (Table 1) comprise several ecological categories.

Some are infrequent vagrants, reaching Mount Piper sporadically as stragglers or migrants outside their usual range: species such as *Acraea andromacha* (F.) (Nymphalidae) and *Appias paulina ega* (Boisduval) (Pieridae) are recorded infrequently in Victoria, and have been found only on one or few occasions. However, 26 species are residents or likely residents. Altogether, 15 species are regarded as "significant" as rare species of conservation interest and concern, as representing populations (possibly remnants) on the southern fringe of their recorded range, or as rare or notable vagrants. The importance of Mount Piper for butterflies is thereby two-fold: as a habitat for nearly a third of Victoria's resident butterfly species, and as a focus or hilltopping site for additional vagrant and migrant species. A number of the rarer species were found only on the summit, and their breeding habitat can only be inferred to occur in the Mount Piper site. The most significant taxa are noted individually.

TABLE 1. The butterfly species recorded from Mount Piper, to April 1993. (Species asterisked have not been collected during our survey.)

Taxon	Status
Hesperiidae	
<i>Trapezites phigalioides</i> Waterhouse	Resident, common
<i>T. luteus luteus</i> (Tepper)	Resident, localized
<i>Dispar compacta</i> (Butler)	Resident, common
<i>Signeta flammeata</i> (Butler)	Resident, sparse
<i>Taractrocerca papyria papyria</i> (Boisduval)	Resident, common
<i>Ocybadistes walkeri sothis</i> Waterhouse	Possible resident, sparse
Papilionidae	
<i>Papilio anactus</i> W. S. MacLeay	Vagrant, rare
<i>P. demoleus sthenelus</i> W. S. MacLeay	Vagrant, rare
Pieridae	
<i>Delias aganippe</i> (Donovan)	Resident, common
<i>D. harpalyce</i> (Donovan)	Resident, common
<i>Anaphaeis java teutonia</i> (F.)	Vagrant, common
<i>Pieris rapae</i> (L.)	Vagrant, common
* <i>Appias paulina ega</i> (Boisduval)	Vagrant, rare
* <i>Eurema smilax</i> (Donovan)	Vagrant, rare
Nymphalidae	
<i>Geitoneura klugti klugti</i> (Guérin-Méneville)	Resident, common
<i>Heteronympha merope merope</i> (F.)	Resident, common
<i>Vanessa kershawi</i> (McCoy)	Possible resident, common
<i>V. itea</i> (F.)	Vagrant, common
* <i>Acraea andromacha andromacha</i> (F.)	Vagrant, rare
<i>Junonia villida calybe</i> (Godart)	Resident, common
<i>Danaus chrysippus petilia</i> (Stöll)	Vagrant, rare
Lycaenidae	
<i>Acrodipsas brisbanensis cyrilus</i> (Anderson & Spry)	Possible resident, sparse
<i>A. myrmecophila</i> (Waterhouse & Lyell)	Possible resident, rare
<i>Hypochrysops delicia delos</i> (Waterhouse and Lyell)	Possible resident, common
<i>Ogyris olane ocela</i> Waterhouse	Resident, common
<i>O. genoveva genoveva</i> Hewitson	Possible resident, rare
<i>O. abrota</i> Westwood	Resident, localized
<i>Neolucia agricola agricola</i> (Westwood)	Possible resident, sparse
<i>Theclinesthes miskini miskini</i> (T. P. Lucas)	Possible resident, sparse
<i>T. serpentata serpentata</i> (Herrich-Schaeffer)	Vagrant, common
<i>Lampides boeticus</i> (L.)	Vagrant, sparse
<i>Zizina labradus labradus</i> (Godart)	Resident, common
<i>Nacaduba biocellata biocellata</i> (C. & R. Felder)	Possible resident, common
* <i>Candalides hyacinthinus simplex</i> (Tepper)	Possible resident, rare
<i>Lucia limbaria</i> Swainson	Resident, localized
<i>Jalmenus evagoras evagoras</i> (Donovan)	Resident, common
<i>J. icilius</i> Hewitson	Resident, rare

Lycaenidae

Acrodipsas myrmecophila (Waterhouse & Lyell), the small ant-blue. This rare species has been recorded from only three localities in Victoria, and habitat loss has resulted in its extinction at two of these, Ocean Grove and Ringwood (Fig. 2a), so that Mount Piper harbors the only known colony in Victoria. It is known also from New South Wales, Queensland, and the Northern Territory (one record), but is very rare throughout this wide range (Common & Waterhouse 1981, Dunn & Dunn 1991).

At Ocean Grove, caterpillars were associated with small black ants (*Papyrius* [formerly *Iridomyrmex*] *nitidus* -group) and may be predatory on ant larvae. Little is known of the biology of *A. myrmecophila*, but adults have been recorded over the period of late October to February in Victoria. *Acrodipsas myrmecophila* is extremely rare at Mount Piper; one individual male was seen on the summit in 1991–1992 (11 March 1992, representing a seasonal extension over known specimens) and (possibly) two males in 1992–1993 (31 December 1992, 2 January 1993), all flying around eucalypts in company with the following species.

Acrodipsas brisbanensis cyrilus (Anderson & Spry), the large ant-blue. This species, possibly not truly distinct from the nominate subspecies, *A. b. brisbanensis* (Miskin) (Common & Waterhouse 1981, Dunn & Dunn 1991), has been recorded from about eight hilltop localities in Victoria from December to February. Recent records are from only five localities (Mount Piper, The Paps, Genoa Peak, Kangaroo Ground, Wedderburn: Fig. 2b), and it is believed to be extinct at other localities. *Acrodipsas b. brisbanensis* occurs in Queensland, New South Wales, and Western Australia, but is rare throughout this range. At Kangaroo Ground, oviposition on a stump infested with *P. "nitidus"* ants was observed by Douglas and Braby (1992), and a northern Queensland individual was reared from a pupa found in an arboreal ant nest (Dunn & Dunn 1991). Otherwise, nothing is known of the life history of *A. brisbanensis*. It was not found at Kangaroo Ground in 1992–1993; the oviposition site there had been destroyed by housing development.

At Mount Piper, *A. b. cyrilus* males were recorded on four occasions during the first season (14, 23 December 1991, 11, 13 March 1992) around the two largest eucalypts on the western and southern sides of the summit (Fig. 4), and on five occasions during the second season (31 December 1992, 2, 14, 20, 22 January 1993), around the top of the highest eucalypt on the summit. No females were observed, although this sex has been captured hilltopping by other workers; they are thought to remain on summits for only short periods and do not settle on vegetation, as do males (Braby pers. comm.).

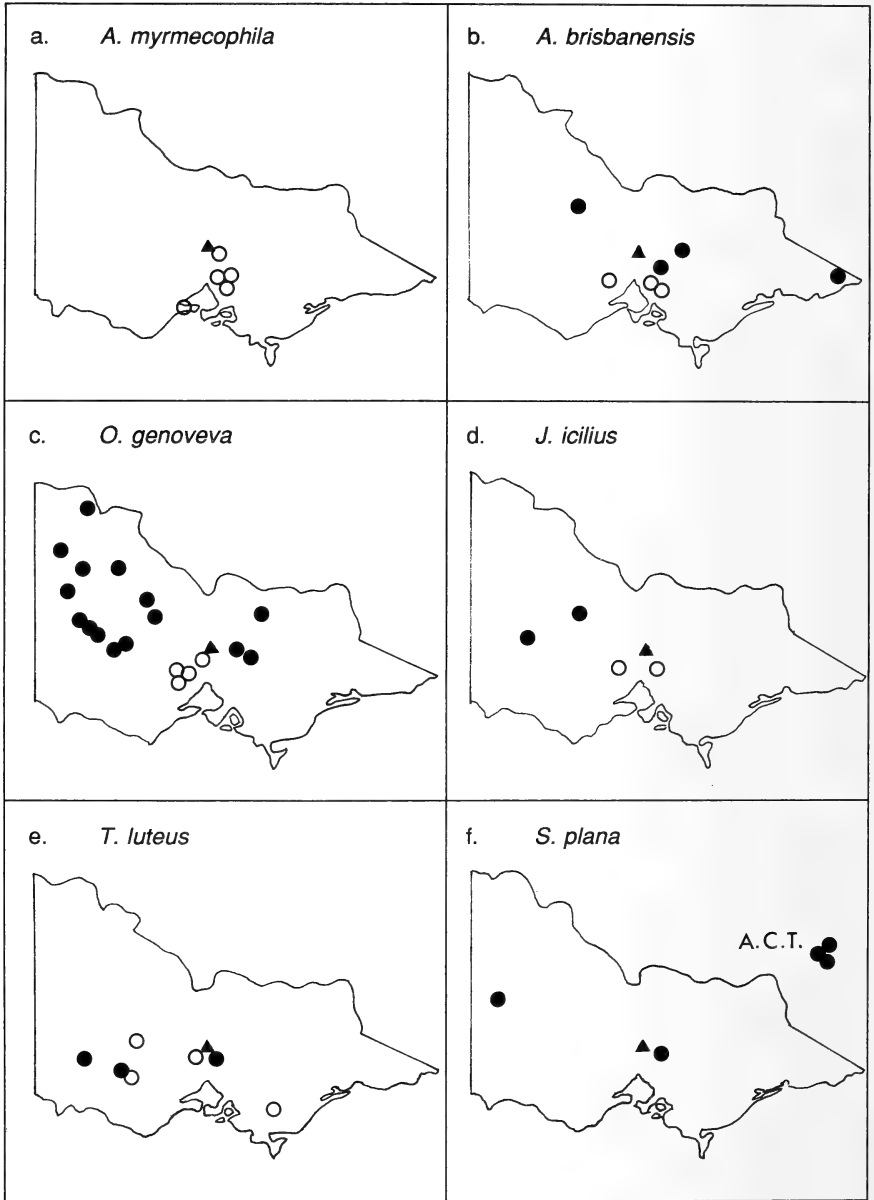


FIG. 2. Distribution in Victoria of selected species of significant Lepidoptera found at Mount Piper: see text for details. Mount Piper: ▲; extant known distribution ●; historical distribution records ○. (Australian Capital Territory populations of *S. plana* indicated).

Ogyris genoveva genoveva (Hewitson), the genoveva azure. This rare species has been recorded from about eight localities in Victoria, and is uncommon also in New South Wales and Queensland. Larvae, in common with those of most other species of *Ogyris*, feed on foliage of mistletoes, and those of *O. genoveva* are attended by sugar ants (*Camponotus* spp.) and shelter in ant nests near the base of host trees during the day. It is believed to be extinct at some of the Victorian localities (Fig. 2c). At Mount Piper, it was not observed during 1991–1992, but hilltopping males were seen in the late afternoon on three dates in 1993 (29 January, 2, 7 February), all of them defending territories on dead or dying *Acacia implexa*.

Jalmenus icilius Hewitson, the icilius blue. Only three extant colonies of this rare species are known in Victoria (Douglas & Braby 1992) (Fig. 2d), and it is probably extinct in two other areas where it was known previously. A breeding colony was discovered on *Acacia pycnantha* at Mount Piper as a result of observing adults flying around a small area of grassland on the northeastern base in December 1992. Larvae are tended by *Iridomyrmex* ants, referred to tentatively to *I. vicina*, a common species around Mount Piper. The colony of *J. icilius* at Mount Piper is very small, and local conditions may not be optimal for this species.

Hesperiidae

Trapezites luteus luteus (Tepper), rare white-spot skipper. This species is rare throughout its range: there are two records from South Australia over the last half century (Fisher 1978), and only four Victorian populations are likely to be extant (Fig. 2e) (Crosby pers. comm.). The skipper was found in March 1993 on farmland near the Mount Piper reserve area, but not connected with it—this species was last recorded in the Broadford area in 1953, and is included here as a scarce taxon warranting conservation measures in the State. Part of its apparent rarity may be due to its very short flight season, only about two weeks at Mount Piper, so that it is unlikely to be found by many collectors.

The remainder of the resident butterfly fauna is composed of generally common and widespread species in Victoria, although one additional lycaenid (*Lucia limbaria* Swainson, the small copper) has a very patchy distribution, and the strong colony in grasslands near Mount Piper merits study to determine possible reasons for this. Larvae there are associated with yellow wood sorrel (*Oxalis corniculata*; Oxalidaceae) and are tended by *Iridomyrmex* ants, possibly *I. "itinerans."*

TABLE 2. Diurnal moths recorded from Mount Piper, to April 1993.

Taxon	Status
Castniidae	
<i>Synemon plana</i> Walker	Resident
Noctuidae: Agaristinae	
<i>Comocrus behri</i> (Angas)	Resident, common
<i>Phalaenoides glyciniae</i> Lewin	Vagrant
<i>Eutrichopidia latinus</i> (Donovan)	Possible resident
Arctiidae	
<i>Nyctemera amica</i> (White)	Resident, common
<i>Asura lydia</i> (Donovan)	Possible resident, common
<i>Utetheisa pulchelloides</i> Hampson	Possible resident, common
Zygaenidae	
<i>Pollanisus viridipulverulentus</i> (Guérin-Méneville)	Possible resident, common

THE DIURNAL MOTHS

Eight species of conspicuous day-flying moths also occur at Mount Piper (Table 2), and one of these is of significant conservation interest.

Castniidae

Synemon plana Walker. This rare grassland moth represents a family of current conservation concern in Australia (Edwards 1991), because most species have declined considerably with alienation of native grasslands. *Synemon plana* is known from about 10 colonies, most of them small, in the Australian Capital Territory (A.C.T.), and two other sites in Victoria (Fig. 2f).

It was discovered in considerable numbers on native grassland patches during December 1992, when numerous males were observed flying. Larvae feed on roots of grasses, at Mount Piper on *Danthonia pilosa* (Poaceae). The colony at Mount Piper is one of the two largest known (the other being at the Belconnen Naval Station, A.C.T.), and may be an important refuge for *S. plana*.

DISCUSSION

Importance of Mount Piper for Diurnal Lepidoptera

The presence of the above notable taxa and a considerable number of other species, renders Mount Piper of unique importance as a site for Lepidoptera in Victoria. However, this must be viewed against a background of incomplete documentation of butterfly distributions in the State, and enhanced knowledge of Mount Piper because of its

TABLE 3. Numbers of butterfly species recorded from other upland localities in central Victoria (shown on Fig. 3) during surveys in 1992–93. (Site 4, omitted, is Mt. Piper.)

Locality	No. species recorded (no. visits)	Notable taxa
1 Brisbane Ranges	10 (1)	—
2 Kangaroo Ground	13 (6)	—
3 Mt. William Ranges	10 (1)	—
5 Warragul Rocks (Tallarook Ranges)	5 (1)	—
6 Yea Spur (Junction Hill)	8 (1)	—
7 Glenaroua	5 (1)	—
8 Mt. Hope	10 (1)	—
9 Seymour Bushland Reserve	6 (1)	—
10 Cathedral Ranges	13 (1)	—
11 The Paps	25 (5)	<i>A. brisbanensis</i> , <i>L. limbaria</i> , <i>O. genoveva</i> ,
12 Blue Range	14 (1)	<i>O. genoveva</i>
13 Mt. Samaria	6 (1)	—

proximity to Melbourne and as a “traditional” collecting site for butterflies.

In an attempt to clarify the conservation interest of the area, visits were made to a number of other isolated hills in central Victoria (Fig. 3), and diurnal Lepidoptera recorded (Table 3). In most cases, only single visits were made but, collectively, 40 species of butterflies were recorded there and/or at Mount Piper. *Acrodipsas brisbanensis* was found at The Paps, near Mansfield (the most intensively investigated site), as was *O. genoveva*. The latter occurred also at the nearby Blue Range. *Acrodipsas myrmecophila* was observed only at Mount Piper, so that the known distribution of the “threatened community” has not yet been extended. However, it is becoming clear that The Paps also may be of significant conservation interest for butterflies. Intensive and extensive surveys are necessary in order to clarify the status of some rare species.

Ant Hosts of Critical Lycaenidae

Systematic collections of ants were made by pit-fall trapping and direct searching throughout the year at a number of sites on the slopes of Mount Piper. An initial survey in 1991–1992 yielded 60 morphospecies representing 27 genera; this total has risen to about 140 morphospecies with recent collecting. However, the recorded host ant of the two *Acrodipsas* has not yet been found there, although it was present from around 1950–1970 on farmland about 3 km to the east, where *A. myrmecophila* also occurred. That colony of butterflies may have been eliminated by agricultural development (D. F. Crosby pers. comm).

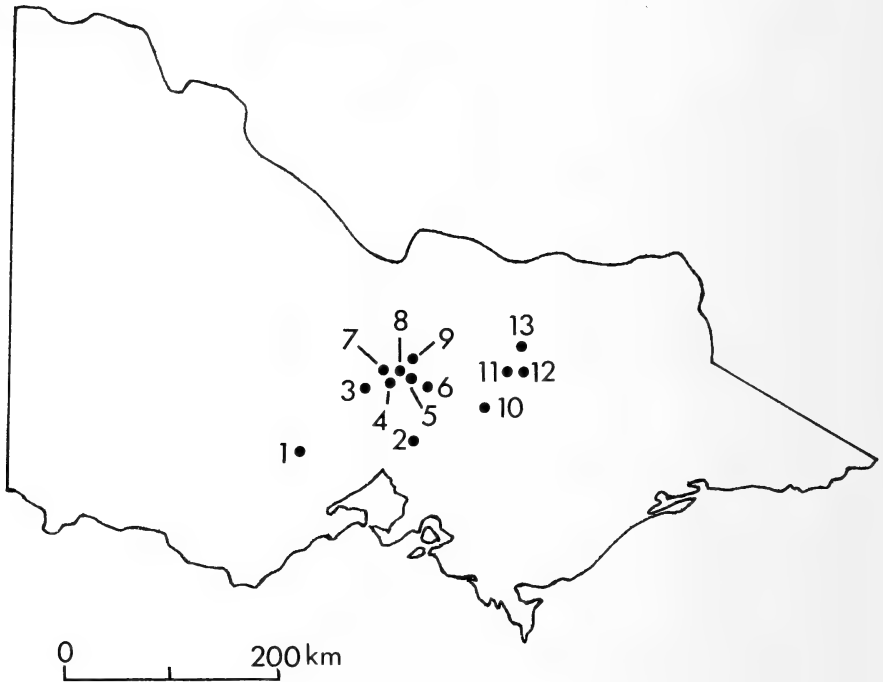


FIG 3. Localities sampled from October 1992—March 1993. 1, Brisbane Ranges; 2, Kangaroo Ground; 3, Mt. William Ranges; 4, Mount Piper; 5, Warragul Rocks (Tallaroek Ranges); 6, Yea Spur (Junction Hill); 7, Glenaroua; 8, Mt. Hope; 9, Seymour Bushland Reserve; 10, Cathedral Ranges; 11, The Paps; 12, Blue Range; 13, Mt. Samaria.

The ant, "*P. nitidus*," formerly occurred in dead *Acacia pycnantha* wood in open country; it is distinctive because of a strong coconutlike odor, and is commonly termed "the coconut ant." Nest structure is also characteristic because of the carton-covered runways made by this species. The apparent scarcity of both species of ant-blues at Mount Piper may reflect the low numbers of the host ant, its restricted distribution, or both these factors.

Two possible host ant species for *O. genoveva* were found around the base of Mount Piper, but examination of nests of *Camponotus "consobrinus"* and *C. "rubiginosus"* in conjunction with the mistletoe hosts did not yield immature stages of the butterfly.

Integrity of the Community

The lack of knowledge of the life histories of the rare ant-blues, and the very low numbers of individuals observed each season at Mount Piper, emphasize the difficulties of studying such taxa, evaluating their

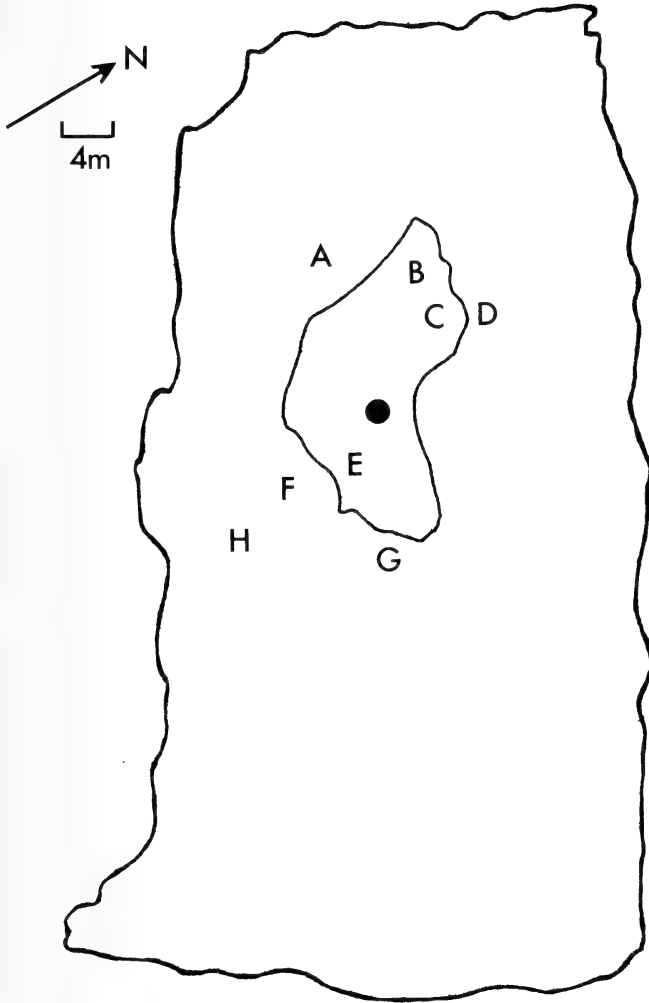


FIG. 4. The summit area of Mount Piper; inner line denotes flat open area; ● trigonometrical point; A-H trees used for hill-topping sites by notable Lepidoptera (see text).

status accurately, and defining their management needs constructively. It is not yet clear, for example, whether either *Acrodipsas* species breeds in the current Mount Piper reserve, or if they congregate from elsewhere to utilize the summit as an assembly site. In common with other hill-topping Lycaenidae, such as various *Hypochrysops* Felder & Felder in Queensland (Sands 1986), some *Acrodipsas* fly fast and stongly, and the distance from which they may assemble is unknown.

In principle, this lack of detailed knowledge does not diminish the

need for conservation of Mount Piper, as its role as a hilltopping site may be vital to the well being of the butterflies, but emphasizes the need for additional exploration around the site as well as within it to define the species' biology more completely. Indeed, observations on hilltopping behavior emphasized that the various species adopted only particular trees from the selection available. Thus (Fig. 4) both *Acrodipsas* were found in 1992–93 only around tree A (a 6 m living *Eucalyptus*); *O. genoveva* on trees B, C and D (a 4 m dead *Acacia*, and two 7 m living acacias); and the other individual trees noted were the foci for other lycaenids, including *O. olane ocela* and *Nacaduba biocellata* (hilltopping generalists), found around all eight trees shown. *Hypochrysops delicia delos* was found mainly around tree A, from November to February. Maintenance of particular features of a hilltop thus may be necessary to assure the availability of territory for a diverse range of species. Management is thus needed to assure the integrity of the habitat both for breeding and assembly of rare butterfly species. It is likely that such isolated hilltopping sites may need to be maintained in sufficiently diverse condition so that a number of distinct territories or perches for individuals and different species are available. A number of common butterflies (*Delias* spp., *O. olane*) also hilltop at Mount Piper and may interact with rare species to the detriment of the latter.

Is the Community Approach Viable?

Conservation of any community necessitates (1) determining the need for management to assure its sustainability, and (2) implementing that management in conjunction with (3) controlling or regulating threatening processes. The important step of preservation of the site and repair of past damage has been accomplished for Mount Piper, but future management for particular rare species must be based, ideally, on detailed knowledge of the needs of those species and placed in the context of broader measures to assure the community's well being. The ant-blues, and other notable Lepidoptera at Mount Piper are the tools whereby impetus can be gained to conserve the assemblage of which they are part.

The major requirement for Mount Piper is to ensure its security as the sole locality currently known to support the two threatened *Acrodipsas* in Victoria. Recommendations for management and research made by Britton and New (1993) include:

- i) Protecting the general environment of Mount Piper and surrounding areas from further despoliation. This includes minimizing disturbance from agricultural activities (including clearing of native trees and native grasslands), subdivision for housing, and pedestrian

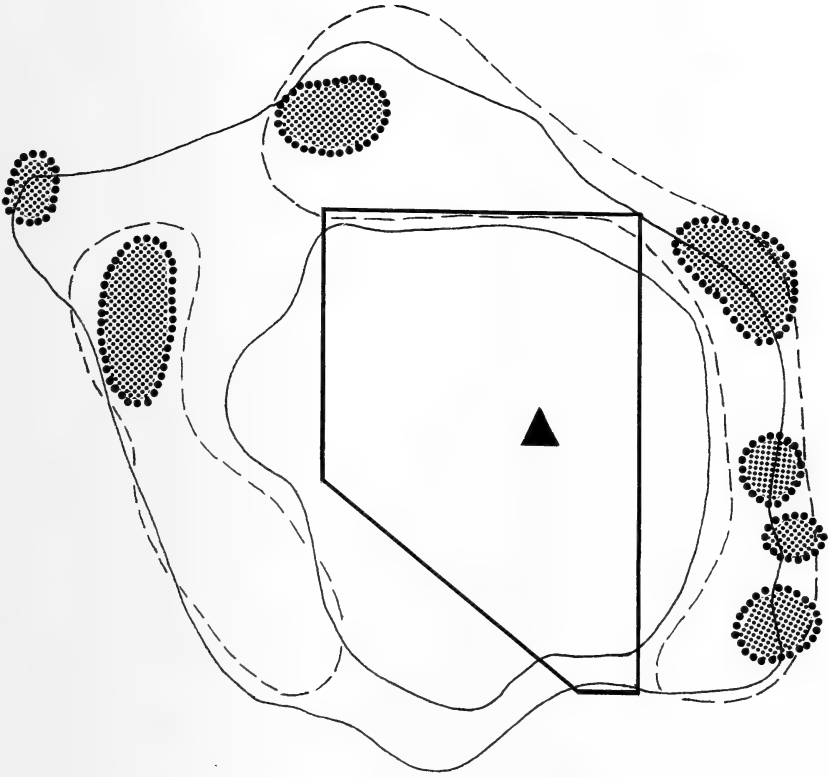


FIG. 5. Distribution of some important habitats for butterflies around Mount Piper. Boundary of reserve shown as in Fig. 1; summit of mountain indicated (\blacktriangle); solid lines, major areas of *Acacia* regrowth (*A. pycnantha*, *A. decurrens*) forming an annulus around the mountain base and extending to areas of uncleared farmland; dashed lines, areas with high densities of mistletoe infestation on eucalypts and acacias; dotted lines (shaded enclosures), areas of native grassland (*Microlaena stipoides*, *Themeda triandra*, *Danthonia* spp.).

and vehicular traffic. Control of exotic biota, and restrictions on collecting are also necessary in order to maintain the environment and the target species in the present condition while more detailed information on biology and distribution of the rare Lepidoptera found there is gathered.

- ii) Some areas are particularly vulnerable to disturbance: the summit, native grasslands around the base of the mountain, roadside verges including the 'corridor' of trees along Jeffrey's Lane (Fig. 1), regenerating acacias, and the large number of mistletoes on which some lycaenids (*Ogyris* spp.) depend (Fig. 5). Fig. 5 shows the

- extent of some elements of the critical habitat for butterflies surrounding Mount Piper, and indicates the need for protection of habitat to extend beyond the boundaries of the present reserve.
- iii) Directions for research on the butterflies include searching for breeding sites (including nests of likely and known ant species) in bushland on and around Mount Piper, and monitoring hilltopping populations and populations of other rare and local species. The first of these is especially difficult and labor-intensive.
 - iv) Continuing to search other localities for the *Acrodipsas* spp. The biology of *P. nitidus* needs further study and, as it has been recorded nesting in dead stumps, any clearing of old stumps around Mount Piper needs to be monitored carefully. One possible clue for this may be the presence of *Hypochrysops ignitus ignitus* (Leach), which is associated with the same ant and is itself scarce and in possible need of conservation in Victoria. *Hypochrysops ignitus* has been recorded at Tallarook, only 10–15 km north of Broadford.

Plans for all these steps, leading to identification of critical habitats for the Mount Piper community, are in train.

An important part of any such practical program is to obtain the support and endorsement of the local people. Mount Piper is an important local emblem, and the interpretative display in the basement carpark of the Education Reserve and a publicity brochure help to increase community awareness of its significance. The local Shire Council is committed to protecting roadside vegetation along Jeffrey's Lane, and a current amendment proposed for the Shire Planning Scheme (amendment L8: Mount Piper Conservation Zone) provides for specific controls to prevent removal of native vegetation (Jelinek et al. 1994). Guidelines within this amendment are far-reaching in assuring the maintenance of a natural environment, including dead timber, epiphytic mistletoes, control of weeds, and encouraging natural revegetation by regulating livestock and minimizing vehicle use. For maintenance of natural grassland and other early successional stages, some controlled grazing may be needed.

The project at Mount Piper highlights the importance in Victoria of isolated hilltop areas for invertebrates and the difficulty of defining the conservation needs of rare, but notable, species. The *Acrodipsas* species exemplify well the much more widespread problem of evaluating the status of inconspicuous hilltopping taxa whose breeding habits are unclear and for which the designation of critical habitat is therefore difficult. The approach of conserving threatened communities (which were discussed and exemplified for invertebrates by Wells et al. 1983) poses problems more complex than for single species conservation and

involves far more than habitat preservation to assure its success. The venture of including a Threatened Butterfly Community under the auspices of the Flora and Fauna Guarantee Act is innovative in helping to develop broader strategies and foresight for furthering invertebrate conservation in Australia. The combination of management based on sound research on the notable species involved and effective support from local, State, and Commonwealth agencies (including the nomination of Mount Piper for listing on the Register of the National Estate based on its significance for invertebrates) is likely to lead to effective protection and understanding of this unique assemblage of Lepidoptera in Victoria.

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A NEW NORTH AMERICAN CLEARWING MOTH AND NOTES ON A RARE SPECIES (SESIIDAE)

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ABSTRACT. A new species of Sesiidae from southwestern United States and northern Mexico, *Carmentia tildeni* Eichlin, is described and salient features illustrated. The female of *Synanthedon arctica* (Beutenmüller) is described and illustrated for the first time, with additional information provided on the species.

Additional key words: Types, genitalia, key, distribution, sex attractant, Ontario, Alaska, Arizona, Texas, Mexico.

Since the most recent revision of the Nearctic sesiid fauna north of Mexico (Eichlin & Duckworth 1988), a previously unknown species from southwestern United States and northern Mexico was discovered. Also, a male and female of a poorly known species, *Synanthedon arctica* (Beutenmüller), came to my attention. Both species are discussed below.

Carmentia tildeni Eichlin, new species

(Figs. 1, 2, 3, 5, 6)

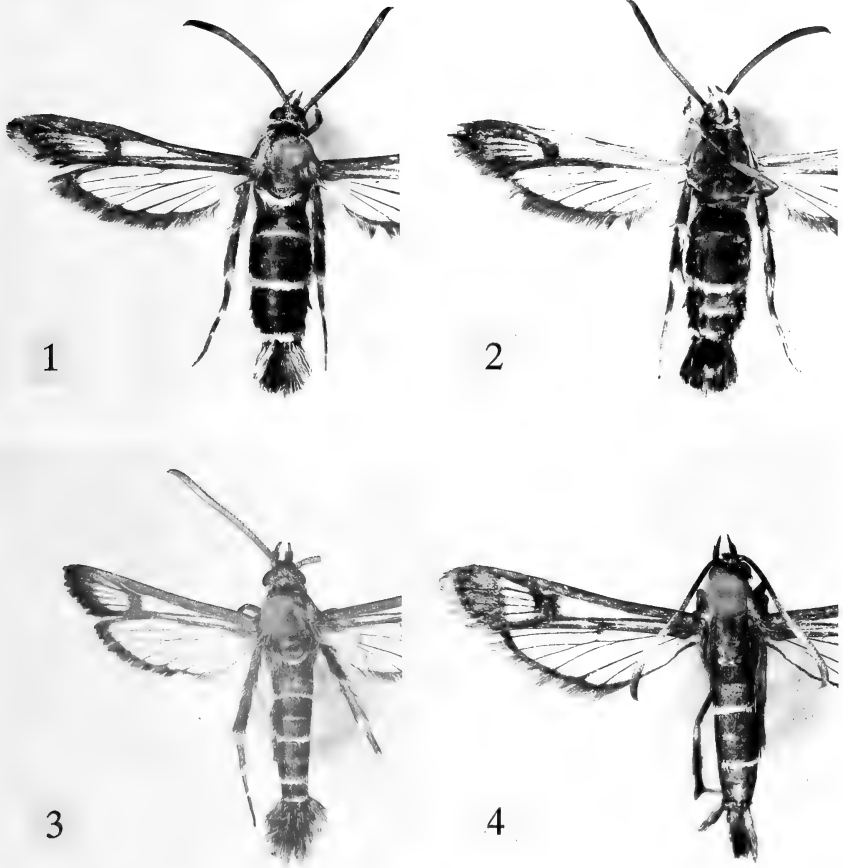
Male (Fig. 3). Head with vertex brown-black; front brown-black; occipital fringe pale yellow; antenna brown-black; labial palpus laterally mostly brown-black or pale yellow with apical half brown-black. Thorax brown-black, much yellow laterally beneath wings; metathorax mostly yellow dorsally. Abdomen brown-black, dorsally with yellow or pale yellow bands on segments 2, 4, 6, and 7; laterally yellow on segments 1 and 2; ventrally pale yellow banding on segments 4–7; anal tuft with yellow laterally. Legs brown-black, usually lacking white or pale yellow on forecoxa; hind tibia with pale yellow at tibial spurs and on joints of tarsal segments. Forewing with margins and broad discal spot brown-black with some pale yellow powdered between veins of apical margin and on distal edge of discal spot; ventrally with pale yellow more extensive on margins and discal spot. Wing length of males 6.5–8.0 mm. Genitalia as in Fig. 5, notably with distal portion of saccular ridge sharply pointed and extending beyond edge of valve; saccus nearly half as long as valve.

Female (Figs. 1, 2). Maculation as described for male but with pale yellow on abdominal segments 2, 4, and 6 dorsally; ventrally, with segments 4–6 mostly pale yellow; anal tuft brushlike, with pale yellow submedially. Wing length of females 8.0–10.0 mm. Genitalia as in Fig. 6.

Types. *Holotype*: ♀ (CAS): Brownsville, Cameron Co., Tex., 30.X.1972; J. W. Tilden collector; James Wilson Tilden Collection, Bequest to California Academy of Sciences—1989.

Allotype: ♂ (CAS): same as Holotype, except “. . . 21.X.1972; CDFA Genitalia Slide #837 by S. A. Kinnee.”

Paratypes (8): 2 ♀♀ (CAS): (1) same as holotype; (1) “. . . southmost Cameron Co., Texas, 29.X.1963.” 1 ♂, 1 ♀ (UCB): (♂) Cordoba, Mex., Vera Cruz, 29.VI.1966; (♀) Temescal, Oax., Mex., 3.X.1963. 1 ♀ (UCD): 3 mi W Sta. Barbara, Chih., Mex., 22.VII.1967; R. C. Gardner, C. R. Kovacic, K. Lorenzen collectors. 1 ♂ (J. R. Heitzman): MEX: San Luis Potosí, 18 km S Tamazunchale, Hwy 85, km 256, 5.VII.1990, coll. J. K. Adams; CDFA Genitalia Slide #838 by S. A. Kinnee. 1 ♂ (R. O. Kendall): MEXICO: Nuevo Leon: Hotel Cola de Caballo grounds/gardens; door light, 5.V.1978, Roy O. Kendall & C. A. Kendall;



FIGS. 1-4. Adults of Sesiidae. 1, Holotype female of *Carmenta tildeni* (wing length 10 mm); 2, Holotype female (ventral view); 3, Allotype male of *C. tildeni* (wing length 8 mm); 4, Female of *Synanthesdon arctica* (wing length 8 mm).

Kp-3. 1 ♂ (NMNH): MEXICO: 7 mi SW Poza Rica, Ver., 200', 20-22.VII.1963, Duckworth & Davis.

Additional material. Unfortunately, 6 conspecific males (CDFA) subsequently were severely damaged: (5) MEX: Nuevo Leon, 18 mi. W Linares, 2700', 24.IX.1975; J. Powell, J. Chemsak & T. Friedlander (1 with Genitalia Slide by M. R. Papp, CDA 018) and (1) MEX: Nuevo Leon, 4 mi. W Iturbide, 13/14.IX.1976. An Arizona male from the collection of Hermann Flaschka is labeled: AZ: St. Cruz Co., 5 mi SE Patagonia, 25.V-20.VII.1993 Lg. J. Brock, L103.

Distribution. Known from southeastern Arizona and southern Texas; in Mexico, from Chihuahua and Nuevo Leon south to Oaxaca.

Etymology. This species is named for the late J. W. (Bill) Tilden, noted teacher, entomologist/lepidopterist. He captured the portion of the type series of *C. tildeni* from Brownsville, Texas (including the Holotype and Allotype). These are from his collection, which he generously donated to the California Academy of Sciences.

Diagnosis. This species superficially resembles several other species of *Carmenta* in the southwestern United States. In the identification key in Eichlin and Duckworth (1988:72), couplets 52 and 53 should be altered to include *tildeni* as follows:

52. Head with front white laterally 53,
 - Head with front lacking white laterally *Carmenta tildeni*
 53. Abdomen dorsally with three pale yellow bands on male, two bands on female;
 male antenna without preapical white spot
 *Carmenta engelhardtii* Duck. & Eich.
 - Abdomen dorsally with more than three pale yellow bands on male, more than
 two on female; male antenna with preapical white spot 53,
 53. (same as for original couplet 53—Eichlin & Duckworth 1988:72)

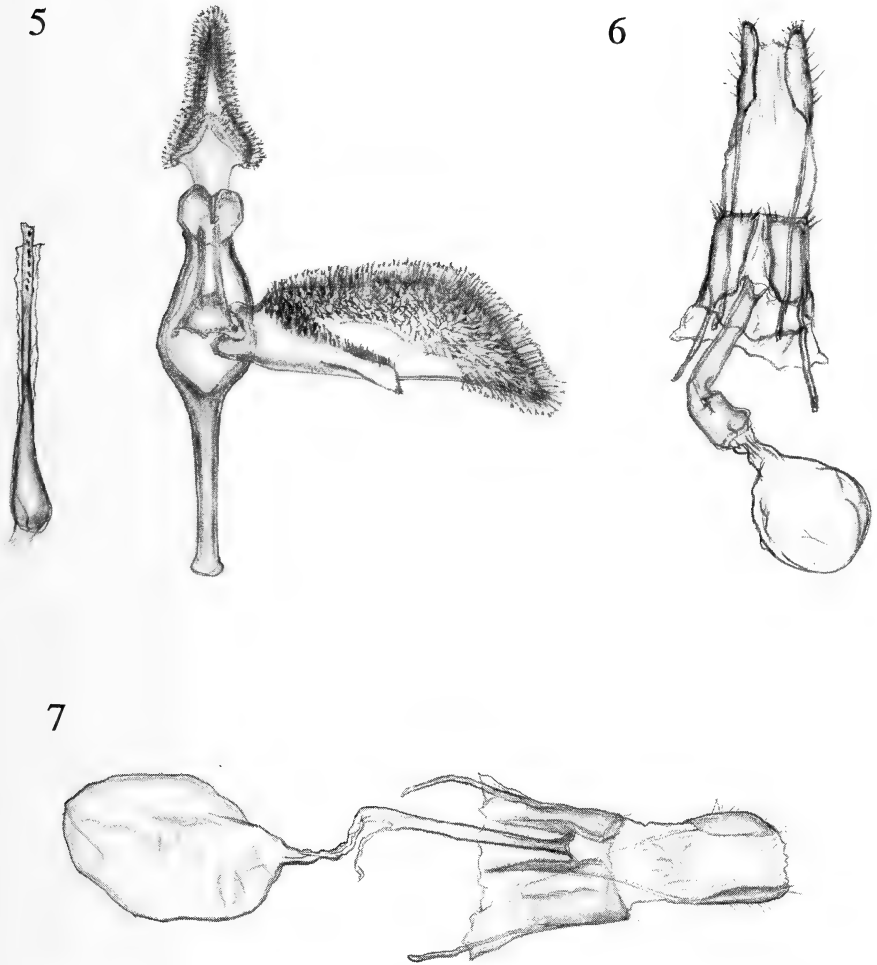
Discussion. No host plant is known for this species. Specimens were collected in the Brownsville, Texas, area at the end of October, and in Mexican localities on different dates from May to October. According to T. Friedlander (pers. comm.), the series of males he collected in late September from Nuevo Leon, Mexico, were taken in the afternoon next to a stream. They responded to a sex attractant containing about 96% of the Z,Z isomer of 3,13-octadecadiene-1-ol acetate (Z,Z-3-ODDA—a major component of the sex pheromone systems of various sesiids). Tumlinson et al. (1974) first elucidated this chemical extracted from females of *Synanthedon exitiosa* (Say).

Synanthedon arctica (Beutenmüller)

(Figs. 4, 7)

Description of female (Fig. 4). Head with vertex brown-black, somewhat roughened; front brown-black; occipital fringe brown-black, mixed with pale yellow laterally; labial palpus somewhat roughened, brown-black, some pale yellow scales mixed ventrobasally; antenna brown-black, variously powdered with pale yellow on apical one-half. Thorax brown-black with yellow beneath wing. Abdomen brown-black with narrow pale yellow bands on posterior edge of segments 2 and 4, some yellow scales on 6; ventrally brown-black; anal tuft brushlike, not broadly truncate as described for the male. Legs brown-black, some pale yellow mesally on hindleg. Forewing with brown-black on broad apical margin and broad discal spot; ventrally strongly powdered yellow on veins and margins and between veins in apical area. Hindwing hyaline with very narrow margins and small triangular discal spot; ventrally with costal margin mostly powdered yellow. Wing length 8.0 mm. Genitalia as in Fig. 7.

Discussion. The female of *S. arctica* is similar to the male (see couplet 24, Eichlin & Duckworth 1988:70). In the same publication (p. 85), the authors wrote that *S. arctica* was known only from the male holotype from Kodiak (NMNH) and one other male from Ruby, Alaska (Carnegie



FIGS. 5-7. Genitalia of Sesiidae. 5, Male of *Carmenta tildeni* (aedeagus detached); 6, Female of *C. tildeni* (ventral view); 7, Female of *Synanthedon arctica* (ventral view).

Museum). The female described above was collected in the vicinity of Healy, Alaska, 8 July 1974, by Hazel I. and J. W. Tilden. These same two collectors captured a male in the vicinity of the Central Steese Highway, Alaska, 29 June 1974. I recently identified a male in excellent condition collected by J. P. Walas from the Thunder Bay area, Ontario, Canada, 20 July 1989. This male, representing a considerable extension in the known range of this species, was captured with the aid of a sex attractant: (E,Z) 2,13-octadecadiene-1-ol acetate (E,Z-2-ODDA), a

chemical first extracted from females of the grape root borer, *Vitacea polistiformis* (Harris) (Schwartz et al. 1983).

ACKNOWLEDGMENTS

Specimens of both species discussed above were made available to me from the California Academy of Sciences (CAS). I thank the following persons and institutions for the loan of specimens used in this study: P. Arnaud (CAS); J. Powell (University of California, Berkeley—UCB); R. Schuster (University of California, Davis—UCD); D. Davis (National Museum of Natural History—NMNH); J. Heitzman (Independence, MO); R. Kendall (San Antonio, TX); H. Flaschka (Decatur, GA); and J. Walas (Thunder Bay, Ontario, Canada).

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DISTRIBUTION OF SELECTED ANTHOCHARIS,
EUCHLOE AND PONTIA (PIERIDAE) IN NEW MEXICO,
TEXAS, CHIHUAHUA AND SONORA

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ABSTRACT. This article presents the collecting history leading to the discovery of *Euchloe guaymasensis* Opler and documents extensions in the known range of four other pierids: *Anthocharis sara*, *Anthocharis pima*, *Euchloe hyantis*, and *Pontia sisymbrii*. *Pontia sisymbrii transversa*, originally described as a form of *P. s. sisymbrii* (Boisduval), is elevated to subspecific status.

Additional key words: *Anthocharis sara*, *Anthocharis pima*, *Euchloe hyantis*, *Pontia sisymbrii transversa*, *Euchloe guaymasensis*.

Prior to 1965, butterfly distribution records from New Mexico and northwestern Mexico (excluding Baja California) reflected the distribution of collectors not butterflies. Extensive collecting in New Mexico had been done only around Albuquerque, Santa Fe, Jemez Springs, Las Vegas, Fort Wingate, and Alamogordo; each of these sites had had resident collectors (see next paragraph). Some field work also had been conducted near Silver City by Bruce Harris and near Los Alamos by Carl Cushing, although the records accumulated by these two lepidopterists were not widely communicated. [The Cushing were reported by Toliver, Holland, and Cary (1994). Some of the Harris records were lost, although many may have been passed on to Cliff Ferris or Dale Zimmerman, who eventually contributed to the Grant County, New Mexico list of Ferris (1976, 1977)]. With the exception of the Townsend collection from Colonia Juarez, Chihuahua (Clench 1965), most pre-1965 collecting in Chihuahua and Sonora was restricted to the vicinity of main highways.

As a result of residents collecting near home, by 1965, discoveries such as *Sandia mcfarlandi* P. Ehrlich and Clench (1960) near Albuquerque and Alamogordo, *Colias scudderi ruckesi* Klots (1937) near Santa Fe and Las Vegas, and *Speyeria nokomis nigrocaerules* W. Cockerell and T. Cockerell (1900) near Las Vegas had been made. Also, *Hesperia woodgatei* Williams was known from both Jemez Springs (Williams 1914) and Colonia Juarez (Clench 1965), and *Speyeria nokomis coerulescens* Holland (1900) had been described from Colonia Juarez. [Nomenclature in this article is based on Miller and Brown (1981), as modified by Ferris (1989).]

RECENT DISCOVERIES AND RANGE EXTENSIONS

The habits of certain species of *Euchloe*, *Pontia*, and *Anthocharis* have led to the underestimation of their ranges in New Mexico. *Euchloe*

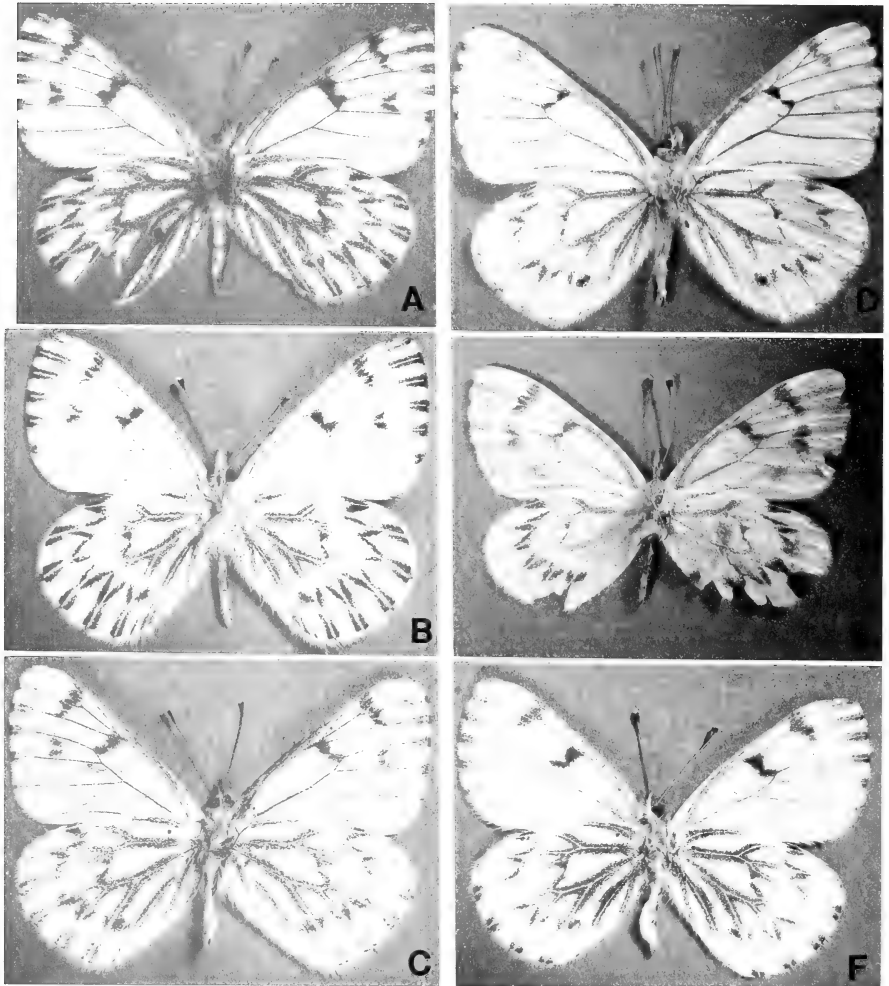


FIG. 1. Ventral surface of *Pontia sisymbrii* phenotypes: A, typical male morph, SW slope, Black Range, USFS Road 152, Grant Co., NM, ca. 7500', 9-iv-89; B, intermediate male, Baylor Canyon, NW slope, Organ Mts., Dona Ana Co., NM, 6000', 16-iii-79; C, *transversa* male paratype, North Franklin Peak, Franklin Mts., El Paso Co., TX, ca. 6000', 1-iv-87; D, male paratype with extreme expression of *transversa* features, Gray Ranch, Deer Creek, SW slope, Animas Mts., Hidalgo Co., NM, ca. 5400', 31-iii-93; E, *transversa* male paratype with an unusually dominating VHW transverse postmedial band, 26 mi. E of Ascencion on Mex. Hwy 2, Mun. Ascencion, Chih., 3800', 1-iv-85; F, *transversa* female paratype, Gray Ranch, Deer Creek, SE slope, Animas Mts., Hidalgo Co., NM, ca. 5400', 31-iii-93.

hyantis lotta (Beutenmuller) occurs 80 miles north and south of Albuquerque, but had not been recorded in the intervening area. Because no one in New Mexico had surveyed hilltops in March or April, *Anthocharis pima* W. H. Edwards also remained unknown from very far east of Tucson, Arizona, until W. A. Baltosser captured one at the Las Cruces, New Mexico city dump in 1977. This capture and the subsequent taking of *A. pima* in El Paso, Texas, generated considerable interest and enthusiasm among New Mexican lepidopterists. Eventually, we discovered *A. pima* in all New Mexican counties and adjacent Mexican municipios on both sides of the Mexico-New Mexico border. *Euchloe hyantis lotta* occurred everywhere *A. pima* did, and was recorded in virtually every other New Mexican county on or west of the Rio Grande, excluding the counties of Valencia, Bernalillo, Santa Fe and Los Alamos. The by-products of this collecting activity were Texas, Chihuahua, and Sonora state records for *Anthocharis sara* Lucas and *Pontia sisymbrii* Boisduval.

The Chihuahua-Sonora specimens of *P. sisymbrii* are of the phenotype *P. s. transversa* (Barnes & Benjamin), with much or all of the distal VHW scaling along the veins absent (Figure 1). This character appears to be sufficiently consistent to justify raising the name *transversa* from synonymy with nominate *sisymbrii*. New Mexican *P. sisymbrii* sometimes have been referred to the subspecies *P. s. elivata* (Barnes and Benjamin), but this subspecies has the ventral hind wing veins even more heavily and uniformly scaled than the nominate subspecies.

During the 1970's and 1980's, I made regular collecting trips in the early spring to Baja California, taking the ferry from the mainland port of Guaymas, Sonora. In March 1974, I drove off Mexico Highway 15 to the Las Avispas (The Wasps) mountain top microwave relay, about half way from Hermosillo to Guaymas. At that time, Sonoran hilltops during March were as much unexplored as those of New Mexico. In the morning, I was startled by the sight of a hilltopping *ausonides*-group *Euchloe*. This group generally is associated with Canadian and Hudsonian life zones, not the Lower Sonoran life zone at one of the hottest, driest places in the New World. A slide of this specimen shown at the 1979 Pacific Slope Meeting of the Lepidopterists' Society in Davis, California, was largely greeted with disbelief. Four more specimens of this *Euchloe* were taken at Las Avispas in 1983 and 1984. Unlike the original worn 1974 specimen, the 1983 and 1984 specimens were in fresh condition. In this condition, they were quite yellow, resembling *Euchloe charlonea* Donzel, illustrated by Sakai (1981) from Afghanistan, and unlike any other Western Hemisphere *Euchloe*.

Opler (1986) described the new species as *Euchloe guaymasensis* (1986), which resulted in a flurry of activity among Tucson collectors

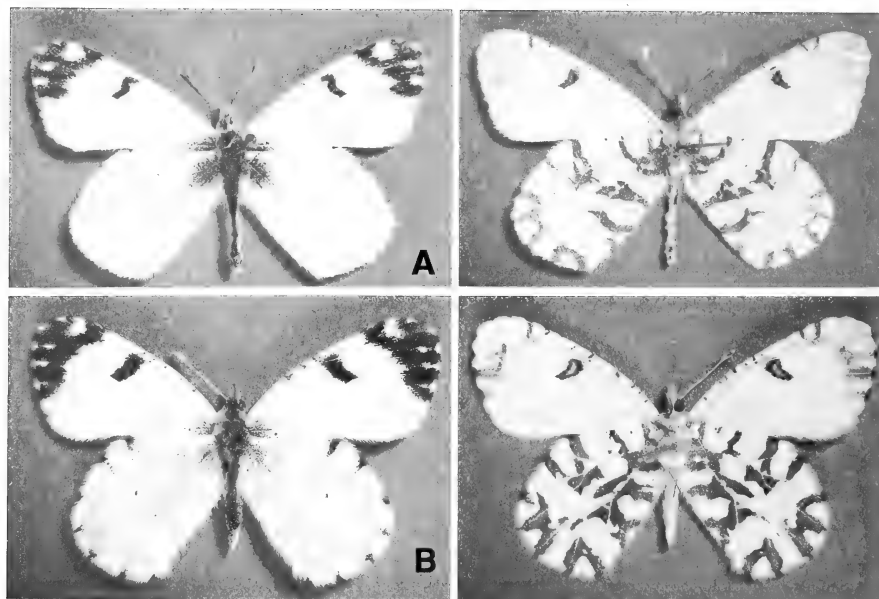


FIG. 2. *Euchloe guaymasensis*: A (top row), toptypical male; B (bottom row), toptypical female.

not unlike that stimulated in New Mexico a decade earlier by the discovery of *A. pima*. Eventually, *E. guaymasensis* was found as far south as Guaymas and north almost to the U.S. border. Figure 2 shows the previously unillustrated female of *E. guaymasensis*. The species is not strongly sexually dimorphic, although the dorsal surface of the female is more intensely yellow than the male, and occasionally has a few orange scales on the hindwing. Also, the female has small black marginal spots at the ends of the DHW veins, which are usually absent on the male.

In 1990, the anthocharine odyssey came full cycle with the taking of *A. pima* at the *E. guaymasensis* type locality, the Las Avispas microwave relay. Figures 3 and 4 show the currently known distribution of *A. sara* and *A. pima*, *E. h. lotta* and *E. guaymasensis*, and *P. sisymbrii* (typical and *transversa*) in New Mexico, Texas, Sonora, and Chihuahua. Widely reported, older records of *A. sara* and *P. sisymbrii* from central and northern New Mexico are omitted on this figure and in the Appendix.

Prior to Spring 1995, I believed that the eastern, northern, and southern limits of distribution for *A. pima* and *E. h. lotta* in Texas, New Mexico, and Chihuahua were accurately known. Searching outside the distribution areas of Fig. 4 had consistently produced negative results

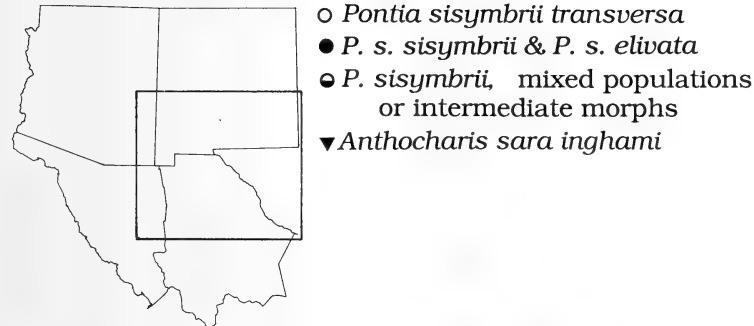
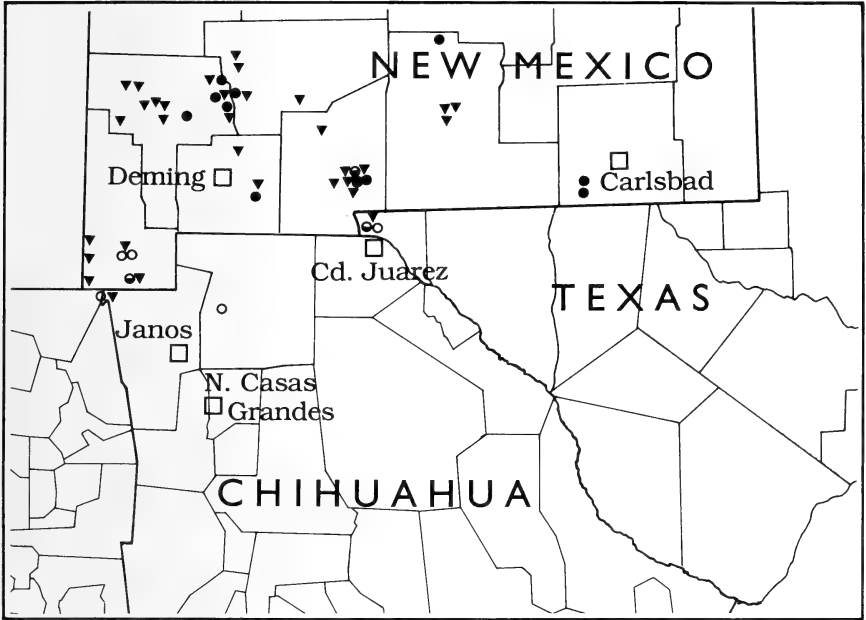


FIG. 3. Distribution of *Anthocharis sara* and *Pontia sisymbrii* (typical and *transversa*) in southern New Mexico, west Texas, Chihuahua, and Sonora.

for 15 years. However, unusually heavy rains in December 1994, followed by an unusually warm mid-winter and early spring changed this outlook. Until 1995, neither of these species was found south into the Sierra Madre winter rain-shadow area across west Texas and Chihuahua beginning about 75 miles south of El Paso. Also, it seemed that *A. pima* did not occur anywhere in New Mexico or West Texas to the north or east of the suburbs of Las Cruces, New Mexico. *Euchloe h. lotta* apparently had a virtually identical eastern limit.

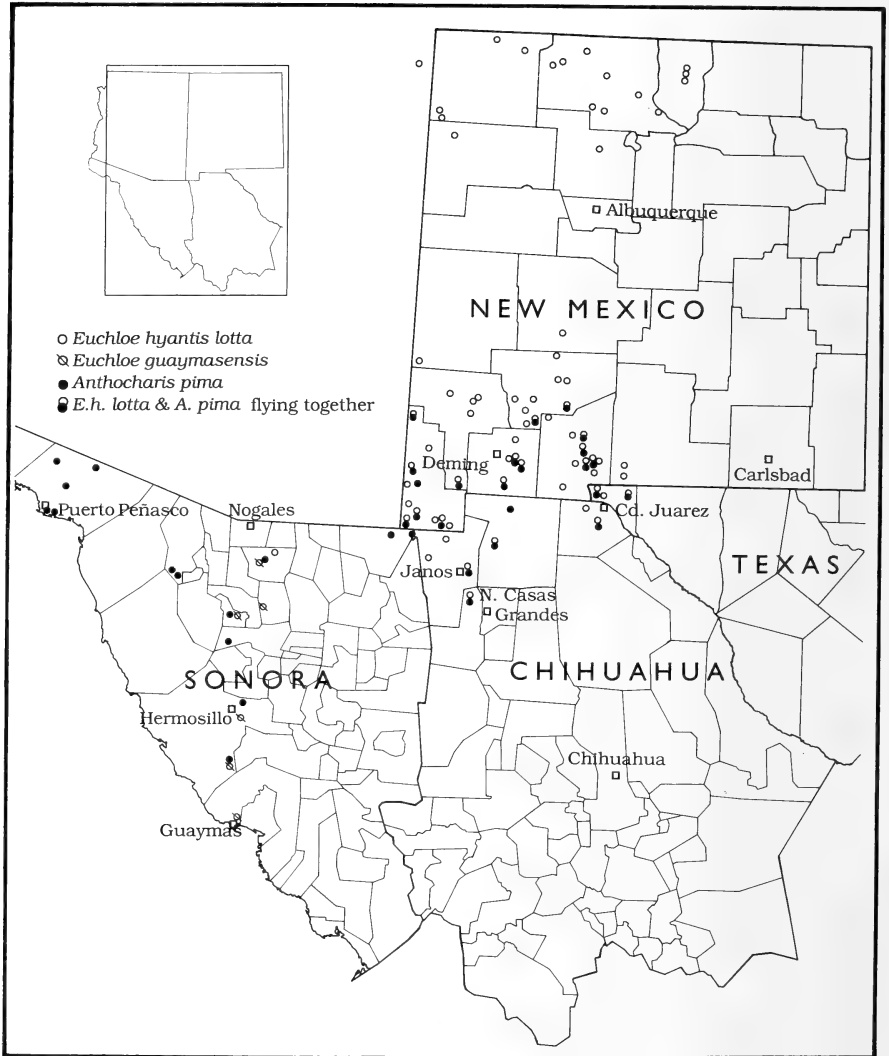


FIG. 4. Distribution of *Anthocharis pima*, *Euchloe hyantis lotta* and *E. guaymasensis* in New Mexico, west Texas, Chihuahua, and Sonora.

Field work in 1995, however, revealed an extraordinary spring plant growth and resulted in the documentation of both species at least 40 miles north and east of all previous observations. These new range extensions coincided with the limits of the abnormal winter precipitation. Consequently, I am now unsure that even the expanded distribution of records reflects the true species distribution; it may merely reflect the distribution of December 1994 precipitation.

There are records of Lepidoptera diapausing over 15 years before emergence from the pupal stage (e.g., Powell 1989). If extraordinary winter precipitation penetrated south into the Madrean rain shadow area (which it did not in December 1994), *A. pima* and *A. hyantis lotta* may have been documented much farther than 75 miles into Chihuahua.

Pontia sisymbrii is widely reported up to the Texas state line in the Guadalupe Mountains of Eddy County in southeastern New Mexico. It likely eventually will be documented from Guadalupe Mountain National Park of Culberson County, Texas. It is possible that the more montane species *P. sisymbrii* and *A. sara* also may extend farther south into the Sierra Madre than is presently confirmed. Sonoran distribution limits are less certain. *Euchloe guaymasensis* could prove to have a much wider range than presently known, especially south of Guaymas, and *A. pima* could be much more widely distributed in Sonora than presently verified. Sonoran collecting of these species seems about a decade behind Chihuahuan work. There are two reasons for this phase lag: the Sonoran terrain is more difficult, and the species in question range much farther south into Sonora than Chihuahua. Connecting the dots on the Sonoran portion of the distribution maps in Figures 3 and 4, even now, leads to a fairly good representation of Mexico Highways 2, 8, and 15.

SYSTEMATICS

Pontia sisymbrii transversa R. Holland, new subspecies

Holotype. Male. Length of right forewing 23.0 mm (Fig. 5). Similar to other subspecies, including nominate *sisymbrii* and *elivata*, except on ventral hindwing (VHW). VHW veins not edged with dark scales posterior of the postmedial chevron band, except at the extreme margin of the wing. VHW vein edging also absent basad of chevron band nearly back to cell along veins arising from cell. General subjective impression is thus to leave postmedial chevron band appearing as isolated transverse maculation—hence the name *transversa*. Holotype bears label “Paradise/Cochise Co./Ariz.” reminiscent of labels on specimens known to have been taken by Otto Poling; see Holland and Forbes (1981). Barnes and Benjamin (1926) declare that the holotype was taken in March, although the specimen currently bears no label so indicating. The specimen, however, does bear another hand-written label, “*A. sisymbrii*/f. *transversa*/Holotype ♂ Br. Benj.” and a third very small printed label “Mcl.” I do not know what this third label indicates.

Female paratype. Length of right forewing 21.5 mm (Fig. 5). Similar to holotype in wing maculation, except the dark scaling along the VHW



FIG. 5. A (top row), holotype of *Pieris sisymbrii* form "transversa" Barnes and Benjamin and *Pontia sisymbrii transversa* R. Holland; B (bottom row), allotype of *Pieris sisymbrii* form "transversa" Barnes and Benjamin. This specimen also included as a paratype of *Pontia sisymbrii transversa* R. Holland.

veins is less reduced, especially basad of postmedial band. In this region, only M_2 has an unscaled section. Female paratype also has considerably heavier scaling on veins around VHW cell, and along $S_C + R_1$, $2A$, and $3A$. Female paratype bears printed locality label identical to holotype, a hand-written label, "*A. sisymbrii*/f. *transversa*/Allotype ♀ Br.Benj.," a third tiny label "Mch.," and a fourth label with only a large "16." Some *P. sisymbrii* females have a slightly cream background dorsally; this paratype is the pure white morph. Barnes and Benjamin (1926) declared that the allotype also was taken in March, although this specimen currently bears no label so indicating, unless the tiny "Mch" label is intended to be an abbreviation for March.

Additional male paratype in the *P. s. transversa* (Barnes and Benjamin) type series bears the label, "Redington/Arizona."

I elevate the name *transversa* from synonymy with *sisymbrii* to subspecific status in the combination *Pontia sisymbrii transversa*. This subspecies is distinguished from other subspecies by the reduction or absence of scaling along the veins of the ventral hindwing, as shown in Figs. 1 and 5. Some populations, especially where the ranges of *P. s. transversa* and *P. s. sisymbrii* or *P. s. elivata* are adjacent, may be phenotypically mixed, and in fact, there may be no populations any-

where which phenotypically are more than 80% *P. s. transversa*. However, New Mexican individuals from north of Las Cruces, New Mexico, are never of the *transversa* phenotype. The percent necessary to be of the *P. s. transversa* phenotype in order to designate the population at a given site as *P. s. transversa* is an issue which will always be open to each worker's personal judgement.

As *P. s. transversa* originally was described as an infrasubspecific form (Barnes & Benjamin 1926), raising it to subspecific status places the elevated name under my authorship (Miller & Brown 1981, note 460). I can, however, see no reason not to retain the Barnes and Benjamin types, which reside at the United States National Museum of Natural History (TL: Paradise, Cochise Co., Arizona), as types for the elevated name. Labels to this effect have been added to three of the four NMNH specimens in question. One of the original *P. s. transversa* (Barnes & Benjamin) paratypes, a female, cannot be found at this time, and thus is not included as a paratype for *P. s. transversa* R. Holland. I also designate the specimens in Figs. 1C, 1D, 1E, and 1F as paratypes. These paratypes will be placed in the AMNH, LACM, AME, and UNAM. Barnes and Benjamin's original description indicates that *transversa* applied to the spring brood. It is now known, however, that *P. sisymbrii* is univoltine (Bailowitz & Brock 1991, Emmel & Emmel 1973). Thus, it is not possible for our material and the original types of *P. s. transversa* to be associated with different broods. What is probable is that the Barnes and Benjamin material, like ours, came from near the southern limit of the range of *P. sisymbrii*, and thus emerged earlier in the spring than most other *P. sisymbrii* populations known to Barnes and Benjamin.

ECOLOGICAL REQUIREMENTS

In much of New Mexico and Chihuahua where *Anthocharis pima* and *Euchloe hyantis lotta* live, both limestone hills and volcanic cinder cones occur. As a general rule, cinder cones are more productive collecting localities, although limestone hilltops are not unrewarding. Both species, as well as *Euchloe guaymasensis*, are thought to use *Descurainia* or *Caulanthus* (both Brassicaceae) as foodplants. Apparently these mustard genera favor volcanic soil, although they do grow and thrive on limestone outcroppings. Recently, Tucson entomologists have reared *Euchloe guaymasensis* on *Descurainia pinnata*. Scarcity of female specimens of *E. guaymasensis*, *E. h. lotta*, and *A. pima* are an artifact of hilltop collecting.

DISCUSSION

This paper describes recent discoveries in the distributions and phenotypes of five pierids in New Mexico, Texas, Chihuahua, and Sonora.

Anthocharis pima is now known to extend as far east as El Paso, Texas and as far south into Sonora as Las Avispas. *Anthocharis sara* is reported for the first time from Chihuahua, Mexico. *Euchloe hyantis lotta* also is now reported from El Paso, Texas, northwestern Chihuahua, northeastern Sonora, and virtually all of New Mexico west of the Rio Grande. The recently described *E. guaymasensis* is reported from much of Sonora north and east of Guaymas, north almost to the U.S. border. In extreme southwestern New Mexico, northwestern Chihuahua, and northeastern Sonora, *Pontia sisymbrii* populations are represented almost purely by the *transversa* phenotype. Hence, I elevate this name, originally proposed as a form by Barnes and Benjamin, to subspecific status.

ACKNOWLEDGMENTS

Tucson collectors generously shared their Sonoran observations, and Steve J. Cary (SJC) his New Mexican records. Steve Cary contributed records he obtained from James A. Scott (JAS), Ray E. Stanford (RES), W. A. Baltosser (WAB), and Kilian Roever (KR). Mike Toliver (MET) records are from Toliver, Holland and Cary (1994). Greg S. Forbes (GSF) collected and retains [at the New Mexico State University (NMSU) collection] the first *Anthocharis pima* taken in Texas. Joanne McCaffrey (JMC) and Bernie Weber donated many of their specimens to the NMSU collection, which was searched by Greg Forbes at my request. Copious data also has been provided by William L. Swisher (WLS). Don Harvey at the NMNH was kind enough to provide me access to the three specimens of the original *Pontia sisymbrii transversa* (Barnes & Benjamin) type series which could be located.

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APPENDIX

Anthocharis sara inghami Gunder

NEW MEXICO (southern counties and low altitude records only):
Dona Ana Co.: Baylor Canyon, W slope, Organ Mts., 6000', 16-iii-79 (9♂♂, 3♀♀); same data, 5-iv-80 (3♂♂, 1♀); same data, 21-iv-79 (1♀); La Cueva Ranch, W slope, Organ Mts., 5500', 18-iii-79 (3♂♂, 1♀); same data, 10-11-iv-82 (SJC); same data, 24-iv-1899 (T.D.A. Cockerell); Finley Canyon, S slope, Organ Mts., 5000', 25-iii-79 (2♂♂); S rim of Soledad Canyon, near Chimney Rock, Organ Mts., 6000', 24-iii-79 (1♂, 2♀♀); Long Canyon, S slope, Organ Mts., 6000', 14-iv-79 (1♂); Fillmore Canyon, W slope, Organ Mts., 7000', 22-iv-79 (1♂); 1 mi. NE of Aguirre Springs, E slope, Organ Mts., 5500', 6-iv-79 (3♀♀); 0.8 mi W of San Augustine Pass, Organ Mts., 5500', 1-iv-83 (1♀, leg. GSF); Aguirre Springs, E slope, Organ Mts., 5500', 9-iii-82 (7♂♂, leg. GSF); same data, 4-iv-82 (1♂, leg. JMC); same data, 6-iv-82 (1♂, leg. JMC); same data, 1-iv-78 (1♂, 1♀, leg. B. Weber); same data, 11-iv-82 (SJC); same data, 13-iii-77 (WAB); Tortugas Mt., 4900', 22-iii-77 (WAB). *Grant Co.*: Devil's Backbone, W slope, Black Range, NM Hwy 151 11 mi. E of San Lorenzo, 6800', 15-iv-66 (2♂♂); Gallinas Canyon, W slope, Black Range, 28-iii-86 (1♂, leg. SJC); Cold Springs Canyon (USFS Road 886), SW slope, Black Range, 7500', 23-iv-88 (2♂♂, 2♀♀); Royal John Mine Rd. (USFS Road 886), SW slope, Black Range, 7000', 23-iv-88 (1♂); Silver City, 3-iv-69 (JAS); same data, 30-iii-74 (WAB); Donahue Canyon, W slope, Black Range, 11-iii-89 (SJC); Ash Spring Canyon, 6700'-6900'; Cherry Creek Canyon and McMillen Canyon, 6700'-7300'; Gila River near Gila, 4250'; Lower Gallinas Canyon, 6400'-6800'; Little Walnut Creek, 6600'; Red Rock, 4000'; Cliff, 4500' (last seven records due to Ferris

(1976)). *Hidalgo Co.*: Clanton Draw, Peloncillo Mts., ca. 5400', 11-iv-81 (SJC); same data, 26-iii-92 (SJC); Gray Ranch, Indian Creek, N slope, Animas Mts., ?-iii-77 (J.P. Hubbard); same data, 14-iv-91 (SJC); Gray Ranch, Deer Creek, SE slope, Animas Mts., 12-iv-91 (SJC); Skeleton Canyon, W slope, Peloncillo Mts., 11-iii-89 (SJC); Guadalupe Canyon, SW slope, Peloncillo Mts., 16-iii-85 (SJC). *Luna Co.*: Ridge E of Spring Canyon, N slope, Florida Mts., 27-iii-86 (1♂, leg. SJC); Spring Canyon, N slope, Florida Mts., 26-iii-86 (1♂, 1♀, leg. SJC); same data, 30-iv-83 (SJC); same data, 24-iii-90 (SJC); Slate Spring, Hadley Draw, NE slope, Cooke Peak, 18-iii-89 (1♂); same data, 19-iii-89 (2♂♂); OK Canyon, Cooke Peak, 12-iii-89 (SJC). *Otero Co.*: Alamo Canyon, SW slope, Sacramento Mts., 6000', 23-iv-73 (1♂, 1♀); same data, 3-iv-75, (5♂♂, 1♀); Dog Canyon, SW slope, Sacramento Mts., 5000', 5-iv-75 (1♀); same data, 11-iv-81 (1♂, leg. JMC); same data, 30-iii-80 (2♂♂, leg. JMC); Mountain Park, 11-iv-82 (JMC). *Sierra Co.* (low altitude records only): Sec. 10, W slope of Brushy Mt., Caballo Mts., 5200', 19-iii-77 (1♂); Granite Spring, W slope of Caballo Mts., 4900', 12-iii-77 (1♂); same data, 9-iv-77 (1♀); Hermosa, E slope, Black Range, 6200', 24-iii-91 (2♂♂); Circle Seven Creek, E slope, Black Range, 6000', 31-iii-91 (2♂♂); vic. of Kingston, E slope, Black Range, ca. 6500', 11-iv-91 (SJC).

TEXAS: *El Paso Co.*: McKelligan Canyon, SE slope, Franklin Mts., El Paso, 5500', 25-iii-81 (1♂, 4♀♀); same data, 27-ii-83 (3♂♂) (early record); Tom Mays Park, W slope, Franklin Mts., 5200', 14-iii-81 (2♂♂).

CHIHUAHUA: *Mun. Janos*: Canyon on Chihuahua side of Puerto San Luis, Mex. Hwy 2, just E of Sonora state line, 5500', 13-iv-85 (2♂♂, donated to UNAM); same data, 7-iv-94 (1♂ taken, 2 more seen).

Anthocharis pima W. H. Edwards

NEW MEXICO (all records for state): *Dona Ana Co.*: Tortugas Mt., N slope, 4000', 22-iii-77 (WAB); 0.5 mi. N of Bishop's Cap, 5300', 17-iii-79 (1♂); S end of Dona Ana Hills at radio tower (Twin Peaks), 4800', 6-iv-80 (1♂); same data, 24-iv-83 (1♂); same data, 10-iii-82 (2♂♂, leg. GSF); same data, 6-iv-80 (1♂, leg. GSF); same data, 5-iv-85 (17♂♂, WLS); same data, 31-iii-87 (5♂♂, 2♀♀, WLS); same data, 1-iv-87 (3♂♂, 2♀♀, WLS); Tortugas Mt., 4900', 5-iv-80 (2♂♂); same data, 6-iv-79 (9♂♂); same data, 12-iii-83 (5♂♂); same data, 8-iv-79 (1♂, leg. GSF); same data, 23-iii-81 (1♂, leg. GSF); hill 1 mi. N of Organ, 4800', 16-iii-95 (4♂♂ taken, 6 more seen, WLS); microwave relay at Rincon, 4800', 2-iv-95 (2♂♂, RH, ESC and SJC). *Grant Co.*: 7 mi. W of Hachita, 5100', 17-iv-83 (2♂♂); same data, 25-iii-93 (16♂♂, WLS). *Hidalgo Co.*: 7 mi. N of Animas and 5 mi. W of NM Hwy 338, Peloncillo Mts., 4600', 17-iv-83 (5♂♂); Guadalupe Canyon, SW slope, Peloncillo Mts., 16-iii-85 (2♂♂, leg. SJC); NM Hwy 9, 6 mi. E of US Hwy 80 (KR); vic. of Playas, 15-iv-80 (Ed Peyton);

Gray Ranch, Smuggler Hills, 3.5 mi. E of Culberson Camp, SE slope, Animas Mts., 5000', 31-iii-93 (15 seen, SJC); 3 mi. N of Gray Ranch Hdq., 5600', 2-iv-93 (2 seen, SJC); 7.5 mi. W of Lordsburg, 3900', 25-iii-93 (4♂♂ taken, 3 more seen, WLS); NM Hwy 92, 1.3 mi. W of Virden, 4500', 14-iii-95 (1♂, WLS); NM Hwy 92, 1 mi. N of US Hwy 70, 4500', 14-iii-95 (1♂ taken, 6 more seen, WLS); NM Hwy 92, 0-1.7 mi. N of US 70, 4500', 17-iii-95 (6♂♂, WLS). *Luna Co.*: ca. 2 mi. SW of Tres Hermanas and 6 mi. NW of Columbus, 4500', 10-iv-83 (13♂♂); Victorio Canyon, E slope, Florida Mts., 24-iii-90 (SJC); Rockhound State Park, 27-iii-86 (RES); 7 mi. NE of Columbus, 4000', 13-iii-85 (2♂♂, WLS); same data, 1-iv-87 (3♂♂, 2♀♀, WLS). *Sierra Co.*: Round Mt., 6 mi. N of Nutt, 4800', 17-iii-95 (6♂♂, WLS); Point of Rocks, Sect. 19-30, T.17S., R.1W., 4800', 2-iv-95 (4♂♂ taken, 4 more seen, RH, ESC and SJC).

ARIZONA: (near *Hidalgo Co.*) *Greenlee Co.*: 5.3 mi. NW of Duncan, AZ, 4300', 25-iii-93 (12♂♂ taken, 12 more seen, WLS).

TEXAS: *El Paso Co.*: Tom Mays Park, W slope, Franklin Mts., 5200', 12-iii-83 (sight); same data, 30-iii-80 (1♂, leg. GSF); E slope, Trans Mountain Rd., c. 4500', 5-iii-95 (11♂♂, RH and SJC); red hill, 2 mi. W of road to Hueco Tanks St. Park, US Hwy 62-180, 4000' (1♂, RH and SJC).

CHIHUAHUA: *Mun. Ascencion*: ca. 12 mi. S of Palomas, Rancho Constitucion 1856, 16-iv-83 (2♂♂); 26 mi. E of Ascencion, Mex. Hwy 2, 3800', 1-iv-85 (2♂♂). *Mun. Ciudad Juarez*: Sierra del Presidio, ca. 25 mi. S of Cd. Juarez, 5000', 21-iii-84 (sight). *Mun. Janos*: Janos microwave relay, 5 mi. E of Janos, 5400', 1-iv-85 (1♂); 25 mi. NW of Janos, Mex. Hwy 2, 4300', 13-iv-85 (1♂); microwave relay at Puerto San Luis, Mex. Hwy 2, Chih.-Son. state line, 6500', 5-iv-91 (1♂) (probable altitude record). *Mun. Casas Grandes*: 25 mi. N of Nuevo Casas Grandes, Puerto Janos, 4500', 2-iv-85 (1♂).

SONORA: *Mun. Altar*: 5 mi. SE of Altar on Mex. Hwy 2, 1500', 1-iii-92 (2♂♂); 7 mi. SE of Altar on Mex. Hwy 2, 1-iii-92 (1♂). *Mun. Agua Prieta*: Microwave relay at Puerto San Luis, Mex. Hwy 2, Chih.-Son. state line, 6500', 5-iv-91 (1♂); mountains S of Guadalupe Canyon, 4200', 6-iv-80 (1♂). *Mun. Benjamin Hill*: Santa Eva Microwave Relay, 10 mi. NE of Benjamin Hill, 3000', 27-ii-92 (4♂♂). *Mun. Hermosillo*: Las Avispas microwave relay, 40 mi. N of Guaymas, 2000', 24-ii-90 (2♂♂); 19.5 mi. N of Hermosillo on Mex. Hwy 15, 14-iii-80 (2♂♂). *Mun. Imuris*: Road to microwave relay E of Imuris, 22-ii-92. *Mun. Puerto Penasco*: Puerto Penasco, 23-ii-93 (1♂); microwave relay ca. midway from Sonoita to Puerto Penasco, Mex. Hwy 8, 24-ii-93 (4♂♂, 1♀, more seen but not taken); Parque del Volcan del Pinacate, Sykes Crater, 12 to 14-ii-83 (1♂ taken, others seen); 6 mi. E of Los Vidrios, Mex. Hwy 2, 9-iii-93 (1♂ taken, others seen); 8 mi. W of Sonoita, Mex. Hwy 2,

9-iii-93 (14♂♂); 6.5 mi. E of Puerto Penasco, Son. Hwy 37, 24-ii-91 (4♂♂, 1♀). *Mun. Opodepe*: 19 mi. S of Benjamin Hill on Mex. Hwy 15, 14-iii-80 (14♂♂).

Euchloe hyantis lotta (W. H. Edwards)

NEW MEXICO (all records for state): *Catron Co.*: N rim of Big Pine Cyn. in section at SW corner of Catron Co., end of USFS Road 106, 5200', 1-iv-95 (6♂♂ taken, 6 more seen, RH, ESC and SJC). *Dona Ana Co.*: 1 mi. NE of Bishop's Cap, 5300', 25-iii-79 (3♂♂); .5 mi N of Bishop's Cap, 5300', 17-iii-79 (6♂♂, 1♀); Baylor Canyon, W slope, Organ Mts., 6000', 16-iii-79 (1♂); Bishop's Cap, 6 mi. E of Mesquite Exit, I-10, 30-iii-78 (1♂, leg. GSF); S rim, Soledad Canyon, near Chimney Rock, Organ Mts., 6000', 24-iii-79 (2♂♂); S end of Dona Ana Hills at radio tower (Twin Peaks), 4800', 6-iv-80 (12♂♂); same data, 24-iv-83 (1♂); same data, 10-iii-82 (1♂, leg. GSF); same data, 6-iv-80 (1♂, leg. GSF); Tortugas Mt., 4900', 5-iv-80 (1♂); same data, 7-iv-79 (2♂♂); same data, 6-iv-79 (6♂♂); same data, 12-iii-83 (5♂♂); same data, 10-iv-80 (2♂♂, leg. GSF); same data, 23-iii-81 (1♂, leg. GSF); same data, 8-iv-79 (1♀, leg. GSF); same data, 21-iii-77 (WAB); N base, Tortugas Mt., 4000', 15-iii-79 (1♂, leg. GSF); same data, 13-iii-79 (1♂, leg. GSF); same data, 28-iii-78 (1♂, leg. GSF); Long Canyon, S slope, Organ Mts., 6000', 15-iv-79 (2♂♂); same data, 14-iv-79 (1♂); radio tower at Rincon, 4600', 24-iv-83 (3♂♂, 1♀); Picacho Peak, W side of Las Cruces, 5000', 25-iv-83 (2♂♂); New Mexico State University Animal Science Ranch, Jornada Experimental Range, 21-iv-73 (1♂, leg. A. Mangini); Jornada Experimental Range, 2.4 mi. W of USDA pillars, 17-iii-79 (1♂, leg. GSF); Potrillo Mts., 1 mi. S of Mt. Riley, 26-iv-77 (WAB); hill on E side, Garfield Exit, I-25, 4600', 24-iv-83 (2♂♂); .5 mi. N of Organ, 4800', 26-iii-93 (1♂, WLS). *Grant Co.*: 7 mi. W of Hachita, 5100', 17-iv-83 (sight); same data, 25-iii-93 (1♂ taken, >100 observed, WLS); Silver City, 3-iv-69 (sight, JAS); Cherry Creek Canyon and McMillen Canyon, 6700'-7300'; Gila River near Gila, 4250'; Signal Peak, 8000'-9000' (last three records due to Ferris (1976)). *Hidalgo Co.*: Rodeo, 9-iii-38 (leg. J.W. Tilden); 7 mi. N of Animas and 5 mi. W of NM Hwy 338, E slope, Peloncillo Mts., 4600', 17-iv-83 (3♂♂); Shakespeare, near Lordsburg, 4800', 17-iv-83 (6♂♂, 1♀); Clanton Draw, E slope, Peloncillo Mts., 5400', 14-iv-73 (MET); Guadalupe Canyon, SW slope, Peloncillo Mts., 16-iii-85 (SJC); Gray Ranch, Deer Creek, 8 mi. NW of Culberson Camp, SE slope, Animas Mts., 5300', 31-iii-93 (3 seen, SJC); Smuggler Hills, 3.5 mi. E of Culberson Camp, Gray Ranch, SE slope, Animas Mts., 31-iii-93 (30 seen, SJC); Gray Ranch, Deer Creek at Granite Pass, SE slope, Animas Mts., 4800', 31-iii-93 (10 seen, SJC); 3 mi. N of Gray Ranch Hdq., 5600', 2-iv-93 (12 seen, SJC);

NM Hwy 92, 1 mi. N of US Hwy 70, 4500', 14-iii-95 (1♂ taken, 10 more seen, WLS). *Luna Co.*: ca. 2 mi. SW of Tres Hermanas and 6 mi. NW of Columbus, 4500', 10-iv-83 (7♂♂); Ridge E of Spring Canyon, N slope, Florida Mts., 27-iii-86 (1♀, leg. SJC); Slate Spring, Hadley Draw, NE slope, Cooke Peak, 19-iii-87 (1♀); same data, 12-iii-89 (SJC); Rockhound State Park, 9-iv-85 (SJC); Little Florida Mts., 23-iii-90 (SJC); vic. Victorio Canyon, E slope, Florida Mts., 24-iii-90 (SJC). *McKinley Co.*: Tohatchi Lookout, SE slope, Chuska Mts., 8300', 4-vi-78 (2♂♂); same data, 22-v-78 (2♂♂). *Otero Co.*: Davis Dome, McGregor Range Camp, 4200', 5-iii-95 (3♂♂, 1♀, RH and SJC); Three Buttes (middle butte), McGregor Range, 4300', 5-iii-95 (2♂♂, RH and SJC). *Rio Arriba Co.*: Below El Vado Dam, 7000', 12-v-85 (1♀); SW of Embudo, 21-iv-62 (JAS); 1 mi E of Capulin, 11-iv-63 (JAS); 3 mi. W of Gallina, 12-iv-63 (JAS); 6 mi. E of Gallina, 25-iv-78 (JAS); 4 mi. N of El Rito, Arroyo Seco, 7600', 14-v-78 (JAS); Gobernador Canyon, 6200', 10-v-83 (JAS); hill 2 mi. SE of Gobernador, 7300', 10-v-83 (JAS); S. Dulce Lake, 7400', 10-v-83 (JAS). *Sandoval Co.*: Pajarito Peak, SW slope, Jemez Mts., 9200', 4-vi-83 (1♂) (late record, probable altitude record); same data, 19-v-84 (3♂♂). *San Juan Co.*: 7 mi. SW of Toadlena, Chuska Mts., 7200', 24-iv-71 (7♂♂, 3♀♀); same data, 23-iv-78 (1♂); NM Hwy 140, 1.3 mi. S of Colorado state line, 9-v-83 (JAS); hilltop E of Aztec, 9-v-83 (JAS); FAA Tower S of Washington Pass, 9000', Chuska Mts., 15-v-71 (1♂). *Sierra Co.*: 3 mi. E of Emory Pass, 5-iv-66 (JAS); Ash Canyon, near Elephant Butte Dam, 4500', 10-iv-77 (1♀); 1 mi. N of NM Hwy 52 and 6 mi. W of Engle, 4600', 23-iv-83 (1♂); 5 mi. NE of Red Rock, SE slope, San Mateo Mts., 4600', 1-v-83 (1♂); NM Hwy 151, 28 mi. E of Emory Pass, 28-iii-86 (2♂♂, leg. SJC); hilltop ca. 20 mi. S of Hillsboro on NM Hwy 27, 18-iii-89 (6♂♂, 1♀); 10 mi. S of Hillsboro on NM Hwy 27, Silby Mt., 5300', 23-iv-88 (SJC); Point of Rocks, Sect. 19-30, T.17S., R.1W, 4800', 2-iv-95 (2♂♂ taken, 10 more seen, RH, ESC and SJC). *Socorro Co.*: 6 mi. NW of San Marcial, 4600', 1-v-83 (3♂♂). *Taos Co.*: 3 mi. NE of Big Arsenic Spring, near Rio Grande Gorge, 8000', 9-v-85 (2♂♂, 1♀); Big Arsenic Spring, Rio Grande Gorge, 7000', 9-v-85 (6♂♂, 1♀); Rio Grande Gorge, SW of Cerro, 7000', 10-v-86 (1♂, leg. SJC); Rio Grande Gorge, 24-iv-85 (SJC).

ARIZONA: *Apache Co.* (near *San Juan Co.*, NM): Ridge 2 mi. SW of Cove, Chuska Mts., 7000', 29-v-78 (4♂♂).

TEXAS: *El Paso Co.*: McKelligan Canyon, SE slope, Franklin Mts., El Paso, 5000', 7-iv-80 (6♂♂); same data, 26-ii-83 (1♂) (early record); same data, 25-iii-81 (2); Tom Mays Park, W slope, Franklin Mts., 5200', 6-iv-80 (3♂♂, 1♀); same data, 24-iii-81 (8♂♂, 1♀); same data, 14-iii-81 (2♂♂); same data, 12-iii-83 (3♂♂); same data, 6-iii-83 (3♂♂); same data, 8-iv-83

(4♂♂); same data, 28-iii-85 (2♀♀); same data, 1-iv-87 (1♀); Scenic View Subdivision, W slope, Franklin Mts., 4000', 8-iv-83 (2♂♂); E slope, Franklin Mts., 3 mi. N of Trans Mountain Rd., El Paso, 5000', 2-iv-87 (7♂♂); red hill, 2 mi. W of road to Hueco Tanks St. Park, US Hwy 62-180, 4000' (1♂, RH and SJC). Note: El Paso Co., TX, and Mun. Ciudad Juarez, Chih., were more intensively searched than other areas in an effort to record *A. pima*.

CHIHUAHUA: *Mun. Ascencion:* 26 mi. E of Ascencion, Mex. Hwy 2, 3800', 1-iv-85 (1♂). *Mun. Casas Grandes:* 25 mi. N of Nuevo Casas Grandes, Puerto Janos, 4500', 2-iv-85 (1♂). *Mun. Ciudad Juarez:* S slope, Cerro Bolas, ca. 20 mi. SW of Cd. Juarez, 5000', 21-iii-82 (1♂); Sierra del Presidio, ca. 25 mi. S of Cd. Juarez, 5000', 23-iii-85 (2♂♂); same data, 13-iii-87 (1♂); same data, 21-iii-84 (several, sight). Note: Approximately the same effort was expended collecting in the Franklin Mts. and the Cerro Bolas, which face each other across the Rio Grande. The only environmental difference I can cite for taking just one specimen in the Cerro Bolas, versus 46 in the Franklin Mts. is that the Cerro Bolas are totally limestone, whereas parts of the Franklin Mts. are volcanic. *Mun. Janos:* Janos microwave relay, 5 mi. E of Janos, 5400', 1-vi-85 (11♂♂); 35 mi. NW of Janos on Mex. Hwy 2, 4500', 12-iv-85 (3♂♂); ca. 10 mi. SW of Ejido Pancho Villa on road to Bavispe, ca. 5000', 6-iv-94 (1♂, RH and ESC).

SONORA: *Mun. Imuris:* 10-12 mi. SW of Cananea, 18-iii-84 (1♂).

Euchloe guaymasensis Opler

SONORA: *Mun. Benjamin Hill:* Santa Eva Microwave Relay, 10 mi. NE of Benjamin Hill, 3000', 27-ii-92 (1♂). *Mun. Cucurpe:* Santo Domingo Canyon, 12 mi. E of Cucurpe, 1-iii-92. *Mun. Guaymas:* El Vigia microwave relay (on ridge between Guaymas International Airport and city), 12-ii-89 (many ♂♂); same data, 19-ii-89 (worn ♂♂); same data, 24-ii-90 (many ♂♂, 6♀♀, ova, larvae, one pupa on *Descurainia pinnata*); same data, 5-ii-90 (few ♂♂, ova larva, and one pupa on *D. pinnata*); same data, 20-ii-92, (several ♂♂ and fourth instar larva); same data, 6-ii-93 (several ♂♂, ova and first or second instar larva); same data, 29-ii-93 (1♀). *Mun. Hermosillo:* Microwave relay on hill NE of Hermosillo, 21-ii-92 (several ♂♂); Las Avispas microwave relay, 40 mi. N of Guaymas, 2000', 24-iii-83 (1♂, holotype); same data, 12-iii-74 (1♂, paratype); same data, 23-iii-83 (2♂♂, paratypes); same data, 5-iii-84 (1♂, paratype); same data, 7 & 8-iii-87 (3♂♂); same data, 11-ii-89 (many ♂♂); same data, 18-ii-89 (many ♂♂); same data, 8-ii-92; same data, 21-ii-92; same data, 28-ii-92 (8♂♂ taken, 20-30 more observed). *Mun. Imuris:* Road to microwave relay E of Imuris, 22-ii-92 (several ♂♂).

Pontia sisymbrii sisymbrii (Boisduval)

NEW MEXICO (southern counties and low altitude records only): *Dona Ana Co.*: S rim, Soledad Canyon near Chimney Rock, Organ Mts., 6000', 24-iii-79 (1♂); Baylor Canyon, W slope, Organ Mts., 6000', 16-iii-79 (1♂) (intermediate to *transversa*); Fillmore Canyon, W slope, Organ Mts., ca. 7000', 28-iv-79 (1♂). *Eddy Co.*: Thayer Hill, E slope, Guadalupe Mts., 5500', 24-iii-86 (1♂); same data, 27-iii-86 (2♂♂); Stone Canyon in Sec. 1, E slope, Guadalupe Mts., 4500', 23-iii-86 (1♂). Note: Eddy County specimens appear to be subspecies *P. s. elivata*. *Grant Co.*: Cameron Creek, 4 mi. N Ft. Bayard, 6700', 16-iv-66 (3♂♂); 9 mi. up McKnight Rd. (USFS Road 152) from NM Hwy 61, W slope, Black Range, ca. 7500', 9-iv-89 (1♂); 3 mi. inside Natl. Forest on Royal John Mine Rd. (USFS Road 886), W slope, Black Range, 7000', 23-iv-88 (1♀); 1 mi. inside Natl. Forest on Royal John Mine Rd. (USFS Road 886), W slope, Black Range, 6500', 23-iv-88 (1♂); Gallinas Canyon, W slope, Black Range, 6000', 28-iii-86 (1♀, leg. SJC). *Luna Co.*: Ridge E of Spring Canyon, N slope, Florida Mts., 27-iii-86 (1♀, leg. SJC). *Otero Co.*: Three Rivers Canyon, Mescalero Reservation, E slope, Sacramento Mts., 6000', 21-iv-73 (3♀♀). *Sierra Co.*: 1 mi. E Emory Pass, E slope, Black Range, ca. 8000', 6-v-89 (1♀).

TEXAS: *El Paso Co.*: Tom Mays Park, W slope, Franklin Mts., 5200', 6-iii-83 (1♂), North Franklin Peak, Franklin Mts., 6000', 1-iv-87 (6♂♂) (intermediate morphs and mixed series, 2 *transversa* and 4 intermediates, as might be expected on a major mountain top drawing males from different drainages).

Pontia sisymbrii transversa R. Holland

NEW MEXICO (all records for state): *Hidalgo Co.*: Gray Ranch, Peaks S of Animas Peak, Animas Mts., 8200', 29-iv-91 (1♂, leg. SJC); Gray Ranch, Deer Creek, 8 mi. NW of Culberson Camp, SE slope, Animas Mts., 5400', 31-iii-93, (3♂♂, 3♀♀, 1 of the males intermediate, leg. SJC); Gray Ranch, Cowboy Rim, 6500', NE slope, Animas Mts., i-iv-93 (3♂♂, leg. SJC).

TEXAS: *El Paso Co.*: McKelligan Canyon, SE slope, Franklin Mts., El Paso, 5000', 27-ii-83 (5♂♂) (early record); same data, 25-iii-81 (1♂).

CHIHUAHUA: *Mun. Ascencion:* 26 mi. E of Ascencion, Mex. Hwy 2, 3800', 1-iv-85 (1♂). *Mun. Janos:* San Luis Microwave Relay, Mex. Hwy 2, Chih.-Son. state line, 6500', 2-iv-85 (2♂♂); same data, 13-iv-85 (1♂); same data, 4-iv-94 (1♂, 2♀♀); canyon on Chihuahua side of Puerto San Luis, Mex. Hwy 2, just E of Sonora state line, 5500', 7-iv-94 (1♂, 1♀, the male intermediate).

SONORA: *Mun. Agua Prieta:* San Luis Microwave Relay, Mex. Hwy 2, Chih.-Son. state line, 6500', 2-iv-85 (2♂♂); same data, 13-iv-85 (1♂).

USING TAXONOMIC DATA TO ESTIMATE SPECIES RICHNESS IN GEOMETRIDAE

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ABSTRACT. A global database of described species was constructed for the Geometridae from the card index to genera and species housed in The Natural History Museum, London. Associated biogeographical data show that compared with existing estimates, marked differences exist in the number of described species in certain of the main biogeographical regions. The *actual* number of geometrid species depends on the number of species yet to be discovered or named and on the number of names of presently accepted species requiring synonymy. Evidence from recent revisionary work on selected Neotropical Geometridae based on both modern samples from Costa Rica as well as older museum material, and a qualitative assessment of taxonomic work on the family globally, suggests that the actual number of valid species is nothing like an order of magnitude greater than the number currently described.

Additional key words: biodiversity, systematics, biogeographical diversity, moths.

A large quantity of taxonomic data lies available but little used in those institutions housing collections and associated reference material. In the present study we have collated such information for Geometridae from card indices and other sources held in The Natural History Museum, London (NHM), an institute housing a large and well curated collection of this group organized on a world basis. From these data we provide a total for the number of *described* species globally and totals for each of the main biogeographical regions. The information indicates taxonomic effort on Geometridae, highlighting strengths and weaknesses in the taxonomy of a large and widely distributed group of terrestrial invertebrates.

The magnitude of *actual* number of species by biogeographical area also is considered by qualitative assessments of the level of taxonomic effort by region, and by using the results of recent sampling and revisionary studies on Costa Rican Geometridae to assess levels of taxonomic change.

The work forms part of a broader project, intended as a response to calls from the wider biological community, conservationists in particular, for systematists to find ways of making their information more accessible and more rapidly available (e.g., McNeely 1992, Wilson 1992, Janzen 1993).

Geometridae were chosen for this study for several reasons. First, they are one of the largest families of Lepidoptera and are distributed in all the main biogeographical regions. Second, much information has been gathered about them: the entire geometrid collection at the NHM is arranged and indexed taxonomically on a world basis, and contains

much unpublished detail on synonymy and generic assignment. Third, recent taxonomic revisions have been undertaken for several subgroups. Over the past few years species-level taxonomy of several Neotropical genera has been undertaken by members of the Geometridae Research Group at the NHM. These studies made use not only of older material housed in museum collections but also modern samples, particularly those of the Instituto Nacional de Biodiversidad (INBio), Costa Rica. The results enabled us to gain some idea of the number of new species to be expected with access to specimens collected during a program of sampling in a biodiverse tropical country. Although the sample of genera studied was limited, it provided us with a guide to the *magnitude* of the number of new species expected with modern collecting.

METHODS

The Database

The foundation for this study is a computerized database, generated principally from the card index to the geometrid collections of the NHM. Names of putatively valid species, already described, were included in the database. The card index is complete, to within a small percentage, to 1985. Names of species from major sources published since then, up to October 1993 when the databasing finished, also were incorporated. As far as possible, the following information was recorded for each species of the six subfamilies (Archiearinae, Oenochrominae *sensu lato*, Ennominae, Geometrinae, Sterrhinae, and Larentiinae): author; date of description; type locality; and biogeographical area. Data were available for over 75% of species names for most variables, and in some cases for over 90%.

Numerous unpublished taxonomic changes, also incorporated in the database, were made to the collection and card index during the course of detailed curation by D. S. Fletcher and his associates over many years. The efforts of these curators added substantially to the pioneering work of L. B. Prout. These unpublished changes include the generic reassignment of many species and much species synonymy.

The biogeographical region for which the type locality was scored is that followed in the NHM collection and card index. These areas are Wallace's biogeographical regions with some subdivision. They are: Nearctic, Neotropical, Afrotropical, Madagascar, Western Palaearctic, Eastern Palaearctic, Indo-Pacific (including New Guinea, i.e., Irian Jaya/Papua New Guinea), Australasia, and New Zealand (see Gaston & Hudson *in press* for a map showing their distribution). The regions were accepted for their expediency rather than their biogeographical reality. Particularly controversial are: (i) the position of the dividing

line between the Nearctic and the Neotropical regions; (ii) the position of the line dividing the Palaearctic from the Indo-Pacific region; (iii) the division between the Indo-Pacific region and Australasia—in particular the inclusion of New Guinea in the former rather than the latter; and (iv) the division between the Western and Eastern Palaearctic.

For the purposes of this work, species were taken to mean 'taxonomic' species. Although there is no agreement over the precise definition of a species for the Geometridae, or any other group of organisms, there is a general consensus among taxonomists as to what constitutes a geometrid species. While most geometrid species can be recognized on wing pattern, species-level decisions have been greatly refined by the study of the genitalia of these insects. The study of genitalia has affected species decisions in two ways. It has resulted in considerable synonymy of 'species' now considered to be just variations and, in contrast, it has led to the recognition of additional species previously unrecognized on the basis of wing shape or color. The study of genitalia has strongly influenced species taxonomy in Geometridae from around the time of the second world war, although A. J. T. Janse made extensive use of these structures in his work on the South African fauna earlier (Janse 1932, 1933–35).

The database took one person about nine months of full time work to complete.

RESULTS

Number of Described Species of Geometridae Globally and by Region compared with Estimates made by Heppner (1991)

Heppner (1991) tabulated the number of described species of Geometridae by biogeographical area and subfamily as part of a collation of described species for all lepidopteran families and subfamilies. Although the *total* number of species for the Geometridae given by Heppner differs by less than 1.5% from our own, the differences between the two sets of figures in some of the biogeographical regions are very great (Table 1). Since the biogeographical areas used by Heppner (1991) differ in some instances from those used in our database, we made our figures comparable by adding and subtracting species numbers where necessary. The source of our regional figures in Table 1 is the database (see Methods), adjusted, for some areas, by those additional sources indicated below.

Nearctic. Our figures (Table 1) are those of the lepidopteran checklist by Hodges et al. (1983). There have been some additions and synonymys since that time, but these are not extensive.

Neotropical. The database includes results of some revisionary work

TABLE 1. Numbers of described species of Geometridae by biogeographical region.

	NEA ¹	NEO	PAL	AFR ²	ORI	AUS ³	Total						
E	750	3318	1361	1556	863	1240	879	520	9710	8984			
L	466	1668	1398	464	501	803	711	300	5749	5723			
S	95	902	526	380	480	564	217	220	2763	2847			
G	73	454	220	561	300	431	404	475	2296	2259			
O	3	87	34	45	100	227	305	350	610	1065			
A	2	4	6	0	0	0	4	0	16	12			
	1398	1417	6433	7956	3545	4243	3106	2144	4151	3265	1865	21,144	20,890

Our figures are not underlined; figures underlined are from Heppner (1991). To equate biogeographical areas used in our database with those of Heppner, we summed species numbers in the following regions: Western and Eastern Palaearctic (combined as Palaearctic by Heppner); Afrotropical and Madagascar (combined as Afrotropical by Heppner); New Zealand and Oceania (including Irian Jaya/Papua New Guinea) (combined into Australasia by Heppner).

E, Ennominae; L, Larentiinae; S, Serrhiniinae; G, Geometrinae; O, Oenochrominae; A, Archhearinae.

¹ Our figures are taken from the *Check List of the Lepidoptera of America North of Mexico* (Hodges et al. 1983).

² Includes Madagascar.

³ Our figures are based on the estimates of described species by Common (1990) for Australia, from the species catalogued by Dugdale (1988) for New Zealand and, for Oceania, from a summation of the type localities with additions of those species listed as endemics from Hawaii in Nishida (1992).

in press. These additions, however, will not have increased significantly the number of names in this region.

Palaeartic. Obtaining figures for numbers of described species in the Western and Eastern Palaeartic is complicated by the existence of various country lists for Europe: figures based on such lists would result in duplication of many species names. Our figures therefore are based strictly on the database of type localities. Many of those localities that we failed to identify in the time available are likely to fall in the Palaeartic, and the position of the border between the Palaeartic and the Indo-Pacific regions is such that some uncertainties exist over the regional designation of some species. We have resolved these problems as far as possible, but they are more likely to bias our figures on the low than on the high side.

Afrotropical (Ethiopian). The number of geometrid species in the database with a type locality in Madagascar is 649, while in the checklist of Madagascan Lepidoptera compiled by Viette (1990) the number is 665. These two figures correspond well, particularly as in the checklist the total would be expected to be somewhat higher by including species occurring both in Madagascar and Africa. The number of geometrid species for Southern Africa (including Namibia, Botswana, Zimbabwe, Mozambique south of the Zambesi, South Africa and the constellation of countries within South Africa) listed by Vári and Kroon (1986) is 914. Thus, total geometrid species for Southern Africa (Vári & Kroon's figure) plus Madagascar (the figure from our database) is 1563, leaving a figure of 1543 further species for the rest of the Afrotropics. By no means does this latter figure seem unreasonable for described species in this area.

Numbers of geometrid species by subfamily estimated by Herbulot (1992) for the Afrotropical region are as follows: Ennominae, 1608; Larentiinae, 467; Sterrhinae, 469; Geometrinae, 572; Oenochrominae, 52. These figures are broadly similar to ours (see Table 1). While our estimate of the total number of species differs by merely 2% from that of Herbulot, it is 45% higher than that of Heppner.

Oriental. Our figures were produced by subtracting from the number of Indo-Pacific records in the database the number of species listed from the Pacific Islands east of, and including, New Guinea.

Australasia. Our figures for the number of described species in Australia are those of Common (1990); those for New Zealand were derived from the checklist by Dugdale (1988). For the Pacific Ocean islands we summed the number of type localities recorded in the database.

The Magnitude of Actual Numbers of Geometrid Species

Understanding the true number of geometrid species depends on the number of species already described, the number of species undescribed

(whether represented in collections or not) plus species needing to be revived from synonymy, and the number of species names requiring synonymy. Accumulation curves of geometrid species numbers by decade (Gaston, Scoble & Crook in press) show that the rate at which species were described rose rapidly from around 1850 and, for several regions, fell sharply around the time of the second world war. There are several possible reasons for the fall in species description rates; a reduction in the number of new species to be described is only one.

Nearctic. Taxonomic knowledge for Geometridae in the Nearctic region is fair to good. The area has benefited from a comprehensive checklist of Lepidoptera (Hodges et al. 1983), in which many revisionary changes to the taxonomy have been incorporated. Nine authors, from a total of over 75, are collectively responsible for the description of around 70% of geometrid species from this region. They are: W. Barnes, S. E. Cassino, J. A. Grossbeck, A. Guenée, G. D. Hulst, J. H. McDunnough, A. S. Packard, F. H. Rindge, and F. Walker. Continued collecting, and study of unworked material stored in institutions, will undoubtedly reveal undescribed species, and further revisionary work will almost certainly identify further synonyms. Nevertheless, fieldwork over a long period by many individuals suggests that the number of species yet to be collected is unlikely to be high.

Neotropical. This region has the greatest number of described geometrid species, although the rate of description declined in the second decade of the century. It is likely also to have the greatest actual number of species.

Taxonomic knowledge of Neotropical Geometridae is fragmentary with modern revisions available for relatively few of the many genera. Eight authors, from a total of around 70, are collectively responsible for the description of over 75% of all geometrid species from the region. They are: P. Dognin, H. Druce, A. Guenée, L. B. Prout, F. H. Rindge, W. Schaus, F. Walker, and W. Warren. Of these, only F. H. Rindge is responsible for modern revisionary work (almost exclusively on selected genera of Ennominae) involving the study of genitalia. To gain a useful estimate of actual geometrid diversity in the Neotropics will require more even sampling over the region and more, and better planned, revisionary work incorporating material from the numerous and scattered collections of Neotropical geometrids.

Palaeartic. In the database, this region is subdivided into Western and Eastern Palaeartic. Assessing the true number of species in the Western Palaeartic is surprisingly difficult given such considerable taxonomic effort, including collecting, over a long period. The rate of description of new species shows no sign of decline in the subregion.

The extensive review of Palaeartic Geometridae by Prout (1912-

16, 1934–39), which did not involve morphological study of the genitalia, provides a useful taxonomic base. Revisionary work since then has been patchy. Few works cover taxa across the region and there are many subregional (often country) treatments. While much valuable information exists for Palaearctic Geometridae, coordination of effort is likely to result in numerous taxonomic changes at the level of species (and genus). The need for coordination and revision is acute in the Western Palaearctic subregion because the taxonomic effort, in terms of species descriptions, is more evenly spread, involving substantially more individual workers than any full biogeographical region.

The species taxonomy of the Eastern Palaearctic is more poorly documented; sampling has been less intense for much of the subregion. Our understanding of the Geometridae of Palaearctic China is relatively poor, while in Japan it is good with numerous revisions particularly by H. Inoue. Nine individuals (A.G. Butler, H. Inoue, J. H. Leech, C. Oberthür, L. B. Prout, O. Staudinger, A. Vojnits, W. Warren, and E. Wehrl) are responsible collectively for the description of around 70% of the named species of the Eastern Palaearctic.

Afrotropical. Our knowledge of Afrotropical Geometridae is uneven across the continent. The work of Janse (1932, 1933–35), which included morphological study of the genitalia, forms an invaluable basis for the Geometridae of South Africa, and has been influential in the taxonomy of the group for the rest of Africa. A recent checklist of Lepidoptera of the subcontinent (Vári & Kroon 1986) incorporates taxonomic changes since the time of Janse's revisionary studies. North of South Africa the geometrids are less well studied although a number of comprehensive revisions have been published. Just four individuals (D. S. Fletcher, C. Herbulot, L. B. Prout, and W. Warren) are collectively responsible for describing around 75% of the species. In Madagascar, treated separately from the rest of the Afrotropical region in the database, the number of names of Geometridae is likely to increase with further collecting and revisionary treatments. Just three authors (C. Herbulot, L. B. Prout, and P. Viette) are responsible for the description of around 80% of the species.

The rate of description of species shows little sign of declining either in Africa or Madagascar, but revisionary work will undoubtedly lead to much synonymy besides additional new species.

Indo-Pacific. Taxonomic knowledge of Geometridae from the Indo-Pacific region ranges from poor to fair across taxa and subregions. Most of the 5123 described species from the area were named before the level of revisionary work was advanced by the study of genitalia. However, revisionary study is particularly good for the Ennominae of Borneo (Holloway 1994). Given the intensity of sampling in Borneo, the number

of geometrid species yet to be collected is unlikely to exceed 10% of the number recognized currently (J. D. Holloway pers. comm.). Other areas that have benefited from modern revision or review of geometrid moths are Norfolk Island (Holloway 1977), New Caledonia (Holloway 1979), Fiji (Robinson 1975), Hawaii (Zimmerman 1958, Nishida 1992), and Nepal (Yazaki 1992, 1993, Sato 1993). Seven individuals are responsible for describing around 75% of the species. They are: G. F. Hampson, H. Inoue, F. Moore, L. B. Prout, C. Swinhoe, F. Walker, and W. Warren.

Among the Pacific islands, the number of new species from New Guinea, especially, is likely to rise substantially given the high level of endemism of its fauna, our relative ignorance of its geometrids, and the number of complexes of closely related, externally similar, species it appears to support.

Australia. The actual number of geometrid species in Australia was estimated as 2310 (Nielsen & Common 1991), a figure based on considerable taxonomic effort in the preparation of a forthcoming checklist of Australian Lepidoptera (Nielsen et al. in prep.). This figure is almost double the number of species described. The existence of many undescribed species is explained by the description of few geometrid species since 1947, a date representing the end of studies by A. J. Turner, and extensive collecting from 1960 onwards (E. D. Edwards pers. comm.). Current collecting activity is resulting in the discovery of very few species that are undescribed or unrepresented in collections. Thus the actual number of geometrid species in Australia is unlikely to more than double the number described.

Around 75% of Australian geometrid species have been described by four individuals: O. B. Lower, E. Meyrick, A. J. Turner, and F. Walker.

New Zealand. The accumulation curve for description of geometrid species reaches an asymptote around the decade commencing 1940 (Gaston, Scoble & Crook in press). It seems unlikely that the number of species will increase greatly, and certainly not by an order of magnitude (J. S. Dugdale pers. comm.).

Around 75% of New Zealand geometrid species were described by four individuals: G. V. Hudson, E. Meyrick, A. Philpott, and F. Walker.

Using Recent Samples and Taxonomic Revision to Estimate Actual Species Numbers

Museum collections of geometrids (and other organisms) are neither comprehensive nor do they represent a random sample of species. The comprehensiveness of taxonomic revisions based on them are, therefore, limited correspondingly. Revisionary works most likely to give a best

TABLE 2. Changes in selected genera of Neotropical Geometridae after recent taxonomic revision.

	<i>Oos</i>	<i>Nem</i>	<i>Lis</i>	<i>Cha</i>	<i>Thy</i>	<i>Per</i>	<i>Phr</i>	<i>Pit</i>	Total
No. of species after revision	72	99	42	14	12	24	13	2	278
No. of new species ¹	3	29	3	0	4	15	4	0	58
No. of names synonymized ²	37	9	11	3	2	1	20	5	88
% new species	4	29	12	0	33	62	31	0	21
% new synonymy	50	9	26	24	16	4	154	250	32

Abbreviations of genera, and sources from which the data were derived. *Oos*, *Oospila* (Geometrinae) (Cook & Scoble in press); *Nem*, *Nemoria* (Geometrinae) (Pitkin 1993); *Lis*, *Lissochlora* (Geometrinae) (Pitkin 1993); *Cha*, *Chacariella* (Geometrinae) (Pitkin 1993); *Thy*, *Thysanopyga* (Ennominae) (Krüger & Scoble 1992); *Per*, *Perissopteryx* (Ennominae) (Krüger & Scoble 1992); *Phr*, *Phrygionis* (Ennominae) (Scoble 1994); *Pit*, *Pityeja* (Ennominae) (Scoble 1994). The figures were derived from results in revisions using material from the NHM and INBio in all genera listed. Material from several North American museums was incorporated into revisions for all genera excepting *Thysanopyga* and *Perissopteryx*.

¹ Includes revived species (names removed from synonymy).

² Refers to names synonymized in the works listed, not necessarily the total number of synonyms. Includes changes of status of species to subspecies.

estimate of numbers of new species are those involving a well organized sampling program.

Taxonomic study of selected neotropical genera incorporating material from recent collecting in Costa Rica shows that for, admittedly, a non-random sample of taxa, the increase in numbers of species can be strongly reduced by the number of species synonymized (Table 2).

DISCUSSION

Described Species

We are unclear as to the sources of many of the species numbers given by Heppner (1991) (Table 1). They were provided for the Neartic region, for Australia, and for New Zealand but there is no convincing explanation as to how the other figures were derived. Robbins already has suggested that the figures in Heppner's tables for butterflies (taxonomically the best known Lepidoptera) should not be used for diversity studies unless the apparent high bias is documented. We urge similar caution in the use of Heppner's figures for diversity studies in Geometridae until it can be convincingly demonstrated that they are more soundly based than our own.

The validity of the species accepted in the database depends on the accuracy of geometrid taxonomy. The number of synonyms in Table 2 suggests that many of the species we accept as valid today may be synonymized with future revisionary work.

Actual Numbers of Species

Accounting for synonymy is of great relevance in attempting to estimate *actual* species numbers (Gaston & Mound 1993). Table 2 shows how synonymy may be much underestimated in species richness as-

assessment. Even with the many unpublished synonymies recorded in the database, detailed revisionary work identifies many more. In a study of ennomine geometrids of Borneo, Holloway (1994) recognized 429 species, 83 of which were new, and 13 of which were revived from synonymy. Fifty-six new synonymies were made. Unlike the situation in Table 2 for certain Neotropical genera, in Holloway's study synonymy was only 13% of the total species finally recognized as valid. Nevertheless, synonymy is evidently of critical importance in estimating species numbers, yet it is widely ignored in the literature on biodiversity—the description of new species being given overwhelming, and uncritical, emphasis.

From Table 2 it is clear that access to extensive modern collections from the tropics does not necessarily result in the description of proportionally large numbers of new geometrid species. When synonymy is accounted for, the overall figure for geometrid species will rise even less. Although most geometrid genera are relatively cryptic, and thus prone to under-description, there are no signs that the total number of species is set to rise by anything remotely like an order of magnitude, even in the Neotropics—the most species-rich of the biogeographical areas.

We emphasize that the figures in Table 2 provide only an indication that species richness is not as great as we are sometimes led to believe. Limitations to sampling in other parts of the Neotropics provide us with little idea as to the true extent of geometrid species richness outside Costa Rica. Nevertheless we find the figures suggestive and hope that a similar exercise will be undertaken for other Lepidoptera and that the work will be expanded to incorporate modern samples from Neotropical sites outside Costa Rica.

Care also should be taken in extrapolating from the results in Table 2 for, as lepidopterists are well aware, brightly colored or strikingly patterned Lepidoptera are far more likely to suffer from variants being described as species. The dramatic synonymy recorded in Table 2 for the genera *Phrygionis* and *Pityeja* is undoubtedly so explained and, in any case, *Pityeja* is a very small genus. In contrast, more cryptic Lepidoptera tend to be underdescribed—as in the ennomine genus *Perissopteryx* in which many new species were described. Table 2, however, includes a spread of genera from those with species often difficult to distinguish on wing pattern (*Thysanopyga*, *Perissopteryx*, *Nemoria*), through *Oospila*, a genus with species that usually can be effectively distinguished on wing pattern, to genera exhibiting marked variation within species (*Phrygionis* and *Pityeja*). Although the sample of geometrid genera is representative neither of the Neotropics nor of geometrid genera globally, nothing in the results suggests that there exists

for this family the massive number of undescribed species estimated by Erwin (1982) to apply to insects generally. However, because collecting falls well short of comprehensive coverage (particularly in diverse regions such as South America), it is impossible to be precise about the actual global number of geometrid species.

A message from this study is that taxonomic data provide a useful source of information about species richness (e.g., Gaston 1991), a theme we are developing further for the Geometridae in particular. A proviso is that such data require careful and critical assessment. Unevenness of sampling is a particular problem, and older taxonomic works require revision to provide a balanced view of species numbers and species identity.

The value of taxonomic revisionary work in the modern biodiversity arena, as opposed to just the description of new species, is immense and not well appreciated (e.g., Albert 1993) by biologists generally. Although, and not surprisingly, its value is far better understood by taxonomists, there are few signs of the coordination and planning necessary to achieve taxonomic coverage sufficiently comprehensive to make a profound impact on our understanding of biodiversity (Mound & Gaston 1993). Furthermore, the usefulness of inventories and 'quick and dirty' lists as a base on which general biological data can be associated depends strongly on the quality of our taxonomic knowledge.

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ON THE RELATIVE ACCEPTABILITIES OF LOCAL BUTTERFLIES AND MOTHS TO LOCAL BIRDS

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ABSTRACT. A total of 162 species of butterflies and moths are classified into 10 acceptability categories, ranging from very highly acceptable to totally unacceptable, on the basis of presentations of dead specimens in over 300 discrete trials to birds coming to a feeding tray in Leverett, Massachusetts. The acceptability categories were defined on the basis of both percentage of specimens taken and the order in which these specimens were taken in the trials. Several behaviors of the birds also were recorded, including whether or not an insect was eaten, and, if eaten, whether it was de-winged prior to being consumed.

Analyses of the data revealed that overall size and wing area/body size ratio were important determinants of acceptability. Bark-like cryptic moths were the most acceptable insects presented, butterflies overall were less acceptable than moths, and mimetic species were among the least acceptable insects presented. A number of presumably warningly colored species were quite acceptable to the birds, and this finding is discussed with reference to the complexities involved in defining this prey defense. Overall, the results are compared with those obtained in earlier studies.

Additional key words: feeding experiments, insect defenses, predator/prey relationships, warning coloration, cryptic coloration, mimicry.

This paper presents the results of over 300 bird-feeding trials involving local butterflies and moths that were carried out from 1982 to 1985 in Leverett, Massachusetts. The major aim of this study was to assess the relative acceptabilities of 162 lepidopteran species to birds selecting from sample arrays presented in discrete trials at a single feeding station.

The most similar prior study was carried out by Jones (1932, 1934) at a feeding station on the island of Martha's Vineyard, Massachusetts. This earlier study, though similar in many respects to mine, involved some inconsistencies in experimental design (e.g., unequal sample sizes and unequal test durations) that precluded rigorous statistical analyses and, therefore, unequivocal interpretations of the results. The present study, while posing some of the design problems inherent in field experiments of this sort, has yielded data that have been subjected to a rigorous discriminant analysis, which some readers may wish to consult (MacLean, Sargent & MacLean 1989). Here I attempt to present results of more specific interest to lepidopterists and persons with primarily behavioral and ecological interests.

A second important aim of the present research was to provide some interpretation of the contributions of various characteristics of butterflies and moths to their relative acceptabilities to birds. Thus, all of the lepidopteran species used were classified within (1) taxonomic, (2) size,

(3) larval hostplant, and (4) appearance categories. While detailed analyses of the relative importance of these characteristics in determining the acceptability of lepidopteran prey to birds were presented in the previously mentioned discriminant analysis, I will here discuss some of the highlights of that work. In particular, I will address the role of appearance (crypsis, warning coloration, and mimicry) in determining prey acceptability to birds. Finally, I hope that a number of questions will emerge from these results that will stimulate further research.

METHODS

All of the moths used in this study were taken at night at 150-watt incandescent spotlights (Westinghouse outdoor projector) at my home in Leverett, Massachusetts. The butterflies were collected by net during the day at several sites up to 10 km from my home. Most of the specimens collected were immediately frozen in small jars in the freezer compartment of a household refrigerator and were thawed just prior to their use in the bird-feeding trials. All of the specimens were utilized within one week of their capture. Thus, as in the studies of Jones (1932, 1934), most of the insects were dead when presented to the birds. However, a few moths were only cooled in the refrigerator and were presented alive in order to determine whether this difference would affect the acceptabilities of the species involved. A total of 213 species of butterflies and moths were used as prey, and 162 of these were tested in two or more trials.

A bird-feeding trial consisted of a 15-minute presentation of six different species (or distinctive morphs) arranged in a circle on a 15.24 cm diameter light blue dish. This dish was set out on an open feeding tray located 1 m from a large glass door through which observations were made. [A photograph of this feeding situation is presented in Sargent (1987).] I observed the feeding tray from approximately 2 m away and recorded the specimens taken, in order, and the bird species taking each insect. In addition other behaviors of the birds were noted when they occurred, as follows: SW = specimen swallowed whole; DWE = specimen taken to perch and there de-winged and eaten; PD = specimen picked up and dropped in place; and TD = specimen taken to perch and dropped. All feeding trials were conducted between 0600 and 0800 h EDST, and no more than four trials were run on any one day.

Two measures of acceptability for each species (or morph) were obtained: the overall percentage of specimens taken, and the average rank of the specimens taken. These two measures were highly correlated (Pearson's correlation coefficient: $r = -0.699$, $P < 0.0001$ for the 69 species tested on more than 10 occasions), indicating that preferred

species were both taken more often and taken earlier in the trials than were less-preferred species.

These two measures of acceptability were then utilized to develop a ten-category classification of all of the species that were tested in the feeding trials. The percentage of specimens taken and the average rank of the specimens taken were scored as follows:

Percent Taken	Score	Average Rank	Score
80-100	1	1-1.9	1
60-79	2	2-2.9	2
40-59	3	3-3.9	3
20-39	4	4-4.9	4
0-19	5	5-6	5

An overall score was then obtained by averaging the percent taken and average rank scores. In this way, nine acceptability categories were created with scores ranging from 1, in 0.5 step increments, to 5. In addition, a category 10 was established for those species that were never taken by the birds. The overall classification is:

Category	Score	Description
1	1	very highly acceptable
2	1.5	highly acceptable
3	2	very acceptable
4	2.5	moderately acceptable
5	3	marginally acceptable
6	3.5	slightly unacceptable
7	4	moderately unacceptable
8	4.5	very unacceptable
9	5	highly unacceptable
10	—	totally unacceptable

The G-test of independence (Sokal & Rohlf 1969) was used in analyzing the data.

RESULTS AND DISCUSSION

A total of 2158 individual butterflies and moths, representing 203 species from 21 families, was presented to birds during this study (Table 1). The birds involved were primarily woodland species, with blue jays contributing the majority of the records (Table 1).

A listing by acceptability categories of the 162 lepidopteran species that were presented more than once to the birds is given in Table 2. Over half of the species tested (55.5%) rated as very acceptable or better (categories 1, 2 and 3). Another large group of species (33.3%) ranged

TABLE 1. Summary of the Lepidoptera presented, and those taken by birds, in feeding trials in Leverett, MA (1982-85).

Family	No. species	No. individuals	% taken	Bird species ¹			
				bj	bcc	tt	others
Sesiidae	1	1	0.0	—	—	—	—
Cossidae	2	2	100.0	2	—	—	—
Hesperiidae	2	16	75.0	11	—	1	—
Papilionidae	3	51	52.9	24	2	1	—
Pieridae	3	124	55.6	36	18	15	—
Lycaenidae	1	7	28.6	2	—	—	—
Nymphalidae	14	115	49.6	39	11	6	1
Satyridae	4	42	57.1	20	2	1	1
Danaidae	1	17	35.3	3	1	2	—
Limacodidae	2	10	50.0	5	—	—	—
Pyralidae	1	11	27.3	2	1	—	—
Thyatiridae	2	2	100.0	—	1	1	—
Drepanidae	3	28	46.4	8	1	4	—
Geometridae	22	259	70.7	131	21	28	3
Lasiocampidae	5	79	94.9	56	9	10	—
Saturniidae	3	76	81.6	53	3	6	—
Sphingidae	15	77	93.5	63	3	6	—
Notodontidae	14	53	98.1	40	6	4	2
Arctiidae	14	229	69.9	133	7	16	4
Lymantriidae	3	72	86.1	45	14	3	—
Noctuidae	88	887	93.5	453	235	121	20
Totals	203	2158	79.6	1126	335	225	31
%s				65.6	19.5	13.1	1.8

¹ bj = bluejay; bcc = black-capped chickadee; tt = tufted titmouse.

from moderately acceptable to slightly unacceptable (categories 4, 5 and 6), while only 18 species (11.1%) fell into the moderately unacceptable to totally unacceptable range (categories 7-10).

Certain subgroups within the 162 species total in Table 2 were singled out and are listed in descending order of their acceptability to birds in Table 3. This ranking indicates that sphingids, notodontids, and noctuids were the most acceptable insects presented, while geometrids and arctiids were less acceptable among the moths. Butterflies, however, were less acceptable than moths overall ($G = 172$, $P < 0.001$). And certain warningly-colored and mimetic insects were among the least acceptable insects presented. This list also includes some well known genera for which there were reasonable samples, and these genera usually fit the generalizations just described (e.g., *Papaipema* and *Catocala* were very highly acceptable like most noctuids). An exception was provided, however, by moths of the genus *Spilosoma* which were far more acceptable than arctiids generally. The high acceptability of these and other supposedly aposematic species will be discussed later.

TABLE 2. Acceptability data on 162 lepidopteran species¹ presented to birds in feeding trials in Leverett, MA (1982-85).

Category	Family Species	N	% taken	Av. rank	
1	Sphingidae				
	<i>Ceratomia undulosa</i> (Walker)	15	100.0	1.5	
	<i>Ceratomia catalpae</i> (Boisduval)	2	100.0	1.0	
	<i>Paonias excaecatus</i> (J. E. Smith)	11	100.0	1.5	
	Notodontidae				
	<i>Nadata gibbosa</i> (J. E. Smith)	4	100.0	1.3	
	Noctuidae				
	<i>Euparthenos nubilis</i> (Hubner)	10	100.0	1.6	
	<i>Catocala epione</i> (Drury)	5	100.0	1.8	
	<i>Catocala ilia</i> (Cramer)	4	100.0	1.8	
	<i>Catocala coccinata</i> (Grote)	2	100.0	1.0	
	<i>Acronicta americana</i> (Harris)	45	100.0	1.7	
	<i>Acronicta morula</i> Grote & Robinson	2	100.0	1.0	
	<i>Apamea amputatrix</i> (Fitch)	7	100.0	1.9	
	<i>Papaipema inquaesita</i> (Grote & Robinson)	5	100.0	1.6	
	<i>Metaxaglea innulta</i> (Grote)	7	100.0	1.3	
	<i>Adita chionanthis</i> (J. E. Smith)	6	100.0	1.8	
	<i>Agrotis ipsilon</i> (Hufnagel)	14	100.0	1.9	
	2	Geometridae			
		<i>Biston betularia cognataria</i> (Guenee)	3	100.0	2.3
<i>Ennomos magnaria</i> Guenee		16	100.0	2.4	
Lasiocampidae					
<i>Malacosoma americanum</i> (Fabricius)		46	93.5	2.6	
Saturniidae					
<i>Actias luna</i> (L.)		9	88.9	2.4	
Sphingidae					
<i>Sphinx gordius</i> Cramer		2	100.0	2.0	
<i>Lapara bombycoides</i> Walker		9	100.0	2.0	
<i>Paonias myops</i> (J. E. Smith)		8	100.0	2.0	
<i>Laothoe juglandis</i> (J. E. Smith)		7	100.0	2.4	
<i>Darapsa pholus</i> (Cramer)		5	100.0	2.2	
Notodontidae					
<i>Peridea ferruginea</i> (Packard)		20	95.0	2.7	
<i>Schizura unicornis</i> (J. E. Smith)		4	100.0	2.8	
Arctiidae					
<i>Pyrharctia isabella</i> (J. E. Smith)		47	93.6	2.6	
<i>Halysidota tessellaris</i> (J. E. Smith)		63	88.9	2.7	
Lymantriidae					
<i>Dasychira obliquata</i> (Grote & Robinson)	14	92.9	2.6		
Noctuidae					
<i>Zale horrida</i> Hubner	8	87.5	2.7		
<i>Catocala antinympha</i> (Hubner)	5	100.0	2.0		
<i>Catocala judith</i> Strecker	10	100.0	2.5		
<i>Catocala resecta</i> Grote	14	100.0	2.4		
<i>Catocala ultronia</i> (Hubner)	39	100.0	2.4		
<i>Catocala crataegi</i> Saunders	9	88.9	2.9		
<i>Catocala grynea</i> (Cramer)	9	88.9	2.6		
<i>Catocala amica</i> (Hubner)	30	93.3	2.8		

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	<i>Panthea pallescens</i> McDunnough	150	97.3	2.5
	<i>Charadra deridens</i> (Guenee)	35	97.1	2.7
	<i>Macronoctua onusta</i> Grote	5	100.0	2.4
	<i>Papaipema speciosissima</i> (Grote & Robinson)	2	100.0	2.0
	<i>Phlogophora periculosa</i> Guenee	10	100.0	2.2
	<i>Amphipyra pyramidoides</i> Guenee	60	98.3	2.4
	<i>Lacanobia grandis</i> (Guenee)	7	100.0	2.6
	<i>Nephelodes minians</i> (Guenee)	12	100.0	2.4
	<i>Feltia jaculifera</i> (Guenee)	7	100.0	2.0
	<i>Xestia adela</i> Franclemont	14	100.0	2.9
	<i>Xestia bicarnea</i> (Guenee)	7	100.0	2.9
	<i>Anaplectoides prasina</i> (Denis & Schiffermuller)	3	100.0	2.3
3	Nymphalidae			
	<i>Polygonia comma</i> (Harris)	5	80.0	3.8
	<i>Vanessa atalanta rubria</i> (Fruhstorfer)	14	85.7	3.6
	<i>Speyeria cybele</i> (Fabricius)	4	100.0	3.5
	Satyridae			
	<i>Cercyonis pegala</i> (Fabricius)	23	73.9	2.9
	Geometridae			
	<i>Lytrosis unitaria</i> (Herrich-Schaffer)	18	100.0	3.1
	<i>Pero honestaria</i> (Walker)	14	78.6	2.8
	<i>Caripeta angustiorata</i> Walker	3	100.0	3.7
	<i>Prochoerodes transversata</i> (Drury)	37	89.2	3.2
	<i>Hydria undulata</i> (L.)	6	50.0	1.7
	Lasiocampidae			
	<i>Phyllodesma americana</i> (Harris)	11	90.9	3.8
	Saturniidae			
	<i>Dryocampa rubicunda</i> (Fabricius)	56	83.9	3.2
	Sphingidae			
	<i>Darapsa myron</i> (Cramer)	5	100.0	3.6
	Notodontidae			
	<i>Pheosia rimosa</i> Packard	6	100.0	3.0
	<i>Nerice bidentata</i> Walker	2	100.0	3.5
	<i>Furcula modesta</i> (Hudson)	4	100.0	3.0
	Arctiidae			
	<i>Spilosoma congrua</i> (Walker)	34	91.2	3.4
	<i>Spilosoma virginica</i> (Fabricius)	17	94.1	3.7
	Lymantriidae			
	<i>Orgyia leucostigma</i> (J. E. Smith)	7	85.7	3.8
	<i>Lymantria dispar</i> (L.)	51	84.3	3.1
	Noctuidae			
	<i>Panopoda rufimargo</i> (Hubner)	15	93.3	3.4
	<i>Panopoda carneicosta</i> Guenee	10	90.9	3.7
	<i>Caenurgina erechtea</i> (Cramer)	6	88.3	3.0
	<i>Catocala residua</i> Grote	2	100.0	3.0
	<i>Catocala palaeogama</i> Guenee	8	100.0	3.0
	<i>Catocala gracilis</i> W. H. Edwards	4	100.0	3.0
	<i>Catocala andromedae</i> Guenee	13	100.0	3.2
	<i>Catocala praeclara</i> Grote & Robinson	5	100.0	3.0

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	<i>Catocala micronympha</i> Guenee	4	100.0	3.5
	<i>Chrysanympha formosa</i> (Grote)	6	83.3	3.0
	<i>Anagrapha falcifera</i> (W. F. Kirby)	8	100.0	3.6
	<i>Acronicta innotata</i> Guenee	36	83.3	3.3
	<i>Papaipema ptersii</i> Bird	11	100.0	3.4
	<i>Papaipema nebris</i> (Guenee)	4	100.0	3.3
	<i>Phlogophora iris</i> Guenee	11	81.8	3.6
	<i>Lithophane grotei</i> Riley	2	100.0	3.5
	<i>Eucirroedia pampina</i> (Guenee)	14	100.0	3.6
	<i>Sunira bicolorago</i> (Guenee)	8	100.0	3.8
	<i>Polia imbrifera</i> (Guenee)	4	100.0	3.0
	<i>Pseudaletia unipuncta</i> (Haworth)	13	100.0	3.6
	<i>Agrotis venerabilis</i> Walker	16	100.0	3.2
	<i>Anomogyna dilucida</i> (Morrison)	19	100.0	3.3
4	Hesperiidae			
	<i>Epargyreus clarus</i> (Cramer)	15	73.3	3.6
	Nymphalidae			
	<i>Speyeria aphrodite</i> (Fabricius)	5	60.0	3.0
	Limacodidae			
	<i>Euclea delphinii</i> (Boisduval)	7	71.4	3.8
	Geometridae			
	<i>Euchlaena serrata</i> (Drury)	6	66.7	3.8
	<i>Tetracis crocallata</i> Guenee	4	50.0	2.5
	Lasiocampidae			
	<i>Tolype vellea</i> (Stoll)	7	100.0	4.3
	<i>Tolype laricis</i> (Fitch)	2	100.0	4.0
	<i>Malacosoma disstria</i> Hubner	13	100.0	4.2
	Notodontidae			
	<i>Macrurocampa marthesia</i> (Cramer)	4	100.0	4.0
	Arctiidae			
	<i>Apantesis virgo</i> (L.)	2	100.0	4.5
	Noctuidae			
	<i>Scoliopteryx libatrix</i> (L.)	2	100.0	4.0
	<i>Synedoida grandirena</i> (Haworth)	7	57.1	2.5
	<i>Parallelia bistriaris</i> Hubner	42	78.6	3.4
	<i>Crymodes burgessi</i> (Morrison)	3	100.0	4.3
	<i>Achatodes zae</i> (Harris)	2	100.0	4.0
	<i>Chytonix palliatricula</i> (Guenee)	9	55.6	2.6
	<i>Polia latex</i> (Guenee)	2	100.0	4.0
	<i>Schinia florida</i> (Guenee)	10	90.0	4.2
5	Papilionidae			
	<i>Papilio troilus</i> L.	18	66.7	4.4
	Pieridae			
	<i>Colias eurytheme</i> Boisduval	19	73.7	4.5
	Nymphalidae			
	<i>Polygonia interrogationis</i> (Fabricius)	3	66.7	4.0
	<i>Vanessa virginiensis</i> (Drury)	9	44.4	3.3
	<i>Junonia coenia</i> (Hubner)	8	50.0	3.8
	<i>Basilarchia archippus</i> (Cramer)	29	51.7	3.5

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
	Satyridae			
	<i>Enodia portlandia</i> (Fabricius)	2	50.0	3.0
	Drepanidae			
	<i>Oreta rosea</i> (Walker)	11	63.6	4.3
	Geometridae			
	<i>Anacamptodes ephyraria</i> (Walker)	10	60.0	4.2
	<i>Xanthotype sospeta</i> (Drury)	17	70.6	4.6
	<i>Caripeta piniata</i> (Packard)	25	72.0	4.1
	<i>Nemoria mimosaria</i> (Guenee)	3	66.7	4.0
	<i>Eulithis explanata</i> (Walker)	3	66.7	4.5
	<i>Coryphista meadii</i> (Packard)	11	72.7	4.0
	<i>Dyspteris abortivaria</i> (Herrich-Schaffer)	2	50.0	3.0
	Saturniidae			
	<i>Hemileuca lucina</i> Henry Edwards	11	63.6	4.9
	Notodontidae			
	<i>Schizura ipomoeae</i> Doubleday	3	100.0	5.3
	Arctiidae			
	<i>Haploa clymene</i> (Brown)	7	42.9	3.7
	Noctuidae			
	<i>Idia lubricalis</i> (Geyer)	3	66.7	4.0
	<i>Leuconycta diphteroides</i> (Guenee)	6	50.0	3.0
6	Papilionidae			
	<i>Papilio polyxenes asterius</i> Stoll	14	57.1	4.2
	<i>Papilio glaucus</i> L.	19	36.8	3.4
	Pieridae			
	<i>Artogeia rapae</i> (L.)	43	46.5	4.3
	<i>Colias philodice</i> Godart	62	56.5	4.2
	Lycaenidae			
	<i>Satyrium calanus</i> (Hubner)	7	28.6	3.5
	Nymphalidae			
	<i>Clossiana bellona</i> (Fabricius)	3	33.3	3.5
	<i>Euphydryas phaeton</i> (Drury)	12	25.0	3.3
	Pyrilidae			
	<i>Desmia funeralis</i> (Hubner)	11	27.3	3.3
	Drepanidae			
	<i>Drepana bilineata</i> (Packard)	7	57.1	4.8
	Geometridae			
	<i>Campaea perlata</i> (Guenee)	41	53.7	4.1
	<i>Ennomos subsignaria</i> (Hubner)	14	42.9	4.3
	<i>Eulithis propulsata</i> (Walker)	8	75.0	5.0
	Sphingidae			
	<i>Hemaris thysbe</i> (Fabricius)	8	37.5	3.3
	Arctiidae			
	<i>Ctenucha virginica</i> (Esper)	7	57.1	4.8
	Noctuidae			
	<i>Agriopodes fallax</i> (Herrich-Schaffer)	8	62.5	5.0
	<i>Callopietria cordata</i> (Ljungh)	4	50.0	4.5

TABLE 2. Continued.

Category	Family Species	N	% taken	Av. rank
7	Nymphalidae			
	<i>Vanessa cardui</i> (L.)	4	50.0	5.0
	Satyridae			
	<i>Megisto cymela</i> (Cramer)	6	50.0	5.3
	Danaidae			
	<i>Danaus plexippus</i> (L.)	17	35.3	4.2
	Geometridae			
	<i>Euchlaena irris</i> (Barnes & McDunnough)	11	54.5	5.3
8	Nymphalidae			
	<i>Phyciodes tharos</i> (Drury)	11	27.3	5.7
	Satyridae			
	<i>Coenonympha inornata</i> W. H. Edwards	11	27.3	5.0
	Drepanidae			
	<i>Drepana arcuata</i> Walker	10	20.0	5.0
	Arctiidae			
	<i>Cycnia tenera</i> Hubner	3	33.3	5.0
9	Geometridae			
	<i>Itame pustularia</i> (Guenee)	6	16.7	5.0
	Arctiidae			
	<i>Haploa lecontei</i> (Guerin-Meneville)	17	11.8	5.0
10	Nymphalidae			
	<i>Clossiana selene myrina</i> (Cramer)	7	—	—
	Limacodidae			
	<i>Apoda biguttata</i> (Packard)	3	—	—
	Arctiidae			
	<i>Hypoprepia fucosa</i> Hubner	19	—	—
	<i>Holomelina laeta</i> (Guerin-Meneville)	3	—	—
	<i>Ciseps fulvicollis</i> (Hubner)	8	—	—
	Noctuidae			
	<i>Paectes oculatrix</i> (Guenee)	2	—	—
<i>Lithacodia carneola</i> (Guenee)	2	—	—	
<i>Cerma cerintha</i> (Treitschke)	3	—	—	

¹ Species are listed sequentially (after Hodges et al., 1983) within each of the 10 acceptability categories defined in the text.

Prey Size

A previous discriminant analysis (MacLean, Sargent & MacLean 1989) revealed that size was the single most important predictor of acceptability for the moths and butterflies used in this study. A comparison of data obtained for small, medium, and large species (based on the wingspans given in Forbes, 1923, 1948, 1954, 1960) shows that medium and large species were taken more often than small species ($G = 28.5$; $P < 0.001$), despite the fact that medium and large species, if eaten, were more likely to be de-winged before being consumed ($G = 28.9$;

TABLE 3. Selected groups of Lepidoptera arranged in descending order of acceptability to birds.

Groups	No. species	No. individuals	% taken
Sphingids (nocturnal)	13	68	100.0
<i>Papaipema</i> spp.	6	24	100.0
Notodontids	14	53	98.1
<i>Catocala</i> spp.	22	169	97.3
Noctuids	88	887	93.5
<i>Spilosoma</i> spp.	2	51	92.2
Moths	175	1786	85.1
Geometrids	22	259	70.7
Arctiids	14	229	69.9
<i>Colias</i> spp.	2	81	60.5
Butterflies	28	372	53.0
<i>Haploa</i> spp.	2	24	20.8
Batesian mimics (non-lepidopteran models)	4	35	20.0

$P < 0.001$) (Table 4). This suggests that any handling costs associated with larger lepidopteran prey are not sufficient to offset the gains (presumably caloric) associated with consuming them.

Another line of evidence for an aversion of the birds to smaller prey is the finding that small prey were three times more likely to be picked up and dropped in place than were large prey ($G = 17.5$; $P < 0.001$) (Table 4), suggesting that small prey were often rejected on the basis of an assessment of their weight (most of the small species used were cryptic (Table 4), and therefore presumably palatable).

A general preference of birds for larger prey, all else being equal, has often been demonstrated (e.g., Marples 1993). However, the trade-offs suggested here between the costs and benefits of sampling, handling,

TABLE 4. Data comparisons for small (<38 mm), medium (38.1–53 mm) and large (>53 mm) Lepidoptera species used in this study.

Characteristics	Small	Medium	Large
No. species	71	90	42
No. individuals	592	1164	402
No. cryptic species	55 (77.5%)	71 (78.9%)	33 (78.6%)
No. cryptic individuals	481 (81.3%)	836 (71.8%)	293 (72.9%)
Percent taken	71.8	82.3	82.8
Percent eaten/taken	32.5	23.9	17.4
Percent de-winged/eaten	13.0	31.0	60.3
Percent picked up and dropped	9.5	4.3	3.0

TABLE 5. Comparative acceptabilities of noctuids and geometrids in two cryptic categories.

Moths	No. species	No. individuals	% taken	picked up & dropped
Barklike noctuids	47	613	96.2	0.5
Leaflike noctuids	33	242	90.9	6.6
Barklike geometrids	3	31	87.1	3.2
Leaflike geometrids	12	158	77.2	8.2

and consuming lepidopteran prey of different sizes would seem to warrant more precise quantitative analyses of this matter in the future.

Wing Area/Body Size Ratio

Jones (1932) speculated that another factor contributing to the relative acceptabilities of various Lepidoptera to birds might be the wing area to body size ratio. Thus, he suggested that the higher ratios characterizing certain groups, such as butterflies (as opposed to moths) or geometrids (as opposed to noctuids), might contribute to the lower acceptabilities of these insects to birds. Other studies have yielded results that are consistent with this suggestion. For example, Chai (1986) noted that within butterflies, acceptability was often associated with "short, stout bodies," whereas unacceptability was often associated with "long, slender bodies."

I previously have pointed out the relatively low acceptability of butterflies (compared to moths) in the present study (Table 3), and data on the relative acceptabilities of geometrids and noctuids are presented in Table 5. Geometrids were less acceptable than noctuids overall ($G = 72.5$; $P < 0.001$), and it is interesting to note that leaflike specimens (with generally higher wing area/body size ratios) in both families were significantly less often taken ($G = 27.5$; $P < 0.001$) and significantly more often picked up and dropped ($G = 19.4$; $P < 0.001$) than were barklike specimens (with generally lower wing area/body size ratios).

The general impression conveyed by these data is that wing area/body size ratio is a contributing factor to the acceptability ratings of lepidopteran prey and, as with size alone, further quantitative study is needed.

Warning Coloration and Mimicry

A peculiarity of this study was the finding of a high acceptability of some presumably aposematic species to birds. In fact, MacLean, Sargent and MacLean (1989) found warning coloration to be the third most important single predictor of acceptability (after large size and barklike appearance) for this entire array of butterflies and moths!

TABLE 6. Comparison of acceptabilities of living and dead specimens of several presumably aposematic moth species.

Species	Living			Dead		
	No.	% taken	Rank	No.	% taken	Rank
<i>Dryocampa rubicunda</i>	4	100.0	1.8	52	82.7	3.3
<i>Pyrrharctica isabella</i>	10	100.0	1.9	37	91.9	2.8
<i>Spilosoma congrua</i>	3	100.0	3.0	31	90.3	3.4
<i>Spilosoma virginica</i>	2	100.0	2.5	15	93.3	3.9
<i>Halysidota tessellaris</i>	6	100.0	2.5	57	87.7	2.7
Totals	25	100.0	2.2	192	88.0	3.1

In part, this finding may have resulted from the erroneous assignment of some species to the warning coloration category (e.g., *Pyrrharctica isabella*). In other cases, however, there were prior reports of unpalatability (e.g., *Halysidota tessellaris* to bats (Dunning & Roeder 1965; Dunning 1968), and *Spilosoma* species to birds (Rothschild 1983), or field evidence of very low acceptability to birds (e.g., *Spilosoma congrua* and *Dryocampa rubicunda* (Jones 1932)).

On the other hand, some of these species may show a form of crypsis that has been described as "special resemblance" (Cott 1940), i.e., resemblance to some distinctive part of the environment. Thus, the white *Spilosoma* species may resemble fallen dogwood bracts on the forest floor (Endler 1984), and the pink-and-yellow *Dryocampa rubicunda* may resemble flowers or flower parts, like the similarly colored *Schinia florida* (Sargent 1969).

Whatever the case, I did attempt to control for the fact that these presumably aposematic moths were presented as dead specimens (and so might have lacked some behavioral or biochemical attribute that would otherwise have deterred the birds) by presenting live specimens (cooled in the refrigerator) of six species in several tests. Although the sample sizes were small, birds found the living moths more acceptable than the dead ones in every case (Table 6).

It is clear that designating a species as warningly colored or aposematic is no longer the simple matter it once seemed to be. We know, for example, that individuals of a seemingly aposematic species may vary with respect to the levels of toxins they possess (e.g., the so-called "palatability spectrum" in danaid butterflies (Brower et al. 1968; Brower 1984)), reflecting, at least in part, variations in the chemistry of their hostplants (see references in Bowers 1990). We also know that predators vary, both within and between species, in the extent to which they find particular prey aversive, reflecting motivational (e.g., Swynnerton 1915, Chai 1986), physiological (e.g., Brower et al. 1985), and behavioral (e.g.,

Brower & Calvert 1985, Brower & Fink 1985) variables in these predators. Further study obviously is needed in order to establish the qualifications that must be applied to any particular case of warning coloration.

Despite these caveats, however, it is important to note that at least a few species that generally are regarded as aposematic were quite unacceptable to the birds in this study. Among these cases were the brightly colored, day-flying saturniid, *Hemileuca lucina* (category 5); the checkerspot butterfly, *Euphydryas phaeton* (category 6), and a number of colorful or boldly patterned arctiids, including *Haploa clymene* (category 5), *Haploa lecontei* (category 9), *Cycnia tenera* (category 8), and *Holomelina laeta* (category 10).

In contrast to the warningly colored insects, Batesian mimics (especially those with non-lepidopteran models) were consistently rejected by the birds in this study. Examples include the bee mimic, *Hemaris thysbe* (category 8); the wasp mimics, *Ctenucha virginica* (category 6) and *Cisseps fulvicollis* (category 10); and the firefly mimic, *Hypoprepia fucosa* (category 10). An unusual case of "special resemblance" (which some might regard as Batesian mimicry (e.g., Edmunds 1974)), involving a noxious element in the environment (bird-droppings) also elicited rejection by the birds (e.g., *Cerma cerintha* (category 10)).

The much-studied mimicry case involving the monarch (*Danaus plexippus*) and viceroy (*Basilarchia archippus*) butterflies, a seemingly inexhaustible source of new insights (e.g., Brower 1969) and new surprises (e.g., Ritland 1991), here yielded equivocal results, with both the putative model and putative mimic being relatively unacceptable to the birds (categories 7 and 5, respectively). This classic relationship will undoubtedly repay yet further investigation.

Comparisons with Jones (1932)

There were a number of similarities between the present study and the earlier one of Jones (1932). The total numbers of lepidopteran species presented on at least two occasions in the two studies were 162 (Sargent) and 118 (Jones). Butterflies made up 15.9% (Sargent) and 7.6% (Jones) of these totals. If Jones' acceptability ratings are converted to 10 categories (10 units each on his 0-100 scale), then 79.1% (Sargent) and 66.1% (Jones) of the species presented were rated as acceptable or better (categories 1-5).

In addition, some of the general findings of Jones were noted here as well. For example, the birds clearly preferred larger to smaller insects in both studies. They also preferred moths over butterflies, noctuids over geometrids, and found large cryptic moths with colorful or boldly patterned hindwings (e.g., *Catocala* and many sphingids) among the

most highly acceptable insects presented. I also obtained data to support Jones' suggestion that wing area/body size ratio was an important factor affecting the acceptability of various lepidopteran prey.

There were 40 species presented to birds that were clearly identical in the two studies. If, as noted above, Jones' acceptability ratings are converted to 10 categories, then comparisons with my ten-category classification are possible. Of the 40 species so compared, 8 were placed in the same category, 17 were placed in adjacent categories (+ or -1), and 8 more were placed in categories no more than two steps apart in the two studies. This leaves 7 species that were classified rather differently (3 steps or more apart), 5 of which were far less acceptable in Jones' study (*Artogeia rapae*, *Dryocampa rubicunda*, *Euchlaena serrata*, *Schinia florida*, and *Tetracis crocallata*), and 2 of which were far less acceptable in mine (*Euchlaena irraria* and *Cerma cerintha*). There seems to be no particular overall significance to these differences, and they may represent only the kind of variation to be expected in studies that are separated in time and place and that involve somewhat different arrays of avian predators.

I believe that the present study, while corroborating many of the findings of Jones, provides stronger evidence for these findings due to the utilization here of more precisely defined acceptability categories, the recording of additional behavioral data, and the use of several statistical methods (see also MacLean, Sargent & MacLean 1989). Hopefully, future studies will continue to move in the directions of increased quantification and more rigorous statistical analyses.

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BIOLOGY OF *URESIPHITA REVERSALIS* (GUENÉE) AND
COMPARISON WITH *U. POLYGONALIS MAORIALIS* (FELDER)
(CRAMBIDAE)

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ABSTRACT. The biology of *Uresiphita reversalis* (Guenee) is described, and the unpublished thesis of Mulvay on *Uresiphita polygonalis maoralis* (Felder) is summarized. The biologies of the two species are identical in many regards. Eggs are cream colored and laid in overlapping clusters of up to 80. Larvae undergo five instars; they are brightly colored, gregarious, and aposematic. Pupae are dark brown. Overwintering usually occurs in the pupal stage. Adults are active nocturnally and are superficially similar, with dark brown forewings and light orange hindwings with brown markings along the outer margin. In contrast to larvae, adults of both species are suspected to be palatable to predators on the basis of their color, nocturnal activity, and absence of sequestered quinolizidine alkaloids in adults of *U. reversalis*. Both species are multivoltine. Larvae of *U. reversalis* are diurnally active but feed throughout the night under warm temperatures.

Additional key words: Pyralidae, Pyraustinae, circadian activity, geographic distribution, *Genista*.

The genus *Uresiphita* Hübner is a small group in the family Crambidae (subfamily Pyraustinae), according to Munroe's (1989) revised classification of the Pyraloidea. The biology of only one species, *Uresiphita polygonalis maoralis* (Felder), has been studied in detail, and the results of those studies are presented in the unpublished Master's thesis of Mulvay (1978). *Uresiphita polygonalis maoralis*, the kowhai moth, is indigenous to New Zealand and is a pest of introduced lupines (e.g., *Lupinus arboreus* Sims; Fabaceae) (Ferro 1976). Mulvay (1978) studied the biology of this species in the context of identifying methods to inhibit damage to lupines. Mulvay (1978) concluded that *U. p. maoralis* undergoes two or three generations per year on the North Island of New Zealand, and overwinters in the pupal stage. Laboratory studies on the circadian activity of individually isolated males and females revealed that adults were nocturnally active when exposed to alternating light and dark conditions or when subjected to constant darkness. Oviposition was primarily on the lower surfaces of *Sophora* (Fabaceae) leaves but on the upper surfaces of *Lupinus* leaves. Eggs have a lacelike pattern on the chorion and are laid in overlapping clusters of up to 75.

Mulvay (1978) described the larvae of *U. p. maoralis* as cryptically colored and suggested that they probably do not use host plant alkaloids, but presented no evidence to support this conclusion. Larvae are orange or green with conspicuous yellow and white lateral lines, and have black tubercles, white patches, long white hairs, and dorsal white spots; they

feed gregariously. Based on coloration and pattern, larvae of *U. p. maoralis* appear to be aposematic. Mulvey described larvae as cryptically colored probably because they are obscured from view on defoliated stems when they orient themselves along the length of the stem.

The number of instars of *U. p. maoralis* varied with the host plant. Larvae reared on *Sophora microphylla* Ait., *Ulex europaeus* L. (Fabaceae), or *Genista monspessulana* (L.) L. Johnson (Fabaceae) underwent five or six instars. Larvae reared on *Lupinus arboreus* had five instars and smaller head capsules than those reared on *S. microphylla*. Larvae reared on *Sophora howinsular* (W. R. B. Oliver) P. S. Green completed six or seven instars. Pupation occurred on host plant leaves, beneath loose bark, or inside crevices of the stem. Pupation did not occur away from the host plants.

Uresiphita reversalis (Guenée), the genista caterpillar, is the only member of the genus known to occur in North America (Munroe 1976). Comstock and Dammers (1933) provide the earliest and most extensive descriptions of the egg, larvae, and pupae. Other descriptions of the early stages are provided by McKenzie (1933) and Bernays and Montllor (1989). The present paper reports the results of studies on the geographic distribution, life history, and circadian activity of *U. reversalis*. Data were gathered primarily in the laboratory on populations originating from northern California. When possible, field data were gathered on populations in the San Francisco Bay region of California, and these are noted in the text.

DISTRIBUTION

Distribution information on *U. reversalis* was obtained through a review of the literature and museum collections (see Leen 1992 for specific sources). *Uresiphita reversalis* is a North American species with a latitudinal distribution from Nova Scotia, Canada, into parts of Mexico. Specimens have been collected from nearly all states in the U.S. except those surrounding and directly west of the Great Lakes. Colorado, Nebraska, Iowa, and Illinois represent the northern limits of distribution in the midwestern U.S. The western range extends to Arizona and California, including the California Channel Islands. I found no records of *U. reversalis* from Nevada or Utah although apparently acceptable host plants are present there.

The current distribution of *U. reversalis* in central and northern California is attributed to a range expansion that occurred in the early 1980s (Powell 1992). According to the California Department of Agriculture identification records, the distribution of *U. reversalis* extended northward during the 1980s. In 1980 and 1982, it was collected in the northern interior county of Shasta. In 1990, the moth was collected

at Fort Bragg in Mendocino County, the northernmost site recorded on the California coast. Freezing temperatures during December 1990 markedly decreased field populations throughout northern California, although *U. reversalis* was collected again in Mendocino County (Ukiah) in October 1991. The eastern limit of its distribution in California lies near the state boundary. Specimens have been collected from the foothills of Placer and San Bernardino counties.

LIFE HISTORY

The developmental rates of *U. reversalis* from egg through adult were observed in the laboratory at 20°C and 16L:8D. Adult longevity and egg productivity were studied under the same conditions.

Eggs

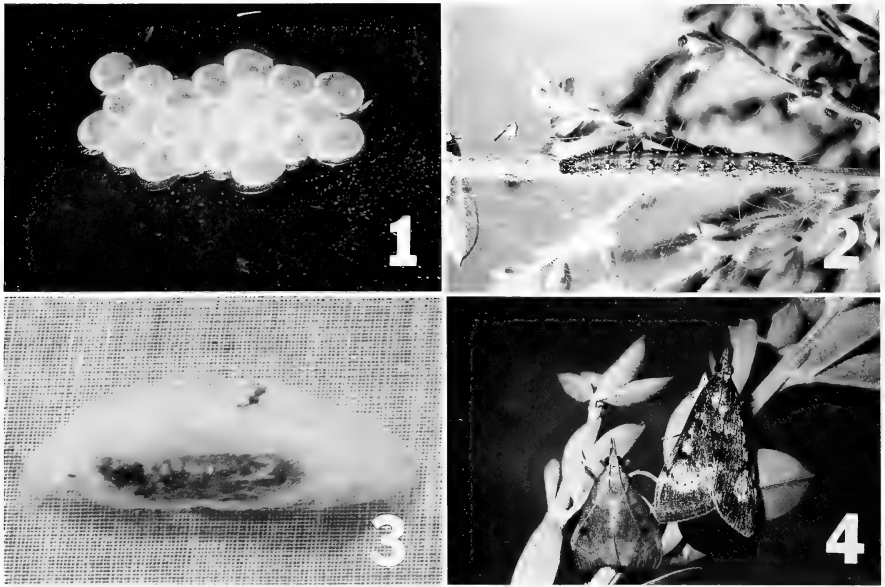
Observations of oviposition patterns and egg numbers were made in both the laboratory and the field. Eggs are shiny and yellow, and laid in clusters in an overlapping pattern resembling fish scales (Fig. 1). Cluster size ranged from 1 to 88 ($\bar{x} = 19$; $n = 91$) in the laboratory. Clusters observed in the field ranged from 3 to 65 ($\bar{x} = 39$; $n = 35$).

Egg clusters are laid on both the lower and upper surface of leaves. On *Genista monspessulana*, 63% (50/79) of clusters observed in the laboratory and 68% (17/25) of clusters observed in the field were on the upper leaf surface. Additional field observations on other host plants also show surface placement is variable. Clusters were observed on the upper surface of *L. arboreus* 67% (4/6) of the time and on the upper surface of *Baptista leucantha* Torr. and Gray 25% (1/4) of the time. None of the laboratory or field values differ significantly from 50% (z-test, $p > 0.05$). Field data were gathered from potted plants maintained in Albany, California.

Larvae

Egg incubation averaged five days ($n = 50$). Newly emerged larvae occasionally cannibalized larvae that were slower to emerge. The chorion often was eaten after emergence, suggesting that cannibalism is probably an indirect consequence of this feeding. The time required for development from larval (Fig. 2) to pupal stage when fed *G. monspessulana* was 28 days (based on 217 larvae from 29 separate clusters of eggs).

Head capsule widths were measured for 205 larvae reared on *G. monspessulana* in the laboratory. Larvae go through five instars with head capsule widths ranging from 0.18 to 0.36 mm for the first instar; 0.45 to 0.72 mm for the second; 0.81 to 1.17 mm for the third; 1.26 to 1.89 mm for the fourth; and 1.98 to 2.34 mm for the fifth.



FIGS. 1-4. Life stages of *Uresiphita reversalis*. 1, Eggs (approximately 1 mm in length); 2, Larva; 3, Pupa; 4, Adult *U. reversalis* (left) (forewing length 17 mm); adult *U. polygonalis* (right) from Masca, Tenerife, Canary Islands, Spain.

Larvae fed on the foliage and flowers of the host and ate bark and other soft stem tissues when foliage was not available. First instars initially fed on the leaf surface (upper or under) upon which the eggs were oviposited rather than exclusively on the upper surface, as implied by Bernays and Montllor (1989). Coloration has been described accurately by several authors (Comstock & Dammers 1933, Bernays & Montllor 1989), and need not be repeated here. Aspects of the aggregative behavior are discussed in Leen (1992).

Pupae

The pupae are dark brown with an average weight of 80 mg ($n = 20$) for males and 92 mg ($n = 49$) for females (Fig. 3). Development from pupa to adult averaged 18 days ($n = 21$). A solid, thick cocoon is formed prior to pupation, which occurs away from the host plant. Pupae were found under wood at 2 and 10 m from the host plant; larvae searched for pupation sites at even greater distances (20 m). Pupation occurred on a host plant when additional shelter (e.g., 5 cm wide tape) was provided but did not otherwise occur there.

In the laboratory, larvae cannibalized pupae, even when host plant foliage was available. Although silk and larvae contain quinolizidine

TABLE 1. Average longevity and weight of adult *Uresiphita reversalis*.

	Females	Males
Live weight after emergence (mg)	47.5 (n = 41)	38 (n = 19)
Life span when fed honey and water (days)	20 (n = 21)	19 (n = 16)
Life span when fed water only (days)	7.8 (n = 52)	7 (n = 42)

n = number of individuals measured.

alkaloids, pupae do not (Wink et al. 1991). When pupae are exposed as a result of damage or movement of the cocoon, the opportunity for cannibalism by larvae was provided and occurred. However, there was no evidence of cannibalism in the field where pupation occurs away from the host plant.

Adults

Adults have velvet-brown colored forewings and light orange hindwings, and are relatively large in comparison to most other crambids (Fig. 4). The forewing of *U. reversalis* is without conspicuous pattern elements. By contrast, the forewing of *U. p. maorialis* and other *Uresiphita polygonalis* Denis and Schiffermüller subspecies (Fig. 4) features an intricate brown and silver pattern. Most *Uresiphita* species have some degree of brown coloring along the margin of the light orange hindwing.

Seventeen pairs of adults were isolated in pint-sized paper cups containing water and honey. A bouquet of *G. monspessulana* was placed outside the cups. Egg productivity was recorded and averages were calculated. Oviposition was initiated three days after emergence; the total egg-laying period was 10 days. The mean number of eggs produced was 276; the mean number of batches produced was 13; mean number of eggs per batch was 21.4; the mean number of eggs per day during the egg-laying period was 30.26; and the mean number of batches per day during the egg-laying period was 1.5.

Additional measurements were made on isolated adults maintained under similar conditions. Average female weight was almost 10 mg greater than male weight (Table 1). Longevity for females exceeded that of males by one day when fed either water and honey or water only. When either sex was provided honey in addition to water, longevity doubled. Females in colony cages were capable of ovipositing viable eggs without imbibing honey or water.

Overwintering Stage

Uresiphita reversalis did not overwinter in the larval stage during the study period 1985–1989. They usually overwinter as pupae and less

often as adults. Collection records for California and Florida indicate adults may be collected throughout the year.

CIRCADIAN ACTIVITY

Methods

The circadian activities of eggs, larvae, and adults were examined over three 24-hour periods: 28 October, 12 November, and 25 November 1989. Observations were recorded at one-half hour to one-hour intervals, depending upon the frequency of activity, with a 16L:8D light regime at 20°C. A red light filter was used for observations during the dark period (2200–0600 h). Activities observed include hatching of larvae; feeding of fourth and fifth instar larvae; and adult emergence, feeding, drinking, mating, and oviposition.

Clusters of eggs laid upon leaflets in the laboratory were placed on moistened filter paper in petri dishes and observed for hatching. Most eggs in a cluster hatch within minutes after hatch of the first egg. The time of hatch thus was recorded as the time the first larva in a cluster hatched. Feeding of fourth and fifth instars was observed by placing a single cutting of *G. monspessulana* in a bottle of water and placing one larva upon the cutting. Larvae were noted as eating if their mandibles were in motion at the time of observation.

Adult emergence was recorded as the presence of new adults in a cage where only pupae were present previously. Adults were not sexed but were observed for mating and oviposition activities. Three separate cages of adults that had emerged on day one, two, and three were observed over a 24-hour period to determine the time between emergence and first oviposition. Additional adults were placed in 0.6 m × 0.6 m cages and observed for mating, oviposition, drinking, and feeding behaviors. Each cage contained a vial of water with a cotton wick for drinking and streaks of honey on the outside of the vial for feeding. Another vial with a branch of *G. monspessulana* was placed in each cage for oviposition. Drinking or feeding was recorded when a moth extended its proboscis onto the wick or honey.

Results

The greatest proportion (95%, $n = 70$ clusters) of eggs hatched during daylight hours, with two peak periods of emergence at 1200 h and 1500 h. Larval feeding also occurred during the daylight hours but continued at the same levels during the night. Feeding is not light dependent for either fourth ($n = 64$) or fifth ($n = 51$) instars.

Adult emergence ($n = 42$) is primarily nocturnal and occurs more frequently after 2400 h than at other times of the night. Emergence

did not occur between 1200 and 1700 h. Mating also is primarily nocturnal but occurs more often during the matinal hours (0430–0630 h). Over 200 adults were observed over the three 24-hour periods, but only 67 pairs mated during the three days of observations. Mated adults ranged from one day to over two weeks old. Occasionally, a pair failed to separate and remained paired long after or permanently after the lights were turned on. Nearly all pairs recorded mating after 0800 h initiated the mating earlier in the night. Curiously, within a half hour of the lights going out, most adults spread the forewings about half way apart, exposing the lighter hindwings. This clearly is not associated with mating since less than 15% of all adults mated in the three observation periods. It also probably is not associated with thermoregulation since it was not related to changes in temperature.

Oviposition was primarily crepuscular, was less frequent during the night, and ceased during midday hours. Thirty-four females oviposited during the three 24-hour periods. General observations of caged females in the laboratory indicate that oviposition occasionally occurred during late afternoon hours as well. The time from emergence to first oviposition was greater than 48 hours but less than 72 hours. Oviposition did not occur during the first 24 hours ($n = 30$) or 48 hours ($n = 60$) after emergence, but did occur after 48 but before 72 hours following emergence ($n = 25$). The exact interval cannot be determined since the exact time of emergence was not known. Mating and feeding began within 24 hours after emergence ($n = 30$). Drinking was almost exclusively nocturnal and increased during matinal hours (0500–0700 h). Feeding was primarily nocturnal and remained steady throughout the night.

DISCUSSION

Many characteristics of *U. reversalis* and *U. p. maorialis* are similar and may be representative of other species in the genus. The color and pattern of larvae and adults of these two species are the same as those of other species of *Uresiphita*, based on published illustrations and examination of museum specimens. The habits of *U. reversalis* and *U. p. maorialis* seem to be associated with their color and pattern. The available data indicate that larvae of *Uresiphita* defoliate their host plants and specialize on quinolizidine alkaloid-bearing plants in the fabaceous tribes Genisteae, Sophoreae, Thermopsidae, and Bossiaceae (Leen 1992). Confirmation of sequestration of quinolizidine alkaloids by *U. reversalis* larvae was confirmed by Montllor et al. (1990), although these chemicals are not transferred to pupae or adults. Other species of *Uresiphita* probably are diurnally active and have gregarious larvae that sequester quinolizidine alkaloids from their host plant, and thus are aposematic. Other *Uresiphita* adults do not appear to be apose-

matically colored, and alkaloids probably are eliminated at the pupal stage as in *U. reversalis*.

Other similarities between *U. reversalis* and *U. p. maoralis* include cream colored eggs laid in overlapping clusters of up to 80, larvae that undergo five instars, and pupae that are plain dark brown. Both species are multivoltine and usually overwinter as pupae. Pupation sites are not uniform between these two species. Data on other species of *Uresiphita* are needed before generalizing further.

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A REVIEW OF *COELOPOETA* (ELACHISTIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT. The genus *Coelopoeta* Walsingham, 1906 (Lepidoptera, Elachistidae), is reviewed. Three species are recognized, two of which are described as new: *C. phacelliae* Kaila, new species (California, USA) and *C. maiadella* Kaila, new species (Yukon, Canada). The genus former was considered monotypic and included only *C. glutinosi* (Walsingham) (California). *Coelopoeta* apparently is restricted to western North America. Diagnoses and descriptions are given for all three species.

Additional key words: diagnosis, taxonomy, systematics.

Walsingham (1908) described the genus *Coelopoeta* for one species, *glutinosi* Walsingham, which occurs in California. He placed the genus in Hyponomeutidae. He also recognized the association of *Coelopoeta* with *Elachista*. Barnes and Busck (1920) and Braun (1948) placed *Coelopoeta* in the Elachistidae, the latter author according to characters of the adult mouth parts, antennae, and wing venation. She recognized, however, differences in genitalia, especially those of the male, between *Coelopoeta* and other members of the Elachistidae. Hodges (1978) doubted the monophyly of Elachistidae sensu Braun (1948), and suggested that *Coelopoeta* might be derived from the Oecophorini. He placed the genus in its own subfamily, Coelopoetinae, and kept it within the Elachistidae. Minet (1989) attempted to redefine the Elachistidae on the basis of the structure of pupal abdominal segments, the spinose gnathos in the male genitalia, the absence of dorsal spines in the adult abdomen, and several homoplastic characters. He excluded *Coelopoeta* from Elachistinae and even from his broadened concept of Elachistidae because of the different shape of the gnathos and the presence of dorsal abdominal spines in the genus. However, he indicated that the correct position of *Coelopoeta* was not unequivocally resolved. Hence, the relationships of this genus to other members of Gelechioidea remain obscure. In this paper I follow Braun (1948), Hodges (1978), and Hodges et al. (1983), and provisionally assign *Coelopoeta* to the Elachistidae until a generally accepted systematic position for the genus is found.

In addition to the type species of *Coelopoeta*, I describe in this paper two new species and present diagnoses and descriptions for all three species. The three species show only relatively small morphological differences.

The following institutions provided material for this study: Zoological Museum (ZMH), University of Helsinki, Finland; Essig Museum of Entomology (UCB), University of California, Berkeley; and United

States National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Coelopoeta glutinosi Walsingham (= *baldella* Barnes & Busck) is the largest and most broad-winged of the species. It is whitish or pale ocherous in color, only occasionally darker brownish. The dusting on the forewing of *C. glutinosi* is formed by the dark tips of scales (Figs. 1-4). *Coelopoeta phaceliae*, new species, is darker, bright yellowish brown, and has narrower forewings than *C. glutinosi*. The forewing scales are almost entirely brown (Fig. 5-8). *Coelopoeta maiadella*, new species, is grey, with a bright whitish spot on the forewing (Fig. 9). The male genitalia of *C. glutinosi* and *C. phaceliae* are most easily separated by the size of the vinculum: longer and broader in *C. glutinosi*, in which the vinculum is broadest near the tip (Fig. 12). The vinculum is narrow and gradually tapered towards the tip in *C. phaceliae* and *C. maiadella* (Figs. 12, 14). The cucullus of the valva is more distended in *C. glutinosi* than in that of *C. phaceliae* and *C. maiadella*. This character is seen most easily in ventral view (Figs. 10, 12, 14). *Coelopoeta maiadella* is separated from the other species by its longer and more slender aedeagus and more tapered juxta (Figs. 14, 15); the cucullus is not distended in *C. maiadella*. The female genitalia appear to be similar in *C. glutinosi* and *C. phaceliae* [the differences in Figs. 16 and 17 are artifacts of preparation]. The female of *C. maiadella* is unknown.

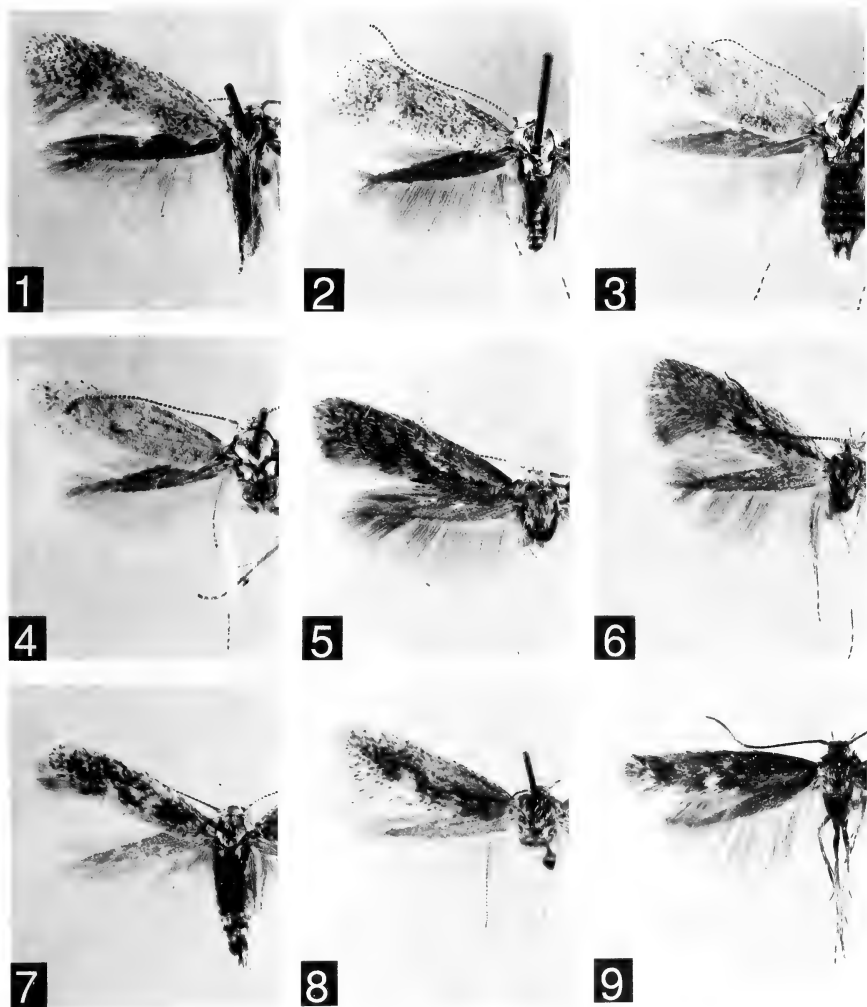
***Coelopoeta glutinosi* Walsingham, 1908**

(Figs. 1-4, 10-11, 16)

Coelopoeta glutinosi Walsingham 1908:218

Coelopoeta baldella Barnes & Busck 1920:248; synonymized by Braun 1948:8.

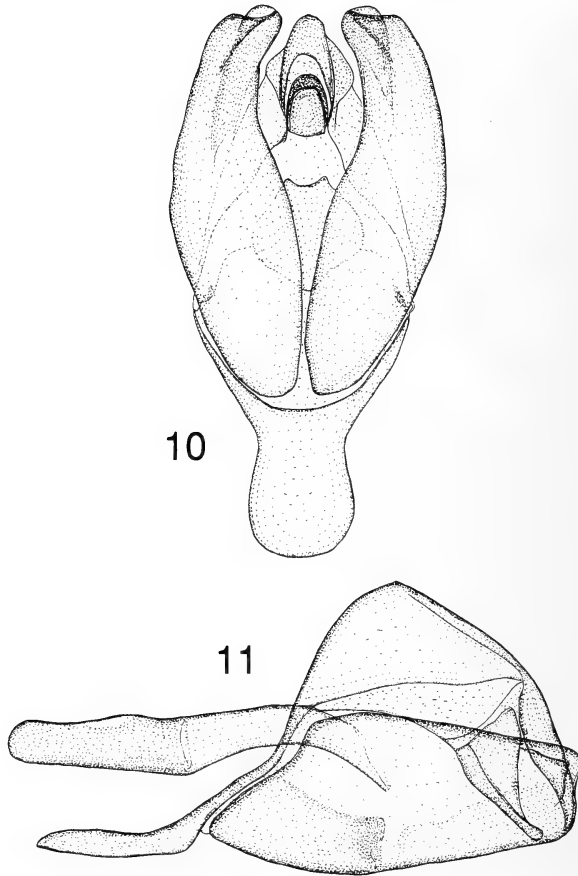
Adult. Labial palpi relatively short, almost straight, white, occasionally with some grayish scales. Head and neck tufts white, mottled ocherous in darker specimens. Antenna white, flagellum annulated with dark gray above. Abdomen white, dorsally with gray transverse fascia at base of each segment, with chitinized spines dorsally, appearing as bare, brown, transverse fasciae. Legs white, fore- and midlegs with gray dusting, tarsal segments with dark gray scales above. Forewing: Costa from base to one-third dark gray; ground color creamy white or pale ocherous, more or less densely dusted with gray or brownish tips of scales, dusting denser in apical half; an irregular darker patch in middle of wing at fold, the patch bound outwardly with an irregular whitish area. Cilia same color as forewing. Forewing length 5.0-6.5 mm. Hind-



FIGS. 1-9. Adults of *Coelopoeta* species. 1, *C. glutinosi*, male, California, Monterey Co.; 2, *C. glutinosi*, male, California, Ventura Co.; 3, *C. glutinosi*, female, California, Monterey Co.; 4, *C. glutinosi*, female, California, Marin Co.; 5, *C. phaceliae*, holotype, male, California, Modoc Co.; 6, *C. phaceliae*, paratype, male, California, Plumas Co.; 7, *C. phaceliae*, paratype, female, California, San Mateo Co.; 8, *C. phaceliae*, paratype, female, California, Plumas Co.; 9, *C. maiadella*, holotype, male, Canada, Yukon Territory.

wing gray. Underside of wings unicolorous grayish brown, except margins and cilia of forewing whitish.

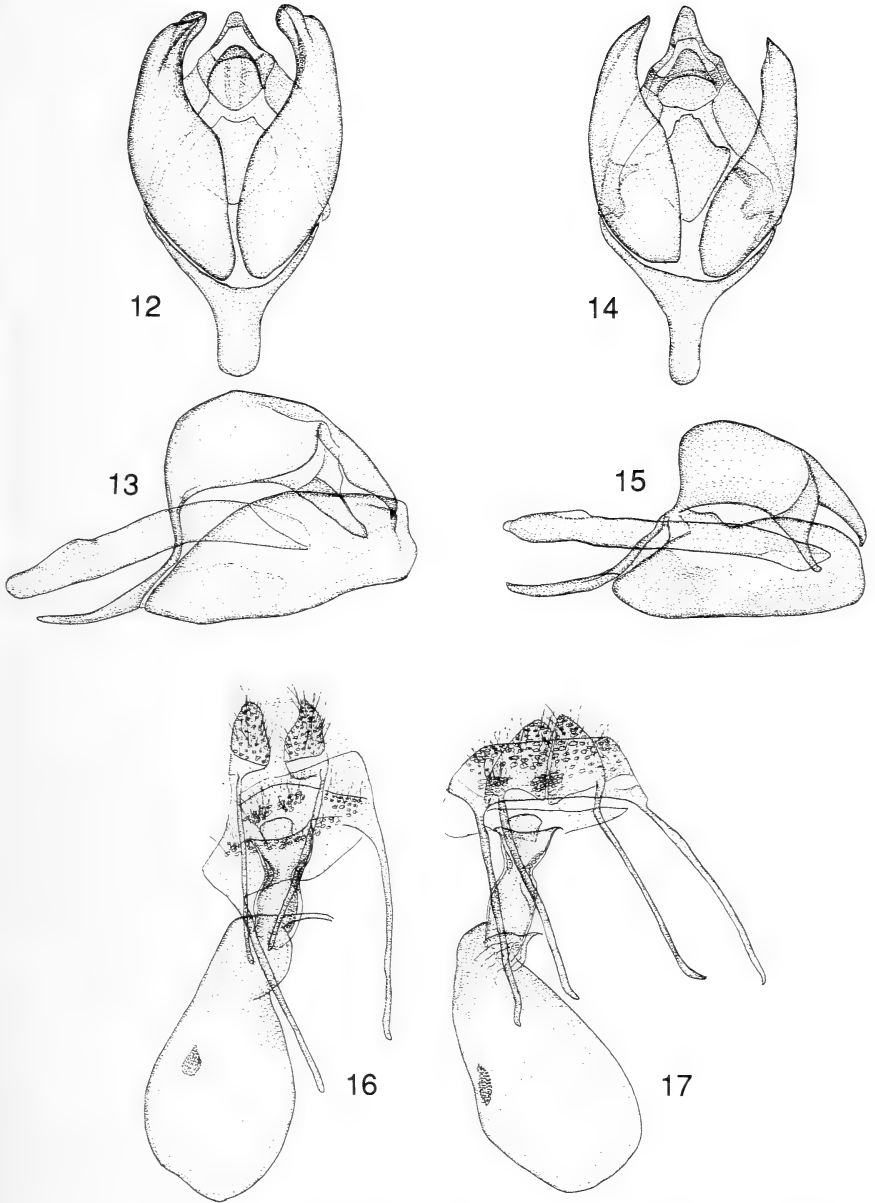
Male genitalia (Figs. 10-11). Uncus elongate, strongly sclerotized, apically tapering, ventrally concave, tip curved. Gnathos strongly sclerotized, tapering towards upturned, concave tip. Valva broad, apically



FIGS. 10-11. Male genitalia of *Coelopoeta glutinosi*, California, Marin Co.; **10**, Ventral view, aedeagus removed; **11**, Lateral view, juxta removed.

bent inward, inner margin gently concave; sacculus lobe apically straight-angled, with a few setae; cucullus prominently distended. Juxta shield-shaped, distally broad, laterally slightly produced. Vinculum strongly sclerotized, medially sharply and broadly produced, forming a broad spoon-shaped plate. Aedeagus with slightly produced caecum, smoothly bent in middle, apex oblique; the length equal to the length of the valva; cornuti absent.

Female genitalia (Fig. 16). As in *C. phaceliae* (see below). In Fig. 16, the length and density of setae on the papillae anales and posterior margin of the eighth segment have been reduced in order to clarify the illustration. The difference in size of the appendix bursae in Figs. 16 and 17 does not represent true interspecific differences; the appendix



FIGS. 12-16. Genitalia of *Coelopoeta* species. 12, Male genitalia of *C. phaceliae*, California, San Mateo Co., ventral view, aedeagus removed; 13, Same as 12, lateral view, juxta removed; 14, Male genitalia of *C. maiadella*, Canada, Yukon Territory, ventral view, aedeagus removed; 15, Same as 14, lateral view, juxta removed; 16, Female genitalia of *C. glutinosi*, California, San Bernardino Co., Kaila prep. #912; 17, Female genitalia of *C. phaceliae*, California, San Mateo Co., Kaila prep. #910.

bursae of *C. phaceliae* collapsed in mounting. The size and shape of the signum vary in both species, and therefore it cannot be used in separating the species.

Material studied. California, Camp Baldy, San Bern. Mts., 24.VI.1930 (6 specimens), 16.VII.1923 (7 specimens); San Bernardino Co., 24.VIII.1931 (2 specimens); Los Angeles Co., San Francisquito Canyon, 6.VII.1937 (2 specimens), E. C. Johnson; San Benito Co., Pinnacles, 11.VI.1936 (1 specimen), E. C. Johnson; Piute Mtns., Kern Co., 10.VI.1936 (1 specimen), E. C. Johnson; Los Angeles Co., Wrightwood, 14.VI.1948 (20 specimens), larvae as leaf miners on *Eriodictyon trichocalyx*, C. M. Dammers (all in NMNH); Monterey Co., Horse Bridge, 1.5 air mi SW Arroyo Seco G. Sta., 1300', 3-7.V.1975 (3 specimens), J. Powell 75E8, reared from *Eriodictyon californicum*; Ventura Co., Hungry Valley, 5 mi S Gorman, 4.V.1959 (2 specimens), J. Powell 69E3, reared from *Eriodictyon crassifolium*, emerged 1.VI.1959; Marin Co., Mt. Tamalpais, 15.VI.1960 (3 Specimens), J. Powell 60E5, reared from *Eriodictyon californicum*, emerged 6-13.VII.1960 (ZMH). Holotype of *Coelopoeta baldella*, female, labeled: June 24-30; Camp Baldy, San Bern. Mts., Calif.; *Coelopoeta baldella* Type. Busck; L. Kaila prep no. 1183 (NMNH).

Remarks. Walsingham (1908) did not designate a holotype from the thirteen syntypes of *C. glutinosi*. Braun (1948) studied the syntypes deposited in the NMNH, as well as the type series of *C. baldella*, and found them conspecific. I have not seen types of *C. glutinosi*, but the original description is unambiguous, as Walsingham emphasizes the white ground color of the species. I have studied the holotype of *C. baldella*. Its appearance falls well within the range of variation of the specimens of *C. glutinosi*, and therefore I confirm Braun's conclusion regarding the synonymy of these two taxa.

Biology. The species feeds on *Eriodictyon* species (Hydrophyllaceae), making a gall-like mine on the leaf. The biology was described in detail by Braun (1948).

Coelopoeta phaceliae Kaila, new species

(Figs. 5-8, 12-13, 17)

Male. Labial palpi relatively short, color varying from creamy white to brownish or grayish, darkest below. Head and neck tufts varying from creamy white to light brown, occasionally mottled with gray scales. Antenna light gray with greenish sheen, flagellum annulated with dark gray. Tegulae and thorax mottled light brown, tegulae with whitish scales, mostly at tip. Abdomen gray, with chitinized spines dorsally, appearing as bare, brown, transverse fasciae. Legs gray with creamy tint, tibia and tarsal segment with scattered dark scales above. Forewing: Costa from base to one-third dark gray; ground color ochreous, densely mottled, mostly with brown scales, making the color bright yellowish brown; a weak, irregular darker brown patch in middle of wing at fold, bound outwardly by a light ochreous area. Cilia concolorous with forewing. Forewing length 4.5-6.0 mm. Hindwing gray. Underside of wings dark chocolate brown, cilia yellowish brown.

Female. As described for male, except forewing narrower, with lighter ground color and more contrasting and irregular dark brown dusting.

Male genitalia (Figs. 12-13). Uncus strongly sclerotized, apically tapered, ventrally concave, tip curved. Gnathos strongly sclerotized, tapered towards upturned tip. Valva broad, apically bent inwardly, inner margin strongly concave; sacculus lobe apically slightly produced, almost straight-angled, with a few setae; cucullus slightly distended. Juxta shield-shaped, apically broad, laterally slightly produced. Vinculum more or less strongly sclerotized, medially sharply produced forming a spoon-shaped plate. The size of the plate varies to some extent, often smaller than in Figs 12-13. Aedeagus with slightly produced caecum; bent in the middle, apex oblique; the length equal to the length of valva; cornuti absent.

Female genitalia (Fig. 17). Papillae anales with long setae (in Fig. 17 the length and density of setae have been reduced for clarity of the illustration); apophyses long, tip bent, length of posteriores equal to anteriores; a pair of papillae posterior to ostium with

very long hairy setae; posterior margin of eighth segment with similar setae; ostium dorsally lined with a sclerotized plate; ventral margin almost straight; antrum sclerotized, funnel-shaped; a narrow membranous zone between antrum and bottle-shaped sclerotized colliculum; in anterior part of colliculum some minute chitinized plates. Base of ductus seminalis with longitudinal lines of minute teeth, in corpus bursae one dentate signum, varying in form and size.

Types. Holotype, male: CAL: Modoc Co., Fandango Pass, 6100', 12-13.VI.1970, J. Powell 70F95, emerged 7.VII.1970, reared from *Phacelia hastata*, R. E. Dietz & P. A. Opler (UCB); "Holotype *Coelopoeta phaceliae* Kaila" [red]. Genitalia preserved in glycerol tube on specimen pin.

Paratypes (23). California, Modoc Co., Fandango Pass, 6100', larva 12-13.VI.1970, J. Powell 70F95, emerged 30.VI.1970, reared from *Phacelia hastata*, 2 ♂, R. E. Dietz & P. A. Opler (UCB); San Mateo Co., San Bruno Mts., J. Powell 62D3, emerged 7.V.1962, reared from *Phacelia californica*, 2 ♂, J. A. Powell (UCB, NMNH), J. De Benedictis 81137-A, emerged 10.VI.1981, reared from *Phacelia californica*, 1 ♂ (L. Kaila, genitalia figured), 3 ♀, J. De Benedictis (♂ and 2 ♀ in UCB, 1 ♀ in ZMH); Siskiyou Co., Ash Crk. Rgr. Sta., 9 mi E McCloud, 3500', 7-9.VI.1974, J. Powell 74F17, emerged 5.VII.1974, reared from *Phacelia mutabilis*, J. A. Powell, 2 ♀ (UCB, ZMH); Plumas Co., Humbug Cr., 5100', 3 mi NW Portola, 7.VII.1982, J. Powell 82G7, emerged 23.VII.1982, reared from *Phacelia hastata* × *mutabilis*, J. A. Powell, 1 ♂ (ZMH), 1 ♀ (UCB); Plumas Co., 1 mi S Meadow Valley, 22.V.1982, J. Powell 82G2, 82G3, 82E98, reared from *Phacelia procera*, 3 ♂, 8 ♀, J. A. Powell (2 ♂, 8 ♀ in UCB, 1 ♂ in ZMH).

Biology. The species has been reared from *Phacelia californica*, *P. procera*, *P. hastata*, and *P. mutabilis* (Hydrophyllaceae).

Coelopoeta maiadella Kaila, new species

(Figs. 9, 14-15)

Male. Labial palpi porrect, slightly curved, gray; head and neck tufts gray; antenna gray, annulated with dark gray; tegulae and thorax gray, abdomen gray, with chitinized spines dorsally, appearing as bare, brown, transverse fasciae. Legs gray, tarsal segments with light gray distal rings. Forewing: Ground color mottled gray, with scattered white and dark gray scales; an elongate, indistinctly limited dark patch beyond the middle in the fold; beyond patch a white spot extending from tornus to the fold. Cilia line absent, cilia gray. Forewing length 5 mm. Hindwing and underside of wings gray.

Female. Unknown.

Male genitalia (Figs. 14-15). Uncus elongate, strongly sclerotized, apically tapered, tip curved. Gnathos strongly sclerotized, tapered towards slightly upturned tip. Valva broad, apically slightly bent inward, inner margin concave, sacculus lobe apically strongly produced, cucullus without dilation. Juxta shield-shaped, apex narrow, medially slightly produced. Vinculum strongly sclerotized, medially sharply produced, forming a narrow, blunt-tipped plate. Caecum of aedeagus slightly produced, with a small node; aedeagus almost straight, apex oblique, distal opening very long; length 1.3 times the length of valva; cornuti absent.

Types. Holotype, male: Canada, Yukon T., 60°45'N, 134°40'W, 20 km SE Whitehorse, light-trap, 16.VII.1985, K. Mikkola; deposited in ZMH.

Biology. Unknown.

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GENERAL NOTE

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OCCURRENCE OF A NEMATODE IN THE TROPICAL TASAR SILKWORM, *ANTHERAEA MYLITTA* (SATURNIIDAE)

Additional key words: silk production, parasitization, India.

The infestation of insects by nematode parasitoids is well documented in the literature (Lieutier & Vallet 1982, McCoy & Kaplan 1983, Simmons & Rogers 1990, Simmons et al. 1991, Stock & Camino 1991, Alm et al. 1992, Parker 1993). However, only Poinar (1975) has mentioned the infestation of Indian tropical tasar silkworm, *Antheraea mylitta* (Drury), by a nematode parasitoid.

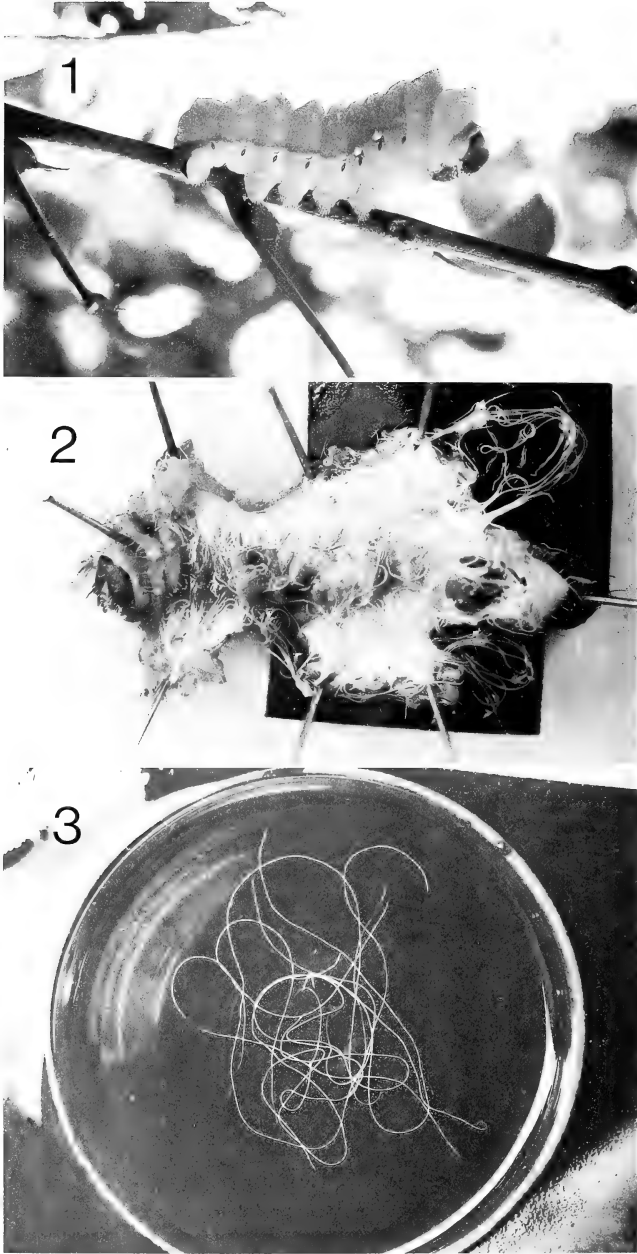
Fifth instar larvae of the tasar silkworm (Fig. 1) were found to be infested with a nematode parasitoid (family Merminthidae) during the first generation (= rearing season) of the year (i.e., July-August). Structure of the nematode and its infectivity are discussed.

Indian tropical tasar silkworm is one of the most important silk producing insects in the world. It usually is reared on *Terminalia tomentosa* (Wt. & Arn., Combretaceae) and *T. arjuna* (Wt. & Arn.) in the field owing to the wild nature of this moth. During a three-year (1990-1992) survey, we observed nematode infestation in larvae of silkworms in the field. The first rearing season of the year generally commences in July, with the larvae reaching fifth instar in August. The second generation (= rearing season) starts in September, with larvae reaching fifth instar in October. It was discovered that fifth instar larvae of the first generation of each year (1990-1992) were infested with nematode parasitoids, while first, second, third, and fourth instar larvae do not show any symptoms of infestation. First generation infestation appears to be related to the high percent relative humidity and high temperature and associated heavy rainfall during July and August. No nematode infestation was detected in the second generation larvae reared during September-October, a period when temperature, rainfall, and percent relative humidity are comparatively low.

Numerous thin, threadlike nematodes were observed inside mature fifth instar larvae after dissecting their abdomens (Fig. 2). The nematodes were whitish, with smooth skin, pointed at both ends, with an unsegmented body (Fig. 3). The length of adult nematodes ranged from 166 to 294 μ m. Most of the fat body mass and silk glands of the host were utilized by the nematodes. Morphometric measurements of the nematodes ($n = 100$) and percentage larval mortality are presented in Table 1. Larval mortality was determined from 100 individuals \times 10 replicates (1000 larvae) in each year.

Parasitism was determined based on symptoms shown by the infested fifth instar larvae. Infested silkworms gradually lose their ability to grip the host plant; ultimately, the larvae fall from the plant. The body of the infested silkworm becomes shortened from the shrinkage of the outer body wall as the parasitoid utilizes the tissue inside the body of the host. Finally, the infested larva dies, and the threadlike adult nematodes exit the host body through its anal opening. Infested silkworms were unable to spin the silk necessary for cocoon production. Only the larvae of the silkworm were found to be infested by nematodes. In contrast, pupal and adult stages of other insects are known to be nematode hosts (Anderson & Laumond 1992, Mannion & Jansson 1992, Poinar 1992). These preliminary data are being augmented by further studies regarding the taxonomy of the nematode.

We acknowledge the support of the Central Tasar Research and Training Institute, Ranchi, India. We also thank two anonymous reviewers for helpful comments on the manuscript.



FIGS. 1-3. Larvae of *Antheraea mylitta* and nematode parasitoids. 1, Healthy fifth instar larva; 2, Infested larva dissected; 3, Nematode parasitoids.

TABLE 1. Morphometric measurements of adult nematodes (n = 100) and larval mortality during 5th larval instar of *A. mylitta* for three years, 1990-92.

Morphometry (mm)		% larval mortality		
Length (mean ± SE)	Breadth (mean ± SE)	1990	1991	1992
238.90 ±9.50	0.223 ±0.006	1.50 ±0.34	2.20 ±0.59	1.70 ±0.56

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Cover illustration: Fifth instar larva of *Podotricha telesiphe* (Hewitson), a heliconiid butterfly that occurs in Ecuador, Peru, and Bolivia. Original drawing by Carla Penz, Department of Zoology, University of Texas, Austin, Texas, 78712, USA.

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FIRE-BURNED HABITAT AND REINTRODUCTIONS OF THE BUTTERFLY *EUPHYDRYAS GILLETTII* (NYMPHALIDAE)

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ABSTRACT. The butterfly *Euphydryas gillettii* (Barnes) lives in moist mountain meadows connected by riparian corridors, thus forming metapopulations in which local extinctions and recolonizations occur infrequently. Following the 1988 fires in the Greater Yellowstone Ecosystem, I chose 8 unoccupied patches of suitable habitat, 4 of which had been burned, and introduced a single eggmass into each. Larvae survived to diapause in at least 4 of the 8 sites, but only one introduction led to the establishment of a new colony the next year. This was at a burned site. The new population increased rapidly for 2 years but then declined and disappeared. These results suggest that: (1) a single, isolated eggmass is sufficient for colonization of open habitat; (2) most single, isolated eggmasses do not survive to produce adults the following year; and (3) recently burned sites provide acceptable habitat for this scarce butterfly.

Additional key words: transplants, fugitive species, dispersal, metapopulation, colonization.

Many organisms live in habitat that is unpredictable in time and space, and for them natural selection is likely to increase rates of dispersal and subsequent colonization of uninhabited areas (Southwood 1962, den Boer 1990). Even in stable habitats there is an advantage to dispersal because individuals then leave copies of their genes in new areas (Hamilton & May 1977, McPeck & Holt 1992). Many dispersive species occur in metapopulations in which individual colonies periodically go extinct while others are newly established, producing a mosaic of occupied and unoccupied habitat patches (Gilpin 1987).

Some butterfly species have such a metapopulation structure. In these insects, dispersing males rarely help found new colonies because they are unlikely to encounter unmated females away from existing populations. Dispersing females, on the other hand, are likely to have already mated, and if they pass through suitable habitat with acceptable host-plants, they may establish new populations with the eggs they leave behind. Females sometimes disperse at higher rates than males due to

behavioral interactions between the two sexes (Shapiro 1970), thereby increasing the likelihood that new sites are colonized. For butterflies that produce eggs in clusters, the existence of a refractory period after ovipositing one large eggmass (Williams in prep.) makes it unlikely that a dispersing female will leave more than one egg cluster in any one new habitat. Thus, each new colony of a cluster-laying species is probably established by a single eggmass.

Euphydryas gillettii (Barnes) (Nymphalidae) is an uncommon, cluster-laying nymphalid butterfly of the northern Rockies which inhabits moist montane meadows. It lives in extended metapopulations along riparian corridors, with low frequency of dispersal up and down stream (unpubl. data) or over longer geographic distances (Holdren & Ehrlich 1981). Its population structure is similar to that of other butterflies (Harrison et al. 1988, Pollard & Yates 1992, Warren 1994) that live in distinct colonies, undergo local extinction, exhibit low levels of dispersal, and occasionally recolonize empty habitat.

Most meadows occupied by *E. gillettii* exist because of disturbance, and the most common form of disturbance is forest fire (Williams 1988). By removing the canopy, fires reduce evapotranspiration and increase sunlight on hostplants and nectar sources. The extensive 1988 fires in the Greater Yellowstone Ecosystem opened up new patches of habitat that are likely suitable for occupancy by *E. gillettii*. To assess colonization in this butterfly, I chose 8 unoccupied sites in this ecosystem, introduced a single eggmass into each, and followed the fate of each transplant. I expected to find that: (1) a single eggmass is sufficient to give rise to a new colony; (2) the probability is small that any single, isolated eggmass will actually give rise to a new colony; and (3) the Yellowstone fires of 1988 produced suitable habitat for *E. gillettii*.

METHODS

To make it likely that the butterflies could survive and reproduce, I chose transplant sites with features that characterize the habitat of *E. gillettii*. The most important features (Williams 1988) are, in order of importance, presence of: (1) the hostplant, *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae); (2) open, sunlit meadows; (3) an abundance of nectar sources; (4) water, usually a small stream; (5) trees for roosting; and (sometimes) (6) south-facing exposure for warmth. Despite occasional use of additional hostplants (e.g., Williams & Bowers 1987), *L. involucrata* is the primary hostplant at every population known. I used field surveys based on U.S.G.S. topographic maps to identify sites in the northern Yellowstone region that provided the above habitat features, including sites burned during the 1988 fires, and for which there

TABLE 1. Summed results of reintroductions of *Euphydryas gillettii*. Reintroductions were made 9–19 July 1989 into patches of open habitat, and the status of each transplant was assessed in August 1990 and July 1991.

Site	Habitat	Eggmass (no. eggs)	Elevation (m)	Fate of eggs	Adults in 1990
1	burned	107	2195	prediapause feeding	no
2	burned	146	2045	prediapause feeding	yes
3	burned	202	2015	unknown	no
4	open	110	2440	prediapause feeding	no
5	burned	104	2445	prediapause feeding	no
6	open	210	2380	unknown	no
7	open	196	2470	browsed	no
8	open	165	2350	browsed?	no

was no evidence of *E. gillettii* being already present. I surveyed more than 25 possible sites before choosing 8 for transplants. Of the 8 sites chosen (Table 1), 4 experienced canopy burns in 1988, while the other 4 had not burned within recent decades. The eight sites, found within 109°30' to 110°40'W longitude and 44°50' to 45°10'N latitude, occur within the Greater Yellowstone Ecosystem (Marston & Anderson 1991). While there was some variation in the size of the 8 sites chosen, what is most important for the survival of *Euphydryas* butterflies is the quality of the habitat, not its extent (Ehrlich 1992). Both limited habitat and restrictions on experimenting in Yellowstone National Park prevented me from increasing the number of sites for transplants as I had planned.

Prior absence of *E. gillettii* was judged by lack of indicators—butterflies, eggs, or evidence of characteristic feeding on the hostplant *Lonicera involucrata*—during two or more visits at each site during the height of the flight period (mid July) in 1989, when all surveys and subsequent introductions were made. Extensive field work with this species (Williams et al. 1984, Williams 1988) has shown that wherever a population occurs, even a small one, evidence of its presence is easily found.

Eggmasses for transplantation were collected from one of the few large populations known (Valley Co., Idaho, 400 km distant) and transported on ice to the study area. At each site, using adhesive tape, I attached one randomly-chosen eggmass-bearing leaf by its petiole to a small twig in the upper middle of a large *L. involucrata* shrub in an open meadow near water. Each site and eggmass was marked and photographed. Eggmasses for the 8 transplants averaged 155 eggs (Table 1). The eggmasses used in this study came from a population at a lower elevation (1615 m), where the adults fly 10 days earlier. Thus, the transplanted eggs may have been developmentally ahead of those ex-

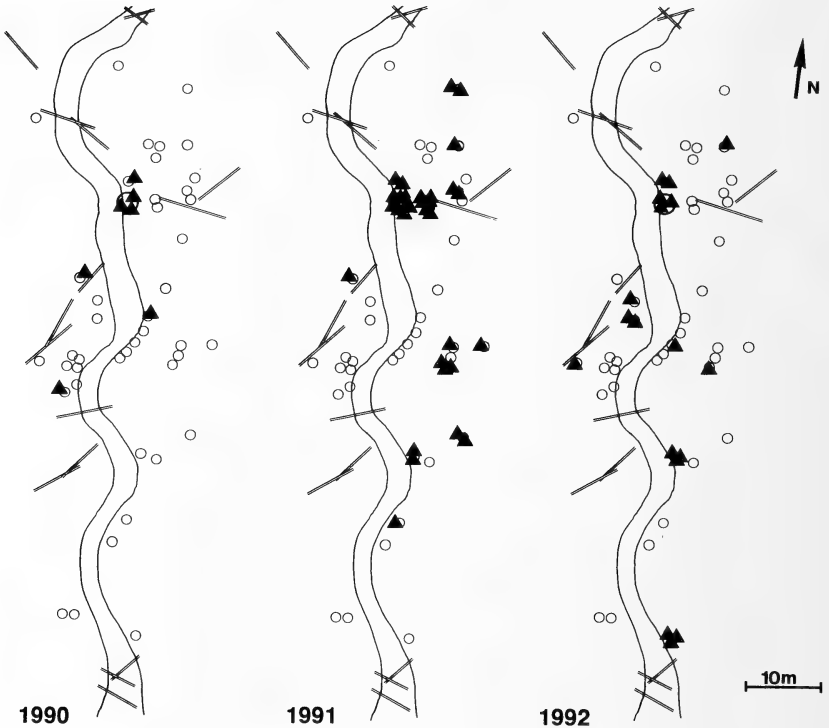


FIG. 1. Eggmass distribution for 1990–1992 at the site with the successful introduction. The stream is shown through the middle of the site, while straight lines represent burned, fallen trees. Triangles show locations of eggmasses. Open circles represent hostplants, *Lonicera involucrata*, with the large circle being the shrub that received the introduced eggmass in 1989. No additional eggmasses could be found within another 100 m up or down stream or to either side (no hostplants occurred away from the stream) in any year.

pected at the transplant sites, yielding a little more feeding time for transplanted larvae to prepare for winter (R. R. White pers. comm.).

For the next three years I revisited the sites near the end or after the flight period. Estimates of brood size were based on the number of eggmasses at each site that could be found from surveying every *L. involucrata* shrub within a 100 m radius (Fig. 1). With this survey technique, I missed long distance dispersers; however, few *E. gillettii* move away from regions of high concentration, and eggmass counts accurately reflect the relative size of each year's population (unpub. data). The most accurate censusing is done at the end of the flight period or soon thereafter, because, unlike adults, eggmasses and larval webs are easily found and censused during periods of variable weather.

RESULTS

In 1990, there was conspicuous evidence at 4 of the 8 sites that the eggs introduced in 1989 had hatched successfully and that prediapause larvae had fed (Table 1). At all 4 of these sites, the twig that received the transplant was leafless or dead the following year, a characteristic result of *E. gillettii* oviposition on *L. involucrata* (Williams et al. 1984). In addition, a partial feeding web remained on the transplant twig at 2 of the 4 sites. Three of these 4 sites had burned in 1988. Judged by evidence of browsing, moose had consumed the transplanted eggs or first instar larvae at a fifth site and possibly a sixth. Such a fate is not uncommon for *E. gillettii* early stages within this ecosystem (Williams et al. 1984). There was no evidence to assess the fate of the final 2 transplants.

I could find surviving *E. gillettii* at only one of the eight sites in 1990, however, despite extensive searching for eggs, larvae, adults, or characteristic feeding on *L. involucrata* (a success rate of about 0.12). Searches of all eight sites again in 1991 and 1992 gave the same results. The site with the successful transplant (near 45°N, 110°30'W) burned extensively in the 1988 fires and as a result provided newly open, sunlit patches of meadow. The introduced eggmass at this site had 146 eggs, fifth largest of the 8 transplanted eggmasses. Flowers were abundant here, including the following common nectar-sources for *E. gillettii*: *Arnica* spp., *Aster occidentalis* (Nutt.) T.&G., *Geranium richardsonii* Fisch. & Trautv., and *Senecio serra* Hook (identification from Hitchcock & Cronquist 1973).

Based on annual counts (1990–1993) of eggmasses after the flight period, the population at the successful site grew rapidly for two years, declined in the third year, and disappeared in the fourth (Fig. 2). The distribution of eggmasses and larval feeding webs indicated that the butterflies remained remarkably close to the transplant site (Fig. 1): (1990) mean distance 9 m, range 0–29 m; (1991) 12 m, 0–46 m; and (1992) 23 m, 0–62 m. No eggmasses or signs of larval feeding were evident more than 20 m from the stream (no hostplants grow away from the stream) or 100 m up or down stream (where the canopy is more closed).

DISCUSSION

The recolonization of empty habitats within a metapopulation structure has been infrequently observed. These results show clearly that a single eggmass can give birth to a new population; thus, with the oviposition of one eggmass, a single dispersing female of *E. gillettii* can colonize a new habitat patch, at least for the short-term. The introduced

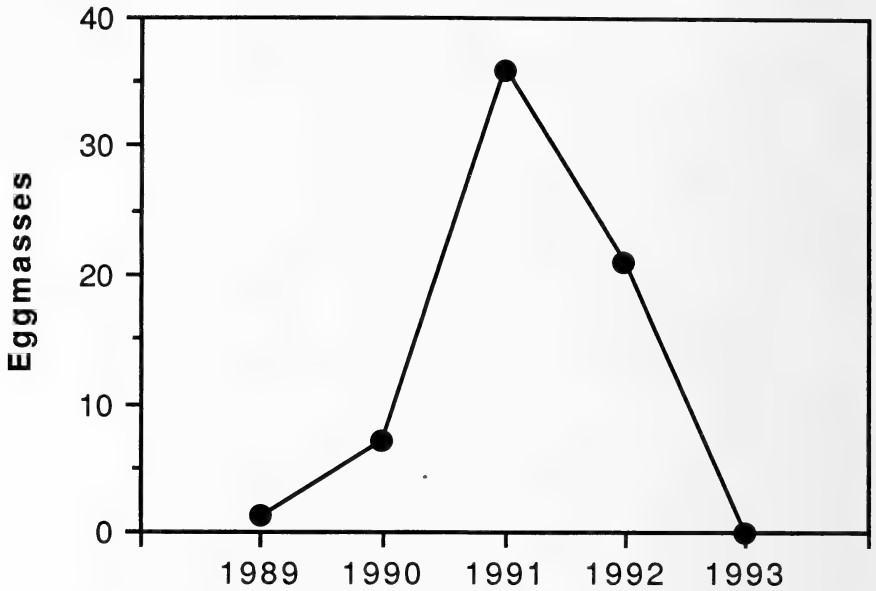


FIG. 2. Growth and decline of the introduced population of *Euphydryas gillettii*. The number of eggmasses found after the flight season is shown for each year since the introduction of a single eggmass in 1989. Population size is proportional to the number to eggmasses.

eggs would have hatched at the same time or slightly ahead of those expected at the transplant elevations, thereby ensuring that the larvae would have enough food of sufficient quality to prepare for diapause. Also, though few introductions were attempted, the probability of a single eggmass surviving and producing a new colony is small, as expected. The number of eggs in the eggmass is probably of secondary importance to the overall fate of the mass itself in determining whether any adults emerge the following year; random events such as browsing by moose exert strong impact on the survival of an eggmass, whereas other factors lead to the survivorship of some but not all eggs within an eggmass.

It is unknown whether the successful site could have supported a population of *E. gillettii* without a recent forest fire (their absence suggests not), but with the canopy burn and felling of a number of trees, the fires of 1988 opened up this habitat conspicuously. Recycled nutrients may have increased plant growth, and tree loss likely reduced evapotranspiration, but the most immediate change in habitat quality as a result of the fires was reduction in tree canopy cover. *Euphydryas gillettii*, like most butterflies, depend on solar warming to remain active,

and they avoid shaded areas (Williams 1981). Larvae of other *Euphydryas* have been shown to bask both to facilitate digestion and growth (*E. aurinia*, Porter 1984) and to develop more rapidly through a limited growing season (*E. editha*, Weiss et al. 1988). It is the presence of hostplants and nectar sources in open, moist meadows that attracts the butterflies, and fire is the most common producer of such conditions. There is a significant history of fire throughout the Greater Yellowstone Ecosystem (Romme & Despain 1989, Despain 1990) as well as the rest of *E. gillettii*'s range. The successful colonization of a recently burned habitat patch supports the expectation that fires produce acceptable habitat for *E. gillettii*. Natural colonization of fire-burned areas have yet to be reported, however.

The introduced population grew rapidly over the first two years (Fig. 2), and though exponential growth cannot continue for long, the decline in numbers in the third year did not appear to result from exhaustion of resources at that site. More likely, rainy weather during the normal flight period of 1992 decreased the opportunity for oviposition, so fewer eggmasses were produced (egg shortfall). Weather is known to limit brood size by restricting oviposition (Courtney & Duggan 1983). The same 1992 reduction in population size was seen in another *E. gillettii* population 80 km east (unpubl. data), and synchronous responses of different populations point to more general controlling factors such as weather (Pollard 1991). Furthermore, the establishment of a colony from a single eggmass produces limited genetic variability that, without subsequent gene flow, diminishes the long-term survival of the colony. The disappearance of the population in 1993 was surprising; a significant factor was that heavy spring flooding led to the collapse of some of the streambank and washed away the shrubs on which there had been the heaviest oviposition. Once it had been established, I did not expect to lose this colony so soon, but the loss reinforces the notion that chance events can exert strong impact on the survival of small colonies that make up metapopulations of this species.

A few introductions of this and related butterflies have been attempted. Holdren and Ehrlich (1981) introduced *E. gillettii* into two sites in Colorado, and while their transplants were successful for a few years, they used nearly 10,000 eggs each (up to 83 eggmasses) to ensure successful colonization. Harrison (1989) introduced propagules of 100 larvae of *Euphydryas editha* to each of 38 empty sites and found only a 6% chance of persistence for two years. Her results are in accord with the low probability of survival I found in *E. gillettii*.

No introduction can be undertaken lightly, however. My study was based on introducing eggs to empty habitat patches within the historic range of the species (Yellowstone National Park is also the source of

the type specimen). *Euphydryas gillettii* is known from sites 24 km to the southwest and 80 km to the east of the transplant sites, for example. Thus, these introductions may be more accurately characterized as "re-establishments" (New 1991) into known range, and they therefore are not fraught with the risks associated with making introductions into non-endemic areas. Nevertheless, genetic variation does occur among populations in sedentary species, and Debinski (1994) has documented low level genetic differences among *E. gillettii* from Idaho, Montana, and Wyoming. I did not regard this variation as a deterrent to attempting re-establishment of a scarce butterfly in its native range.

Even with low rates of success, *E. gillettii* is able to colonize patches of habitat newly opened by disturbance. For animals that vary widely in abundance, such as insects, dispersal and recolonization of new patches are necessary for the longterm maintenance of a metapopulation (den Boer 1990). For insects that occupy disturbed sites, such as *E. gillettii*, the production of newly opened habitat by fire or other means is necessary for their survival. The results reported here provide an example of colonization in *E. gillettii*, illustrate how the Yellowstone fires of 1988 recreated habitat for this scarce butterfly, and, importantly, show how infrequent such re-establishment may be.

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THE EFFECTS OF ELEVATION ON THE BUTTERFLY COMMUNITIES OF A MEDITERRANEAN MOUNTAIN, SIERRA DE JAVALAMBRE, CENTRAL SPAIN

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ABSTRACT. This paper examines altitudinal changes in butterfly communities in the Sierra de Javalambre of central Spain. From May to September 1991 we sampled the butterfly fauna every 15 days at 10 stations located between 1100 and 2000 m. We obtained a total of 2,123 individuals of 101 different butterfly species. Abundance and species richness were highest at low elevations and declined with increasing altitude, while the converse held for habitat breadth. The chorological index was highest at low elevations. Changes in the butterfly communities along the altitudinal gradient of the Sierra de Javalambre are caused by harshness of environmental conditions, changes in the vegetation, and presumably, resource impoverishment. High elevations do not seem to 'select' for an endemic fauna of butterflies. The communities in the lowest places are composed of rare and localized species, while high elevation communities are less original in faunistic composition since they are composed of euryecious and widespread species in this area.

Additional key words: altitudinal changes, habitat breadth, resource poverty, species richness.

Analyses of altitudinal changes in diversity, abundance, and species composition of biotas can provide important information on such phenomena as those aspects of the environment limiting the distribution of organisms, factors influencing the structure of communities, and biogeographical patterns. These problems have been investigated by ecologists for the past 40 years. Several studies (Hagvar 1976, Claridge & Singhrao 1978, Hebert 1980, Ichijo et al. 1982) have concluded that a decrease in species richness with elevation is typical of many groups of animals, including insects, with the exception of bees (Gauld 1987) and tropical psocids (Turner & Broadhead 1974). At least four causes have been suggested for this decrease: reduced habitat area at high elevations, reduced resource diversity, increasingly unfavorable environments, and/or reduced primary productivity at higher altitudes (Lawton et al. 1987). In addition to these, other processes (competition, predation, evolutionary time, etc.) also may influence species richness (Lawton et al. 1987).

Other studies (Janzen 1973, Janzen et al. 1976), however, have concluded that species richness peaks at middle elevations, rather than at low ones. Many distinct processes have been proposed to explain mid-elevational peaks: disturbances caused by human activities in low elevations (Wolda 1987), increasingly unfavorable environments at both high and low altitudes (Gagne 1979, Randall 1982), and even the sam-

pling regimes (short-term vs. long term sampling regimes) (Wolda 1987, McCoy 1990).

The purpose of this paper is to present the results of a study of changes in the structure of butterfly communities along an altitudinal gradient in a Mediterranean mountain. There is a dearth of such studies in these latitudes (see Claridge & Singh Rao 1978).

MATERIALS AND METHODS

The study was conducted in the Sierra de Javalambre, Sistema Ibérico, Teruel province, central-eastern Spain (Fig. 1). The Sierra consists largely of carbonated Jurassic rocks. The climate is typical of mediterranean mountains, with a wide daily and seasonal variation in temperature, with hot summers and cold winters. Rainfall is low and seasonal, varying annually from 400 to over 500 mm. These mountains thus provide a remarkable opportunity for the study of altitudinal distributions and zonation of organisms.

The lower slopes are heavily cultivated with various fruits and vegetables. Elsewhere, forests dominated by holm oak (*Quercus rotundifolia* Lam.) (Fagaceae) and Spanish juniper (*Juniperus thurifera* Linnaeus) (Cupressaceae), and their successional stages dominate the landscape. At about 1300 m the forest is dominated by lusitanian oak (*Quercus faginea* Lam.) (Fagaceae), extremely perturbed and replaced in many cases by bushes of *Ligustrum vulgare* Linnaeus (Oleaceae), *Prunus spinosa* Linnaeus (Rosaceae), *Berberis vulgaris* Linnaeus (Berberidaceae) and *Rosa canina* Linnaeus (Rosaceae).

Spanish juniper and black pine (*Pinus nigra* Arnold) (Pinaceae) form mixed forests at 1400–1600 m, dominated by seminatural black pines. This forest is replaced above 1600 m by Scot pine forests (*Pinus sylvestris* Linnaeus) (Pinaceae). Just below the summit, at about 2000 m, there is a meadow with *Erodium celtibericum* Pau (Geraniaceae). A general account of the natural vegetation of the area is given by Peinado and Martinez-Parras (1985, 1987) (also see Fig. 2).

METHODS

The study was conducted along an altitudinal transect between the village of Camarena de la Sierra and the peak of the highest mountain (Javalambre, 2020 m). Ten stations separated by intervals of approximately 100 m of elevation (from 1100 to 2000 m) were established in the above described habitats.

Every two weeks from May to September 1991 we sampled the butterfly fauna at these 10 stations. Samples were taken on sunny days between 1000 and 1600 h. The sampling scheme was based in sampling subunits (40 min) of collecting effort per site per sample. We obtained

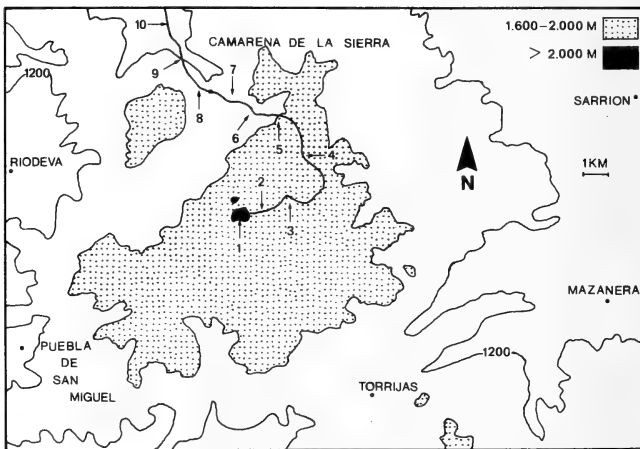
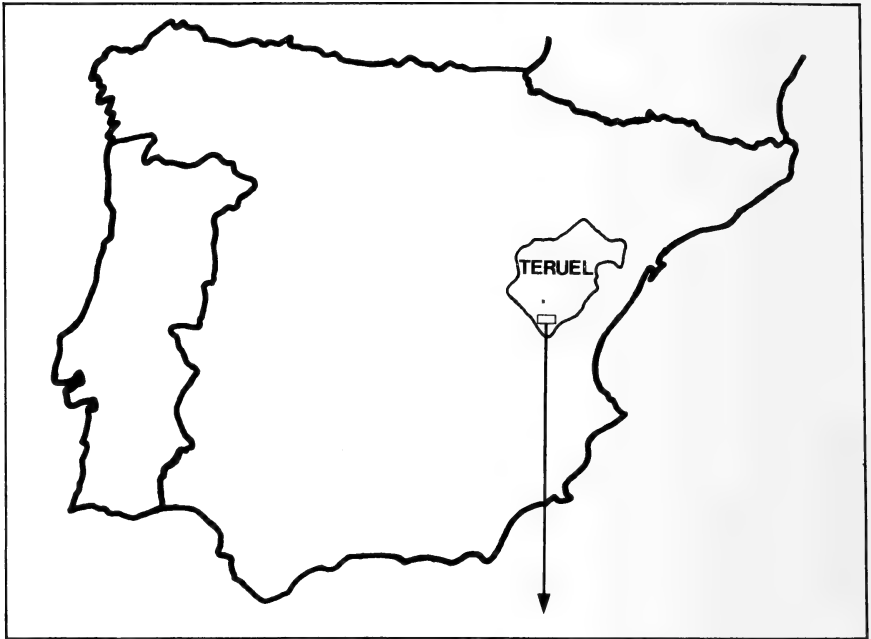


FIG. 1. Map showing the study area. Transect with the numbers of sampling sites are also represented.

a total of 2,123 individuals of 101 different species (Appendix A). From these data, the following variables were calculated:

- Number of species (**S**) equals the total number of species recorded on each site.
- Abundance (**Ab**) equals the total number of individuals.

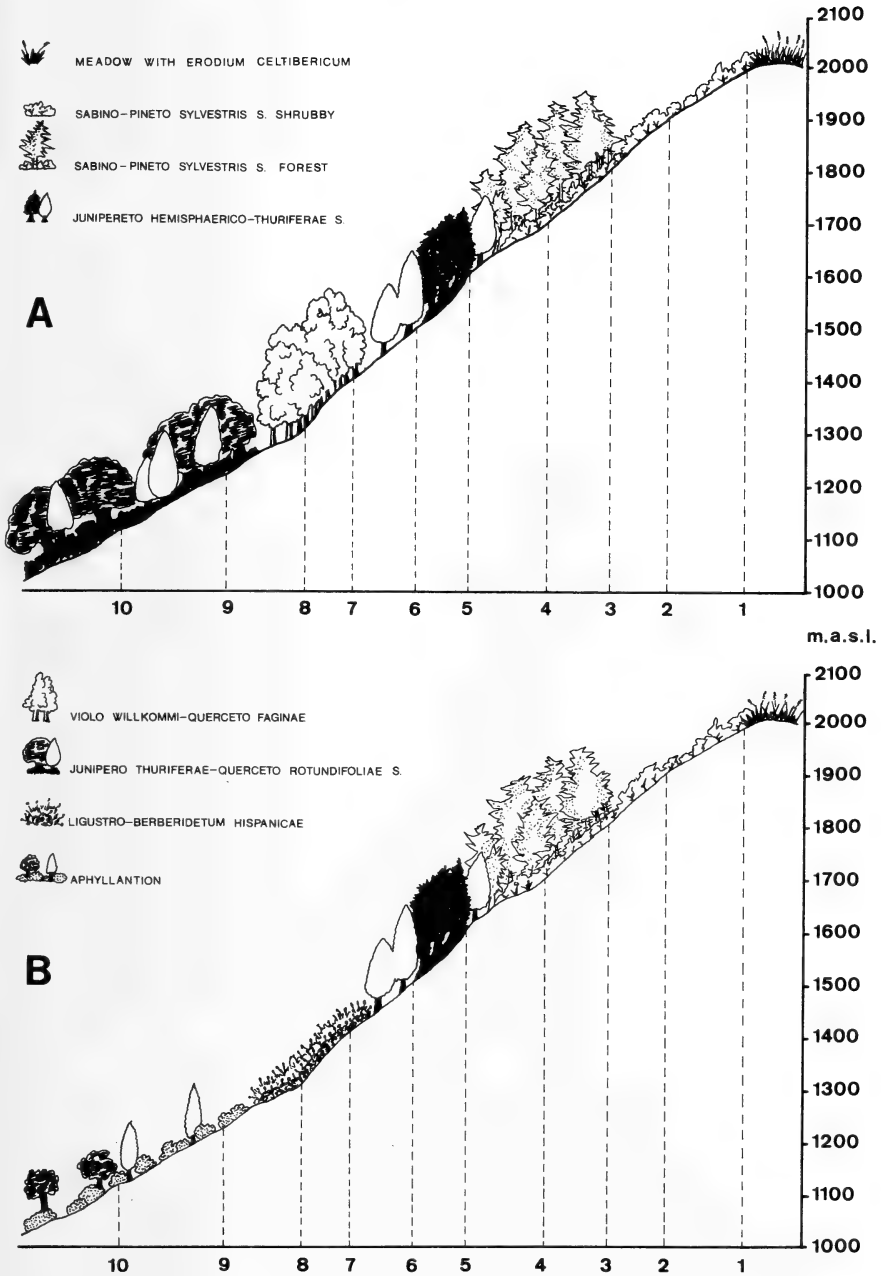


FIG. 2. Schematic representation of both potential (A) and present (B) vegetation along the elevational transect. Numbers 1-10 refer to sampling sites, number 1 being at the highest elevation.

TABLE 1. Values of the 7 variables used in the characterization of butterfly communities on each sampling site, number 1 being at the highest elevation.

	1	2	3	4	5	6	7	8	9	10
S	26	37	47	39	38	58	54	52	45	48
AB	135	158	200	212	173	253	258	258	230	246
D	0.49	0.32	0.35	0.17	0.21	0.16	0.17	0.19	0.26	0.28
H'	3.41	4.29	5.18	4.75	4.61	5.23	5.20	5.05	4.57	4.53
J'	0.72	0.82	0.93	0.89	0.87	0.89	0.90	0.88	0.83	0.81
CI	6.61	6.54	6.76	6.76	7.15	7.24	7.09	6.73	7.20	6.83
HB	4.75	4.54	4.35	4.62	4.65	4.05	4.06	4.02	4.24	3.94

- Dominance (**D**) was obtained from the McNaughton & Wolff's index (1970), expressed as $D = Y_{1,2}/Y$, where $Y_{1,2}$ is the sum of individuals of the two most abundant species, while Y is the total number of individuals.
- Diversity (**H'**) was obtained from the Shannon & Weaver's index (1963), expressed as $H' = -\sum p_i \log_2 p_i$ where p_i is the proportion of the i th species in the total sample
- Equitability (**J'**) expressed as: $J' = H'/H'_{max}$.
- Mean chorological index (**CI**). Calculated for each site by means of the chorological index of each species (data from Kudrna 1986). As Kudrna pointed out, the chorological index allows an evaluation of the biogeographic arrangement of all European butterfly species from a conservation point of view, as well as an evaluation and comparison of habitats (localities) based solely upon the composition of their butterfly fauna. The values of **CI** result from the sum of the numerical values of *range size*, *range composition* and *range affinity* ("sensu" Kudrna 1986). Values for range size vary from 1 (species widespread across Europe) to 5 (species confined to small areas, such as islands, mountain ranges, or single sites in Europe). Range composition evaluates the continuity of the distribution; in other words, the ability of individuals of one population to reach other populations. It ranges from 1 (continuous, or nearly so, distribution over most of the European range of the species) to 5 (widely isolated single populations, small groups of populations, and small stocks of very restricted range). Lastly, range affinity synthesizes the relationship between the species' European distribution and its world range as a supplementary indicator of the relative importance of these populations for the overall survival of the species. Its value ranges from 1 (extra-European species as defined by Kudrna 1986) to 4 (species endemic to Europe). Thus, the chorological index varies from 4 (most widespread species) to 14 (endemic European species restricted to very small territories).
- Mean habitat breadth (**HB**). Obtained from the habitat breadth of each species after Simpson's (1949) formula, expressed as $HB = 1/\sum p_i^2$, where p_i is the proportion of individuals on each site.

The values of all these variables are summarized in Table 1.

RESULTS

Table 2 shows the results of the regression analysis between altitude and variables of community structure. Significant negative relationships were found between altitude and both species number and abundance (i.e., species number and abundance decrease with altitude), whereas mean habitat breadth increased with elevation (Fig. 3). However, no correlations between altitude and dominance, species diversity or equitability were found. This is due to the fact that number of species (species

TABLE 2. Results of the regression analysis between altitude and the 7 variables considered. CI* represent results of the regression after the localities 8 and 10 were removed (see text for explanations).

	S	AB	D	H'	J'	HB	CI	CI*
<i>r</i>	-0.66	-0.82	0.48	-0.44	-0.20	0.81	-0.53	-0.88
<i>R</i> ²	42.82	68.46	23.9	19.5	34.24	66.0	29.12	—
P	0.03*	0.003*	0.15	0.20	0.56	0.004*	0.10	0.005*

* $P < 0.05$. R^2 = Coefficient of determination (in %).

richness) and equitability (evenness in abundance) are the two components defining H' . Diversity increases as species are added, as well as when the species abundances are evenly distributed. In diverse situations, single species do not dominate; in contrast, where one or two species are much more abundant than the rest, there is low diversity (see Price 1984). Thus, the absence of a relationship between elevation and equitability is the result of the absence of a relationship between elevation and butterfly species diversity as expressed by H' .

As regards the mean chorological index, no significant relationships were found when all 10 sampling sites were included in the analysis. However, when localities 8 and 10 (both located close to human-perturbed habitats) were removed from the analysis, a highly significant negative relationship between elevation and mean chorological index was found (Fig. 4).

To evaluate the effect of the resource impoverishment (i.e., decrease in the abundance of suitable host plants) on the variation in species numbers along the gradient, we proceeded as follows. We assigned each butterfly species to one of four groups based on their larval host plants: 1) plants of the class Dillenidae (families Brassicaceae, Resedaceae, Primulaceae, Malvaceae); 2) plants of the class Rosidae (families Rosaceae, Fabaceae, Rutaceae, Umbelliferae); 3) plants of the class Asteridae (families Caprifoliaceae, Valerianaceae, Dipsacaceae, Boraginaceae, Lamiaceae, Escrofulariaceae); and 4) plants of the class Lillidae (family Poaceae) (Appendix B). Figure 5 shows that in the lowest elevations the percentages of the four different butterfly groups are close to those expected (high values of equitability), while at the highest altitudes some groups are proportionally better represented than expected (low values of equitability).

DISCUSSION

Studies on the distribution of insects along elevational gradients have yielded differing results (see McCoy 1990 for a review). Recent long-term sampling studies have concluded that previously identified mid-

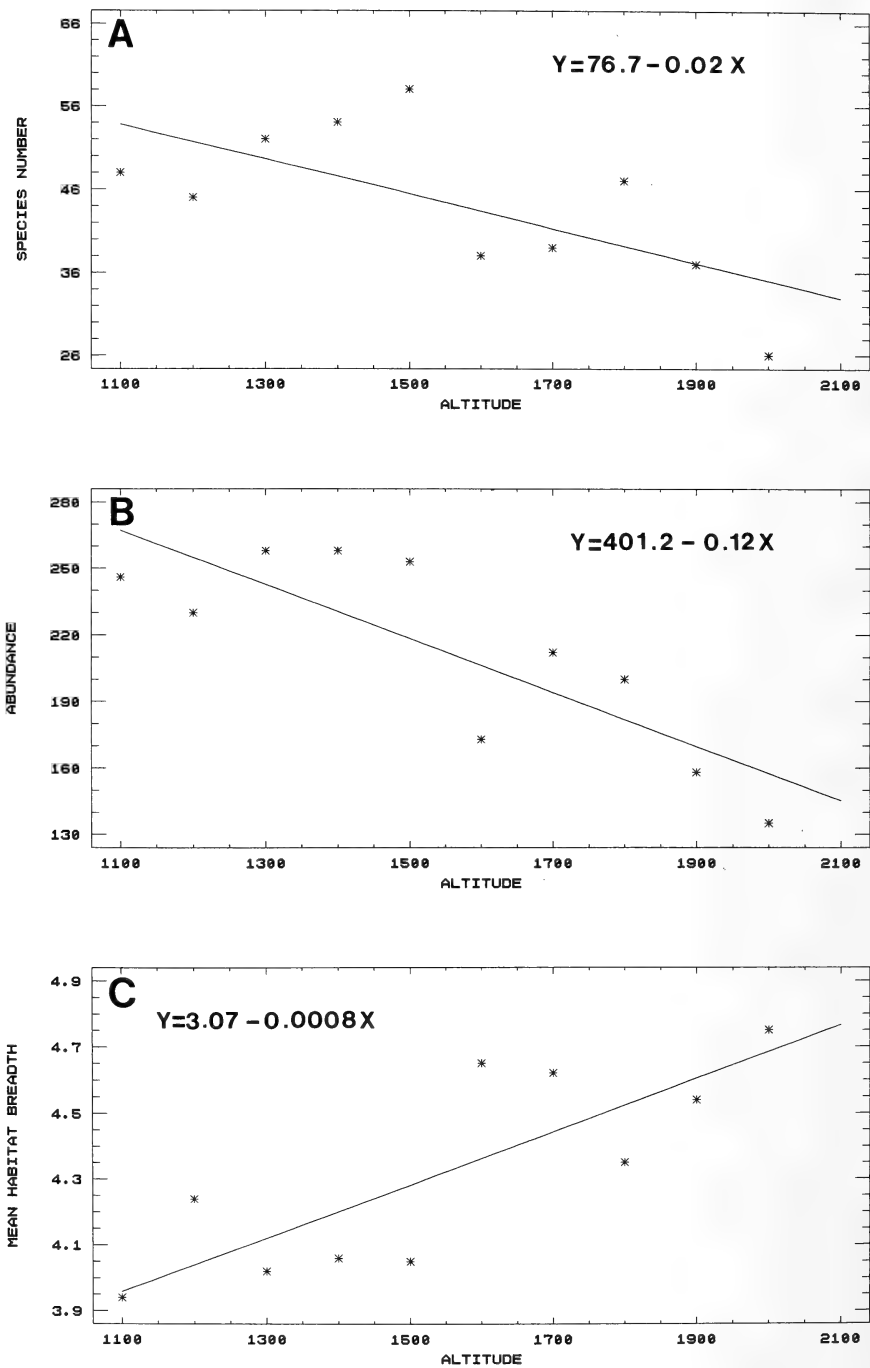


FIG. 3. Relationships between altitude and species number (A), abundance (B), and mean habitat breadth (C).

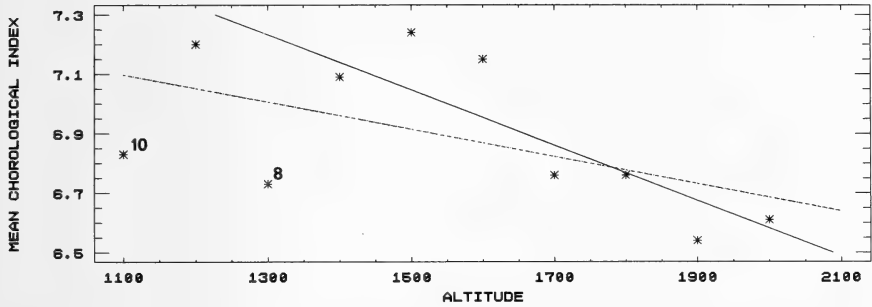


FIG. 4. Relationships between altitude and the mean chorological index. Dashed line obtained from all 10 sampling sites. Bold line obtained after sampling sites 8 and 10 were removed (see text for explanations).

elevational peaks in species richness may have resulted from the short-term sampling regimes that were employed (Wolda 1987). However, mid-elevational peaks have been documented for organisms that should be less affected by factors such as sampling regime and disturbance, for example, birds of the Páramos (Vuilleumier & Ewert 1978, Terborgh 1977).

Our data indicate that both richness and abundance of butterflies decrease with altitude, although the greatest number of species was found at 1500 m. This may be interpreted as a result of the interaction of two different variables—habitat and disturbance. The lowest places of Javalambre have been human-managed historically for agricultural uses, thus the climax vegetation has been replaced by its seral stages, which support lower butterfly species richness (Baz 1986). On the other hand, habitats at mid-elevations are deciduous woodlands (*Quercus faginea*) that contain the richest butterfly faunas, at least in the Iberian peninsula (Baz 1987, Viejo et al. 1989). If the habitat at lower elevations were in a natural stage, one would expect to find more butterfly species there. The continuous decrease in the number of species with increasing elevation may be caused by the harshness of environmental conditions and area reduction, but also as a consequence of a reduction in resource diversity (Lawton et al. 1987). In the absence of more detailed inventories of plant species, Fig. 5 may serve as an example to illustrate this point, showing that at the highest elevations a trophic group of species dominates community composition (ca. 55% of all species).

An interesting pattern found in this work is an extension of Rapoport's latitudinal rule to altitude (i.e., the tendency for latitudinal ranges to become smaller with decreasing latitude [Rapoport 1982, Stevens 1989]) which has been reviewed recently by Stevens (1992). Mean habitat

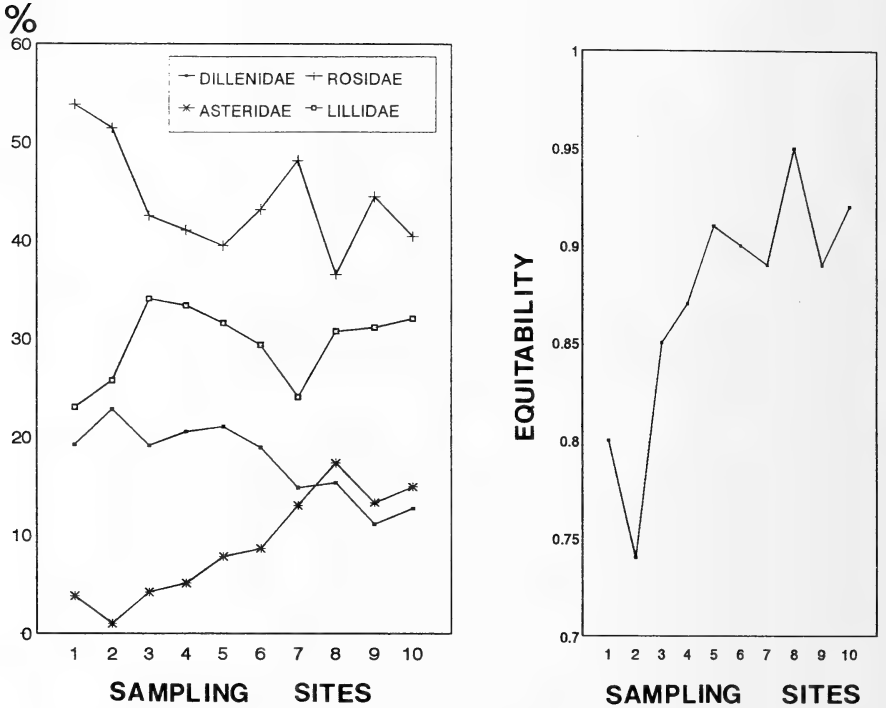


FIG. 5. Altitudinal changes in the relative importance of the 4 butterfly groups in relation to their caterpillar host plants. The altitudinal changes of equitability of the butterfly assemblage are also represented. Sampling site number 1 is at the highest elevation.

breadth increases with altitude (Fig. 3), hence the butterfly communities are composed primarily of common and eurycious species in the highest elevations (see Baz 1987 and Thomas & Mallorie 1985a who found the same pattern in other Mediterranean mountains). Stevens (1989) indicates that the latitudinal Rapoport's rule arises as a result of the narrowing range of climatic conditions the individuals experience with decreasing latitude. Since non-migratory individuals must be physiologically or behaviorally capable of tolerating the full range of conditions the seasonal changes impose on them, natural selection has favored broad tolerances at high latitudes. The consequence is that species from high latitudes have large latitudinal ranges because each individual of the species must have broad climatic tolerances just to survive at any latitude location.

At the other extreme, the breadth of climatic conditions each individual of a tropical species experiences is so narrow that there is no penalty for possessing narrow climatic tolerances. As Stevens (1992)

pointed out, if this explanation for Rapoport's latitudinal rule is correct, a pattern conforming to the altitudinal Rapoport's rule should be found, since the breadth of climatic conditions experienced by mountain residents does increase with increasing elevation. Certainly, our data support this idea.

Lastly, an interesting pattern in relation to the value of mountains for conservation purposes has been observed. Figure 5 shows that after man-managed localities (i.e., 8 and 10) are eliminated from the analyses, an inverse correlation between the mean chorological index and altitude exists, so that communities in the piedmont are composed of more rare or localized species (in a European context) than those at the highest elevations which probably is due to the peculiarities of basal habitats (Baz 1987, Thomas & Mallorie 1985b). In Iberia, mountains chains have acted as corridors for butterfly species of predominantly European origin (Martin & Gurrea 1990), and have facilitated the expansion in range of many European species. As a consequence, low altitudes seem to have inhibited dispersal of banal European butterflies (Martin & Gurrea 1990) and nowadays harbor a more original Mediterranean butterfly fauna. However, more detailed studies in undisturbed habitats within altitudinal ranges 8 and 10 of our study are necessary to prove this hypothesis.

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APPENDIX A. List of the 101 butterfly species recorded, with their distribution along the elevational gradient. Values of habitat breadth and the chorological index for each species are also included.

	1	2	3	4	5	6	7	8	9	10	Total	CI	HB
Papilionidae													
<i>Iphiclides feisthamelii</i> (Duponchel, 1832)	1				2	1	4	2	1		11	8	4.48
<i>Papilio machaon</i> Linnaeus, 1758						2	1			1	4	5	2.66
<i>Parnassius apollo</i> (Linnaeus, 1758)	14	15	22	11	10	4					76	8	5.05
Pieridae													
<i>Anthocharis cardamines</i> (Linnaeus, 1758)						4					4	5	1
<i>Anthocharis euphenoides</i> (Staudinger, 1869)						6	10	5	2		40	10	5.47
<i>Aporia crataegi</i> (Linnaeus, 1758)	1	3	14	20	15	22	21	16	9	3	124	5	7.31
<i>Colias alfacariensis</i> (Berger, 1948)	1	1	2		2	1	4	7	11	3	32	7	4.97
<i>Colias crocea</i> (Geoffroy, 1785)	3	1	2	9	4	4	8	5	19	19	74	6	5.83
<i>Euchloe ausonia</i> (Hübner, 1804)					1						1	10	1
<i>Gonepteryx cleopatra</i> (Linnaeus, 1767)			1	3	2	1	4		2	1	14	7	5.44
<i>Gonepteryx rhamni</i> (Linnaeus, 1758)				2	2						4	4	2
<i>Leptidea sinapis</i> (Linnaeus, 1758)	1							2	3	1	7	5	3.26
<i>Pieris brassicae</i> (Linnaeus, 1758)										1	1	4	1
<i>Pieris daphidice</i> (Linnaeus, 1758)				5	3	2	3	11	15	6	45	5	4.72
<i>Pieris rapae</i> (Linnaeus, 1758)			1	7	2	2	6	11	7	13	49	4	5.54
Lycaenidae													
<i>Aricia allous</i> (Geyer, 1837)	3	8	1			6	5	1	1	1	26	8	4.89
<i>Aricia cramera</i> (Eschscholtz, 1821)			6		3	6	2		2	2	21	9	4.79
<i>Callophrys rubi</i> (Linnaeus, 1758)						1		1			2	4	2
<i>Celastrina argiolus</i> (Linnaeus, 1758)				1						2	3	4	1.8
<i>Cupido osiris</i> (Meigen, 1829)							1		1		2	9	2
<i>Cyaniris semitargus</i> (Rottemburg, 1775)						1	1	2			4	5	2.66
<i>Glaucopsyche alixis</i> (Poda, 1761)	1					1	8	2	10	2	25	7	3.57
<i>Glaucopsyche melanops</i> (Boisduval, 1828)						1			2		3	10	1.8
<i>Lampides boeticus</i> (Linnaeus, 1767)			1							2	3	6	1.8
<i>Lycaeides idas</i> (Linnaeus, 1761)	2	5	2	1		3	2	2			17	5	5.66
<i>Lycaena alciphon</i> (Rottemburg, 1775)	2	4	1		1	7		3			18	7	4.15

APPENDIX A. Continued.

	1	2	3	4	5	6	7	8	9	10	Total	CI	HB
<i>Hipparchia statilinus</i> (Hufnagel, 1766)			1	4	3	5	4	4	1	1	23	8	6.22
<i>Hyponephele lupina</i> (Costa, 1836)			1		1		1	2	2	2	9	9	5.4
<i>Hyponephele lycaon</i> Muschamps, 1915	3	6	12	13	2	14	2	4			56	7	5.48
<i>Kanetisa circe</i> (Fabricius, 1775)		1	1			1	1	2	3	7	16	9	3.87
<i>Lastommata megera</i> (Linnaeus, 1767)	1	3	4	8	11	4	4	7	1	3	46	4	7
<i>Maniola jurtina</i> (Linnaeus, 1758)							1	10	6	20	37	4	2.54
<i>Melanargia ines</i> (Hoffmannsegg, 1804)		1	11	18	10	20	24	19	17	37	157	10	6.96
<i>Melanargia lachesis</i> (Hübner, 1790)		1	2	2		1	2				8	9	4.57
<i>Melanargia russiae</i> (Esper, 1784)			1	1		4			1		7	4	2.57
<i>Pararge aegeria</i> (Linnaeus, 1758)						1	1	6	2	1	11	9	2.81
<i>Pyronia bathseba</i> (Fabricius, 1793)						1			1	3	4	9	1.6
<i>Pyronia cecilia</i> (Vallantin, 1894)							11	2	2	6	21	7	2.67
<i>Pyronia tithonus</i> (Linnaeus, 1771)			1	1	3	2					7	8	3.26
<i>Satyrus actaea</i> (Esper, 1780)													
Nymphalidae													
<i>Aglais urticae</i> (Linnaeus, 1758)		1	1	3							5	4	2.27
<i>Argynnis adippe</i> (Denis & Schiffermüller, 1775)	5	17	10	11	5	10	8	10	5	12	93	5	8.71
<i>Argynnis aglaja</i> (Linnaeus, 1758)	5	3		1		1	7	2	1	3	23	5	5.34
<i>Argynnis niobe</i> (Linnaeus, 1758)		1	4							2	7	5	2.33
<i>Argynnis pandora</i> (Denis & Schiffermüller, 1775)				1		1					2	2	5
<i>Argynnis paphia</i> (Linnaeus, 1758)					2	4	4				10	5	2.77
<i>Brenthis hecate</i> (Denis & Schiffermüller, 1775)								2	1	1	3	8	1.8
<i>Euphidryas aurinia</i> (Rottemburg, 1775)							6	6			12	10	2
<i>Euphidryas desfontainii</i> (Godart, 1819)							2	2			34	4	4.89
<i>Issoria lathonia</i> (Linnaeus, 1758)	1	2	1	9	5	8	2	2	1	1	3	8	3
<i>Limenitis reducta</i> (Staudinger, 1901)						1		1			23	5	2.43
<i>Melitaea athalia</i> (Rottemburg, 1775)					1	3	8	12	8	18	34	5	2.71
<i>Melitaea cinxia</i> (Linnaeus, 1758)						1	6	1	1	1	3	10	3
<i>Melitaea deione</i> (Geyer, 1832)							1	1			3	7	4.26
<i>Melitaea didyma</i> (Esper, 1779)								2	1		1	10	1
<i>Melitaea parthenoides</i> (Keferstein, 1851)							1						

APPENDIX A. Continued.

	1	2	3	4	5	6	7	8	9	10	Total	CI	HB
<i>Melitaea phoebe</i> (Denis & Schiffermüller, 1775)	13	2	2	1	3	3	3	5		4	16	7	4.26
<i>Vanessa cardui</i> (Linnaeus, 1758)							1			2	23	4	2.76
Hesperiidae													
<i>Carcharodus alceae</i> (Esper, 1780)								1			1	5	1
<i>Carcharodus boeticus</i> (Rambur, 1839)								1	1		2	8	2
<i>Erynnis tages</i> (Linnaeus, 1758)								3			3	4	1
<i>Hesperia comma</i> (Linnaeus, 1758)	5	6	5	3	3	3	1	1	3	1	30	5	7.25
<i>Pyrgus albeus</i> (Hübner, 1803)		3	1								4	5	1.6
<i>Pyrgus armoricanus</i> (Oberthür, 1910)			1	2				1	2	2	8	5	4.57
<i>Pyrgus carthami</i> (Hübner, 1819)	4	2	3	1		1					11	4	3.9
<i>Pyrgus cirsii</i> (Rambur, 1839)	1	2		12		5	3	2	1	1	27	8	3.94
<i>Pyrgus onopordi</i> (Rambur, 1839)								1			1	8	1
<i>Pyrgus serratalae</i> (Rambur, 1839)	2	16	3		2						23	6	1.93
<i>Spialia sertorius</i> (Hoffmannsegg, 1804)	1	1	2	3	1	1	1	11	3		24	5	3.89
<i>Syrichthus proto</i> (Ochsenheimer, 1816)									1		1	7	1
<i>Thymelicus acteon</i> (Rottemburg, 1775)							1			3	4	4	1.6
<i>Thymelicus flavus</i> (Brünnich, 1763)		2	1			8	4				15	4	2.64

APPENDIX B. Butterfly species included in each group of caterpillar host plant. Sources from Takhtajan (1980), Gomez-Bustillo and Fernandez-Rubio (1974) and Higgins and Riley (1980).

Dilleniidae	Rosidae	Asteridae	Lillidae
<i>A. cardamines</i>	<i>I. feisthamelii</i>	<i>P. panoptes</i>	<i>P. hispana</i>
<i>A. euphenoides</i>	<i>P. machaon</i>	<i>A. urticae</i>	<i>A. arethusa</i>
<i>E. ausonia</i>	<i>P. apollo</i>	<i>E. aurinia</i>	<i>C. briseis</i>
<i>P. brassicae</i>	<i>A. crataegi</i>	<i>E. desfontainii</i>	<i>C. arcania</i>
<i>P. rapae</i>	<i>C. alfacariensis</i>	<i>L. reducta</i>	<i>C. dorus</i>
<i>P. daphidice</i>	<i>C. crocea</i>	<i>M. cinxia</i>	<i>E. epistygne</i>
<i>L. alciphon</i>	<i>G. cleopatra</i>	<i>M. didyma</i>	<i>E. triaria</i>
<i>L. phaleas</i>	<i>G. rhamnii</i>	<i>M. parthenoides</i>	<i>E. zapateri</i>
<i>A. adippe</i>	<i>L. sinapis</i>	<i>M. deione</i>	<i>H. fidia</i>
<i>A. aglaja</i>	<i>A. allous</i>	<i>M. athalia</i>	<i>H. hermione</i>
<i>A. niobe</i>	<i>A. cramera</i>	<i>M. phoebe</i>	<i>H. semele</i>
<i>A. pandora</i>	<i>C. rubi</i>	<i>V. cardui</i>	<i>H. statilinus</i>
<i>A. paphia</i>	<i>C. argiolus</i>	<i>C. boeticus</i>	<i>H. lupina</i>
<i>I. lathonia</i>	<i>C. osiris</i>	<i>S. proto</i>	<i>H. lycaon</i>
<i>C. alceae</i>	<i>C. semiargus</i>		<i>K. circe</i>
<i>P. alveus</i>	<i>G. alexis</i>		<i>L. megera</i>
<i>P. carthami</i>	<i>G. melanops</i>		<i>M. jurtina</i>
	<i>L. boeticus</i>		<i>M. ines</i>
	<i>L. idas</i>		<i>M. lachesis</i>
	<i>N. acaciae</i>		<i>M. russiae</i>
	<i>N. spini</i>		<i>P. aegeria</i>
	<i>P. argus</i>		<i>P. bathseba</i>
	<i>P. pylaon</i>		<i>P. cecilia</i>
	<i>P. amandus</i>		<i>P. tithonus</i>
	<i>P. bellargus</i>		<i>S. actaeae</i>
	<i>P. damon</i>		<i>P. onopordi</i>
	<i>P. dorylas</i>		<i>T. acteon</i>
	<i>P. fabressei</i>		<i>T. flavus</i>
	<i>P. icarus</i>		
	<i>P. nivescens</i>		
	<i>P. ripartii</i>		
	<i>P. thersites</i>		
	<i>S. orion</i>		
	<i>S. pirithous</i>		
	<i>L. celtis</i>		
	<i>B. hecate</i>		
	<i>E. tages</i>		
	<i>H. comma</i>		
	<i>P. armoricanus</i>		
	<i>P. cirsii</i>		
	<i>P. serratulae</i>		
	<i>S. sertorius</i>		

A REVISION OF THE NORTH AMERICAN *PERITTIA*
(=*ONCEROPTILA*), WITH FIRST NEARCTIC RECORDS OF
THE GENUS *MENDESIA* (ELACHISTIDAE)

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ABSTRACT. The genus *Onceroptila* Braun, 1948, is synonymized with *Perittia* Stainton, 1854. Four *Perittia* species are recognized as occurring in North America: *Perittia cygnodiella* (Busck, 1921) (**new combination**) in western Canada and United States; *P. eremonoma* (Braun, 1948) (**new combination**) in western United States; *P. passula*, **new species**, in California; and *Perittia herrichiella* (Herrich-Schäffer, 1855) in eastern Canada. *Perittia passula* is compared with the related *P. andoi* Kuroko, 1982, which occurs in Japan and the Russian Far East. *Perittia herrichiella* is widespread in Europe, from where the species probably has been introduced to North America with honeysuckle plants. Two species of *Mendesia* Joannis, 1902, are recognized from North America: *Mendesia serica*, **new species**, from Colorado, and *M. metaxea*, **new species**, from Texas. The genus *Mendesia* (s.l.) previously was known only from the western Palaearctic and South Africa.

Additional key words: systematics, taxonomy, introduced species, new species, *Lonicera*.

Since Braun's (1948) revision of the Elachistidae of North America, little has been published on this group, although extensive material has been collected. The aim of this and coming papers is to revise and redescribe the species recorded in former works and describe the new material. The present paper treats the small genera *Perittia* and *Mendesia*, which belong to a group of Elachistinae (sensu Hodges 1978) that feed on dicotyledonous plants.

MATERIAL

Material for this study was obtained from following museums:

ANSP—Department of Entomology, Academy of Natural Sciences of Philadelphia, USA (D. Azuma).

CNC—Canadian National Collection, Agriculture Canada, Ottawa, Canada (J.-F. Landry).

Sakai University of Osaka Prefecture, Sakai, Osaka, Japan (T. Hirowatari).

UCB—Essig Museum, Division of Entomology and Parasitology, University of California, Berkeley, USA (J. A. Powell).

NMNH—Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (R. W. Hodges).

ZMH—Zoological Museum, University of Helsinki, Finland (L. Kaila).

Genus *Perittia* Stainton

Perittia Stainton, 1854:177. Type species: *Apheloseitia obscurepunctella* Stainton, 1848. *Scirtopoda* Wocke in Heinemann, 1876:465 (nom. praeocc.). Type species: *Tinagma herrichiella* Herrich-Schäffer, 1855.

Onceroptila Braun 1948:10, **new synonymy**. Type species: *Apheloseitia cygnodiella* Busck, 1921.

Swezeyula Zimmerman and Bradley, 1950:194. Type species: *Swezeyula lonicerae* Zimmerman and Bradley, 1950.

Braun (1948) described *Onceroptila* for two Nearctic species, *O. eremonoma* Braun, 1948, and *Apheloseitia cygnodiella* Busck, 1921. She distinguished the new genus from the closely related *Perittia* Stainton, 1854, by the conspicuously developed manica in the male genitalia and two characters in wing venation: veins R_4 and R_5 are long stalked in *Onceroptila* but are coincident in *Perittia*; and $1A+2A$ is furcate in *Perittia* but without any indication of basal forking in *Onceroptila* (Braun 1948).

Of the Palearctic species included in *Perittia*, the manica is well developed in at least *P. herrichiella* (Herrich-Schaffer, 1855), *P. biloba* Sruoga, 1990, *P. andoi* Kuroko, 1982, *P. lonicerae* (Zimmerman & Bradley, 1950), *P. unicolorella* Sinev, 1992, *P. petrosa* Sruoga, 1992, and *P. obscurepunctella*. The stalk of R_4 and R_5 in *P. andoi* and *P. herrichiella* is as long as in *O. cygnodiella*. The length of stalking shows intraspecific variation at least in *Perittia herrichiella* (L. Kaila, unpubl.), and therefore this character is not particularly useful in separating the two genera. The basal forking is clearly present in *Perittia herrichiella* and to some extent in *P. obscurepunctella*, but in *P. petrosa* Sruoga it is absent (venation of other species have not been studied).

The species *obscurepunctella* and *cygnodiella* are nearly indistinguishable in characters of the male genitalia. However, they appear to represent distinct species on the basis of the following differences in female genitalia: ostium bursae is very wide, as wide as the 8th sternum in *O. cygnodiella*, much narrower and rounded in *P. obscurepunctella*; ductus bursae is several times longer than abdomen and spirally coiled in *O. cygnodiella*, much shorter and straight in *P. obscurepunctella*.

Therefore, as I have found no reliable characters that would support separation of the genera *Perittia* and *Onceroptila*, *Onceroptila* is hereby proposed to be a junior subjective synonym of *Perittia*, **syn. n.**

SYSTEMATICS

Key to North American species of *Perittia*

1. Forewing unicolorous dark gray, except a whitish or light grayish patch on posterior margin (Figs. 5-8) (3)
- 1'. Forewing light or leaden gray, with scattered light scales and a dark streak in the fold (Figs. 1-4) (2)
2. Head gray; valva tapered into a curved, strongly sclerotized cucullus (Fig. 10); apex of each lobe of juxta unilobed (Fig. 16); ostium bursae very wide; ductus bursae very long, spirally coiled (Figs. 22-23) *P. cygnodiella*
- 2'. Head creamy white; cucullus of valva broad, rounded (Fig. 11); apex of each lobe of juxta bilobed, one a sclerotized thorn (Fig. 19); ostium bursae small, rounded, ductus bursae short and straight (Fig. 24) *P. eremonoma*
3. Valva tapered into a curved, strongly sclerotized cucullus (Figs. 12-13); apex of

each lobe of juxta unilobed, without setae (Figs. 17–18); ostium bursae narrow, with parallel sides and V-shaped ventral margin (Fig. 26); ductus bursae straight; signum a laterally dentate, elongate, medially broadened patch (Fig. 34) *P. herrichiella*

- 3'. Valva smoothly rounded, with no distinct cucullus (Fig. 14); apex of each lobe of juxta with a sclerotized, broad thorn and a rounded lateral lobe with setae (Fig. 20); ostium bursae funnel shaped, tapering toward colliculum (Fig. 28); ductus bursae spirally coiled (Fig. 29), signum a sclerotized, oval plate with two or three strong thorns in the middle (Fig. 35) *P. passula*

Perittia cygnodiella (Busck, 1921), n. comb.

Figs. 1–3, 10, 16, 22–23, 32

Apheloseitia cygnodiella Busck, 1921:280

Onceroptila cygnodiella; Braun 1948:11

Labial palpi light gray, drooping, straight, length of third segment equal to second; head and neck tufts gray, tips of some scales often whitish; antenna gray, segments of distal third with slightly raised scales; tegula, thorax and abdomen gray; legs gray, tibia and tarsal segments with slightly lighter distal rings; forewing gray, in the middle of wing at fold an elongate dark spot, surrounded by bluish-white scales forming an irregular light patch; at three-fourths of forewing another weak and irregular dark spot, which may be reduced to a few dark scales or expanded as a large dark patch; very dark grey line in cilia, prominent around apex, weak near tornus; cilia gray. Forewing length 3.5–5.5 mm. Hindwing gray, basally often lighter; underside of wings gray.

Male genitalia. Uncus small, with some setae; gnathos rather large, elongate, setose; valva short and broad; costa proximally convex, weakly sclerotized, in the middle almost straight angled, forming a strongly sclerotized, distinct, narrow, blunt-tipped cucullus; sacculus weakly sclerotized, broad, convex to two-thirds from base, apically concave; digitate process visible only because of a small, dense group of setae; juxtal lobes longitudinally folded, long, sclerotized, each with a sharp, curved tip; vinculum rounded, slightly broadened ventrally; aedeagus long, slightly bent, without cornuti, caecum with a bilobed manica.

Female genitalia. Posterior margin of eighth segment with some large setae; papillae anales with small setae; apophyses stout, the length of apophyses anteriores two-thirds of the length of apophyses posteriores; ostium very broad, antrum funnel shaped, tapering into a very long, spirally coiled ductus bursae, which is partly lightly sclerotized, with longitudinal folds; corpus bursae with small inwardly directed spines; signum large, dentate, elongate, broadening medially.

Life history. Unknown.

Material examined. Canada, British Columbia: Holotype male, labelled: "Victoria B.C./23. April 1920/W. Downes", "388," [red] "Type no. 1133," "Apheloseitia/cygnodiella/Type Busck", "L. Kaila/prep.nro 886" (CNC).

Victoria, 26 April 1920, 1 M (W. Downes, ANSP); Victoria, 5 May 1923, 1 F (E. H. Blackmore, ANSP).

Alberta: Edmonton Whitemud, Crash ravine, 25 May 1983, 1 M (J.-F. Landry, CNC).

USA: Washington: Wawawai, 18 April 1929, 1 F (J. F. G. Clarke, ANSP).

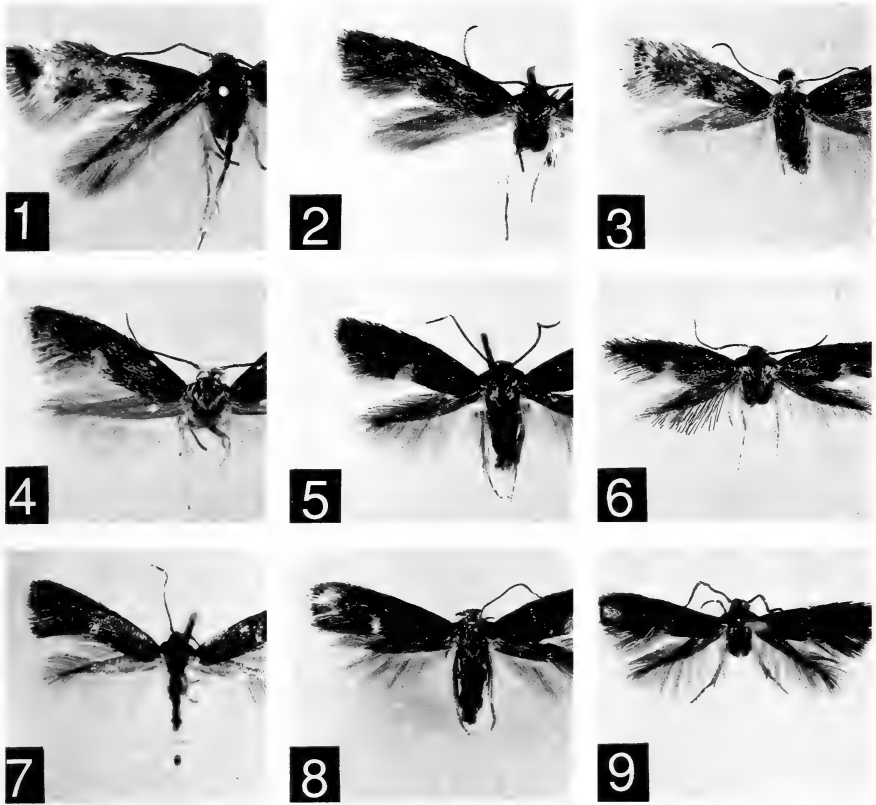
California: Plumas Co.: 1 mi. S. Meadow Valley, 18–19 May 1982, 1 F (J. A. Powell, UCB).

Perittia eremonoma (Braun, 1948), n. comb.

Figs. 4, 11, 19, 24–25, 33

Onceroptila eremonoma Braun, 1948:12

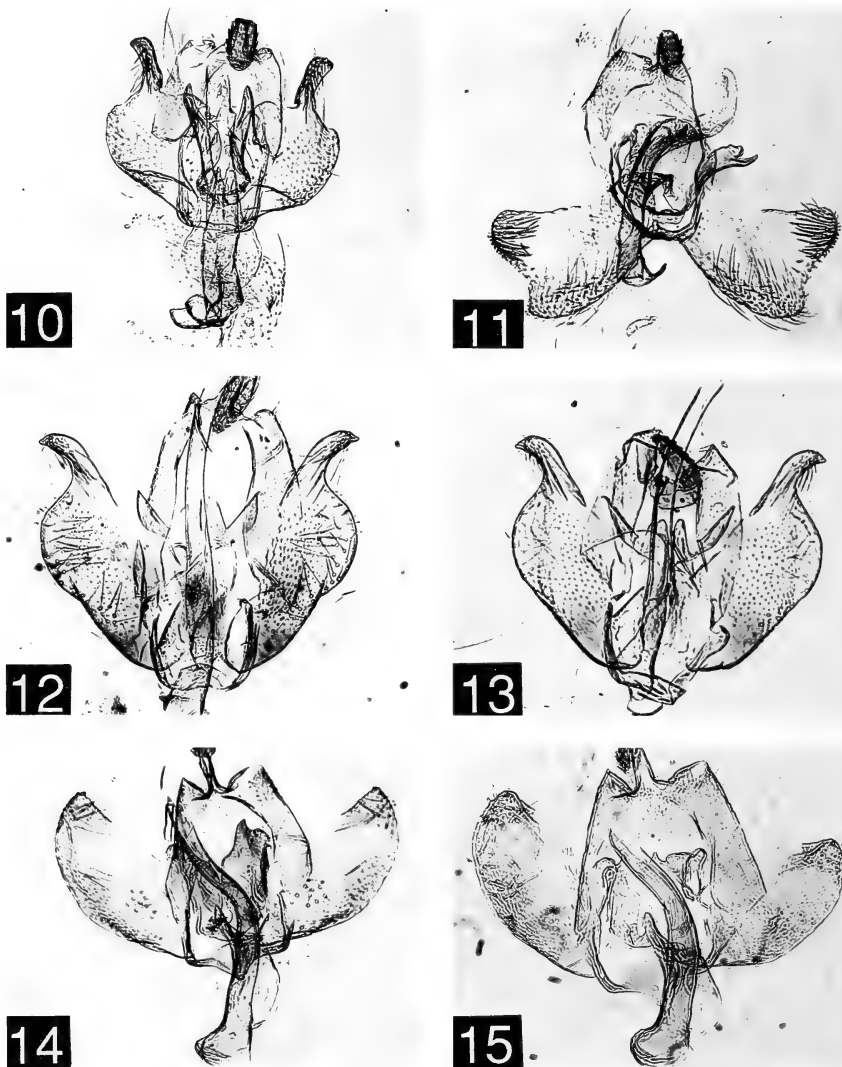
Labial palpus creamy white or slightly grayish, drooping to straight, length of third segment equal to second; head and neck tufts creamy white; antenna unicolorous gray,



FIGS. 1-9. *Perittia* species. 1, *P. cygnodiella*, holotype male, Canada, British Columbia, Victoria; 2, *P. cygnodiella*, male, Canada, Alberta, Edmonton Whitemud; 3, *P. cygnodiella*, female, USA, California, Plumas Co.; 4, *P. eremonoma*, male, USA, Nebraska, Cherry Co.; 5, *P. herrichiella*, male, Poland, Breslaw; 6, *P. herrichiella*, Canada, Quebec, dr. Terrebonne, Lac Brulé nr. Ste-Agathe; 7, *P. passula*, holotype male, USA, California, Monterey Co.; 8, *P. passula*, paratype female, USA, California, Marin Co.; 9, *P. andoi*, paratype male, Japan, Sugadaira.

segments on distal third with scales slightly raised apically; tegula gray basally, creamy white apically; thorax creamy white dorsally, gray ventrally; abdomen and legs gray; forewing whitish, densely mottled with dark-gray tips of scales making the wing gray; in the middle of wing at fold an oblique, dark spot, bound outwardly by an irregular whitish spot extending to posterior margin; line in cilia indistinct, dark gray; cilia gray. Forewing length 4.0-4.5 mm. Hindwing and underside of wings gray.

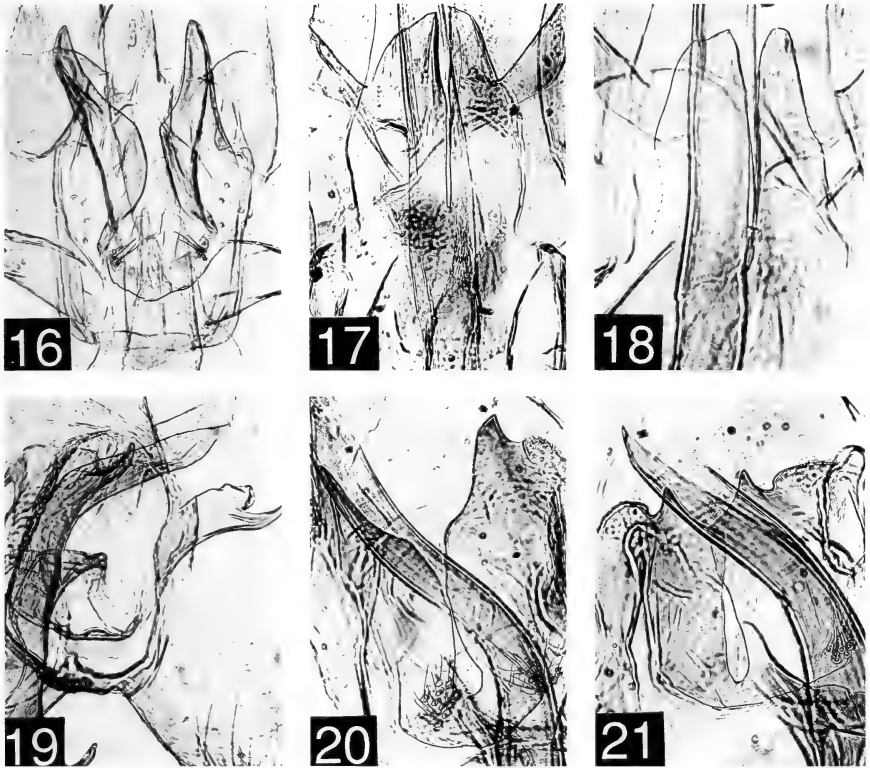
Male genitalia. Uncus reduced to a small, triangular setose swelling; gnathos rather small, elongate, setose; valva broadening proximally; costa not sclerotized, weakly concave; sacculus forming a large, rather weakly sclerotized lobe, with strong setae; termen of valva slightly concave, cucullus rounded, with strong setae; digitate process very small, with about five setae; juxta U-shaped, median margin strongly sclerotized, tapering as a strong, bent thorn apically; outer margin of apex distally enlarged as a blunt, weakly sclerotized, setose dilation; vinculum rounded; aedeagus without cornuti, bent at two-



FIGS. 10-15. Male genitalia of *Perittia* species. 10, *P. cygnodiella*, holotype, Victoria, British Columbia; 11, *P. eremonoma*, Colorado, Chaffee Co; 12, *P. herrichiella*, Quebec, Gatineau; 13, *P. herrichiella*, Finland, Helsinki; 14, *P. passula*, holotype, California, Monterey Co.; 15, *P. andoi*, paratype, Japan, Sugadaira.

thirds, tapering as sharp-tipped lobe on ventral side; distal opening very long and oblique; with a small, bilobed manica.

Female genitalia. Papillae anales short, triangular, setose; apophyses stout, length of apophyses anteriores two-thirds length of apophyses posteriores; ostium bursae rounded,



FIGS. 16-21. Juxta in male genitalia of *Perittia* species (the same specimens as in Figs. 10-15). 16, *P. cygnodiella*; 17-18, *P. herrichiella*; 19, *P. eremonoma*; 20, *P. passula*; 21, *P. andoi*.

antrum funnel shaped, well sclerotized; ductus bursae not sclerotized, less than three times the length of apophyses posteriores; corpus bursae rounded, with small inwardly directed spines and retinaculation; signum very large, dentate, elongate, broadened medially.

Life history. Unknown.

Material examined.

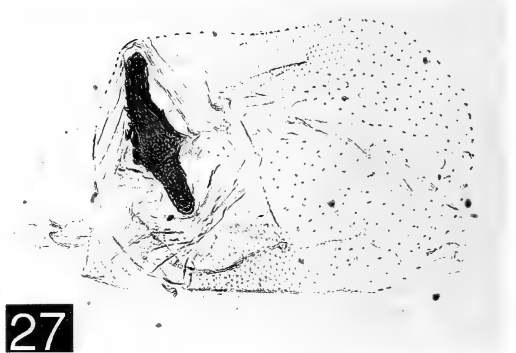
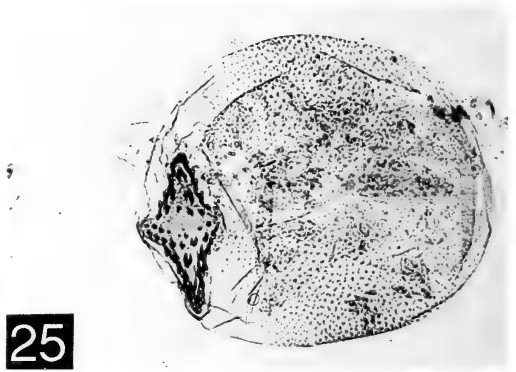
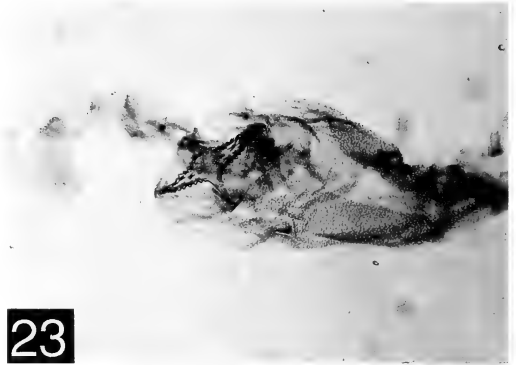
USA: Oregon: Baker Co.: Spring creek, 24 July 1968, 1 M, 3 June 1969, 1 M 1 F, 9 July 1969, 1 M, 7 July 1970, 1 M, 7 July 1970, 1 M (J. H. Baker, NMNH).

Utah: Sanpete Co.: Ephraim Can, 7100', Major's Flat, 20-21 July 1981, 2 M, 7500', Willow Cr. Road, 21-22 July 1981, 4 M (R. W. Hodges, NMNH).

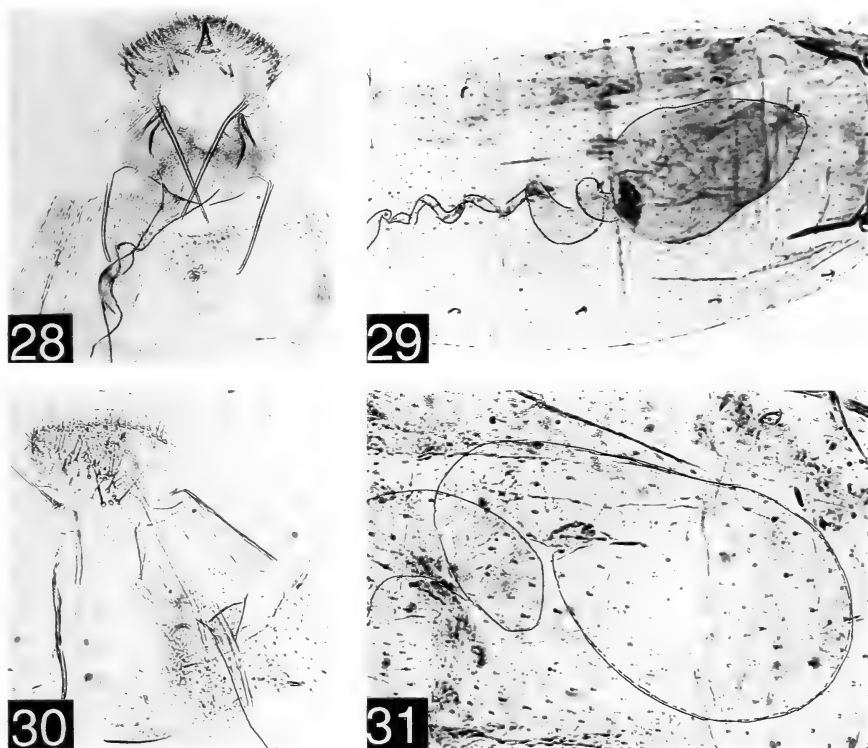
Nebraska: Cherry Co.: Ft Niobrara NWR, 2-19 June 1983, 8 M (R. W. Hodges, NMNH).

Colorado: Chaffee Co.: base Mt. Yale, 4 km W Rainbow Lake 2900 m, 13 July 1982, 1 M; Poncha Ck., 3 km S Poncha Springs, 14 July 1982, 1 M, (J.-F. Landry, CNC).

California: Tuolumne Co.: Baker Campgr. nr. Kennedy Meadow, 28 Aug. 1983, black light, 1 M (J. A. De Benedictis & J. A. Powell, UCB).



FIGS. 22-27. Female genitalia of *Perittia* species. 22-23, *P. cygnodiella*, California, Plumas Co; 24-25, *P. eremona*, Oregon, Baker; 26-27, *P. herrichiella*, Quebec, Gatineau.



FIGS. 28-31. Female genitalia of *Perittia* species. 28-29, *P. passula*, paratype, California, Strawberry Co.; 30-31, *P. andoi* Japan, Honshu, Sugadaira.

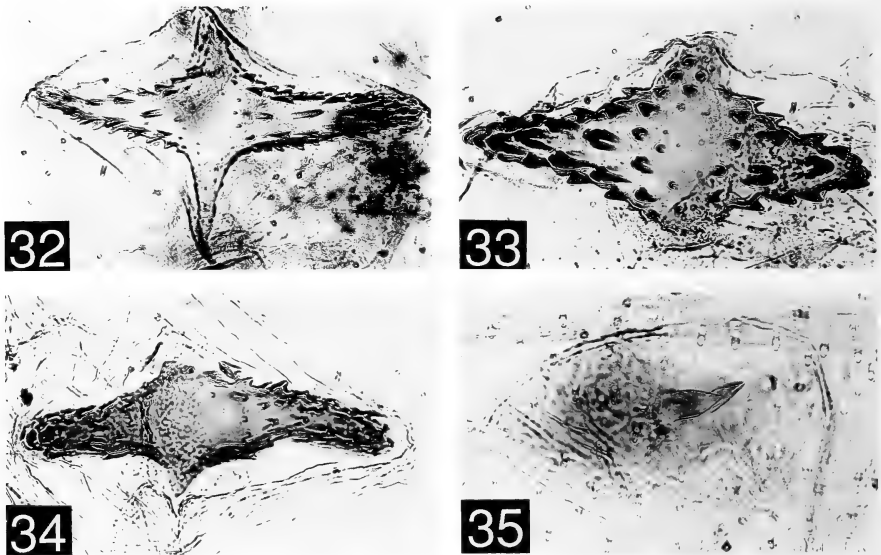
Perittia herrichiella (Herrich-Schäffer, 1855)

Figs. 5-6, 12-13, 17-18, 26-27, 34

Tinagma herrichiella Herrich-Schäffer, 1855:260

Labial palpus brownish gray, slightly lighter above, drooping, weakly curved, third segment two thirds length of second; head and neck tufts brownish gray, with slight bronzy sheen; antenna brownish gray, segments on distal third with apically raised scales; tegula and thorax brownish gray, with bronzy sheen; abdomen brownish gray, with bluish or greenish reflection; legs gray, tibia and tarsal segments with lighter distal rings; forewing dark gray with slight bronzy sheen, weakly mottled with very dark gray tips of scales; a creamy white triangular spot in the middle of posterior margin; in cilia indistinct, dark brownish gray line, cilia gray; forewing length 3.5-4.0 mm; Hindwing and underside of wings gray.

Male genitalia. Uncus small, rounded, tip setose; gnathos elongate, setose; valva short and broad; costa strongly convex proximally forming a membranous lobe, apically almost straight, sacculus strongly concave, tapering into a narrow, sclerotized, setose cucullus; digitate process reduced as a very small swelling without setae; juxta U-shaped, lobes broadly fused basally, long, rather broad, inner margin almost straight, apical margin oblique, rounded; vinculum rounded, enlarged anteriorly; aedeagus long and narrow,



FIGS. 32-35. Signum in female genitalia of *Perittia* species (the same specimens as in Figs. 22-31). 32, *P. cygnodiella*; 33, *P. eremonoma*; 34, *P. herrichiella*; 35, *P. passula*.

weakly bent, S-shaped, with blunt, rounded and bent caecum, without cornuti; with manica.

Female genitalia. Posterior margin of eighth segment with some large setae; papillae anales triangular, with small setae; apophyses anteriores rather short and stout, apophyses posteriores more than twice length of apophyses anteriores; ventral margin of ostium bursae V-shaped, antrum sclerotized, with almost parallel lateral margins, gradually tapering into a narrow colliculum; colliculum densely covered with small chitinized spines internally beyond a short, membranous zone; ductus bursae narrow; corpus bursae with very small inwardly directed spines, signum large, dentate, elongate, broadened medially.

Life history. The species is widespread in Europe (Traugott-Olsen & Nielsen 1977). *Perittia herrichiella* is a leaf-miner on *Lonicera* spp. (Caprifoliaceae). It hibernates as a pupa in a cocoon under the bark of the host plant. At this stage the species may easily have been introduced to eastern Canada with *Lonicera* plants.

Material examined. Canada, Quebec: d.r. Gatineau, Aylmer, 15 June, 6 M, 2 F (J.-F. Landry, CNC); d.r. Terrebonne, Lac Brulé nr. Ste-Agathe, 8 July 1988, 1 M, MVL (J.-F. Landry, CNC).

Perittia passula Kaila, n. sp.

Figs. 7-8, 14, 20, 28-29, 35, 36

Labial palpus gray, rather long, drooping, second segment slightly curved basally, third segment two thirds length of second; head and neck tufts unicolorous gray; antenna gray, segments of distal half with apically slightly raised scales; tegula, thorax, and abdomen unicolorous gray; legs gray, tarsal segments with lighter distal rings; middle spurs of hind tibia at one-fourth from base, inner spur more than twice the length of outer spur; distal spurs shorter, outer spur two-thirds length of inner spur; ground color of forewing light gray, densely mottled with dark-gray tips of scales making the color dark gray; beyond



FIG. 36. Cocoon of *Perittia passula* on a twig of the host plant, California, Strawberry Co.

middle of posterior margin a small triangular white patch; line in cilia dark-gray, cilia gray; forewing length 3–4 mm. Hindwing and underside of wings gray.

Male genitalia. Uncus lobes small, triangular, tip without setae; gnathos elongate, setose; costa of valva weakly sclerotized, almost straight, valva rather short proximally, sacculus smoothly rounded, tapering distally into a blunt cucullus with a small distal thorn; digitate process very small, setose; lobes of juxta large, broad, lateral margin rounded, setose, apical margin strongly sclerotized, tapering into a thorn-shaped prolongation; vinculum sclerotized, tapering medially into a short saccus; aedeagus long, strongly bent in the middle, caecum with a small manica, distal opening oblique, without cornuti.

Female genitalia. Eighth sternum sclerotized; apophyses slender and rather long, length of apophyses anteriores two-thirds length of apophyses posteriores; ostium rounded, very large; antrum funnel shaped, ventral margin straight; ductus bursae long, spirally coiled, in posterior part sclerotized for short distance; corpus bursae with small inwardly directed spines, signum a sclerotized patch with two-three strong thorns.

Diagnosis. *Perittia passula* is closely related to *P. andoi* Kuroko, 1982, which occurs in Japan and Russian Far East in the Palaearctic. They differ in following characters: the thorn-shaped prolongation in the juxta of the male genitalia is larger in *P. passula*, and the aedeagus is longer and more strongly bent in *P. passula* compared to *P. andoi* (Figs. 14–15, 20–21). There is no signum in bursa copulatrix of *P. andoi* (Fig. 31); in *P. passula* the signum is a sclerotized, non-dentate plate with two or three strong thorns (Fig. 35).

Life history. The species is a leaf-miner feeding at least on *Lonicera hispidula* (Caprifoliaceae). Pupation occurs in a dense cocoon that the larva makes under the epidermis of a twig of the host plant. The cocoon appears as a shuttlelike swelling, covered with epidermis of the twig (Fig. 36).

Material examined. Holotype: Male: California: Monterey Co.: 17.5 mi W of Solon, 19 March 1969, J. Powell No. 69C87, dead XI.1969, reared from *Lonicera hispidula* (P. Opler, UCB); L. Kaila, prep. nro 1015; Holotype *Perittia passula* Kaila [red]; Coll. UCB.

Paratypes: USA: California: Alameda Co.: Strawberry Cyn., 8 Feb. 1968, 2 M, 6 F, J. Powell No. 68B48-49, larva on *Lonicera* sp. (P. Opler, UCB, ZMH); Tilden Park, Berkeley Hills, 14 and 23 March 1969, 4 F, J. Powell 69D35.1; 69C91; reared from *Lonicera* (P. Opler, UCB).

Marin Co.: Marin Id., 13 Apr 1989, 1 M, J. Powell No. 89O20, reared from *Lonicera hispidula* (J. Powell & M. Prentice, UCB); 26 May 1989, 1 F, J. Powell No. 89E11, reared from *Lonicera hispidula* (J. Powell & M. Prentice, UCB).

Marin Co.: Carson Ridge nr. Woodacre, 30 March 1985 1 M, J. A. Powell No. 85C50, reared from *Lonicera hispidula* (J. Powell, ZMH).

Monterey Co.: 17.5 mi. W of Solon, 19 March 1969, 1 M, J. Powell 69C87, larva on *Lonicera hispidula* (J. Powell, UCB); Big Creek Res., 21-22 Feb 1988, 2 M, coastal scrub, J. Powell 88J19, reared from *Lonicera hispidula* (J. A. Powell UCB).

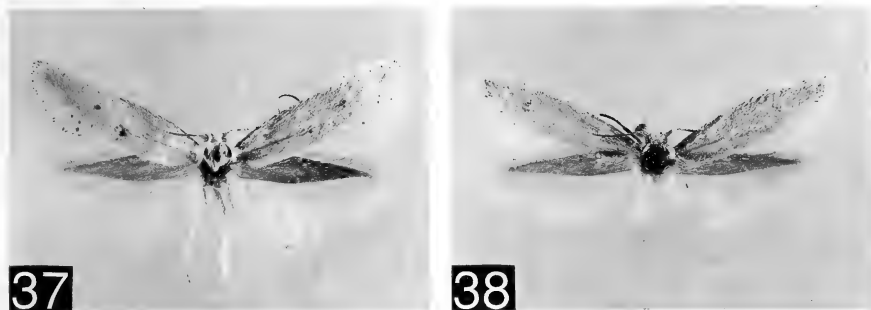
Los Angeles Co.: Sta. Catalina Is., middle cyn., 500-750', 1 May 1978, 1F (J. Powell, UCB).

Genus *Mendesia* Joannis

Mendesia Joannis, 1902:231. Type species: *Mendesia echiella* Joannis, 1902.

Triboloneura Walsingham, 1908:54. Type species: *Elachista sepulchrella* Stainton, 1872.

Previously recognized species of *Mendesia* are distributed in the Western Palaearctic region (Traugott-Olsen & Nielsen 1977, Traugott-Olsen 1990, Klimesch 1990). In addition, a species currently assigned to *Mendesia* (Parenti 1988) has been reported from South Africa. No species of *Mendesia* or the closely related *Polymetis* Walsingham, 1908, have been reported from North America (Braun 1948, Hodges et al. 1983). Elachistidae material collected by R. W. Hodges (NMNH) and J.-F. Landry (CNC) from the southern United States contain two undescribed species that I provisionally assign to this genus, although both species share characters not present in previously described species of *Mendesia* or related genera. These characters are a tuft of scales above the eyes, the sharply produced, long saccus in male genitalia, and a long, tongue-shaped appendix in the costa of the valva. The same or a similar structure also is present in *Mendesia aganope* Meyrick, 1911, from South Africa (see Parenti 1988). The generic names of this group of Elachistidae have not been revised, and the genera in current use probably do not represent monophyletic natural groups. Moreover, I believe that a number of species belonging to this group await description, and the taxonomic value of the characters on which the genera in current use are based on is unknown. Therefore, I shall not introduce a new generic name for the present species solely on the basis of the



FIGS. 37-38. *Mendesia* species. 37, *M. serica*, holotype male, USA Colorado, 1 mi S Poncha Springs; 38, *M. metaxea*, holotype male, USA, Texas, Brewster County, Chisos Mts.

characters mentioned, especially since the females of both these species remain unknown.

Diagnosis

The two species described below are apparently closely related. Both are silky white, with some darker scales. In *M. serica* the darker scales are very dark brown; in *M. metaxea* they are light brownish. The sacculus is concave beneath the cucullus in *M. metaxea*; straight or slightly convex in *M. serica*.

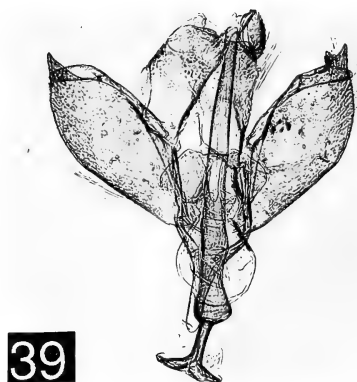
Mendesia serica Kaila, n. sp.

Figs. 37, 39-40, 42

Labial palpus short, brownish white, the length of third segment equal to second, third segment drooping; head and neck tufts white; scape of antenna with long white scales, flagellum pale brownish gray, in distal third segments with distally slightly raised scales; tegula, thorax, and abdomen white; foreleg white above, gray below, tarsal segments gray, distally white; midleg whitish, tibia with two apical spurs, length of inner spur twice that of outer, tarsal segments gray, distally white; hindleg white, middle spurs of tibia long, arising at one-third distance from base, inner spur twice the length of outer, apical spurs short, inner spur slightly shorter than outer. Forewing: ground color silky white, with scattered yellowish scales especially near apex, and some scales with blackish brown tip, forming an irregular line in cilia and two dark spots, one before middle of fold and another at two thirds length of wing; cilia white. Length 6 mm. Hindwing slightly translucent, gray; underside of wings gray.

Male genitalia. Uncus lobes small, triangular, with setae; gnathos elongate; tegumen tapering toward uncus; costa of valva slightly curved, forming a long, curved, blunt-tipped appendix with setae at tip beyond middle; costa concave beyond appendix; sacculus rounded, tapering distally into a sharp, setose cucullus; digitate process small, setose; lobes of juxta large, setose, median margin slightly rounded toward apex, apical margin rounded, slightly produced laterally; vinculum well sclerotized, produced into a long, blunt-tipped saccus; aedeagus long, narrow, slightly bent medially, without cornuti; caecum ventrally with a large, apically dilated, bilobed manica.

Female genitalia. Unknown.



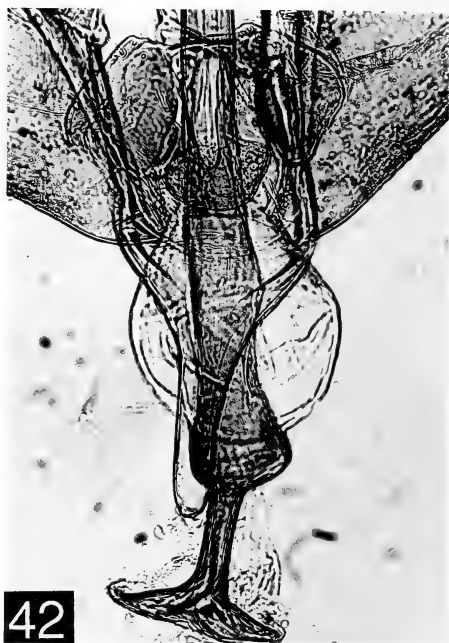
39



40



41



42



43

FIGS. 39-43. Male genitalia of *Mendesia* species. 39, *M. serica*, holotype male, Colorado, Poncha Springs; 40, *M. serica*, paratype, Colorado, Poncha Springs; 41, *M. metaxea*, holotype male, Texas, Brewster County; 42, *M. serica*, holotype male: lobes of juxta, vinculum and manica; 43, *M. metaxea*, holotype male: lobes of juxta, vinculum and manica.

Life history. Unknown.

Material examined. Holotype: Male: Colorado: Chaffee Co.: 1 mi S Poncha Springs, 7000', 6 July 1982 (Ronald W. Hodges, NMNH), Pinyon-juniper/oak-cottonwood/willow-Rhus; L. Kaila prep. nro 923; Holotype *Mendesia serica* Kaila [red].

Paratypes. Colorado: Chaffee Co.: 1 mi S Poncha Springs, 7000', Pinyon-juniper/oak-cottonwood/willow-Rhus, 13 July 1982, 1 M (R. W. Hodges, NMNH), L. Kaila prep. nro 946; Poncha Ck. 3 km S Poncha Springs, 14 July 1982, 1 M, at black light, pinyon-juniper-oak forest (J.-F. Landry, CNC), L. Kaila prep. nro 931.

Mendesia metaxea Kaila, n. sp.

Figs. 38, 41, 43

Labial palpus short, white, straight, length of third segment equal to second; head and neck tufts white; scape of antenna with long white scales, flagellum pale brownish gray, on distal third segments distally with slightly raised scales; tegula, thorax, and abdomen white; fore- and midlegs brownish, tarsal segments gray with white distal rings; midtibia with two apical spurs, inner spur longer than outer; hindleg whitish, middle spurs of tibia at one-fourth distance from base, outer spur twice the length of inner spur, apical spurs short, inner spur longer than outer. Forewing: ground color silky white, scattered scales with light brown tip, forming an irregular spot at two thirds wing length and an irregular line in cilia. Length 5 mm. Hindwing slightly translucent, gray; underside of wings gray.

Male genitalia. Uncus lobes small, setose; gnathos short, rather broad; costa of valva curved, forming at two thirds from base a long and broad, curved, gradually tapering appendix with setae at inner margin; costa concave beyond appendix; sacculus slightly rounded from base to two thirds length where it forms a gentle angle; sacculus concave beyond angle, tapering distally into a sharp, bare cucullus; digitate process very small, setose; lobes of juxta large, setose, median margin slightly convex toward apex, apical margin rounded, lateral margin straight; vinculum sclerotized, produced into a long, clavate saccus; aedeagus long, narrow, medially slightly bent, without cornuti; caecum ventrally with a large, apically dilated bilobed manica.

Female genitalia. Unknown.

Life history. Unknown.

Material examined. Holotype: Male: Texas, Brewster Co.: Chisos Mts, K-Bar Ranch, 3400 ft, 1 June 1973 (R. W. Hodges, NMNH); L. Kaila prep. nro 939; Holotype *Mendesia metaxea* Kaila [red].

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PREDATION OF *ANETIA BRIAREA* GODART
(NYMPHALIDAE: DANAINAE) AT AGGREGATION SITES:
A POTENTIAL THREAT TO THE SURVIVAL OF A RARE
MONTANE BUTTERFLY IN THE DOMINICAN REPUBLIC

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ABSTRACT. Evidence of predation on *Anetia briarea* was discovered at the single known aggregation site on Pico Duarte in the Dominican Republic. In addition to birds, feral rats (*Rattus rattus* L.) are hypothesized to be involved in predatory activity affecting the aggregation. Analyses show no biases in the sex, size, or color of *A. briarea* taken as prey. Steps that can be taken to protect the aggregating butterflies include removal of exotic rats from the colony area.

RESUMEN. Evidencia de predación de *Anetia briarea* fue descubierta en el único sitio conocido de agregación en Pico Duarte en la República Dominicana. Además de pájaros, se cree que ratas (*Rattus rattus*), están involucradas en la predación de las colonias. Un análisis de predación de las colonias de *A. briarea* muestra no tendencia por el género, tamaño, o color de la presa. Actividades para proteger las mariposas que se están agregando incluyen la eliminación de las ratas extrañas del sitio de agregación.

Additional key words: rats, conservation biology, West Indies.

Predation on butterflies, although thought to be important evolutionarily, is rarely observed in the field (Brown & Vasconcellos 1976, Bowers et al. 1985, Brower & Calvert 1985). With the exception of the observations documenting predation of monarchs at overwintering sites (Brower & Calvert 1985, Sakai 1994) most of our knowledge regarding predation on butterflies is obtained indirectly by analysis of the evidence of predation, such as beak-marked (e.g. Shapiro 1974, Smith 1979) or tooth-marked (e.g. Brower et al. 1985) wings. Laboratory investigators, studying the acceptability of various butterflies to vertebrate predators, have found great variation in palatability within and between butterfly species (e.g. Brower & Brower 1964, Duffey 1970, Bowers 1980, Brower 1984).

Anetia briarea Godart (Nymphalidae) is a rare montane danaine butterfly of the Greater Antilles (Riley 1975, Schwartz 1989, Alayo & Hernadez 1987, Vane-Wright et al. 1992, Smith et al. 1994). It shares with several other danaines the characteristic of forming seasonal aggregations, often at high altitudes (e.g., species of *Anetia*, *Euploea*, *Tirumala*, *Ideopsis*, *Salatura*, *Parantica*, and *Danaus*) (Brower et al. 1977, Ivie et al. 1990, Wang & Emmel 1990, Llorente-Bousquets et al. 1993). However, in sharp contrast to such common species as the monarch (*Danaus plexippus* L.), with colonies estimated to number up to 20 million individuals (Brower & Calvert 1985), and *Danaus genutia* (Cramer) and *Euploea* spp. with colonies of up to 50 thousand (Wang

& Emmel 1990, Ishii & Matsuka 1990), the only known colony of *A. briarea* contains a mere 500–2,500 individuals (Ivie & Sikes unpublished data). Even such a small aggregation potentially offers a rich concentration of resources for predators.

The exact role of seasonal aggregation is not well understood in *A. briarea*, but since aggregations occur yearly at the same sites (Ivie & Sikes unpublished data), it is currently assumed to be an obligate life history trait. The monarch butterfly maintains large populations in temperate habitats by withdrawing to an amenable climate and diapausing in aggregations during the winter (Calvert et al. 1989). Migrations by *A. briarea* seem to be related to wet/dry cycles, and we expect that they are comparatively local in extent. In any case, such high densities in an exposed setting would be expected to require the butterflies to have evolved some type of predator deterrent (Vulinec 1990).

This hypothesis has only been tested with one of the aggregating danaine species, the monarch butterfly. This species is somewhat protected from predation by sequestered cardiac glycosides obtained from asclepiadaceous larval host-plants, although individual bird and mammal predators sometimes overcome this defense (Fink & Brower 1981, Brower & Calvert 1985, Brower et al. 1985, Sakai 1994). Although the Hispaniolan host-plant of *A. briarea* remains unknown, Brower et al. (1992) recently have reared *A. briarea* larvae on Floridian *Cynanchum angustifolium* (Pers.) (Asclepiadaceae), and spectrophotometric analysis of wild collected *A. briarea* adults shows they contain small quantities of cardenolides (L.P. Brower, M.A. Ivie, A. Alonso & D.S. Sikes unpublished data). However, during visits to the only known *A. briarea* aggregation site in July and August 1992 and July 1993, evidence of predation was found in the form of beak and tooth marks on living individuals and discarded wings. These findings mirror those of Brower and Calvert (1985) on the Mexican monarch.

METHODS

Observations were made during visits to the 2670 m aggregation site described by Ivie et al. (1990), in July and August 1992 and July 1993. During the daylight and crepuscular hours of 25–29 July 1993, the colonies were monitored for evidence of predation.

To investigate the incidence of bird predation attempts, we collected a subsample of 78 butterflies from a sample of 195 (with a bias towards individuals with undamaged wings) on 8 July 1992. Another sample (lacking bias) of 179 individuals was taken and released on 28 July 1993. Each sample was from a single cluster of butterflies occupying

one branch (see Ivie et al. 1990), and data were collected as an adjunct to sex-ratio studies. The individuals from these two samples were scored for bird beak-marks, and analyzed following procedures outlined by Shapiro (1974).

To examine sex, size, and coloration as predictors of beak-marking [which may affect predation bias (Smith 1979, Bowers et al. 1985)], data from the July 1992 sample were analyzed using SAS, release 6.08, (SAS 1990). Both parametric (ANOVA) and non parametric (Chi^2 , Mann-Whitney) analyses were performed.

We found seven middens of "shucked" wings left below clusters by one or more predators on 26 August 1992, and considered them to be evidence of successful predation (Fig. 1, 2). Damage to the wings (Figs. 3-5) was consistent with small mammal tooth marks observed by Brower et al. (1985). Lincoln Brower examined the wings, and agreed with this interpretation (L.P. Brower, pers. comm.). The middens were photographed and collected for analysis. The wings from each group were then scored for wing-type (e.g. right-front, etc.) and counted. A minimum number of individuals represented in each group was determined by the maximum occurrence of a wing-type. For example, if there were 8 right-fore wings in a midden, and less than 8 of the 3 other types, then 8 would be the minimum number of individuals represented.

RESULTS

Of the 78 live butterflies taken 8 July 1992 (and selected for relatively intact specimens), 32 (41%) showed distinct beak-marks and an additional 22 (28%) showed indistinct marks that may have been made by birds. This sample did not show a significant difference between the damaged wing frequencies on males versus females ($\text{Chi}^2=0.28$, $df=1$, $P>0.50$), although we found the wing length of females to be greater than that of males (45.8 ± 1.8 mm, $n=38$ vs. 44.2 ± 1.4 mm, $n=40$; Mann-Whitney $S=1902.5$, $Z=4.00$, $P=0.0001$). No significant differences were found between the mean lengths of damaged versus undamaged wings, both between and within sexes, nor did we find a difference between the damage frequencies of darker morphs versus lighter morphs (ANOVA, all $P>0.05$).

The 28 July 1993 sample of 179 live individuals showed distinct beak marks on 84 (47%) specimens and indistinct marks on 13 (7%). The ratio of beak-marked males ($n=88$) to females ($n=91$) did not differ significantly from 1:1 ($\text{Chi}^2=0.135$, $df=1$, $P>0.50$). Because these specimens were released or held for life history studies, to minimize handling, color-morph and size were not recorded.

Of the seven middens of disembodied wings found beneath clusters, two were ca. 60 cm apart beneath a cluster and the other five, also



FIGS. 1-2. Middens of *Anetia briarea* wings found beneath colonies on Pico Duarte, Dominican Republic.

within 60 cm of each other, were found beneath clusters located in a different tree. The seven middens contained 16, 8, 19, 23, 40, 26, and 32 wings. These wings were determined to represent the consumption of at least 47 (4, 2, 7, 7, 11, 8, 8) butterflies.

The total aggregation documented during August consisted of six clusters in four trees, with an estimated total population size of 2000–2500 individuals. The individuals consumed by the predator that made the middens thus represent a ca. 2% mortality to the aggregation.

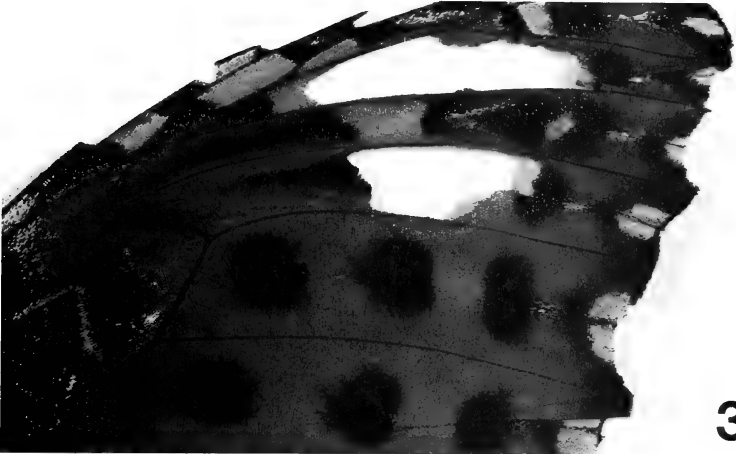
Predator surveys at the aggregation site on 25–29 July 1993 provided few suspects. Two bird species occasionally vocalized in the vicinity, but no birds were seen close to the butterflies. A single *Anolis* sp. was observed on the ground in the area, but seemed too small (ca. 5 cm snout-vent length) to account for the *Anetia* predation. Although bats may be present near or at the site, observations made during crepuscular hours revealed no evidence of bats. In addition, because the piles of wings were 3–5 meters below the branches, bats probably did not make the middens. Bats dropping butterfly wings from feeding roosts in the branches above would produce a dispersed refuse area, not the tight groups observed (Figs. 1, 2).

Lastly, DSS observed an individual of the introduced rat, *Rattus rattus* L., at the site on 28 July 1993. Since the marks on the wings are consistent with small mammal attacks, and since no other small ground-dwelling predacious mammal is known to be present in the area, the evidence points toward *Rattus rattus*.

DISCUSSION

Smith (1979) investigated beak-marks on the wings of an African population of *Danaus chrysippus* (L.). He concluded that larger individuals of both sexes were more frequently beak-marked. Bowers et al. (1985) found that birds attacked more females than males of the checkerspot butterfly, *Euphydryas chalcedona*, but the effect of prey size was not investigated. Brower and Calvert (1985) found the opposite for aggregating monarchs, with birds selecting for the more palatable males in a population without significant sexual dimorphism in prey size. Sakai (1994), reported that predatory birds preying on monarchs at a California overwintering site showed no preference for the sex of prey. In agreement with Sakai's findings on monarchs, our data showed no patterns of preference by birds for sex, size, or color of *A. briarea*. This may be due to a lack of obvious sexual dimorphism and predicts no difference in palatability between the sexes.

Brower and Calvert (1985) reported high predation on the colonies of *D. plexippus* in Mexico by birds and mammals. They conservatively calculated a 9% annual mortality from predation at the colonies. At a



3



4



5

California monarch overwintering site Bell and Dayton (1986) reported a range of 0.345–2.21% annual mortality due to chestnut-backed chickadees. Sakai (1994), also working at a monarch overwintering site in California, documented an estimated annual mortality of 6.51–7.43% due to a single pair of rufous-sided towhees. Our conservative estimate of 2% annual mortality for 1993 falls within these estimates.

Predation on aggregating monarchs is spatially divided into those taken from the arboreal clusters by birds and those taken by mice and voles from fallen groups on the ground below the clusters. This is consistent with observations of *A. briarea*. Those individuals with evidence of attempted bird predation (i.e. beak-marked wings) were found within arboreal clusters, while the suspected rat predated individuals were found in piles below. These later individuals must have been “shucked” on the ground or the disembodied wings would have dispersed as they fell from the branches, thus not forming the tightly clumped middens we observed. Sakai (1994) reported middens created by birds dropping remains from perches. However, the middens he observed consisted of the remains of only a single butterfly, generally with four wings per midden and numerous middens scattered beneath perches.

Clumps of monarch butterflies may fall to the ground due to low temperatures (Masters et al. 1988), lipid depletion (Brower & Calvert 1985), wind, or heavy precipitation (Calvert et al. 1983). Many *A. briarea* were observed in July 1992 that had been knocked to the ground by a heavy hail storm (M.A. & R.O. Ivie unpublished data). Our guides reported hail to be common in the area.

We suspect that the piles were formed by cold temperatures or precipitation having knocked groups of *A. briarea* from the clusters and rats found them before they could warm up to escape. This is further supported by wing damage consistent with small mammal feeding on the piled wings (L.P. Brower pers. comm., Figs. 3–5).

The introduced, anthrophilous, omnivorous, and aggressively colonizing *Rattus rattus* may have only recently reached this area. Hispaniola has perhaps the longest history of European rat infestation in the New World. An archeological dig at Christopher Columbus’s alleged first encampment in the New World (La Navidad, occupied 1492–1493 in

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FIGS. 3–5. Examples of wings from middens showing wing damage hypothesized to be caused by *Rattus rattus* feeding on *Anetia briarea*. Note the parallel scratches/tears on the wings.

what is now Haiti) yielded the jaw of a black rat (*R. rattus*) dated to pre-1510 (Deagan 1987, Deagan 1988, Wing 1989). However, its presence at high elevations may be tied to human disturbances, which have only recently been important in the Pico Duarte area. In 1988 we saw no rats at the Park cabin, La Compartación, located at 2290 m and an hour's hike below the aggregation site, nor in the area above the cabin. However, by 1992, rats were present at La Compartación, and in 1993 they were obnoxiously abundant. In recent years, the cabin has hosted hundreds of tourists annually, mostly in the winter months, and hundreds of overflow tourists camp above the aggregations in El Vallecito de Lilis (Zanoni 1990). The transport of foodstuffs and gear afford the opportunity for rats to reach the uninhabited aggregation site, and the accumulated refuse at the cabin provides an excellent rat habitat. Feral populations can then spread from these human-use sites. In an analogous situation, introduced rats which have wiped out populations of lowland insects in New Zealand have had little success in invading uninhabited high elevation zones (Watt 1979). The increase in tourism, and the accompanying disturbances on Pico Duarte may have only recently created an opportunity for rat invasions into the area.

Ideally, data on abundance, diet, and local ecology of rats at the aggregation sites should be collected before raising an alarm about their potential impact. However, we lacked the necessary traps and other equipment to do such a study, and other constraints preclude returning to conduct such a study in the near future. Due to the small population size of the only known aggregation of this extremely rare and poorly known butterfly (see Ackery & Vane-Wright 1984, Ivie et al. 1990, Brower et al. 1992), the knowledge that the aggregation is subject to predation is important. The incidence of predation by native birds, bats and lizards can be considered a normal part of the biology of the species, but we hypothesize that rat predation is a new and dangerous escalation. If *Rattus rattus* has no aversion to the defense evolved in response to the few native predators, the future of the colonies may be in danger.

Introduced rats have a long history of negative impact on island species (Day 1981, King 1984, Howarth & Ramsay 1991). The extinction of numerous species of birds, tortoises, mammals and an iguana have been blamed, at least in part, on feral rats which gained access to islands via European sailing ships (Day 1981). Paramonov (1958, 1963) reports that rats caused the extinction of a phasmid (Orthoptera) on Lord Howe Is., and Watt (1979, see also Moffett 1991) implicates them in the expatriation of wetas (Orthoptera, *Deinacrida*) and other insects from historic range in New Zealand. Kuschel (1987) reported the discovery of the remains of three weevil species in New Zealand, that he posits were made extinct by the Polynesian rat. To our knowledge, this study

is the first report of a New World insect species being impacted by Old World rats.

The rapid human population growth and consequent destruction of native habitat on the island of Hispaniola (Kurlansky 1992) threaten to impact the survival of *A. briarea*. Although the aggregations are protected by their remote location in the Parque Nacional Armando Bermudez, the butterflies leave the aggregations to fly to areas lower on the mountain (Schwartz 1989, MAI and DSS pers. obser.). These mid-elevation areas are increasingly cultivated for export crops of vegetables and fresh flowers. The pesticide loads associated with export-quality requirements are bound to be detrimental to non-target species such as *A. briarea*. Any additional pressure on this species could place it in danger of extinction, and we feel the presence of rats at the aggregation site is cause for alarm. Eradication of rats from the mountain, discovery of and protection of other *Anetia* aggregation sites, if they exist, and the location of and protection of host-plant stands, should be made a high priority. The conservation of this species need not become a rescue situation if appropriate measures are taken now.

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POPULATION ECOLOGY OF *ANAEA RYPHEA*
(NYMPHALIDAE): IMMATURES AT CAMPINAS, BRAZIL

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ABSTRACT. I studied a population of *Anaea ryphea* (Nymphalidae) for three years in Campinas, Brazil, to identify the extent and causes of egg and larval mortality. Life tables showed the highest level of mortality occurred during the first instar, but key-factor analysis demonstrated that both first and third instars were responsible for the greatest variation in density between months. There was a high and significant correlation between monthly rainfall indices and total k-values for larvae ($r^2=0.79$ and 0.88 for 1989 and 1991 respectively), suggesting a strong influence of rainfall on mortality. Disappearance accounted for a reduction of 53.7% in the total number of marked eggs, and parasitism was observed in 55.9% of the remaining eggs. A positive and significant correlation was found between the number of new eggs and the relative humidity of the previous night ($r^2=0.55$, $p<0.05$), suggesting that changes in humidity could serve as a cue for oviposition.

Additional key words: *Bracon*, mortality, parasitism, predation, *Trichogramma*.

There are few published papers treating population ecology and dynamics of phytophagous insects in natural tropical systems. Most of the information about phytophagous insect population dynamics comes from pests of agroecosystems (Stiling 1988, Hassell et al. 1989). These studies suggest that regulation through natural enemies—predators, parasitoids, pathogens—is common (Risch 1980, Crawley 1989). Results obtained from agroecosystem studies usually cannot be applied to natural systems because natural hosts usually are more dispersed and present more effective defenses against herbivores. These defenses may slow development (Rausher et al. 1993) and help natural enemies control outbreaks (Hassell & Waage 1984).

Parasitism in larvae is reported commonly for temperate and tropical insects (Young & Moffett 1979, Maltais et al. 1980, Strong et al. 1984, Stiling 1988, Hassell et al. 1989) and is seen as a typical mechanism of regulation in herbivorous species (Clark et al. 1967, Dempster 1984, Strong et al. 1984, Hassell 1986, Waage & Greathead 1986). Recent works (Crawley 1989, Karban 1993) also show that, for many herbivorous insects, population densities are maintained at a low level by quality and not quantity of food.

Variation in population numbers also can be due to meteorological and climatic factors. Seasonal variations in insect population size are usually a consequence of climatic conditions. These can act directly as stress or mortality sources, serve as cues and induce adaptive changes (such as diapause), or influence resources and natural enemies. Even in the tropics there can be highly unfavorable abiotic conditions, such

as a strong dry season or wind and rain storms. These can cause density dependent or density independent mortality (Clark et al. 1967), and there are several possibilities of indirect effect of climate on the interactions with enemies, competitors, and resources (Wolda 1978). These can influence the population size in the present (Courtney & Duggan 1983) or future generations (Pollard 1979).

I studied a population of the tropical butterfly *Anaea ryphea* (Nymphalidae: Charaxinae) for 3 years, in order to gather information on natural regulation of a tropical insect. The goal was to assess the main mortality factors acting on immature stages and to search for evidence of density dependent processes.

Adult Charaxinae butterflies feed on rotten fruits, carrion, and feces, rarely on nectar (DeVries 1987). They have a cryptic coloration ("dry leaf" pattern) on the underside of the wings that seems to confer protection from predators when the butterflies are perched. Larvae feed on various families of plants, but mainly Euphorbiaceae. These butterflies can be found from sea level to 2000 m, and some species have large geographic distributions. *Anaea ryphea* was used for this study because it is a phytophagous insect easily found in tropical forests from Mexico to southern Brazil (DeVries 1987). Its abundance and widespread occurrence will allow further studies about variation in mortality factors among populations under different climatic and geographic conditions. Although this butterfly is common in my study area, and its larval food plant was abundant along the forest margins, little is known about the population ecology of this and related species (DeVries 1987, Caldas 1994).

STUDY SITE AND METHODS

The study area consisted of a semideciduous subtropical moist forest in successional mosaic, left undisturbed for the past 12 years. Along the central 1,160 m trail of the 2.5 km² Reserva Mata de Santa Genebra, Campinas, São Paulo state, Brazil (22°54'S and 47°05'W, elevation 650m), I marked 186 individuals of *Croton floribundus* (Euphorbiaceae), the main larval food plant of *A. ryphea*, with numbered plastic tags. Plants more than 2 m high were not included in the study because of difficulty in examining the higher leaves. Observations on larvae started in November 1988 and observations on eggs started in November 1990; both continued until May 1991. Census information on adults was difficult to obtain. Trapping within the reserve was not very successful (insufficient number of individuals for population studies), and capture with an aerial net was not practical because adults usually fly high in the canopy for most of the time, and hence are very difficult to see. No

adults were observed within the reserve from June to November. Since adjoining forested areas have the same climatic pattern, with dry and wet seasons occurring at the same time of the year as in Campinas, adults would have to fly long distances in order to find suitable food plants to oviposit and remain reproductively active. Migration does not seem to occur in Charaxinae butterflies (Baker 1969), and no individuals were captured in traps located around the reserve. A likely explanation for the absence of adults is reproductive diapause, as observed in *Anaea andria* populations (Riley 1988). This diapause was observed by the author when a reduction in the number of females occurred, toward the end of the reproductive season, when the whole population was declining. Further studies are needed to clarify whether the apparent absence of adults from June to November is due to a low number of reproductive diapausing females or to a complete absence of the species in the area.

The number of plants censused varied from year to year because of plant mortality during the dry season and recruitment during the rainy season. However, the total number of plants included in the study never deviated by more than 10% from the initial 186 marked in November 1988.

During each weekly census, all leaves of tagged plants were searched for larvae, and during 1990 and 1991 for eggs and larvae. Eventually censuses reached a 2-day interval, so that each individual's fate could be assessed more accurately. All larvae were individually identified by tying a numbered plastic band on the petiole of the host leaf, and, if more than one egg or larva were on the same leaf, the position and stage of each was noted. Eggs were identified by writing numbers next to them on the leaf with indelible ink.

This methodology allowed easy identification of parasitized larvae and eggs. Larvae attacked by *Bracon* sp. (Hymenoptera: Braconidae) could be recognized from the fourth instar by two characteristic features: 1) they became lethargic and stayed inside their rolled leaves, and 2) the leaf tube, which usually is clean inside, was covered with silk and accumulated debris. Eggs parasitized by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) changed color from translucent green to yellowish and finally to a metallic gray.

Because no adults or immatures of *A. ryphea* were found during August and September of 1988, 1989, and 1990, the biological year used for the analyses was from September of one year to August of the next.

Vertical (time-specific) life tables (see Table 1) were constructed for *A. ryphea* larvae for the seasons 1988/89 and 1990/91. The intermediate season (1989/90) was not analyzed by this method because of sampling

problems, namely a gap in data because larvae were not followed. Life tables provide an easy way of displaying mortality in different age intervals for a constantly reproductive population. It shows the age interval (X), the total number of individuals belonging to that age interval found in the field (N), the number of individuals that "die" in a certain age interval (meaning do not reach the next age interval), and the most probable causes for the deaths in each age interval. After calculating the log of each N, the difference between logs of successive N's is called the "killing power" (k-value) of the mortality factor(s) acting in that age interval. Vertical life tables are constructed from the age distribution in the field for each census, as opposed to horizontal (age specific) life tables, where a cohort is marked and followed. From direct observations in the field and from inferences based on the pattern of larval disappearance, the probable main causes of mortality throughout the season were listed for each age class.

The life tables built for each month were then used for a Key-factor analysis (Morris 1959, Varley and Gradwell 1960), a method meant to show which factor would be responsible for changes in numbers of individuals between generations in that population. This is not necessarily the factor that kills most (has higher "killing power"), but the one whose "killing power" correlates more with the overall mortality of the population (the total value for k).

Meteorological data on monthly temperature, rainfall, and relative humidity were obtained from FEAGRI/UNICAMP meteorological station, approximately 3 km from the Reserve. All data obtained from *A. ryphea* in the field and subsequent calculations (estimates of mortality, percent parasitism) were analyzed in relation to the meteorological data using correlation analysis and multiple regression (Sokal & Rohlf 1981). With these procedures I tried to identify possible climatic and weather factors associated with changes in population density.

RESULTS AND DISCUSSION

In each of the three years of study, oviposition started in November/December, reaching levels considered suitable for my study ($n > 5$ new eggs and larvae per census) in January. Although strongly variable, maximum recruitment happened between February and April. After that, oviposition declined more or less rapidly before winter started. The oviposition pattern each year did not provide evidence of pulses that could be identified as generations.

There was dramatic variation in the number of larvae censused in each year of study (Fig. 1). In the first year (September 1988 to August 1989), the population increased abruptly in January, and de-

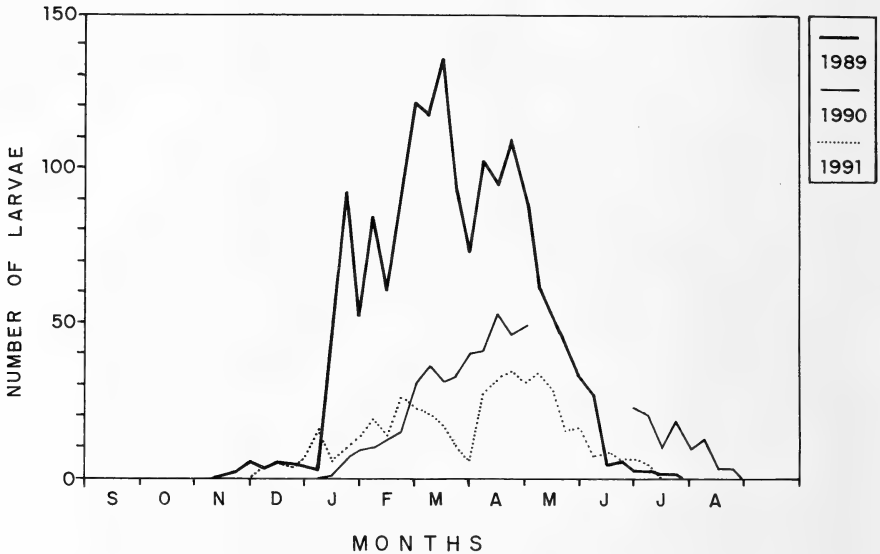


FIG. 1. Total number of *Anaea ryphea* larvae censused at Campinas during the three years of study.

creased abruptly in May. The abundance peak was in late February/early March. In the second year (September 1989 to August 1990) population growth was gradual from January to April and so was the decrease, from late June until September, with a peak in April. During the third year (September 1990 to June 1991), increase was still more gradual. The highest densities were found in April and May.

The beginning of the rainy season affects many tropical species' abundance (Wolda 1983). For *A. ryphea* this could be the best time for a populational increase, because the host plant population not only grows during this period, but also the individuals leaf out. But strong rains are not favorable to the survivorship of *A. ryphea* younger immatures, which can be mechanically dislodged from the leaves by the force of the raindrops. Strong rains might also affect oviposition behavior, although this was not measured. In this sense, an *A. ryphea* population might be adversely impacted during the beginning of the rainy season and prevented from reaching higher density levels. Perhaps the observed variations in population growth in this study could be

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FIG. 2. Climographs for the three years of study at Campinas.

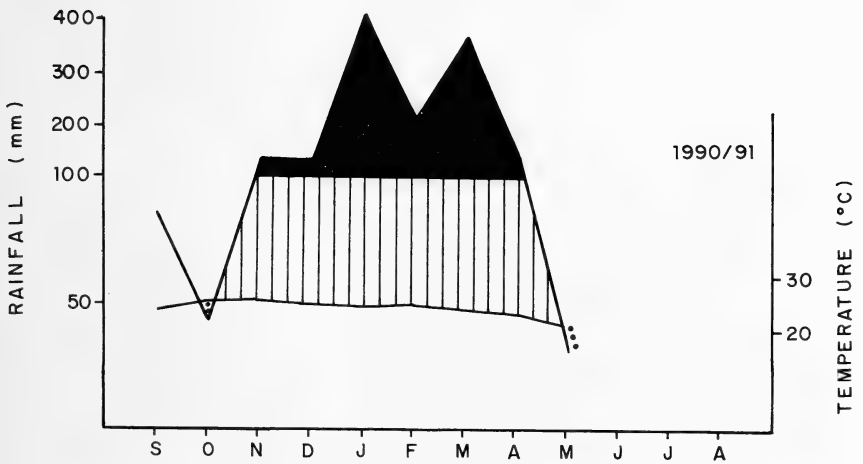
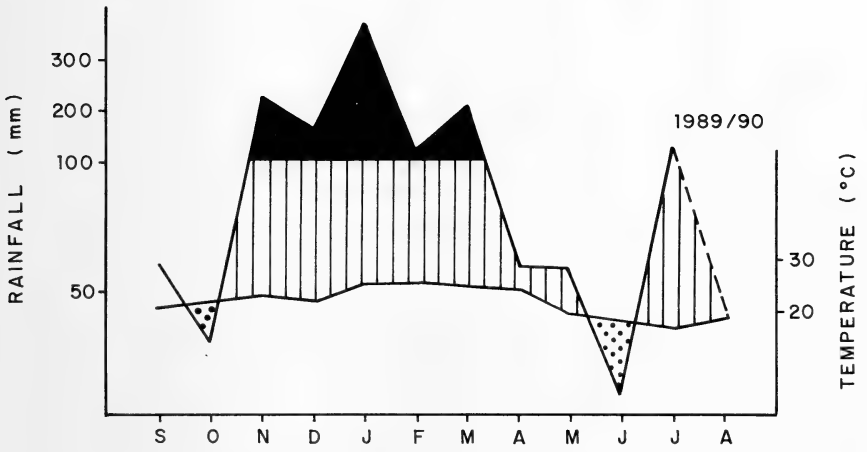
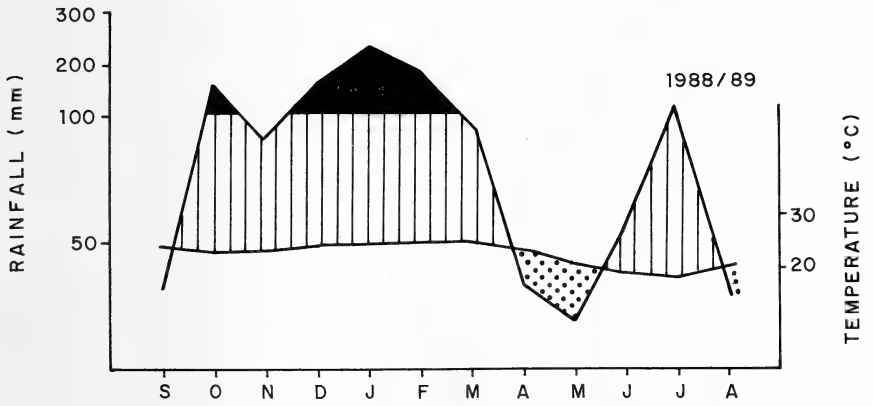


TABLE 1. Vertical life tables for *Anaea ryphea* for the three years of study at Campinas (* = total value for k ; 1S, first instar; 2S, second instar; etc.).

X	Total (N)	"Dead"	Mortality facator	$\log N_x$	k_x
Year 1988/89					
1S	1161			3.065	
2S	598	563	Rain(+)/Predation	2.777	0.288
3S	308	290	Rain(-)/Predation	2.489	0.288
4S	301	7	Virus (?)	2.479	0.010
5S	273	28	Parasitism	2.436	0.043
					0.629*
Year 1989/90					
1S	184			2.265	
2S	74	110	Rain(+)/Predation	1.869	0.396
3S	66	8	Rain(-)/Predation	1.819	0.050
4S	63	3	Virus (?)	1.799	0.020
5S	58	5	Parasitism	1.763	0.036
					0.502*
Year 1990/91					
1S	154			2.187	
2S	93	61	Rain(+)/Predation	1.968	0.219
3S	87	6	Rain(-)/Predation	1.939	0.029
4S	78	9	Virus (?)	1.892	0.047
5S	36	42	Parasitism	1.556	0.336
					0.631*

related to the rainfall pattern of each year, which follow. In the first year, the rainy season started in mid-September (Fig. 2), reaching a maximum of 229.2 mm in January 1988; the dry season started between March and April 1989, and lasted for 2 months. The following year was different: it was dry until mid-October 1989, then a very humid period (maximum 373.1 mm in January 1990) persisted until May. The third year was similar to the second: a dry period somewhat milder in September and October 1990, then a strong rainy period (maximum 418.3 in January 1991) until April. The fact that the rainy season started earlier and was of lower intensity in 1988 could have allowed a higher recruitment of *A. ryphea* in 1988/1989, leading to a population peak higher than during the other two years, when it rained heavily during spring and recruitment levels were low. Indeed, correlation coefficients between monthly k -values and rainfall proved significant both in 1989 and 1991 ($r^2=0.79$ and 0.88 respectively, $p<0.05$), but this hypothesis needs further examination during shorter intervals of time, in order to assess the full impact of rain on a daily basis.

Highest mortality was recorded during the first stadium, as shown by vertical life tables over the 3 years of study (Table 1). Recruitment pattern in first instar larvae of *A. ryphea*, which is the percent of

TABLE 2. K -values for *Anaea ryphea* life tables constructed at Campinas. n = number of individuals marked; k_x = k -value for instar x ; T , total k -value for the month.

	Jan 89 n = 144	Feb 89 n = 371	Mar 89 n = 445	Apr 89 n = 167	May 89 n = 34
k_1	0.266	0.382	0.266	0.214	0.171
k_2	0.194	0.396	0.308	0.197	0.282
k_3	0.066	0.102	0.011	0	0
k_4	0.520	0.430	0	0	0
T	1.046	1.310	0.585	0.411	0.453
	Jan 91 n = 45	Feb 91 n = 23	Mar 91 n = 53	Apr 91 n = 35	May 91 n < 5
k_1	0.423	—	0.278	0.266	
k_2	0.23	0.158	0.031	0	
k_3	0	0.090	0	0	
k_4	0	0.336	0.375	0.278	
T	0.654	0.584	0.684	0.544	

individuals in this instar that survive to the next one, is in part dependent on the abundance of females and their oviposition behavior in the study area, which were not fully assessed. Nevertheless, their level of mortality was high. Survivorship of second and later instars was generally high (90% or higher per instar), but in 1988/89 second instar individuals had a 48.5% mortality, and in 1990/91 53.7% of fourth instar larvae died. There was no record of high mortality for this instar in prior years of the study. In 1991, first instar mortality was highest in January but fourth instar parasitism was the dominant source of mortality in February and March. Fifth instar could not be evaluated because individuals abandoned the foodplant to pupate.

Monthly life tables show higher mortality in the rainy period of January and February 1989, followed by relatively high survivorship between March and May (Table 2). The decrease in mortality was due to a strong reduction in parasitism of fourth instar larvae together with increased survivorship of first and second instars, the latter apparently related to the reduction of rainfall during the same period. Pollard (1979) found that, in four years of study of the white admiral in England, weather conditions were the main cause of population fluctuations between years. When weather conditions became unfavorable, larvae took a longer time to complete development and were exposed to predators for a longer period of time. Thus, the combination of adverse weather and increased exposure to predation led to striking differences in population sizes between years.

Key-factor analysis for monthly life tables showed that first and third instars were the stages most responsible for variation in abundance between months for the years of 1989 and 1991 respectively (Table 3).

TABLE 3. Key-factor analysis through coefficient of variation using vertical monthly life tables in different years.

Age	Average number of individuals per census	Coefficient of variation per census
a. 1989		
1S	232.20	73%
2S	119.62	69%
3S	61.66	62%
4S	57.00	66%
5S	44.80	90%
b. 1991		
1S	39.00	33%
2S	21.75	22%
3S	17.75	37%
4S	18.75	29%
5S	8.50	28%

It is important to note that in vertical life tables (counting individuals in the same stadium at certain time intervals), the same larva may be counted more than once. That is, because parasitism and disease tend to lengthen the duration of the affected instar, attacked individuals are likely to remain in the same instar (before they died) longer than "normal" larvae, and may be responsible for an underestimation of the mortality for those instars in sequential counts, which were then gathered within each month. Because I knew which larvae had been parasitized, they could be excluded from counts made after the average time of duration for that stadium. This means that there is no underestimation of mortality for any instar.

In each of the 3 years of study there was a different oviposition pattern, probably due to variation in the abundance of females during the season and to meteorological conditions. The correlation coefficient between number of new eggs and relative humidity of the night before censuses in the third year of study was 0.74 ($r^2=0.55$, significant for $p<0.05$), suggesting that relative humidity positively influences oviposition. It has been shown that, for some lepidopteran species, certain environmental conditions trigger or enhance oviposition. The number of eggs of the pierid *Leptidea sinapis* found in the field in a 8-year study was highly correlated with the maximum temperature of that day ($r = 0.73$) (Warren et al. 1986), and for *Anthocaris cardamines* the number of eggs laid is dependent on the insolation during the oviposition period (Courtney & Duggan 1983). Whether relative humidity acts as a cue or just influences oviposition rates cannot be assessed with the present data.

Censuses enabled me to calculate the percentages of parasitized,

TABLE 4. *Anaea ryphea* egg survivorship at Campinas in 1990/91 (actual values; * = total k -value for eggs).

Total (N)	"Dead"	Mortality factor	log N	k
653	351	disappearing	2.814	
302	169	parasitized	2.480	0.334
133	31	nonfertile	2.123	0.357
102			2.008	0.115
				0.806*

disappeared, and non-eclosing eggs (Table 4). The percentage of disappeared eggs (53.7%) was almost the same as the incidence of parasitism in the remaining ones (55.9%), an unusually high level for Lepidoptera. In most cases, parasitism was under 20%, predation being the main mortality factor. Hassel et al. (1989) found only 3 cases in 28 Lepidoptera studies where egg parasitism was considered an important mortality source, acting in a density-dependent way. But even in those cases its impact was low, as opposed to my study where it is almost as high as predation, the main mortality factor.

Competition is seldom considered a mortality factor in life table studies. Interspecific competition is rarely seen among phytophagous insects in the field, at least directly. *Hypna clytemnestra* (Lepidoptera: Nymphalidae) could be considered a potential competitor when it co-occurs with *A. ryphea* (Caldas 1991, 1994). Observations on asymmetric competition between these two species indicate a low-intensity interaction, because the *H. clytemnestra* population was never higher than 10% of the *A. ryphea* population in the area (Caldas 1991). Yamamoto (1981) found that the co-occurrence of two pierid species on the same foodplant affects the number of eggs laid on these plants and the larval survivorship.

The population of *A. ryphea* at Campinas seems to be well below the limits imposed by availability of its larval foodplant, as not a single defoliated plant was found. Larval feeding damage by *A. ryphea*, although not measured or tested, is not thought to adversely affect the food plants in a significant way. Larvae do not feed on apical parts of the plants (Caldas 1994), and therefore have little direct impact on plant growth or reproduction. Also, the fact that females tend to oviposit on leaves free of other eggs or larvae (Caldas 1994), together with high larval mortality, results in reduced herbivore impact on the plants.

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DESCRIPTION OF THE EARLY STAGES OF *PODOTRICHA TELESIPHE*
(NYMPHALIDAE: HELICONIINAE)

Additional key words: *Passiflora*, Ecuador, instar duration, oviposition behavior.

The genus *Podotricha* Michener includes two species that are found in mid-elevations in the Andes: *P. euchroia* (Doubleday) in Colombia and Ecuador (Vane-Wright, Ackery & Smiles 1975), and *P. telesiphe* (Hewitson) in Ecuador, Peru, and Bolivia (Vane-Wright, Ackery & Smiles 1975, Brown 1979). The adults of *P. telesiphe* have mimetic affinities with the distantly related *Heliconius telesiphe* Doubleday, which is aposematic on both surfaces of the wings. Unlike *H. telesiphe*, *P. telesiphe* adults have a cryptic, mottled brown pattern on the under surface of the wings (for more information on mimicry and a color plate of the adults, see Vane-Wright, Ackery & Smiles 1975). Neither species of *Podotricha* has received much attention from butterfly ecologists, and the life history of *P. euchroia* remains unknown.

This study provides descriptions of the egg, larva, and pupa of *Podotricha telesiphe* collected in August–September 1992 in Ecuador. Observations on instar duration, leaf damage by larvae, and oviposition behavior are presented. Positive identification of the host plant is not available, although vegetative parts resemble those of *Passiflora montana* Holm-Nielsen & Lawesson, *P. reticulata* Mast., and *P. sprucei* Mast. (S. Knapp per. comm.). Live specimens of the host plant are being maintained in greenhouses at the University of Texas, Austin.

The study site is located in Baeza, Napo, Ecuador (1800 m), on the bank of the Río Quijos. The forest is patchy, interspersed with pasture. Six species of *Passiflora* were found in the immediate vicinity; eggs were found on only one of these. During the study, ambient temperature ranged from 16°C at 0900 h and 1400 h to a maximum of 20°C at 1200 h. September 1992 was rainy and frequently overcast, with only occasional sunlight. Butterflies were observed flying at the edge of the forest, where both males and females were captured, as well as crossing open fields.

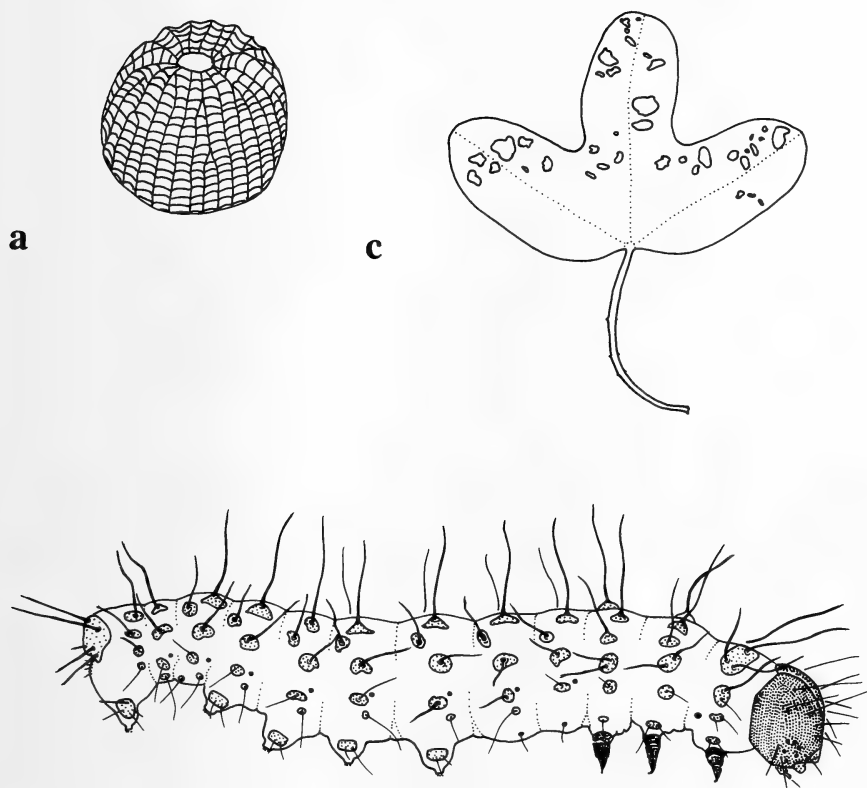
Females were observed on several occasions searching for host plants in areas of high humidity where the *Passiflora* host plants occur. However, only one oviposition event was observed, on 19 September 1992, at 1400 h, during overcast skies following a period of light rain. The female found the host plant on a trail (near the “camino antiguo a Borja”) at the edge of a patch of forest. She flew around the plant repeatedly, inspecting leaves from ground level to a height of 4 to 5 m, alighting both on the surrounding plants and on the host plant. During a 12-minute period of observation, the female alighted on the host plant nine times, apparently laid four eggs, and departed. About five minutes later, presumably the same female (based on wing condition and its ability to immediately locate the plant) returned to the site, inspected the plant again, laid one egg on a branch that was not used during the first observation period, and immediately left.

The following descriptions are based on eggs and larvae collected in the field and reared at ambient temperature (16–20°C) in plastic containers. Examples of the early stages were preserved in 70% ethanol.

Egg (Fig. 1a). Creamy white, adorned with vertical and horizontal ridges; 0.8 mm x 0.8 mm (n = 5). Duration of egg stage approximately 10 days.

Eggs are laid singly, usually on the underside of mature leaves, but occasionally on the upperside, from ground level to over 4 m high. More than one egg was commonly found on the same leaf. The damage produced by larval feeding is characterized by holes in the leaf surface away from the edges (Fig. 1c). The larvae typically rest under the leaf.

Larva (Fig. 1b). *First instar*. Head dark brown; body translucent white when newly hatched, later developing milky white patches and brown spots (especially noticeable in



b

FIG. 1. Early stages of *Podotricha telesiphe* and typical leaf damage. A, Egg, drawn from a specimen preserved in 70% ethanol, approximately 1 month after it was collected; B, First instar larva, drawn from a specimen preserved in 70% ethanol, approximately 1 month after it was collected; C, Leaf damage produced by first and second instar larvae, drawn from a pressed leaf.

dorsum of abdominal segments 3, 5 and 7); body setae black, long, thick, linear to slightly bowed, sharply pointed. Duration of first instar 11–14 days ($n = 2$). *Second instar*. Head black, with scoli approximately one-third the length of head; body white, spotted with black; body scoli thick, adorned with black spinules; dorsal scoli entirely black, approximately one-half the length of head; subdorsal scoli black, approximately the same length as dorsal scoli; lateral scoli lighter in color, approximately the same length as dorsal scoli. Duration of second instar 5 days ($n = 2$). *Third instar*. Head mostly black, adfrontal region gray, gray spot on apex on both epicrania posterior from the insertion of the head scoli; head scoli slightly longer than head; body white with numerous black spots; yellow spot at base of dorsal scoli; body with faint yellow lateral line; dorsal scoli black with black spinules, yellow at base, except on segment 10, where dorsal scoli are white with black tips and white spinules; dorsal scoli approximately 1.25 times the length of head; subdorsal scoli black, slightly shorter than dorsal scoli; lateral scoli white, approximately



FIG. 2. Fifth instar larva of *Podotricha telesiphe*, drawn from a specimen preserved in 70% ethanol, approximately 1 month after it was collected. [Note that there is a discrepancy in the length of the head scoli between the written description (accurate) and the figure, which is due to the three-dimensional structure of the specimen.]

two-thirds the length of dorsal scoli; anal cap white. Duration of third instar 7–9 days ($n = 5$). *Fourth instar*. Same as third instar, except yellow areas more strongly developed on dorsum and sides of body; lateral scoli white with black tips. Duration of fourth instar 8–9 days ($n = 5$). *Fifth instar* (Fig. 2). Head creamy white; head scoli and setae black, approximately 1.5 times the length of head; dark ocular area; body white with numerous black spots, large yellow spots at base of dorsal scoli, body with well-developed yellow lateral line; basal one-fourth of dorsal body scoli yellow, distal three-fourths black, dorsal scoli approximately 1.3 times the length of head; subdorsal scoli black, white or yellow at base, approximately three-fourths the length of dorsal scoli; lateral scoli generally black, approximately two-thirds the length of dorsal scoli; anal cap white; ventral side of thoracic segments, A1–2, and A7–9 black. Two or three days before pupation the white areas of the body become faint blue. Duration of fifth instar 9–10 days ($n = 3$).

Pupa (Fig. 3). Light brown, mottled with white; white ventral line on A5–7; paired gold spots on A1; head ornaments approximately 1.3 times the length of head, round at tip, with three ridges that reach the tip; thick, round flanges on A3, flanges less developed on A4–7, knobbed on A6–7; cremaster pointed, with small round crown projecting ventrally. Duration of pupal stage 16 days ($n = 2$).

Brown (1981) presents abbreviated information on the morphology of the egg, fifth instar larva, and pupa of *P. telesiphe* based on his observations and those of L. E. Gilbert of a sample of eggs and larvae collected, reared, and photographed by Gilbert in Pedro Ruiz, Amazonas, Peru, in 1975. Unfortunately, the only larva reaching maturity produced a deformed pupa that did not develop into an adult (Gilbert pers. comm.). A comparison of the color slides of the fifth instar larva taken by Gilbert with material I collected in Ecuador confirms that the photographs are of a *Podotricha* larva. *Podotricha euchrota* is not found in Peru (K.S. Brown pers. comm., G. Lamas pers. comm.) suggesting that the identification of the specimens described by Brown (1981) is correct. There are a few differences between the Peruvian sample (Brown 1981 and color slides of Gilbert) and those described in this study. The egg is described as 1.0 mm in height, 0.8 mm in diameter, and yellow-white by Brown (1981: Table 1). In contrast, eggs collected in Baeza, Ecuador were 0.8 in height, 0.8 mm in diameter, and white. The description of the fifth instar presented by Brown (1981), based on the color photograph by Gilbert, includes the following: background coloration green-white; yellow strips; black spots; black, white,

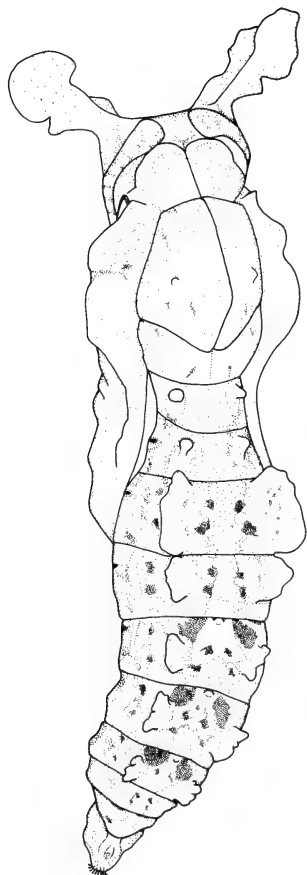


FIG. 3. Pupa of *Podotricha telesiphe*, drawn from a specimen preserved in 70% ethanol, approximately 1 month after it was collected.

yellow scoli; yellow head. However, a closer examination of the photograph by Gilbert indicates the following: (1) bluish background coloration, which is observed before pupation in Ecuadorian samples; (2) completely black dorsal spines inserted in the center of a yellow spot in the body, while the spines of the Ecuadorian larvae differed only in that they were yellow at the base; and (3) head white (not yellow as described by Brown), with a dark blotch below the horns at the edge of the epicrania, which is lacking in the Ecuadorian samples. The general color pattern is similar and the larvae most likely represent the two subspecies: *P. telesiphe telesiphe* (Peru) and *P. telesiphe tithraustes* (Ecuador). The description of the pupa given by Brown (1981) reads only "non-*Heliconius*." Both the Peruvian and the Ecuadorian larvae were found on *Passiflora* with trilobed leaves. However, the leaf shape of the two plants differ in that the leaves of the Peruvian *Passiflora* has longer lobes than that of the Ecuadorian one.

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BERINGIAN TORTRICIDAE: A NEW SYNONYMY IN
EPIBLEMA AND A RECOUNT OF
HOLARCTIC SPECIES

Additional key words: *Epiblema arctica*, *E. simplonianum*, nearctic, palearctic.

Beringia consists of Alaskan, Yukonian, and Siberian lands next to the Bering and Chukchi seas. Its east and west boundaries are inexact, but it includes the present sea floor, which emerged several times as a land bridge during Pleistocene time (Hopkins et al. 1982). Today, high proportions of Beringian biota are represented on both sides of the Bering Straits. Two examples are plants and Noctuidae: 57 percent of Beringian plants are holarctic (Matthews 1982), and 26 percent of Beringian noctuids are holarctic (Lafontaine & Wood 1988).

Kuznetsov and Mikkola (1991) recently summarized Beringian Tortricidae collected on the Siberian side. They reported 66 species in all, of which 39 percent were counted as holarctic. Some Beringian Tortricidae have been described on each side of the Straits under different names. I report one new synonymy of this kind here as well as five other species whose holarctic occurrence was not included in the above count.

Epiblema simplonianum (Duponchel) is among the many Tortricidae reported for the first time from Beringia by Kuznetsov and Mikkola (1991). This taxon was said to be a transpalearctic arctoalpine species (type locality nr. Simplon, Switzerland). As the lone Beringian *Epiblema*, it begged comparison with *E. arctica* Miller, previously the lone arctic *Epiblema* (type locality Anaktuvuk Pass, Alaska). I found that illustrations of *E. arctica* wings and genitalia (Miller 1985a) matched those of *E. simplonianum* (Kuznetsov 1987). Further comparison of male and female Alaskan and Yukonian *E. arctica* specimens with Siberian, Finnish, and Swedish *E. simplonianum* specimens confirmed that both taxa are the same morphospecies. These results are summarized as follows:

Epiblema simploniana (Duponchel)

Carpocapsa simploniana Duponchel 1835:259.

Epiblema simploniana; Obraztsov 1965:380, Kuznetsov 1987:741.

Epiblema simploniana; Kuznetsov and Mikkola 1991.

Epiblema arctica Miller 1985a, Brown and Powell 1991. **New Synonymy.**

A more extensive nomenclatural review for the palearctic region can be found in Obraztsov (1965). Among specimens examined in this study and listed below are previously undetermined ones that extend the known nearctic distribution of *E. simploniana* beyond Alaska to Yukon Territory.

***Epiblema* specimens examined.** ALASKA: Eagle Summit, 65 mi [105 km] SW Circle, 2 July 1979, [P. A.] Opler & [J. A.] Powell, female genit. prep. WEM 298843, *Epiblema arctica* Miller PARATYPE, forewing length (FL) 7.5 mm; same data as preceding except male genit. prep. WEM 298842, FL 7.5 mm, *Epiblema arctica* Miller PARATYPE; 4 mi [6 km] N Cantwell, 2000–2200 ft [610–670 m], 27 June 1979, P. Opler, J. Powell, male genit. prep. JAP 4460, *Epiblema arctica* Miller PARATYPE, FL 9.0 mm (Essig Museum of Entomology, University of California, Berkeley [UCB]). FINLAND [Lapland]: Saana [mountain], 10 July 1936, coll. E. Lankiala, female genit. prep. WEM 214941, FL 8.0 mm, Kilpisjärvi, 10 July 1938, coll. Lingonblad, male genit. prep. WEM 214922, FL 8.0 mm; all above in University of Minnesota Entomology Museum, St. Paul (UMEM), except where noted otherwise. RUSSIA [Siberia]: Chukchi Peninsula, 64° 55' N, 172° 30' W, 45 km N Provideniya, Pestsovaya Riv. valley, 11 July 1991, K. Mikkola coll., male genit. prep. WEM 214944, *Epiblema simploniana* Dup., det. V. Kuznetsov, FL 6.0 mm. [SWEDEN:] Sarek [mountain], Poppius, male genit. prep. WEM 214945, FL 7.5 mm. CANADA: Yukon Terr., 65° 06' N, 138° 15' W, Ogilvie Mts., 1050 m, Dempster Hwy., km 155, 7 April 1985, K. Mikkola, male, FL 8.0 mm; same data as preceding except male genit. prep. WEM 214943, FL 9.5 mm; all in Zoological Museum Helsinki, Finland (ZMH).

Additional holarctic Beringian species. Five species reported from Siberian Beringia by Kuznetsov and Mikkola (1991) that are actually holarctic went uncounted as such by them. These species are as follows: (1) *Olethrutes metallica* (Hübner) (= *O. murina* [Packard]), *O. puncticostana major* [Walsingham], whose known nearctic occurrence includes British Columbia, Alberta, Colorado, and Labrador (Miller 1985b); (2) *O. obsoletana* (Zetterstedt) (= *O. kennethana* McDunnough), known in the nearctic from Alaska, Alberta, and Northwest Territories (Great Bear Lake) (Miller 1985b); (3) *Ancylis geminana* (Donovan) (including *A. diminutana* [Haworth], a widely presumed junior synonym), known to be transnearctic (Bradley et al. 1979, Heinrich 1923, Kuznetsov 1987); (4) *Epinotia cruciana* (Linnaeus), known to be transnearctic (Brown 1980, Kuznetsov 1987); (5) *Notocelia cynosbatella* (Linnaeus), known from British Columbia. Apparently the last-named species was introduced accidentally into the nearctic (Mutuura 1980), but the preceding four undoubtedly are natively holarctic. Of the above five senior synonyms, only *Epinotia cruciana* was known to be holarctic in time to be included in the nearctic check list of Lepidoptera (Powell 1983).

The six species discussed here raise the holarctic percentage of Beringian Tortricidae from 39 to 48. It seems likely that a collecting effort in nearctic Beringia as comprehensive as that of Kuznetsov and Mikkola (1991) in palearctic Beringia would disclose both more Beringian and more holarctic Tortricidae.

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DONATION OF THE AUBURN E. BROWER COLLECTION TO THE
SMITHSONIAN INSTITUTION

Additional key words: *Catocala*, Maine.

Acquisition of the Auburn E. Brower Collection of insects by the Smithsonian Institution has now been completed with the recent transfer of the last portion of the collection, consisting mostly of North American *Catocala* (Noctuidae). Since 1981, collections manager Gary Hevel, sometimes assisted by museum specialist William Rowe, has transported a total of 130,104 miscellaneous arthropods (including 10 spiders) in five separate trips from A. E. Brower's home in Augusta, Maine to Washington, D.C. The collection had been stored in a variety of containers that filled three separate rooms in Brower's home. The Brower Collection consists of a variety of arthropod orders (see Table 1), but is exceptional in its representation of Lepidoptera (115,282 specimens). The collection is clearly the most complete survey of the Lepidoptera ever assembled from the state of Maine.

Throughout his career, Brower's dominant interest in entomology was field biology. Brower early began his lifelong passion of fieldwork in the Ozarks region of Missouri. The results of these efforts formed the basis of some of his earliest entomological papers (Brower 1925, 1930). He received a B.S. degree in Education and an A.B. degree in Science from the Southwest Missouri State College in Springfield, Missouri in 1927. Following a short period of teaching (1927-1928), he continued his studies at Cornell University, receiving a Ph.D. degree in Entomology in 1932. His thesis was on the biology of North American *Catocala*, a genus that remained a special interest throughout his long career. The emphasis on *Catocala*, or "cats" as Auburn fondly referred to them, is particularly evident in his collection, with approximately 21,900 specimens of that genus represented.

Brower's work in Maine began with his employment as director of the Bar Harbor Field Laboratory in May 1931. Early in his career he also assisted in a few major insect surveys, notably with William Procter on the insect section of the Mt. Desert Region Survey and Donald Farquar with his list of the Lepidoptera of New England.

The largest survey project ever engaged by Brower began in April 1941 when he was charged with laboratory responsibilities of the Forest Insect Survey (Brower 1953). Assisted by several Forest Service personnel and numerous volunteers, Brower began to receive more than 2,000 lots each year from various parts of the state (Nash et al., 1971). In addition to the Forest Insect Survey, Brower began in 1943 to process collections from as many as 25 light traps each year. To assist collaborators in the field, Brower would provide collecting boxes with instructions for collecting and preserving specimens written inside the lid. After the material was processed in his laboratory, he would then identify

TABLE 1. Principal composition of Brower collection.

Araneae	10	Mecoptera	125
Coleoptera	5634	Neuroptera	3
Dermaptera	2	Odonata	118
Diptera	2252	Orthoptera	1656
Hemiptera	500	Plecoptera	862
Homoptera	307	Thysanoptera	110
Hymenoptera	3237	Trichoptera	6
Lepidoptera	115,282		
		Total	130,104

each specimen as best he could. Often this involved spending his vacations at the National Museum of Natural History and other museums (Brower 1983). Brower's efforts over more than 50 years to survey the insects for the state of Maine aptly culminated with the publication of *A List of the Lepidoptera of Maine* (Brower 1974, 1983, 1984). The collection records of 2,987 species are summarized in those reports.

Auburn Brower's lifelong fascination with entomology finally ended on 8 April 1994, when he passed away at the age of 93. He is survived by his devoted wife, Lurana, who ably assisted her husband over the years in the rearing, labelling, and general curation of their impressive collection of "cats" and related creatures. The Smithsonian Institution is grateful to the Brower family for this valuable donation. We are indebted to Auburn's son, Dr. John H. Brower, a research entomologist with the U.S. Grain Marketing Research Laboratory, Manhattan, Kansas, for much of the biographical information used in this report.

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OBITUARY

FRED T. THORNE (1909-1994)

The world of lepidopterists, especially those interested in the butterflies of southwestern North America, lost a great friend and accomplished lepidopterist in the passing of Fred T. Thorne on 29 April 1994. At the age of 84, he was a charter and sustaining member of the Lepidopterists' Society, and served in key positions in that Society as well as many other professional and amateur entomological groups.

Fred Thorne was born on 25 June 1909 in Casper, Wyoming. He moved to San Diego County in southern California as a youngster, eventually marrying Dorothy Mary Argo in 1931. They established their residence on a hill overlooking El Cajon, a suburb east of San Diego. Fred attended San Diego State College from 1937 to 1941, but did not complete the degree program. He then worked from 1946-1964 as an entomologist and Deputy Agricultural Commissioner for San Diego County. He later served as Museum Entomologist at the San Diego Natural History Museum from 1972-1975 following the retirement of Charles F. Harbison.

Fred joined the Lepidopterists' Society as a charter member in 1947 and remained a sustaining member throughout his life. In 1958, he became the First Vice President of the Society, and served as a member of the Executive Council during 1967-1969. His most notable contribution to the Society was his service on the Journal's Editorial Committee from 1957-1969. He was Associate Editor from 1957 to 1966 and developed one of the most popular sections of the Journal for amateur and professionals alike, a quarterly feature called "Especially for Collectors." He actively sought contributions from those who had made interesting collecting trips within the United States and abroad, and also developed articles featuring life history and behavioral notes, for this section. Fred also served as the Zone One Season Summary Coordinator from 1961 through 1968. He was one of the key activists on the Program Committees for the Pacific Slope Section of the Lepidopterists' Society, planning annual meeting programs for 1954, 1955, 1956, 1960, 1965, and 1969. He also served on the Program Committee for the national Society meetings in 1953 and 1962. In addition to his activities in the Lepidopterists' Society, Fred was active in the Entomological Society of America, the Lepidoptera Research Foundation, the Lorquin Entomological Society (in Los Angeles), and Los Entomologos (in San Diego), and was elected a Fellow of the San Diego Natural History Museum. Fred's extensive collection of over 9,000 butterflies was donated to the museum's Entomology Department in



FIGS. 1-3. Fred Thorne. 1, San Diego, California, 1928; 2, Grand Canyon, Arizona, 1935; 3, El Cajon, California, 1971.

1973, and the San Diego Society of Natural History unanimously elected him a patron of the museum in 1976.

Fred is best remembered by his multitude of friends for his warm and friendly personality. He invited many younger collectors to go with him on field trips over the years, and one always learned an amazing amount from such experiences in the desert or mountains of San Diego

County. He published a number of papers on southern California species, but probably his most notable contribution was on the distribution and biology of San Diego's endemic Hermes' copper, *Lycaena hermes* (published in 1963 in the *Journal of Research on the Lepidoptera* 2:143-150). He also published notable papers on the Catalina Island endemic hairstreak, *Strymon avalona*, and the small blue, *Philotiella speciosa* (Lycaenidae), in the Mojave Desert. He loved to rear Lepidoptera and gave a considerable amount of living material to John Adams Comstock for description in Comstock's life history papers. Fred's publications appeared in the *Bulletin of the Southern California Academy of Sciences*, *Journal of Research on the Lepidoptera*, *Journal of the Lepidopterists' Society*, *Los Entomologos*, *The Mid-Continent Lepidoptera Series*, and in various popular articles. Fred also was the contributor of accounts of several lycaenid genera in William Howe's classic *Butterflies of North America*.

Much of his careful work on life histories of *Euphydryas editha quino* (Nymphalidae) populations in San Diego County, as well as *Papilio* species (Papilionidae) and the giant skippers (Megathymidae), *Megathymus* and *Agathymus*, in the desert areas of southern California and Baja California remains unpublished, although Charles Harbison used much of Thorne's material to describe two new species of *Agathymus* from Baja California, *A. stephensi* and *A. comstocki*. Fred's interests in, and rearing of, the genus *Mitoura* (Lycaenidae) led to the description of the patronym *Mitoura thornei*, endemic to Otay Mountain in southern San Diego County.

Wherever Fred is right now in the great hereafter, we can envision him pursuing diminutive orange-tips or blues across the desert floor and carefully showing his companions how to identify and handle specimens in the field. Back at the car, we can see him writing up his detailed field notes and showing us how to store material for proper curation later. And we can even expect to see in the mail, perhaps tomorrow, another handwritten letter from him thanking the recipient for sending an interesting note or article for the Field Collector section of the journal, perhaps with some gently-made corrections and suggested changes (which one would never dream of rejecting, because they seem so apt and gracefully suggested). Surely Fred Thorne's legacy lives on in the lives of such well-known western lepidopterists as Ray E. Stanford, Oakley Shields, John Brown, and many others who grew up in San Diego exposed to his help and guidance. He will be sorely missed.

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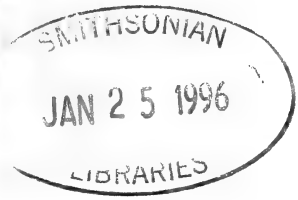
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Cover illustration: A favorite of Charles Remington's—the elm leaf butterfly (*Polygonia interrogationis* Fabr.) on elm in the "Elm City," New Haven, Connecticut, USA. Original line drawing by William Vars.

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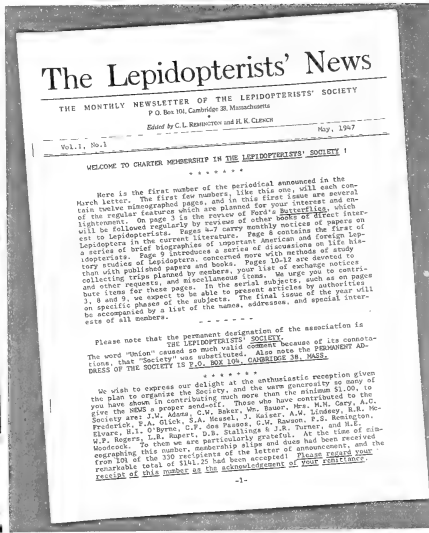
NOTULAE REMINGTONIO OBLATAE

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Over time, each scientific discipline passes through moments that alter its focus and course. One such defining moment for the study of butterflies and moths came in 1947, when the Lepidopterists' Society was hatched at Harvard University under the watchful tutelage of Charles Lee Remington and Harry Kendon Clench (the Society's home base moved shortly thereafter to Yale University, where Charles continued to shepherd the fledgling group through its early metamorphoses in the 1950s). Today, nearly half a century later, the Lepidopterists' Society still prospers even as some other similar organizations have waxed and waned. In no small part, the Society can trace its vitality to a long tradition of fostering collegial interaction among all segments of its membership. Harry and Charles both personified this commitment to "... facilitating the exchange of specimens and ideas by both the professional worker and the interested amateur ..." (from their letter of 24 March 1947 inaugurating the Lepidopterists's Union, as the Society was initially known).

The idea for a Remington issue of the *Journal of the Lepidopterists' Society* began to take shape early in 1992. At the time, I was in the midst of planning a mid-year bash in New Haven for Charles, who was retiring as Professor of Biology and Forestry & Environmental Studies, and Curator of Entomology at the Peabody Museum, after 44 years of service to Yale University. In that context, it seemed appropriate to acknowledge Charles' contributions to the Society via the *Journal*, as had been done posthumously for Harry in 1980. The authors who have contributed herein are all students of Charles' at one or another level, or several levels, and their papers stem from talks presented in an honorarial symposium at that 1992 event (they have been given



latitude to depart somewhat in style and substance from the straight and narrow).

In introducing this issue, I will omit a biography of Charles and the earliest history of the Society, as both are available elsewhere e.g., in the *Lepidopterists' Society Commemorative Volume (1945–1973)* and Issue 2, Volume 34 of the *Journal* for 1980. Rather, I would like to point briefly to a few aspects of Charles' persona that I feel have helped him contribute so richly to lepidopterology, and science in general. A foreshortened bibliography of Charles' principal scholarly publications can be found at the end.

I should make it clear from the outset that, although he is nominally and officially "retired," I would scarcely consider Charles to be "retiring" in even the remotest sense of the word. That label will never fit the man. As I write this, he is: completing a third year of developing and teaching a new and popular course on endangered species with Tim Clark at the Yale School of Forestry & Environmental Studies; preparing a book on lepidopteran conservation with Bob Pyle; inaugurating baseline arthropod sampling surveys in a new shoreline park that he helped to establish in the city of New Haven; assisting in the launch of the Connecticut Butterfly Atlas Project, a five-year effort to record and georeference the occurrence of the state's butterfly fauna; researching novel aspects of insect color vision with Gary Bernard at the Yale School of Medicine. . . . I'll stop there arbitrarily.

Take note of three themes interwoven in the paragraph above: (1) Charles habitually innovates and explores uncharted territory; (2) he has diverse and eclectic pursuits; and (3) he draws himself and others into synergistic collaboration. These characteristics, along with his broad base of acquired comparative biological knowledge (he is indeed one of those rare naturalists with a world perspective on most groups of living creatures), have for years enabled Charles to energize people of all stripes. In the lead article below, Ward Watt, one of Charles' first graduate students, defines, analyzes and discusses the importance of this "Remingtonian tradition" as an empowering paradigm for mentoring and conducting research. Evidence for Charles' success with this model can be seen in Table 1, which lists students who obtained their

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FIG. 1. Remingtonian reminiscences. Clockwise from top: a reunion in 1992 for Bob Pyle (left), Charles Remington (center), and Lincoln Brower (right); the mimeographed *News* of May 1947, first publication of the Lepidopterists' Society; adult *Celerio lineata* (Fabr.) and friends lined up in tribute; the poet, Robert Frost, absorbing a few pointers on hybridization theory from Charles in the collection rooms at the Peabody Museum of Natural History, Yale University. Photography courtesy of Paul and Sandy Russell, William Sacco, and Charles.

TABLE 1. Intellectual progeny of Charles Remington. In the first group, an asterisk indicates a partially completed Ph.D. degree. In the middle group, an asterisk indicates non-Ph.D. degrees (mostly Masters). In the last group, an asterisk indicates that a more advanced degree was also obtained subsequently (when known). The degrees were obtained primarily from the Biology (formerly Zoology) Department and the School of Forestry & Environmental Studies at Yale University. This list is derived from departmental records at Yale, and from Charles' files and recollections.

Individual	Subject
<i>Ph.D. degrees (Remington as principal advisor)</i>	
Shigeru A. Ae	Evolutionary genetics of <i>Colias</i>
Peter F. Bellinger	Soil fauna, Collembola
Denis E. Berube*	Insects and bird behavior
Barbara J. Hibbs (Blake)	Environmental physiology of ground squirrels
Jane Van Zandt Brower (Dingman)	Experimental analysis of mimetic butterflies
Lincoln P. Brower	Evolutionary biology of the <i>Papilio glaucus</i> group
William S. Brown*	Ecology of mountain goats
Donald S. Chambers*	Evolutionary biology of <i>Speyeria</i>
Frances S. Chew (Bryan)	Pierid butterfly relations with cruciferous plants
Christopher J. Durden	Roach paleoentomology
Lawrence F. Gall	Evolutionary ecology of <i>Catocala</i>
Edward L. Goldstein	Ecology of Thimble Island ants
John P. Kochmer*	Biochemical evolution in <i>Chautognathus</i>
Toni Lincks (Taylor)*	Sexual morphology in Lepidoptera
Lesley A. Morgan-Thompson	Pollinator ecology of milkweed beetles
Russell B. Miller	Evolutionary ecology of Colorado <i>Aquilegia</i>
Russell M. Norton*	Ecology of cave crickets
Charles G. Oliver	Geographic and genetic distance in Lepidoptera
Carolyn M. Osborne	Predation ecology of marine snails and crabs
Roger W. Pease, Jr.	Evolutionary genetics of <i>Utetheisa</i>
Robert M. Pyle	Lepidoptera conservation
William N. Ryerson*	Larval foodplant choice in <i>Manduca</i>
Ward B. Watt	Evolutionary genetics and physiology of <i>Colias</i>
Richard E. Wetzel	Ecology and movement in terrestrial arthropods in the Bahamas
Paul F. Whitehead*	Locomotorily physiology and genetics of <i>Cercopithecus</i> monkeys
Bruce A. Wilcox*	Conservation ecology of insects

TABLE 1. Continued.

Individual	Subject
<i>Ph.D. degrees (Remington on doctoral committee), and other graduate degrees</i>	
Carol A. Abruzzese*	Pitcher plant pollinators
Robin Absher	Molecular geography of <i>Lemur fulvus</i>
George D. Amato	Molecular biology of vertebrate conservation
Diane M. Beaudoin	Adaptive divergence of <i>Drosophila</i> behavior
Peter P. Blanchard*	Island entomofauna of Maine
Richard L. Borowsky	Size and growth rates in fish
Andrew Van Zandt Brower	Danaid butterfly systematics
Philip V. Brylski*	Biogeography of island owls
Alice Louise Bull	<i>Drosophila</i> embryology
Joan R. Burchenal*	Dragonfly naiad antennal morphology
Adalgisa Caccone (Powell)	Systematics and molecular genetics of cave crickets
Tchaw-ren Chen	Karyology of teleost fish
Terry L. Chester*	Experimental analysis of mantid predation
Raymond D. Clarke	Autecology of Fowler's toad
Marlene B. Cole*	Alien desert flora and <i>Welwitschia</i> in Namibia
W. Floyd Conner*	Territorial ecology of dragonflies
Matthew A. Cronin	Molecular systematics of deer
Dean R. Cummins	Troglobitic crayfish
David C. Culver	Cave Collembola
Change-feng Dai	Coral biology in southern Taiwan
Amy R. Dumas*	Nature interpretive education
Michael Gregonis*	Museum entomology, Lepidoptera
Melissa M. Grigione*	African and other manatees
Achyut Gyawali*	Natural history museum design for Nepal
Mark Harding*	Museum entomology, Coleoptera
Willard D. Hartman	Sponges of Long Island Sound
Daniel J. Howard	Evolutionary ecology of crickets
Jennifer A. Jacoby*	Nature preserve interpretive education
Michael S. Johnson	Stickleback fish molecular genetics
Charles J. Kara*	Mountain top African insects

TABLE 1. Continued.

Individual	Subject
Robert H. MacArthur	New England warbler niche ecology
Pamela H. Manice*	Neotropical fig insects
Frederick A. B. Myerson*	Human populations
Christopher D. Nagano*	Tiger beetle and Lepidoptera museology
Paul E. Olsen	Triassic fossil ecology
Eric J. Olson	Sphinx moth classification
Katherine J. Patey*	Coyote museology
Naomi E. Pierce	Ant-tended lycanid larval ecology
Stan P. Rachooin	Charles Darwin's embryology
V. Louise Roth	Gigantism and dwarfism in island vertebrates
Stephen I. Rothstein	Ecology of cowbird egg patterns
Kathleen M. Scott	Bovid adaptive allometry
James B. Shackle	Costa Rica sphinx moth ecology
James H. Shaw	Red wolf biology and conservation
Eric J. Sity*	Museum science
Jennifer B. Slade (Belovsky)*	Insects of Isle Royale
Triono Soendoro*	Hormones and steroidogenic ovarian signals
Eleanor J. Sterling	Madagascar Aye-aye biology
Geerat J. Vermeij	Evolution of shell form in molluscs
Laurie R. Walter	Limb adaptation in fossil dicynodonts
George E. Watson III	Island biogeography of Aegean birds
David A. West	Transisthmian bigeminate crabs
Jane M. Whitehill*	Aroid pollinators
Gary Wolinsky*	Museum entomology, Diptera
Carol A. Yoon	Triassic paleoentomology
<i>Yale undergraduate Senior Honors Theses</i>	
Braden R. Allenby '72*	The environmental movement
Elizabeth M. S. Andrews '94	Ants and seed predator insects in Colorado <i>Helianthella</i>
Kenneth K. Asplund '61*	Garter snake biogeography
May R. Berenbaum '75*	Foodplant biology of Chrysomelidae
Elizabeth W. Bokman '88	Coyote and wolf skull comparisons

TABLE 1. Continued.

Individual	Subject
Linda Carr '62	<i>Papilio</i> biology, insect palatability to birds
Jonathan A. Coddington '73*	Spider paleontology
Sara I. Cohen '94	Global population, male sexual attitudes
John R. Cooley '90	Biochemical phylogeny of insect orders
John G. Coutsis '56	Antillean lepidopteroLOGY
Bruce E. Davis '83	Butterfly geography, vertebrate biomechanics
Mark W. Dickinson '78	Paleoichthyology, medical bioengineering
Alice W. Doolittle '89	Manual for museum education
Michael A. Dora '89	Field ecology of caddisflies
L. F. Boker Doyle '53	Butterflies of Fisher Island
Thomas P. Ducker '75	Arthropods and evolution
Barbara Gastel '74	The DNA age in society
James R. Gorman '87*	Human behavioral immunology
William L. Krinsky '67*	Insects and medicine
Frederick D. Krupp '75	Legal solutions to environmental crises
Katarzyna S. Kubzdela '90	Wolf ecology
Krista L. Longnecker '93	Marine invertebrate ecology, <i>Limulus</i> vision
Thomas E. Lovejoy III '64*	Spring territory in <i>Nymphalis</i>
Timothy D. Male '92	Entomofauna of Greater Gull Island
Ryan W. McCue '95	Insect soil fauna of <i>Phragmites</i>
Adam C. Messer '80*	Insects of Moluccan islands
Andrew O. Miller '93	Arizona entomology
Adam R. Moore '92	Experiments with insects and pesticides
N. Ronald Morris '55*	Tyrosine-tyrosinase control of <i>Cynthia</i> wing patterns
Daniel P. Muhonen '57	Butterflies of Idaho, Colorado, and Arizona
Eugenia F. deS. Naro '94	Sea turtle biology in Brazil
Thomas Niemann '79	Entomogeography of Newfoundland
Alfred T. Ogden '94	Hybrid experimental analysis of birch and aspens
Krista L. Olson '92	Endangered sea turtles, biomedicine
David C. Oren '74*	Insect biology, <i>Hyrax</i> ethology
Gustav Paulay '79*	Insects of Rapa Island
Dan Perlman '81*	Pacific island Odonata

TABLE 1. Continued.

Individual	Subject
Judy Penny '62	Insect palatability to Colorado birds
Jennifer Pett-Ridge '93	Insect cave biology
James W. Porter '69*	Colorado moth biology
Robert A. Raguso '87*	Molecular genetics of butterflies
Megan M. Reilly '95	Endangered species of island organisms
Jessica R. Ruvinsky '95	Pollination and genetics in Colorado <i>Delphinium</i>
Benjamin A. Salisbury '92	Insect conservation in Cape Cod
Gail C. Schwartz '74*	Yankee sexuality
Aaron P. Scott '89	Diagnostic tools for human digestive disorders
Mary M. Shaffer '86	Plant ecology of Pelham Bay Park
Janine E. Shissler '91	Geographic ecology of muskrat skulls
Sacha H. Spector '93	Palatability of tropical roaches
Pamela C. Steele '79	Physiology in marine stress environments
Krenin K. Stowe '81	Bush medicine
Matthew M. Taylor '92	Environmental activism, fungus culture
Wendy Todaro '89	African mammal biology, biomedicine
Scott W. Wing '76*	Tertiary paleontomology

TABLE 2. Estimated present holdings of the collections amassed by Charles Remington and his associates in the Entomology Division at the Peabody Museum of Natural History, Yale University. From a 1990 collections survey conducted by divisional staff. Numbers are rounded, inc = incomplete.

Entotrophi	inc
Microcoryphia	inc
Thysanura	inc
Ephemera	260
Odonata	4,440
Plecoptera	520
Embiaria	10
Dermaptera	310
Blattaria	1,200
Isoptera	70
Mantodea	340
Orthoptera	3,600
Phasmatodea	130
Grylloblattodea	1,450
Zoraptera	10
Corrodentia	20
Phthiraptera	10
Thysanoptera	20
Hemiptera	23,520
Megaloptera	510
Raphidioidea	240
Neuroptera	5,040
Coleoptera	114,400
Strepsiptera	90
Hymenoptera	36,740
Mecoptera	400
Diptera	46,780
Siphonaptera	inc
Trichoptera	1,970
Lepidoptera	250,030
unsorted	27,790
Semi-curated holdings (all groups)	279,850
Acquired since 1990 (all groups)	105,000
Estimated total	904,750

university degrees and/or initial training under his guidance, including their topic of research at the time.

Charles has also always stressed the importance of collecting and collections as irreplaceable tools for exploring evolutionary processes. The nearly one million specimens in the Entomology Division at the Yale Peabody Museum largely reflect four decades of effort on the part of Charles, his students and colleagues. Peabody ranks among the two dozen largest entomological collections in the United States and Canada (see S. E. Miller, 1991, *American Entomologist* 37:79; and Table 2). However, size alone does not guarantee that a collection will signifi-

cantly advance science. Charles knew this well when he began as Curator of Entomology in the 1950's, and he set out to acquire material on the philosophy that a university collection must serve as a resource that contributes intimately to the dual missions of teaching and research.

Toward that goal, Charles amassed collections at Peabody that offer taxonomic breadth for comparative work, taxonomic depth for microevolutionary studies, and in general illustrate ecological or evolutionary principles by emphasizing patterns of naturally occurring variation in invertebrate populations. To paraphrase him on these three points: be sure you keep at least one specimen of each different taxon that you have the opportunity to collect or acquire; make large collections of different exemplary taxa from several geographic parts of their ranges; sample as many taxa as possible from unique habitats and ecosystems (e.g., island chains, bogs, ridgetops); and sample for unusual evolutionary characteristics and intrigue (e.g., polymorphs, gynandromorphs, size variants). Although the Lepidoptera are certainly the strongest suit in the Peabody collections, Charles' acquisition philosophy has yielded synoptic or better representation of most arthropod groups, often down to the family or generic level.

Charles has also sought specimen material with special theoretical, historical and/or regional significance, and maintained particular vigilance for collections either "orphaned" or in various states of divestiture. Thus, for example, Peabody has significant holdings in the insect groups (e.g., *Abraxas* moths, corixid bugs) that caught the eye of the late G. Evelyn Hutchinson, a close friend of Charles' and a principal architect of much of modern-day ecological and evolutionary theory. Peabody also recently became home for the entomological collections of the United States Forest Service's Northeastern Experiment Station (85,000 specimens; rich in parasitic hymenopterans), and the Lepidoptera collection of the Bridgham family from Rhode Island (1,800 specimens; a source utilized for type descriptions by W. H. Edwards, A. R. Grote, and their contemporaries in the 19th century). Because of Charles' close involvement in the early decades of the Lepidopterists' Society, the Peabody is also the repository, in whole or part, for the personal collections of a number of lepidopterists (including, for example: M. M. Cary, S. A. Hessel, C. G. Oliver, T. R. Manley, F. E. Rutkowski, D. B. Stallings and J. E. Turner, and H. P. Wilhelm).

As you browse through this issue you will spot a number of personal testimonials by the authors. I'll confess too. My parents were always in cahoots with Charles. This makes it difficult to pinpoint a first event, but certainly my die had been irretrievably cast by 1968, when as a pre-teen I was propelled into summer sleepaway camp in the wooded Berkshires of Massachusetts with a net and copies of the classic Nearctic

works by Klots and Holland. That July, by chance, the cabin of eight boys included a fellow by the name of Jeff Ingraham, who, to my sheer astonishment and delight, proved to be another incipient lepidopterist of equal conviction. Five more summers in the Berkshires followed. Each summer found the two of us again sharing a cabin, generally haranguing our bunkmates with larval escapees, endless latinized names, and tales of pre-dawn forays into the camp's "automats"—the brightly lit bathrooms that invariably attracted the choicest moths (Jeff, I still kick myself knowing you snagged that *Sthenopsis auratus* Grote one step ahead of me!).

To close the circle, it turned out that Jeff's independent source of inspiration was his pediatrician, Dave Winter, a colleague of Charles' and a longtime active member in the Lepidopterists' Society (including Editor of the *News* from 1980–1982). So, matters quickly became hopelessly entangled, for as Jeff and I began to meet other lepidopterists, there didn't seem to be a one among them who hadn't crossed paths with Charles. Before going away to the west coast in the mid 1970s for college, I did volunteer work at the Peabody Museum pinning specimens, joined the Lepidopterists' Society, and got swept into the excitement of the newly formed Xerces Society. I left without a doubt in my mind that I would somehow eventually return to work with Charles on a doctoral project. That came to pass, and our close collaboration continues to date. I can't thank him enough for his guidance and wisdom over the years. Charles, on behalf of the authors and your many other friends and associates, it is an honor and pleasure to dedicate this issue of the *Journal* to you. Long may The Rem's net keep swinging!

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DESCENT WITH MODIFICATION: EVOLUTIONARY STUDY OF *COLIAS* IN THE TRADITION OF CHARLES REMINGTON

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ABSTRACT. Studies of pierid butterflies have for several decades been at the center of diverse advances in the understanding of microevolutionary processes. An important ingredient of this success is the intellectual model—a way of thinking—that Charles Remington has passed to his students and colleagues. This paper reviews the Remington paradigm as applied to research on the bioenergetics of natural populations of *Colias* butterflies, focusing on the impact of thermal and related environmental constraints on the allocation of metabolic resources, and the function and genetic variability of enzyme polymorphisms.

In 1951, Alexander Klots' landmark *Field Guide to the Eastern Butterflies* appeared. Therein, Klots remarked (p. 183) of *Colias*: "I know no other genus of butterflies that presents so many baffling, and stimulating, problems." Five years later, an aspiring high school student and lepidopterist, interested in natural polymorphism in *Colias* as the topic of a science fair project, wrote to Klots for information, and was referred to Charles Remington, who recently had published a major review (Remington 1954) on polymorphism in *Colias*. Because of Remington's legendary ability at encouraging imaginative study of Lepidoptera by amateurs and professionals, students and senior scholars alike, the rest is, as they say, history—for I was that student. Charles has been my friend and professional colleague for all of my adult life and more than half of his. It is a privilege to join his many other friends and intellectual descendants in marking his entry into his eighth decade with thanks and best wishes.

THE REMINGTON SCIENTIFIC TRADITION

If we want to understand Charles' success at fostering others' understanding as well as his own, we must go beyond well-deserved personal tributes to ask how he does it. Much of the work reported in this issue of the *Journal* embodies a clear, active tradition of scientific work in which Charles, and those who have learned from him, participate alike. This is a tradition in the best sense: doing things in the same grand style as one's forebears, but not necessarily doing the same things, or repeating particular deeds again and again.

First among the Remington themes is the importance of detailed knowledge of particular groups of organisms as well-understood "test beds" for study of general problems both in basic and applied science.

This is a very Whiteheadian (1938) viewpoint, emphasizing the human importance of both specific knowledge and general patterns of such knowledge. Charles' focus on the study of Lepidoptera, in context of both evolutionary studies and conservation biology, embodies this theme.

This in turn synergizes with Charles' long-standing commitment to the continuity of communication and intellectual effort between amateur and professional biologists, which we see in his co-founding of the Lepidopterists' Society. This positive sense of "scientific democracy" also has been important in his welcoming of generations of Yale University students into enthusiastic research collaboration.

Finally, we see qualities which revolve around Charles' enthusiasm for eclecticism of concepts and techniques in the broad study of evolution. He emphasizes the importance of large databases as sources of ideas: his students are encouraged to acquire much data, but to think about their meaning even as they come in, and his commitment to building the insect collections of Yale's Peabody Museum has been extremely successful. But Charles is no hyper-empiricist. He has long held that the prime importance of experimental or observational data in evolutionary biology is its use to test ideas, concepts, and theories. Yet, he insists, data must *drive* theory and not the reverse—if a theory clashes with new findings, so much the worse for that theory.

All the contributions to this *Journal* issue show many of the hallmarks of this tradition. My own work, using *Colias* as a "test bed" to study evolutionary mechanisms, has turned out to require all of them in order to address its central questions.

THE STUDY OF EVOLUTION, USING *COLIAS*, IN THE REMINGTON TRADITION

Klots' "baffling and stimulating problems" presented by *Colias* have their sources in the evolutionary biology of this apparently rapidly evolving group of butterflies. Naturally occurring variation can be a uniquely powerful probe with which to explore evolutionary problems like these. A wide variety of such natural variation in *Colias*—from dramatic color polymorphisms, to clinal variation in other aspects of color pattern or morphology, to polymorphisms in the enzymes that process energy in support of flight—all turns out to fit into a context of bioenergetics i.e., the study of energy flow through living systems. Complex patterns of such variation, within and among species, have indeed caused much of the confusion about *Colias*' classification to which Klots referred. However, we will see that, finally, careful study of the mechanisms and the molecular basis of this variation holds much promise for resolving the systematic confusion, as well as illuminating new general principles about the workings of evolution.

Cold Habitats, Hot Butterflies—Temperature Regulation and Flight in *Colias*

In the winter of 1962–1963, my first graduate student year, after four years as a Yale undergraduate with Charles' advice and tutelage, I was spending an afternoon with the *Colias* collections at Yale's Peabody Museum. After a while, I noticed that *Colias* from cold habitats tended to have dark (melanic) hindwing undersides. I already knew from much observation that *Colias* rest with their wings folded dorsally, and the thought occurred to me that this might be an adaptation for absorbing sunlight to warm up in cold climates. I mentioned this idea to Charles the next morning; he enthusiastically recommended I think of some way to run an initial biological test of the idea.

In the next few months, preparing for a (second) summer of field work at Rocky Mountain Biological Laboratory, in Colorado, it occurred to me that if *Colias* were using this hindwing underside patch as a thermoregulatory device, then when cold, they should turn to expose it perpendicular to sunlight, giving maximum warmup advantage. In late July 1963, then, I spent a morning at 12,200 feet on the south edge of the Mesa Seco, in Hinsdale County, Colorado, working with the alpine, heavily melanic *Colias meadii* Edwards. I put half a dozen fresh males, alive, each into a metal 35mm film can, then put them in the shade to cool down to ambient temperature in the cold alpine air. Releasing them one by one onto the sunlit tundra, I saw each one turn itself like a small sailboat, orienting perpendicular to the solar beam! Moreover, each was warm enough to fly off in only two or three minutes, though if they were tossed into the air directly out of their cans, they simply fell helplessly to the ground.

Here I had strong evidence that my idea was worth pursuing. Again, Charles was helpful. This sort of "environmental physiology," as it was then known, was beyond his personal experience, but he knew of an entomologist, Phillip Adams, who was experimenting with the implantation of minute thermistor devices non-destructively into flight muscles of butterflies, so as to monitor their thoracic temperatures during various activities. Adams kindly sent me plans and advice for building the needed field-portable equipment. Summer 1965 found me in northwestern Canada deploying this gear for the first time, to study the thermal biology of a series of *Colias* species which differed altitudinally in hindwing melanization: *C. alexandra christina* Edwards, *C. palaeno chippewa* Kirby, and *C. nastes streckeri* Grum-Grshmailo.

To make a long story short (see Watt 1968, 1969, Kingsolver 1983a, 1983b, Kingsolver & Watt 1984 for details), *Colias* of all species studied (the aforementioned, plus *C. a. alexandra* Edwards, *C. eurytheme*

Boisduval, *C. meadii* Edwards, and *C. philodice eriphyle* Edwards) require a high and narrow body temperature range for optimal flight—35–39°C—and do not fly voluntarily at all outside about 29–40°C. This in itself was remarkable: “environmental physiology” of the time led to the expectation that cold habitat populations would fly at lower body temperatures than warm habitat ones, but not so!

All *Colias* also proved to display the same behavioral responses to habitat temperature, orienting perpendicular to sunlight to warm up when cold, and orienting parallel to sunlight, or seeking shade, when overheated. Populations in different thermal habitats differ in their adaptive morphological mechanisms for achieving the common thermal optimum. The darkened hindwing underside in cold habitats, brighter in warm habitats, is indeed a temperature-regulating device, changing absorptivity for sunlight. Moreover, cold habitat populations have thicker thoracic “fur” (actually modified scales, of course) than do warm habitat populations, thus modifying their rates of heat loss via convective cooling. We now have been able to build a computer software model which, with a few measurements of a *Colias*’ solar absorptivity, “fur” thickness, and the like, together with recorded data on air and ground temperatures, wind speed, and sunlight intensity in a habitat, can accurately predict when during the day that *Colias* will have the opportunity to fly (Kingsolver & Watt 1984). This is useful not only for understanding *Colias*’ thermal habitat structure in its own right, but for carrying out other experiments in that context (see below, Watt 1992).

This analysis allows us to understand *Colias eurytheme*’s seasonal forms, “spring-fall” (=form “ariadne”) versus “summer” (=form “amphidusa”), which Ae (1957) first showed to be due to photoperiodic sensitivity of *C. eurytheme* larvae. The light hindwing undersides of the summer form are less absorptive of sunlight, compared to the dark spring-fall phenotype (Watt 1969; this mechanism also cues the difference between light summer and dark spring-fall hindwing undersides of *C. p. philodice* Latreille (Watt, unpublished data)). Hoffmann (1973) showed that photoperiod alone controls this, reproducing the natural field alternation of forms quantitatively by reference to the response curve of hindwing color versus photoperiod under which larvae are reared in the lab. Recently, we have found (Jacobs & Watt 1994) that in *C. eurytheme*, photoperiod also cues deeper thoracic “fur” (giving more insulation against spring-fall convective cooling) in the short-day spring-fall forms than in the long-day summer ones. Both these differences contribute to greater flight time for each photoperiod form in the season in which it is produced and in which it flies (Jacobs & Watt 1994).

I think it is significant that the whole business of understanding *Colias*' thermoregulatory adaptations had its origin in the Yale Peabody Museum's extensive collection of Lepidoptera, which owes its existence to Charles Remington's tireless activity. This use of collection material to provoke active experimental study is a scientific value of collections which is all too often overlooked, but which will be of increasing importance in the future. I also note that all the original work was done with home-built, shoestring-budget equipment and direct behavioral observation, in a way perfectly accesible to serious amateur lepidopterists—indeed, even quite modern and sophisticated equipment for monitoring thermistor or thermocouple probes, usable for such work, remains relatively inexpensive and accessible.

The Sex-limited "Alba" Female Polymorphism

The white-female "alba" variant was really the first focus of my interest in *Colias*, leading me to write first to Klots and then to Remington when in high school. For a science fair project, I was trying to apply what was then a new, powerful biochemical separation technique—paper chromatography—to analyzing the effects of "alba" on *Colias*' yellow, orange, or white wing pigments (a class of compounds called pteridines, first isolated from the wings of European pierids).

The "alba" morph has a distinguished history in biological study, beginning with John Gerould's (1911) use of it to make the first demonstration of sex-limited Mendelian inheritance. William Hovanitz (trained as a physician, illustrating yet another position along the amateur/professional continuum, which has been so important to Lepidopteran evolutionary study) demonstrated in 1950 that many North American *Colias* species show parallel biogeographic gradients of "alba" frequency, with the coldest-habitat populations of any one species having the highest frequency of this morph, yet often with little correlation between species in this respect. When I first wrote to Remington, he had recently published his survey (1954) of the genetics of *Colias*, including a summary of what was known about "alba." This paper was a major stimulus to my own approach (and later, those of my students as well) to the "alba" problem.

Hovanitz (1948) also reported that "alba" had a propensity to fly in cooler parts of the day than its yellow or orange sisters. Unhappily, he was misled by deficiencies in his observational technique, as Leigh and Smith (1959) showed. In fact, having applied field thermal monitoring technique to address the meaning of *Colias*' underwing coloration, I then used the same technique to test Hovanitz' idea in another way (Watt 1973): the two morphs do not differ in their preference for flight temperatures, and moreover the color difference, to the extent it influ-

ences the insects' thermal balance, would force "alba" females to fly less in the cooler parts of the day. At this same time, my early interest in the chemistry of the wing pigments paid off: data obtained by paper chromatography and spectral analysis showed that "alba" is, biochemically, *not* a "simple oxidation" of colored to colorless pigments (cf. Ford 1953) but a redirection of expensive pigment precursors out of pteridine synthesis into other physiological uses during pupation. This might plausibly lead to physiological advantages for "alba" when pupae develop under cold stress.

Our next look at "alba" grew out of these results. Graham, Watt, and Gall (1980) found that, indeed, when *C. eurytheme* pupae develop at low temperature, "alba" are superior to their orange sisters in speed of maturation and in maturity of eggs when females eclose—but such effects diminish or vanish at warmer temperatures. In addition, we compared "alba"'s eclosion times, fat body sizes, and mating successes in the wild in two near-sympatric Colorado *Colias* which differ greatly in "alba" frequency: *C. a. alexandra*, which has "alba" frequency of 5% or less, and *C. scudderi* Reakirt, with "alba" frequency often in excess of 90%. Moreover, we made these comparisons in populations whose numbers, age distributions, and movement or dispersal patterns had already been studied (Watt et al. 1977) with the aid of yet another Remington doctoral student, Frances Chew (who was my first undergraduate research student).

We found that the physiological and developmental advantages for "alba" at low temperature were indeed seen in the wild, and "alba"'s advantage in emergence time was more pronounced in *C. scudderi*, which has a colder pupal habitat than *C. alexandra*. We also found an advantage to "alba" in mean fat body size for each adult age class, in both species. Following some data of Taylor (1972), another former Remington associate, we also examined the behavior of male *Colias* toward "alba" as compared to its yellow sisters (to do this, we developed a "tethering" technique for studying behavioral interactions between individual butterflies). We found that male *Colias* discriminate against "alba" in the initial visual phases of courtship, 5:1 in *C. alexandra* and 10:7 in *C. scudderi*; once the insects close in to centimeter distance (at which range their pheromones become effective; Silbergeld & Taylor 1978), the difference in male behavior toward the female morphs vanishes. The discrimination seems to be effective, in that "alba" have fewer matings than yellows in each age class (as we found by dissecting females and counting their spermatophores, in the manner of Burns 1968) in both species. Thus "alba"'s developmental advantages in the wild are opposed by behavioral disadvantages.

Claims of pierine distastefulness (e.g. Marsh and Rothschild 1974),

despite the observations of Wourms and Wasserman (1985), led some of our colleagues to suggest that mimicry of pierines by "alba" might be important to this polymorphism. With several students, I explored various implications of this idea: are *Colias* indeed more palatable to visual predators, notably birds, than pierines which are sympatric with them, so that mimicry might result?; and, what is the relation between "alba" frequency and sympatric pierine density? In pursuing the former idea, we developed techniques for studying butterfly palatability in a controlled fashion in natural populations (Ley & Watt 1989), and found that in a Colorado mountain ecosystem, there is no difference in palatability among *Pieris napi mcdunnoughi* Remington, *Pontia occidentalis* Reakirt, *C. a. alexandra*, and *C. scudderi*, and that none of these display the least sign of being distasteful to Canada jays (*Perisoreus canadensis* L.), though larger, heavier butterflies are eaten preferentially to these small pierids. Moreover, Watt, Kremen, and Carter (1989) found that "alba" frequency is negatively correlated, both in space and in time, with the density of these pierines. Thus we could definitively reject the 'mimicry' hypothesis for "alba." Indeed, we collected anecdotal observations to suggest that pierines constitute competitors with "alba," but not other *Colias* morphs, for reproductive space, based on visually mediated behavioral interactions.

The idea that "alba" and pierines are interference competitors may explain why male *Colias* are often selected to discriminate against "alba." This idea is now under further study, along with aspects of the biochemistry and physiology of "alba." The story is far from over, because what we know of the selection pressures should fix either one allele or the other in any given habitat, not maintain the polymorphism. But of course, we do see the polymorphism, in parallel, in many *Colias* species. Therefore there are still many important things to discover about this polymorphism, and we are still hard at it. Indeed, so are others: for example, Sappington & Taylor (1990) report the remarkable fact that "alba" and orange females of *C. eurytheme* preferentially mate with males having differing mixes of short-range courtship pheromones. How this might affect the mix of selection pressures maintaining the "alba" polymorphism is not yet clear.

Enzyme Variation, Energy Supply, and Fitness Measurement in *Colias*

Enzymes, the protein catalysts which control energy processing and other metabolic functions in all organisms, vary genetically in *Colias*' natural populations just as do visible morphology or color pattern. To visualize this variation, one uses the technique of gel electrophoresis, separating the proteins in an electric field on a gel support, followed

by enzyme-specific staining. In earlier decades, there was much debate about whether such enzyme variation, in a variety of organisms, is acted on directly by natural selection, or whether instead it is neutral in the course of evolution. Extreme positions on both sides of this debate are now widely thought to be misguided, with many workers arguing for a broad spectrum of situations, from intense selection on enzyme variation down to little or none (Endler 1986, Gillespie 1991, Watt 1994). In any event, in at least some cases such enzyme variants can be powerful probes of the organization of energy processing. We have found this to be so in *Colias*, exploring yet another aspect of our theme of bioenergetics.

We know by far the most about natural genetic variants in one enzyme, phosphoglucose isomerase or PGI, which occupies a place in the early part of the reaction pathway called glycolysis, the primary route for supplying carbohydrate-derived fuel to *Colias* adults' flight. Four alleles, hence ten genotypes, are frequent to common in the lowland species complex (*C. eurytheme*, *C. philodice eriphyle*). To summarize much detailed biochemical information, among these 10 genotypes there is 3–4-fold variation in the speed with which their PGI enzymes process energy-rich sugar phosphate compounds, and in general, the more effective a genotype's enzyme is in this task, the less stable it is in turn against thermal stress due to high body temperature (Watt 1983; this trade-off of kinetic power against thermal stability was predicted from general considerations of protein structure by Hochachka and Somero in 1973; ours is one of the best studied examples involving variation within a single species). From these biochemical data and consideration of the dependence of *Colias*' flight on its energy supply, in context of its thermal biology as already analyzed (above), we were able to predict that carriers of these enzyme genotypes should differ, in characteristic ways, in their ability to fly over the broad span of the day in the wild. These predictions have been amply supported by direct experimental field test in both *C. eurytheme* and *C. p. eriphyle* (Watt et al. 1983). In turn, since all *Colias* adult activities depend on flight in one way or another, we were able to predict that each of the components of Darwinian fitness—survivorship, male mating success, and female fecundity—should differ among these genotypes in ways predictable from their effects on flight. These predictions, too, have been tested in diverse populations and supported with great statistical significance (Watt 1977, 1983, 1992, Watt et al. 1985, 1986). In the most recent work, on female fecundity effects of the PGI genotypes, we used our computer model of *Colias*' thermal balance to separate out genotype-specific effects from the thermally determined variation in opportunity for all females to lay eggs each day (*Colias* lay single eggs

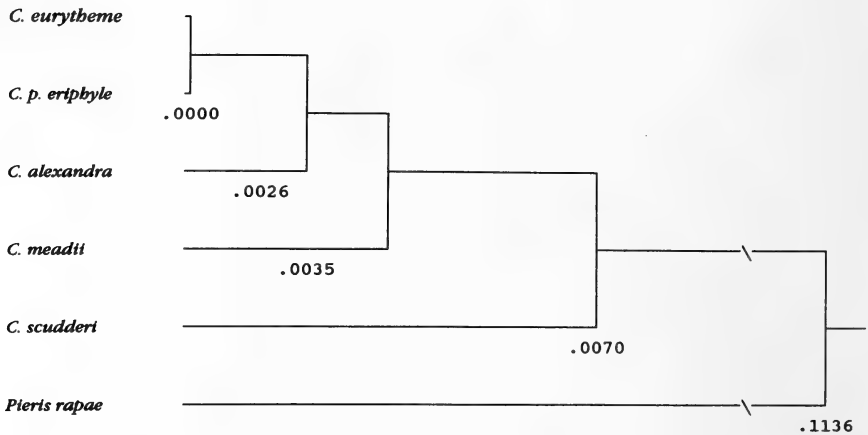


FIG. 1. Unweighted pair group, arithmetic mean distance tree of relationships among the given *Colias* taxa, with *P. rapae* as outgroup, based on initial mitochondrial DNA data of M. Ford, D. Pollock, W. Watt, and D. Rand (unpublished, summarized here by permission). A total of 757 base pairs is compared in this data set, drawn from portions of the 12s and 16s ribosomal RNA genes and the NADH dehydrogenase subunit 5 gene. Note that distances are very short within *Colias* (indeed, *C. eurytheme* and *C. p. eriphyle* show no differences as yet), reflecting a small number of differing sites in, and therefore specially conservative nature of, the sequences sampled. This is promising for the utility of more such sequence data in ordering relationships among species complexes. A cladistic analysis of the site variation patterns is also consistent with this tree.

and must fly between ovipositions). Thus, initially quite different parts of our research program are mutually reinforcing, showing with great clarity how natural selection can reach right down to the level of particular proteins.

A New Path for Re-exploring Old Problems—*Colias* and Molecular Systematics

The enzyme-level polymorphism just discussed occurs in parallel, just as does the "alba" polymorphism, in many different *Colias*, not just the North American lowland species complex. The opportunity to compare such evolutionary adaptations across a broad range of species seems attractive—but here problems arise, as the systematics of the genus is far from clear. Despite informative work in recent years by Ferris (1973) and others, often using new diagnostic characters such as those revealed by ultraviolet photography (Silbergleid & Taylor 1978), the placement of some *Colias* taxa into the proper species complexes is still controversial, and the relationships among species complexes are not at all clear. Indeed, the systematic reliability of some morphological characters that have been used to group taxa may be newly suspect. For example, some authors have grouped *C. nastes* Boisduval and *C. behri*

Edwards because of the very heavy melanization of their wings, which obscures the usual light pteridine pigment pattern. But this may well be the result of convergent evolution because of similarity in their bearers' thermal habitats, and not reflect close relationship.

We are beginning to deploy new molecular methods to resolve systematic problems in *Colias*, analyzing the insects' very DNA itself to generate data on the variation of DNA sequences at a variety of specific genes as a potentially powerful source of systematic characters (which at the least will not likely be subject to the same kinds of biasing selection pressures as some morphological characters). Figure 1 displays a very preliminary tree of relationships among several North American *Colias* taxa, using *Pieris rapae* as an outgroup. These data, so far as they go, at least suggest that the North American legume-feeding *Colias* may share closer common ancestry than any of them do with the willow-feeding *C. scudderi*. Note also that in just over 750 base pairs of data thus far, no differences were seen between *C. eurytheme* and *C. p. eriphyle*, supporting an extremely close relationship between these "semi-species" (cf. Mayr 1963). Much more data-gathering and analysis will be needed to resolve the systematic difficulties of *Colias*, but these techniques do hold great promise for such resolution.

Environmental Applicability of *Colias* Research

Not only does the above work have implications for fundamental Darwinian biology at large, and for specific understanding of these pierid butterflies, but much of it appears to be applicable to environmental problems as well. I give two examples.

First, one of the great problems confronting the management of endangered species of small animals is that because of their fragile condition, one cannot study their population genetics—thus leaving us ignorant as to what genetical difficulties their population size restrictions may be running them into. For example, this situation plagues attempts to conserve *Boloria acrocynema* Gall and Sperling in central Colorado (A. Seidl, personal communication). A number of montane or alpine *Colias* occur in some parts of their ranges as isolated local populations, though none of the taxa as a whole are yet near danger of extinction in North America. Genetical study of such isolated populations might be informative, in context of our population genetic insights in other *Colias*, as models for genetical constraints that may be occurring in local populations of already endangered Lepidoptera or other creatures.

Second, our finding of support, in the *Colias* PGI polymorphism, for Hochachka and Somero's tradeoff of enzyme kinetic function against thermal stability raises the possibility of unanticipated genetic consequences of global warming, should this occur. The most thermally stable

PGI genotypes, because of their disadvantages in energy processing rate at normal temperatures, have far lower male mating success or female fecundity than do other genotypes in the system—yet these are the genotypes which would best survive the increase in acute overheating which even moderate global warming would quickly impose on *Colias*. The initial result of this “selection for poor reproduction” would be a dramatic drop in population sizes, probably throughout the range of whole species. How fast natural selection could work on the insects’ thermoregulatory adaptations to recover population size would then be an open question. In any case, this would raise the probability of their extinction, especially for cold-habitat montane and alpine species which may already occur in separated local populations. We are beginning to explore this grim possibility quite actively, with respect to *Colias* and other butterflies, and also to see how far such effects might run through the animal and plant world at large.

SUMMARY AND CODA

Colias butterflies now appear as a “test bed” system with great potential for ever-diversifying future work in fundamental and applied biology alike. Our results re-emphasize the importance of collections in sparking new scientific ideas, the importance of applying diverse analytic techniques to complex scientific problems, and the crucial interaction of extended databases with a sufficient variety of alternative explanations for natural phenomena. Again, I would emphasize that many of these kinds of study are accessible to the serious amateur lepidopterist just as much as to the professional. All these things are very much in the Remington tradition.

Let no one suppose, however, that in inspiring those of us who represent the Remington tradition in this *Journal* issue, Charles has completed his scientific and educational tasks. No indeed—he is still actively innovating, in path-breaking ways, in his own tradition, as shown by his recent brilliant work with Gary Bernard (see Bernard & Remington 1991) on the visual physiology of *Lycæna* coppers in relation to their mate choice mechanisms and other aspects of their behavioral biology. Moreover, he continues to inspire enthusiasm in new students and colleagues, by daily interactions at Yale and elsewhere, as well as by example not only to us, his intellectual offspring, but to our students in turn, Charles’ intellectual grand- and greatgrandchildren. Thus, by intellectual “descent with modification,” there will be even more young scientists forthcoming who owe thanks to this versatile, energetic scholar-teacher. Who knows what he will do next? For certain, it’s worthwhile to watch and find out. . . .

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FROM WEEDS TO CROPS: CHANGING HABITATS OF PIERID BUTTERFLIES (LEPIDOPTERA: PIERIDAE)

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ABSTRACT. Butterflies in the genus *Pieris* offer a model system for assessing the impact of agricultural expansion on the foodplant-linked biology of insects, notably why certain species become crop pests and others do not. Factors that influence the likelihood of attaining pest status when habitats change are reviewed, including hostplant density, climate, voltinism, larval diet breadth, and fecundity. The relative importance of these are explored in two now cosmopolitan species on agricultural crops, *Pieris rapae* and *P. brassicae*.

Anthropogenic changes to the landscape, particularly those associated with European colonization of the Americas, have brought numerous biological consequences. Some were intentional, such as clearing of forest in eastern North America (Cronon 1983); but others were not. For example, forest cutting brought into contact closely related species from opposite sides of the natural hardwood forest barrier in eastern Canada and the USA (Remington 1968). Anticipating unintended consequences of disrupting natural processes now applies to many human activities including agricultural control of insect pests. If we make agroecosystems more like natural ecosystems, we hope, we will promote effective natural regulation of potential insect pests.

One major challenge is the limited applicability of available information. Information obtained about one level of organization is not always sufficient to predict consequences at a higher level and vice versa (Power 1992, Vitousek 1994). For example, consumption rates of insect prey by predators may not enable us to predict predation's impact on prey population dynamics; similarly, knowing predation's impact on a prey population may not predict whether a predator population is sustained on that prey population (Hunter & Rice 1992). On one hand, most studies of insect ecology are case studies of populations or species in a restricted context, without necessarily accounting for the heterogeneity observed at each trophic level (Hunter & Rice 1992, Vitousek 1994). Limits of time and logistical support force us to focus on relatively small numbers of factors, interactions, populations, species or habitats. Few investigations of crop diversity effects on pest abundance examine mechanisms by which pest abundance changes (Risch et al. 1983, Andow 1988). On the other hand, the size of agroecosystems and the dispersal capacities of insects require that we view these systems at larger scales (Woiwod & Stewart 1990, Allen & Hoekstra 1992).

What lessons from natural populations and communities can we apply

to agroecosystems? Can we expect to alter dramatically the primary resource base of a community while controlling potential change at higher trophic levels? In this paper, I apply ecological research on pierid butterfly communities to speculate on the following questions: 1) What ecological traits enable some species to become pests when their resource base changes from "natural" to "agricultural;" and 2) What lessons from ecological work can we use to manage these pest species?

ECOLOGICAL PORTRAITS OF POTENTIAL PEST SPECIES

Of perhaps several dozen species or geographic subspecies of crucifer-feeding pierid butterflies studied by ecologists during the past several decades, only two species of Palearctic origin—*Pieris brassicae* L. and *P. rapae* L.—attain economic pest status on crucifer crops worldwide, particularly vegetables (Bonnemaison 1965, Oatman & Platner 1969, Takata 1962, Feltwell 1982, Thomas 1984, Finch 1988, Lamb 1989). *Pieris rapae* is now a cosmopolitan species. Figure 1 shows these two species as part of an indigenous community feeding on crucifers (Brassicaceae) in the High Atlas region of Morocco at one of the geographic centers of crucifer diversity (Tsunoda et al. 1980). Interactions among these species and between butterflies and potential hostplants were studied over several seasons (Courtney & Chew 1987, Chew & Courtney 1991). Comparable species richness occurs in pierid communities in the South American Andes and in California, USA. In these latter places, however, populations of *Pieris rapae* or *P. brassicae* are naturalized rather than indigenous. The Moroccan community thus represented an opportunity to observe these two pests in their native habitats where the resource base has not been converted to crucifer agroecosystems (although grain farming, fruit-tree orchards, evergreen tree farms, and grazing are conspicuous activities in some habitats). Further, these species could be observed together with other indigenous crucifer-feeding pierine and euechloeine butterflies.

One general result is that we found no evidence that hostplant use was altered when butterfly species co-occurred. Diet breadth and specificity were unrelated to the composition of the pierid community and are better understood in terms of individual butterfly species adaptation to habitats and potential hostplants (Courtney & Chew 1987; Chew & Courtney 1991). In comparison with other species, *Pieris rapae* and *P. brassicae* differ in a number of traits that together promote rapid response to changes in hostplant abundance: 1) multivoltinism; 2) broad diet (euryophagy); 3) adult preference for mesic habitats with apparent crucifer populations; 4) potentially high fecundity. Euryophagy and fecundity correspond directly to two of four traits that contribute to

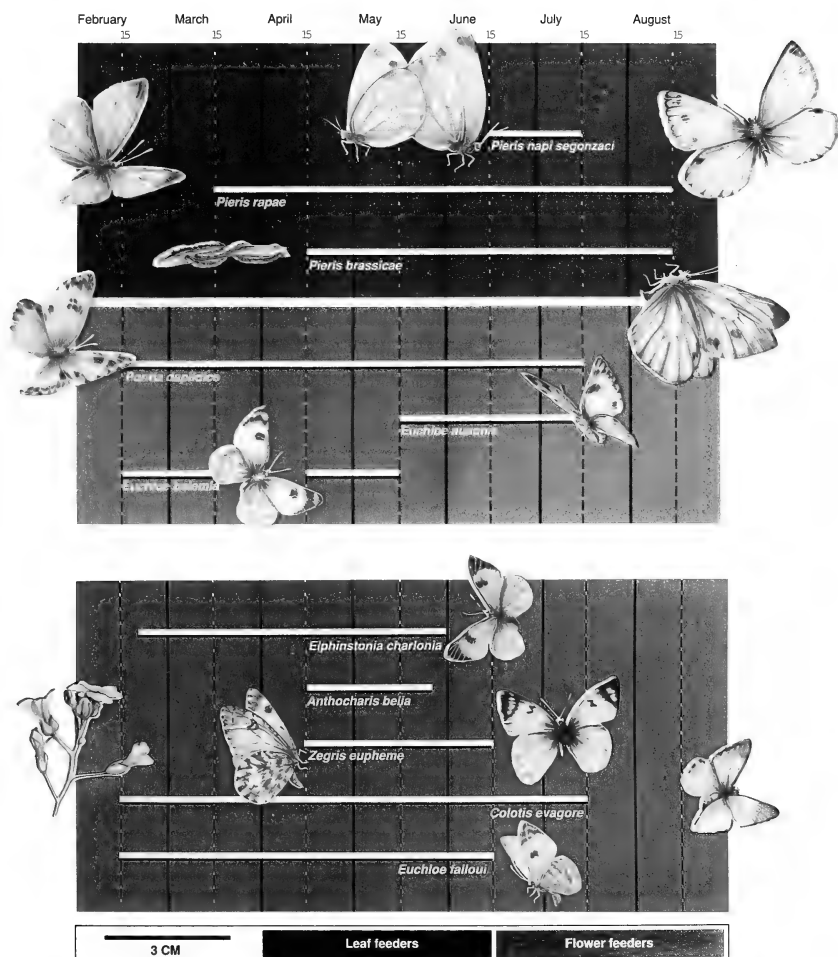


FIG. 1. Crucifer-feeding pierid community in the High Atlas region of Morocco, showing flight seasons of each species as white bars. Butterflies figured in top panel, clockwise from top left, the leaf-feeding guild includes *Pieris rapae* L., *P. napi segonzaci* Le Cerf, and *P. brassicae* L.; continuing clockwise, the inflorescence-feeding guild includes *Euchloe ausonia* Hubner, *E. belemia* Esper, and *Pontia daplidice* L. Lower panel, clockwise from top, *Elphinstonia charlonia* Donzel and *Anthocharis belia* L., both inflorescence feeders; *Colotis evagore* Lucas, a folivore on *Capparis spinosa* bushes, and the inflorescence feeders *Euchloe falloui* Allard and *Zegris eupheme* Lederer. Nomenclature follows Higgins & Riley (1980).

the major pest status of *Heliothis* species (Lepidoptera: Noctuidae) (Fitt 1989); multivoltinism and habitat selection are likely analogs of two traits named by Fitt for major *Heliothis* pests—facultative diapause and nocturnal migration between areas.

Multivoltinism Increases Outbreak Potential

The multivoltinism of both *Pieris* species in Morocco enables them to expand populations early in the season and to produce numerous offspring that colonize new habitats as the season progresses. In addition, multivoltinism together with euryophagy promotes local persistence of these species in years when other insects and their hostplants are asynchronous. We observed that sometimes univoltine butterflies and their hostplants were both abundant, but that the hostplants did not appear in a specific locality until after the butterflies had flown at that site (Chew & Courtney 1991)

Population expansion on alternative hosts in an earlier generation contributes to the rapid response of these *Pieris* species to crop hostplants and to their ability to exploit agricultural crops. This ecological trait also was noted for *Pieris rapae crucivora* Bdv. in Japan (Ohsaki 1982) and for *Pieris napi oleracea* Harris, a pierine that is locally extirpated in parts of the eastern USA, where it used to be an agricultural pest (Harris 1841). In northern Vermont, USA, this latter species occurs in low density early in the season, but flies with *P. rapae* in great abundance in July and August (Chew 1981).

Flight season or multivoltinism alone do not promote attainment of pest status. *Pontia daphidice* L., a multivoltine species with the longest flight season in Morocco, is not usually a pest. However, multivoltinism may permit exploitation of otherwise unused resources and changes in host availability may favor multivoltinism. Native *Pieris napi* in California has extended its vernal flight season into summer near riparian habitats containing naturalized watercress (Shapiro 1975). Based on data showing that late emergence from overwintering puparia is controlled by a single gene locus, Finch (1988) suggests that trivoltine *Delia radicum* (cabbage root fly, Diptera: Anthomyiidae) evolved, in response to agricultural practices extending the season for cruciferous crops, from ancestors restricted to two generations per year.

Euryophagy Promotes Pre-adaptation to Crop Hosts

Both *Pieris rapae* and *P. brassicae* exploit a wide range of crucifers compared to other Moroccan pierids. They utilize all the hosts preferred by pierids with narrower diet breadth, and utilize additional hosts. Neither species exhibits strong negative or positive correlations in larval performance on hosts, a general finding for many herbivorous insects (Via 1990). Diet breadth maintains larval adaptation to a range of hostplants and increases the likelihood of successful colonization of a novel host. Available evidence suggests individual egg-laying pierid females oviposit on all the hostplants used by their population (*Pieris*

napi macdunnoughii Remington, Chew 1977a), but more extensive work on *Colias eurytheme* Bdv. (Pieridae) demonstrates heritable variation for oviposition preference among conspecific individuals of this family (Tabashnik et al. 1981).

Temporal variation in host availability between years is the most prominent correlate of diet breadth for Moroccan pierids. Some host species occur at nearly the same density in a given locality from year to year; in other species, some population densities may differ by several orders of magnitude from year to year. Crucifer species whose densities are numerically stable in a given locality are chosen by all the Moroccan pierids in this community. Exceptions are representatives of a few genera known to contain secondary compounds atypical of the Brassicaceae, some of which deter oviposition or larval feeding of *P. rapae* (Sachdev-Gupta et al. 1990, 1993). Thus pierids with narrow diet confine themselves to using numerically stable plant species in preference to less predictable species. Pierids with broader diet utilize these stable species, and add less predictable species. Only the most euryphagous pierid in this community, *Pontia daplidice*, uses highly unpredictable plant species, where population-level variation in crucifer density averages more than an order of magnitude from one year to the next. This pattern is similar to observations of three *Pieris* species living in the same region in central Japan (Ohsaki 1979).

Crucifer damage caused by unidentified herbivorous invertebrates shows the same pattern (Chew & Courtney 1991). Plant species with the least numerical stability from year to year have the least damage from unidentified invertebrate herbivores (by visual inspection of magnified photographs, $r = -0.66$, $p < 0.01$, $n = 19$ crucifer species); these plant species also accumulate fewer pierid eggs than species with more numerical stability. When the average population-level plant density varies more than four-fold (almost half an order of magnitude), only the most euryphagous pierid butterflies use that plant, and mean infestation rate (average number of eggs per host individual) drops from the range of 0.4–1.1 to less than 0.05–0.2.

Two exceptions to this general finding increase the likelihood that *Pieris rapae* and *P. brassicae* attain outbreak proportions on crops. First, despite its broad diet, *P. rapae* uses the most numerically stable populations of its hostplants. In this habit it resembles butterflies that exploit a much narrower range of hostplant species, except that *P. rapae* differentiates between more and less numerically stable populations within each hostplant species, while euechloines and pierines with more restricted diets differentiate between more and less numerically stable hostplant species. This adult behavior promotes consistent exposure of *P. rapae* larvae to a wide array of host species so larval adaptation to

these species is maintained by natural selection. This pattern of adult oviposition behavior is similar to the contrast observed by Ohsaki (1979, 1980) between the pest *P. rapae crucivora* and *P. melete* Menetries, which uses a wider range of hosts but does not specialize on crop hosts. When abundant, densely planted novel hosts occur in agricultural systems, *P. rapae* females exploit these resources as an extension of their behavior in natural habitats. Because their larvae are adapted to many natural hosts, there is high probability of larval success on the novel resource. In combination, adult and larval adaptation promote rapid, successful colonization. For *P. rapae crucivora*, however, Ohsaki and Sato (1994) also note that host use is a trade-off between the high quality of agricultural plants and the heavy parasitoid load encountered in agricultural situations. Possibly it is the only species sufficiently fecund to tolerate the exposure to parasitoids and still maintain local populations.

Pieris brassicae presents a second departure from the general findings about euryophagy and host numerical stability noted above, with consequences for numbers of larvae on individual hosts. *Pieris brassicae* uses hostplant populations with relatively less numerical stability compared to the host species averages. This occurs because some of its host species are annuals whose populations can attain high densities and very large individual size (>1.5 m) in wet years, but not during intervening dry years. Large individual hostplants support larval growth until *P. brassicae* must disperse from the plant they have consumed, so ovipositing on a large host increases the size larvae will attain before dispersal (Davies & Gilbert 1985). Typical cluster size on wild hosts in Morocco is a dozen eggs (Courtney 1986, personal observation), while in Europe egg clusters are several times that size (Davies & Gilbert 1985). The speculation that individual butterflies might adjust the size of egg clusters to the size of hosts is intriguing, but evidence is lacking (Courtney 1986). Selection may favor large cluster size where hosts are consistently large and dense because large clusters may increase female oviposition efficiency (Rothschild 1987) without negative consequences for dispersing larvae. *Pieris rapae* lay more eggs per alighting where climate limits flight activities (Jones 1987).

Pontia daplidice uses the broadest range of host species of any pierid in this community, yet it does not attain pest status. However, it differs from the two potential pests in two ways. First, it is an inflorescence feeder rather than a leaf feeder. It thus exploits resources that are individually short-lived in most crucifers; it is not pre-adapted to colonize (leafy) vegetable crops. Second, adults do not concentrate in dense crucifer populations (see habitat choice, below). Instead, *P. daplidice* occupies many habitats at very low density (Courtney & Chew 1987).

Euryophagy, like multivoltinism, may permit pest status, but is evidently not sufficient for pierid butterfly pest status.

Pests Prefer Dense Hosts in Mesic Habitats

Of all Moroccan pierids, *Pieris rapae* occurs most abundantly in a wide range of habitats. Populations of *P. rapae* are widespread, although not ubiquitous at high latitudes, high elevations or islands (missing, for example, from Alaska, USA; K. Philip, pers. comm.). With the exception of wooded areas, it is a habitat generalist in Morocco, as well as in Japan and eastern North America (e.g., Takata 1962, Cromartie 1975, Ohsaki 1979). Given the open population structure of *P. rapae* in Japan and North America (Chew 1981, Yamamoto 1981, Ohsaki 1982, Thomas 1984), this butterfly's dispersal capabilities permit rapid spread to new sites (Scudder 1889) and reduce local genetic differentiation (Vawter & Brussard 1983) that might restrict adaptation to its many hosts. Because it favors open areas and is euryophagous, multivoltine and fecund, its frequent colonization of agroecosystems is not surprising.

Pieris rapae prefers open, sunny habitats, in contrast with *P. napi nesis* and *P. melete* in Japan (Ohsaki 1986) and *P. napi macdunnoughii* (Chew 1977a), *P. napi oleracea* (Chew 1981), and *P. virginiensis* Edw. (Klots 1951, Cappuccino & Kareiva 1985) in eastern North America. When ambient temperatures are too high, *P. rapae* adults intercept solar radiation by closing the wings over the body (Ohsaki 1986; cf. *Colias*, Watt 1968). By contrast, *P. melete* and *P. napi nesis* adults regulate body temperature by flying in and out of shaded areas (Ohsaki 1986). Because the oviposition sites of these two butterflies are in shaded areas, Ohsaki (1986) concluded that adults sought sunlight in order to elevate body temperatures above the minimum needed for flight activities such as oviposition. However, these observations raise the possibility that of the three *Pieris* species examined, only *P. rapae* adults are able to prevent overheating in open, sunny areas. Rates and spatial patterns of oviposition in *P. rapae* have diverged adaptively among British, western Canadian and eastern Australian populations (Jones 1977, 1987). Populations in cool or cloudy climates where temperature limits flight activities tend to dump eggs to reduce egg shortfall while butterflies in sunny Australia disperse eggs more widely (Jones 1987).

Pieris rapae's preference for sunlit habitats extends to choosing sunlit oviposition sites, where elevated ambient temperatures reduce the time required to complete larval development to only two-thirds the requirement of larvae growing in shaded habitats (Ohsaki 1982). Elevated temperature of the larval habitat appears to be a key factor in increasing the number of generations achieved in central Japan by *P. rapae crucivora* in comparison with *P. napi nesis* and *P. melete* (Ohsaki 1982;

cf. *Euphydryas gillettei* Barnes, Williams 1981). Similar developmental acceleration could result from females choosing only those hosts that support the most rapid development (Scriber & Lederhouse 1992, van der Reijden & Chew 1992). By choosing a narrow range of microhabitats, *P. rapae* crucivora exploits a large range of hosts evidently without compromising rapid larval development (Ohsaki 1979, 1980, 1982). Curiously, when faster growing female *P. rapae* larvae from Australia and Britain developed into adults, they laid more eggs per alighting than adults from more slowly developing larvae (Jones 1987). Under lab conditions, higher ambient temperatures result in increased forewing length, pupal weight, and subsequent adult fecundity in *P. rapae* (Jones et al. 1982, Kimura & Tsubaki 1986), but possible trade-off between these measures of fitness and the advantage of short generation time in a multivoltine population with overlapping generations (Ohsaki 1982, Jones 1987), and the relation of fecundity to tolerance of parasitoid load (Ohsaki & Sato 1994) is not known.

Pieris brassicae is most frequently associated with fertile open sites where individual crucifers attain great size and density in mesic years (Courtney & Chew 1987). Because larvae of *P. brassicae* leave individual plants after defoliating the plant (Davies & Gilbert 1985), high hostplant density increases likelihood of larvae locating alternative hosts. Crucifer agroecosystems mimic these natural conditions of abundance, soil moisture, and fertility to which *P. brassicae* are attracted. Davies and Gilbert (1985) argue that *P. brassicae* more efficiently uses larval resources than does *P. rapae*, a trait they attribute to the gregariousness of *P. brassicae* caterpillars, which frequently use hosts to which they've dispersed. These latter host individuals are not oviposition sites, but their use permits higher larval survival than if the population were restricted to host individuals that receive eggs. A similar theoretical argument by King (1971), adapted by Chew (1975) for pierid butterflies that disperse to novel hosts in late instars, proposes that additional novel resources increase the equilibrium population size.

Where *P. brassicae* and *P. rapae* co-occur, encounter rates between the two species may be reduced by two mechanisms. First, *P. brassicae* may occupy large plants while *P. rapae* chooses smaller plants or species. In Morocco *P. rapae* often oviposit on tiny individual crucifers (<2 cm height). In the USA, *P. rapae* also sometimes oviposit on tiny crucifers, as do other Nearctic pierine species (*P. napi macdunnoughii*, *P. napi oleracea*, *P. virginiensis*). Second, oviposition deterrent pheromones (ODPs) have been isolated from eggs of both *P. brassicae* and *P. rapae*. Tarsal and antennal receptors of both species responded to the ODPs from their own as well as the other species' eggs (Klijnstra & Roessingh 1986, Schoonhoven et al. 1990a), so it is possible that these pheromones

influence the local distribution of eggs where the two species fly together. Chemical studies show the active compounds are water soluble, relatively non-volatile, and relatively stable (Schoonhoven et al. 1981); they are identified as novel cinnamic acid derivatives (J. J. A. van Loon, personal communication). While laboratory studies of behavior and electrophysiology of European and North American *P. rapae* show that both populations produce and respond to extracts containing ODP (Schoonhoven et al. 1990b), field studies of *P. rapae* behavior and eggs distribution in Australia and the USA have cast doubt on the importance of ODP in oviposition behavior of *P. rapae* (Ives 1978, Root & Kareiva 1984). These results leave unanswered the possible role of ODPs in interspecific interactions under field conditions.

Unlike both *Pieris brassicae* and *P. rapae* in Morocco, *Pontia daplidice* is everywhere, but never dense or abundant anywhere. While both other species are abundant as adults in their preferred habitats, we observed *P. daplidice* in the widest range of habitats, but always in very low numbers. This low-density population structure, combined with lack of preference for mesic habitats or high densities of crucifers, is probably one factor that prevents this insect from reaching pest status in densely planted agroecosystems.

High Fecundity Increases Colonization Potential

Because temperate butterfly population sizes are limited by recruitment into the population (number of eggs laid) (Wiklund & Åhrberg 1978, Hayes 1981, Courtney & Duggan 1983, Courtney 1986), high fecundity in the field enables butterflies to respond rapidly to new abundant resources. *Pieris rapae* is the most fecund butterfly I have ever reared; laboratory and field fecundities of 800+ eggs per female are reported (Norris 1935, Richards 1940, Yamamoto 1978, Yamamoto & Ohtani 1979). High fecundity is achieved partly by allocation to small eggs. In central Japan, *P. rapae* eggs are half the volume of eggs from *P. napi* and *P. melete* (Ohsaki 1982). In the northeastern USA, measurements of egg heights (Scudder 1889, Chew 1981) suggest conservatively that *P. napi oleracea* eggs are 25% larger than those of *P. rapae*. *Pieris rapae* pupae are also larger than many pierines, and its larvae develop faster than *P. napi oleracea* on a wide range of Palearctic crucifers if grown at 20–25°C (van der Reijden & Chew 1992). Developmental rates may constrain the voltinism of species like *P. napi oleracea*, by limiting it to two or three discrete generations, while *P. rapae* occurs continuously from late spring to hard frost in the same areas of eastern North America, a pattern also observed for *P. rapae crucivora* in comparison to *P. napi* and *P. melete* in Japan (Ohsaki 1982). *Pieris rapae*'s overlapping generations may favor individuals

that develop quickly enough to produce an additional generation (Ohsaki 1982, van der Reijden & Chew 1992), further improving *P. rapae*'s ability to respond rapidly to increased availability of host resources. *Pieris brassicae* lays up to 500 eggs per female (Gardiner 1963), a higher lifetime fecundity than the 240–400 eggs per female recorded for *P. napi nesis* (Yamamoto & Ohtani 1979).

In addition to high lifetime fecundity, *Pieris rapae* females are successful colonists because their age-specific fecundity, dispersal behavior, and oviposition behavior permit them increase fecundity in response to increased resources. First, age-specific fecundities peak early during adult life in *P. rapae crucivora* compared to *P. napi nesis* (Yamamoto 1978, Yamamoto & Ohtani 1979). Age-specific fecundity peaks the third or fourth day of adult life, about the time when adult female dispersal often occurs (Root & Kareiva 1984), often as emigration from locally dense populations (Shapiro 1970, Ohtani & Yamamoto 1985). Second, egg-laying rates of *P. rapae crucivora* in the field increase with increasing ambient temperature (from 20 to 25°C) and hours of sunny weather. Thus improved conditions result in higher realized fecundity for this species.

For many other crucifer-feeding pierid butterflies including *Pontia daplidice*, larval cannibalism and the accompanying pierid "red-egg syndrome" may limit the egg density (Shapiro 1981, Courtney 1986) even in areas with dense host populations. By contrast, ample rain may reduce activity of the water-soluble oviposition deterrent pheromones of *P. rapae* and *P. brassicae*, permitting greater density of eggs where available hostplants and mesic conditions will support more larvae.

FROM NATURAL TO AGROECOSYSTEMS

Agroecosystems mimic environments where crucifers flourish—vernal conditions in fertile habitats. In addition, most agricultural practices do not promote plant symbiosis with vesicular-arbuscular mycorrhizal fungi (VAM) because VAM establishment retards early crop growth (Bethlenfalvey et al. 1982) and its later benefits are neutralized by fertilizer and water. Unlike more than 80% of other angiosperm taxa, crucifers do not support symbiosis with VAM (Tommerup 1984, Glenn et al. 1985, 1988), perhaps because they have evolved specialized nutrient uptake capacity (Nye 1981) to exploit lush, but temporary, conditions (Grime 1977). Thus crucifer agroecosystems very closely resemble natural habitats preferred by *P. brassicae* and *P. rapae*.

Multiple Infestation Occurs in Crops and Apparent Plants

Multiple infestation by different pierid species and species from other orders occurs for many crucifer crops (e.g., Bonnemaïson 1965, Williams

& Free 1979, Andow et al. 1986, Andow 1988, Lamb 1989) and for the most apparent and heavily utilized crucifers in the Moroccan pierid-crucifer community. For a multiply infested plant, it is not obvious which herbivores have greater impact. First, infestation by one herbivore species may make host individuals more vulnerable to damage by others e.g., *P. brassicae* damage makes *Brassica oleracea* hosts more susceptible to subsequent aphid damage (Mitchell 1977); however, herbivore damage also may attract parasitoids (Keller 1990). Second, herbivore effects on plants may be unpredictably severe; for example, in a study of herbivore impact on *Solidago altissima* (Asteraceae), Meyer (1993) found that of three herbivores—a xylem-sap feeding spittlebug (*Philaenus spumarius*; Homoptera: Ceropidae), an aphid (*Uroleucon caligatum*; Homoptera: Aphididae), and a leaf-chewing beetle (*Trirhabda* spp.; Coleoptera: Chrysomelidae)—the spittle bug had by far the greatest impact on growth because its activities reduced water transport needed for leaf expansion in growing plants.

Any species under selection from multiple sources and directions will be constrained evolutionarily. Partly for this reason, Moroccan pierid larvae are best adapted to the plants they are most likely to encounter—the same plants with the heaviest herbivore loads. These are conspicuous crucifers whose populations are persistent and numerically stable (Chew & Courtney 1991). This general finding completes the partial picture explored by earlier apparency theory (Feeny 1975). Inverse relationships between palatability and apparency may occur in depauperate communities where a hostplant is under strong directional selection from only one species (Courtney 1982) because these frequently encountered (apparent) plants evolve unpalatability under strong directional selection from a single herbivore source. But in the species-rich Moroccan community there is a stalemate: the most heavily utilized plants cannot respond evolutionarily to directional selection from multiple sources—a situation that applies to crucifer crops in agroecosystems (Andow 1988) as well as to apparent crucifer species in natural habitats.

The Resource Base is the Primary Factor

Even if no evolutionary response is desired (crop plants), frequent encounter enables insect pests to track more easily any changes in resistance of the cultivar. Lamb (1989) reports that the expansion of canola (oilseed brassicas) has been accompanied by vast expansion of the insect fauna attacking these plants. Recent introduction of zero-glucosinolate Canola varieties to large scale cultivation in Canada should have presented brassica pests with hosts lacking this major chemical class of oviposition and feeding stimulants (reviewed by Chew 1988).

However, after introduction of these cultivars, the fauna of oilseed brassicas did not change. Lamb notes that major changes have accompanied shifts in the resource base and cultural management, rather than changes in phytochemical traits of the cultivars (Lamb 1989).

Another observation supporting this view is that many heavily infested crops are not preferred by their pests in laboratory tests where alternative hosts are equally available. Experimental assessments of *P. rapae* oviposition and larval preference conclude that agricultural crops e.g., cabbage (*Brassica oleracea* cultivars), are not preferred by either butterflies (Renwick & Radke 1985) or larvae (Chew, unpublished observations), although some *Brassica* cultivars contain specific glucosinolates that are strong stimulants for ovipositing *P. rapae*. Similarly, cotton is severely damaged by several *Heliothis* species but is not a preferred host of any *Heliothis* species (Fitt 1989); and cranberry plants are not preferred hosts of a major pest, cranberry weevil (*Anthonomus musculus*; Coleoptera: Curculionidae) (Mechaber & Chew 1991). These findings argue that outbreak populations occur on crops because of their abundance and phenology, not because of their intrinsic palatability to the potential pest.

The crucial role of phenology in resource base management is illustrated by what occurred in the United Kingdom after widespread introduction of Canola® (oilseed brassica). Cabbage root fly (*Delia radicum*; Diptera: Anthomyiidae) is a major pest. Finch (1989) reports that only serendipity averted a potentially serious pest situation that might also have provided a crucifer reservoir for increased pest problems on cruciferous vegetable crops. Because the harvest of spring-sown oilseed brassica crops coincided with cereal harvests, oilseed brassicas were sown in the fall so that harvesting machinery could be used on both cereals and oilseed crops. Nearly all of the British crop of oilseed brassicas, which now totals about five times the acreage planted with vegetable crucifers, is sown in the fall (Finch 1989). Because *D. radicum* cannot easily attack seedlings in the fall, it cannot become established on overwintering oilseed crops. Finch notes that if oilseed brassicas were rotated in Canada, similar phenology management could be useful in controlling *Delia* species, which in Canada have a single midsummer generation (Finch 1989).

Could Wild Crucifers Harbor Potential Pest Populations?

Do weedy or indigenous crucifers act as reservoirs for crucifer crop pests? Finch (1988, 1989), in a detailed commentary on *Delia radicum*, calculates the proportion of infestation likely to arise from weedy crucifers in hedgerows. He concluded it is trivial because hedgerow cru-

cifers are sporadic and rare, and because *D. radicum* develops poorly on these weeds.

In the case of the crucifer-feeding Moroccan butterfly community, most are unable to respond to increased host resources by rapidly increasing population density. In the case of *Pieris napi oleracea*, prior to cutting of hardwood forest and destruction of the herbaceous understory, native *Cardamine* and *Dentaria* species supported the vernal brood of *P. napi oleracea*. *Pieris napi oleracea* propagated on these wild hosts and then emerged in large numbers as pests on summer cole crops near wooded areas. But unlike hedgerows, these wooded areas were extensive and their crucifer stands were large. Earlier observers supposed that *P. napi oleracea* was victim to competition with its naturalized congener *P. rapae* (Scudder 1889, Klots 1951). More recent evidence shows the two species use similar resources, but the forest is a vernal refugium for *P. oleracea*. Where woods or native herbaceous understory have been destroyed and supplanted by naturalized weeds unsuitable for *P. oleracea* larvae, this species has disappeared (Chew 1981). Local extirpation occurs when *P. oleracea* are deprived of a vernal host. Nearly all hosts now available in urban and suburban areas where *P. oleracea* used to fly are naturalized crucifers on which females oviposit and larvae die (Bowden 1971, Chew 1977b). A possible exception is the garlic mustard *Alliaria petiolata*, which grows at woodland edges, to which larvae of some *P. oleracea* appear to be adapting (Courant et al. 1994). Were *P. virginensis* larvae able to adapt to this weed, it would gain a large larval resource (Porter 1994) and perhaps become multivoltine (Courant & Chew 1995). Where habitat change has eliminated suitable native hostplants, other indigenous North American pierids, *P. virginensis* and *Anthocharis midea* Hubner, oviposit on naturalized crucifers, but many of these support larval growth poorly if at all (Chew 1977b). When native vegetation in their wooded and rock ledge habitats is destroyed or severely reduced, they likewise disappear locally.

From a viewpoint of promoting biodiversity, destroying native herbaceous understory is an ecologically unacceptable mechanism for regulating an agricultural insect pest (Gilpin, Gall & Woodruff 1992). But since most wooded areas of the world have been cut at least once, and their understories—including native crucifers—are often destroyed, populations of *Pieris oleracea* and its many relatives in the *P. napi* complex are now reduced compared to earlier periods (Ohsaki 1979, Chew 1981, Yamamoto 1981). Even if these crucifer-feeding pierid populations were not reduced by suburbanization, their inability to tolerate broad expanses of open habitat (pierines) and egg dispersion (especially among euschloeines, Shapiro 1981) make it extremely un-

likely that these species would attain pest status in open agricultural habitats.

CONCLUSIONS

Conspicuous, dense, numerically stable crucifer stands support the largest herbivore loads (Root 1973, Chew & Courtney 1991). If these stands happen to be crops, pierids and other herbivorous invertebrates are only exhibiting the same behavior observed in indigenous habitats. Changing plant defense mechanisms may be ineffective or result in rapid adaptation to plant resistance, a concern expressed about broad-scale applications of some biological control methods (Altman, 1992, Abbot 1994). By manipulating the numerical stability of the crop, for example by rotation in different seasons or years, we may reduce attainment of outbreak proportions by these insects. But these large-scale manipulations of the resource base—the only kind of change that seems likely to control these two pierid pests and other crucifer pests in large agroecosystems, requires implementation at landscape scales (Allen & Hoekstra 1992). On a local scale, manipulating the apparency of the stand, for example by small scale (single row) intercropping (Tahvanainen & Root 1972, Vandermeer 1990), may reduce colonization by crucifer herbivores including *Pieris brassicae* and *P. rapae*. But as Finch (1988) observes, inexpensive, short-term floating row covers have superseded intercropping for many vegetable crops. These row covers directly reduce crop apparency and butterfly access to oviposition sites and thus are very effective at controlling pierid colonization.

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UNDERSTANDING AND MISUNDERSTANDING THE MIGRATION OF THE MONARCH BUTTERFLY (NYMPHALIDAE) IN NORTH AMERICA: 1857-1995

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ABSTRACT. Since 1857, amateurs and professionals have woven a rich tapestry of biological information about the monarch butterfly's migration in North America. Huge fall migrations were first noted in the midwestern states, and then eastward to the Atlantic coast. Plowing of the prairies together with clearing of the eastern forests promoted the growth of the milkweed, *Asclepias syriaca*, and probably extended the center of breeding from the prairie states into the Great Lakes region.

Discovery of overwintering sites along the California coast in 1881 and the failure to find consistent overwintering areas in the east confused everyone for nearly a century. Where did the millions of monarchs migrating southward east of the Rocky Mountains spend the winter before their spring remigration back in to the eastern United States and southern Canada? Through most of the 20th century, the Gulf coast was assumed to be the wintering area, but recent studies rule this out because adults lack sufficient freezing resistance to survive the recurrent severe frosts.

Seizing the initiative after C. B. Williams' (1930) review of monarch migration, Fred and Norah Urquhart developed a program that gained the interest of legions of naturalists who tagged and released thousands of monarchs to trace their migration. Just as doubts in the early 1970s over whether there really were overwintering aggregations of the eastern population, on 2 January 1975 two Urquhart collaborators, Kenneth and Cathy Brugger, discovered millions of monarchs overwintering high in the volcanic mountains of central Mexico. This allowed a synthesis of the biology of this remarkable insect, including its migration and overwintering behaviors, its spread across the Pacific Ocean to Australia, its coevolution with milkweeds, and its elaborate milkweed-derived chemical defense which probably makes possible the dense aggregations during the fall migration and at the overwintering sites.

Many important questions remain. Can monarchs migrate across the Gulf of Mexico? Can they migrate at night? Do they exploit strong tailwinds? Do they migrate to Central America? Do they overwinter elsewhere in Mexico or Central America? How much interchange is there between the eastern and western North American populations? How important is the fall migration along the Atlantic coast compared to the migration west of the Appalachian Mountains? What causes annual fluctuations in the size of the fall migrations?

Beautiful and mysterious, the monarch's overwintering colonies in Mexico rank as one of the great biological wonders of the world. Unfortunately, these colonies are the monarch's Achilles' heel because of human population growth and deforestation in the tiny Oyamel fir forest enclaves. Additional risks arise from the increasing use of herbicides across North America which kill both larval and adult food resources. As a result, the migratory and overwintering biology of the eastern population of the monarch butterfly has become an *endangered biological phenomenon*. Without immediate implementation of effective conservation measures in Mexico, the eastern migration phenomenon may soon become biological history.

In writing this paper for Charles Remington's honorarial issue of the *Journal of the Lepidopterists' Society*, fond memories flood forth of my days as his graduate student at Yale University from 1953 to 1957. My very first seminar lecture was on the migration of the monarch butterfly, *Danaus plexippus* (L.), and this set the stage for what will soon be 40 years of studying diverse aspects of the biology of this

fascinating creature (reviews in Brower 1977a, 1984, 1985a, 1985b, 1986, 1987b, 1988, 1992).

The present paper reconstructs the history of understanding the migration of the monarch butterfly in North America. To my knowledge, a detailed analysis of the ideas and the people who developed them has never been attempted. The story, a result of the combined observations of professional and amateur lepidopterists over more than a century, reflects the spirit in which Charles Remington, then a graduate student at Harvard, and his friend and colleague Harry Clench founded The Lepidopterists' Society in 1947 (Clench 1977). My purpose is to weave together the strands, to follow some of the red herrings, and to discuss several aspects of the migration biology that are still incompletely understood. Timely resolution of these questions should enhance efforts to preserve the monarch's mass migratory and overwintering behaviors which, regrettably, have become an endangered biological phenomenon (Brower & Pyle 1980, Brower & Malcolm 1989, 1991).

The first great student of the monarch butterfly was Charles Valentine Riley, who emigrated from England and rose to lead midwestern, and then national entomology in the USA (Packard 1896, Essig 1931). In addition to being a first rate scientist, Riley was a talented artist who beautifully illustrated his descriptions of insect natural histories, and he fostered the English tradition of collating and publishing letters from a diversity of field observers, including many on the migration of the monarch. Anecdotal science on the monarch predominated well into the 20th century. In 1930, C. B. Williams of Edinburgh University reviewed monarch migration in his book, *The Migration of Butterflies*, which he periodically updated (Williams 1938, 1958, Williams et al. 1942). Shortly after the founding of The Lepidopterists' Society, Williams (1949:18) called for information from members and defined questions for much of the migration research that would follow: "What happens to the butterflies that fly through Texas in the fall? Do they go on to Mexico? If so, do they hibernate there, or remain active, or breed?"

University of Toronto entomologist Fred A. Urquhart and his wife Norah took up the Williams challenge in 1940 and began tracing the fall migration of the monarch via a long-term tagging program, which would come to involve more than 3,000 research associates (Urquhart 1941, 1952, 1960, 1978, 1979, 1987, Anon. 1955). The Urquharts communicated with their collaborators through an annual newsletter, published numerous papers on monarch biology, and carried on the tradition of incorporating amateurs' notes in their writings. According to Urquhart and Urquhart (1994), the final newsletter to their Insect Migration Association was issued as Volume 33 in 1994.

Speculations about the destination of the eastern monarch migration

became increasingly confused throughout the first three quarters of the 20th century because of the mysterious disappearance of what had to be vast numbers of butterflies that annually bred over an area of at least three million square kilometers. Many tortuous hypotheses were devised until resolution came in Urquhart's August 1976 *National Geographic* article announcing the discovery of the phenomenal overwintering aggregations in Mexico. This culmination of the Urquharts' lifetime efforts was one of the great events in the history of lepidopterology.

FIRST OBSERVATIONS OF THE FALL MIGRATION:
REPORTS FROM KANSAS TO CONNECTICUT

Aside from a possible sighting of monarchs migrating in eastern Mexico during one of Christopher Columbus's expeditions (Doubleday & Westwood 1846–1852:91), D'Urban (1857) was apparently the first to report a migration of monarch butterflies. He described the butterflies appearing in the Mississippi Valley in "such vast numbers as to darken the air by the clouds of them" (p. 349). During September 1867 in southwestern Iowa, Allen (in Scudder & Allen 1869) described monarchs gathered in several groves of trees bordering the prairie "in such vast numbers, on the lee sides of trees, and particularly on the lower branches, as almost to hide the foliage, and give to the trees their own peculiar color" (p. 331). Although this clustering behavior was initially interpreted as a means of avoiding strong prairie winds, it soon became evident that it was associated with large southward movements of monarchs in the fall.

The first collated evidence of massive fall migrations was published in 1868 by two American entomologists, Benjamin Dann Walsh and Charles Valentine Riley, who had independently emigrated from England to Illinois and were both keen to establish entomology as a science useful to farmers. Additionally, as evidenced in Darwin's correspondence (in F. Darwin and Seward 1903a:248–251, 1903b:385–386), Walsh and Riley were both influenced by *The Origin of Species* (Darwin 1859). Walsh, born in 1808, developed his interest in insects when he was nearly 50 years old, and launched his career in 1865 as associate editor of the *Practical Entomologist* in which he wrote, reprinted and edited numerous articles and letters, and answered letters from curious people and farmers besieged by insect pests. Within a decade he became the first Illinois State Entomologist (Riley 1870, Darwin and Seward 1903a). In contrast, Riley, born in 1843, had left his family home in England at the age of 17. By the time he was 20, he had begun publishing entomological notes in the Chicago-based *Prairie Farmer* (Ashmead 1895) and shortly thereafter became the journal's prolific entomological editor. In September 1868 the two men founded *The American Entomologist*, which Riley continued after Walsh died prematurely in

1869 (Riley 1870). In 1868 Riley was appointed State Entomologist of Missouri, in 1876 he moved to Washington, D.C. to become Chief of the newly founded U.S. Entomological Commission, and shortly thereafter he founded the Smithsonian Institution's insect collections.

Beginning in 1864, Riley used the *Prairie Farmer* to establish a correspondence network with midwestern farmers who were plagued by the migratory Rocky Mountain Locust. Combining his observations and high quality drawings with the information in hundreds of letters from farmers and lay people, Riley generated enormous interest in insect life histories in both the United States and Canada. He also published prolifically in virtually all the major biological journals of the period: Derksen and Scheiding-Göllner (1968) listed 50 pages of Riley's references. Among his many achievements was rescuing the French wine industry by unraveling the life history of the grape *Phylloxera* (Phylloxeridae) which had 19 distinct forms (Riley 1874, Smith 1992). In what may be considered the founding paper on the broad study of the biology of the monarch, Riley (1871) described and illustrated the life histories and mimicry of the monarch and viceroy butterflies. Darwin wrote Riley on 1 June 1871 saying "I am struck with admiration at your powers of observation. . . . The discussion on mimetic insects seems to me particularly good and original" (in Darwin & Seward 1903b:386).

As pointed out by Dr. Edward Smith, (letter to LPB, 10 June 1994), the garnering of information on monarch movements and numbers was a valuable outcome of the network of farmers that Riley had set up. Correspondents indicated that monarchs appeared in great abundance in several midwestern states during September 1868. Thus in Riley (1868) and in Walsh and Riley (1868), Davis described the sudden appearance of vast swarms in different parts of Madison, Wisconsin; Barnard noted great multitudes in Manteno, Illinois; and Sibley recounted millions flying over St. Joseph, Missouri. Peabody (1880) independently recalled having seen another large swarm in Racine, Wisconsin in the first week of September, 1868 (Racine is on the western shore of Lake Michigan south of Milwaukee). Westcott (1880) reported large flights and clustering in Racine during September or October in two of the seven years between 1873–1880. Although Bethune (1869) noted monarchs as abundant in the Toronto area in July 1869, no swarms were reported that year. During September and October 1870, Wells (in Riley 1871) noted large numbers of monarchs flying overhead in a S/SW direction through both Manhattan, Kansas and Alton, Illinois.

New reports during the 1870s extended the range of the fall swarming behavior farther east. Monarchs were exceedingly common during the summer of 1871 throughout New England (Sprague 1871), and in September, Saunders (1871:157) observed "vast numbers—I might safe-

ly say millions" clustering on a semicircle of trees on the Canadian shore of Lake Erie, about 130 km NNE of Cleveland, Ohio. This was the first report that associated overnight roosting with the swarming behavior. Werneburg (in Scudder 1889:1083) had also noted endless masses migrating southwesterly through Connecticut in 1871. The following fall (1872) an immense swarm was observed in flight over Cleveland, Ohio, where the butterflies remained abundant for several days (Ison, in Riley et al. 1875). Ison speculated that the monarchs had flown across Lake Erie from Canada. He was undoubtedly correct because Point Pelee, Ontario, to the northwest of Cleveland, was later determined to be a major concentration point for the fall migration across Lake Erie (Moffat 1901b, Saverner 1908).

ESTABLISHING THE MONARCH AS A BIRD-LIKE MIGRANT

In relating numerous accounts of the monarch congregating in "immense swarms or bebies" in the prairie states, Riley (1871:151) struggled to understand the significance of this annual "assembling" behavior. As was then in vogue in the entomological community (cf. Hall 1887), Riley considered insect movements as largely irruptive, and initially eschewed the idea that the monarch butterfly could perform directed long distance flights comparable to the migration of birds. He tentatively hypothesized (p. 152) that during "the seasons when the milkweeds are either destroyed [i.e. in the fall] or have not yet started to grow [i.e. in the early spring] . . . low temperatures of the seasons instinctively prompt them to wend their way southwards. The probabilities are that these swarms are eventually destroyed" . . . Re-establishment of monarchs the following spring in the north, therefore, had to depend on the survival of hibernating "impregnated females" that begin laying their eggs early in May. Riley thus initially propounded an emigration-death hypothesis for the "migrating bebies" and assumed that the re-establishment of the monarch populations the following spring was by the breeding of the non-migrant individuals which had successfully hibernated through the winter in the north.

In August 1875, Riley, Saunders, Scudder and others exchanged ideas on the swarming behavior at a sub-meeting of the Cambridge Entomological Club held in Chicago (Anon. 1875). William Saunders, the preeminent Canadian entomologist of his time, founded the Entomological Society of Ontario and later, along with Charles Bethune, would found the influential *Canadian Entomologist*. Samuel H. Scudder (1889) published *The Butterflies of the Eastern United States and Canada with Special Reference to New England* and became one of the most famous 19th century U.S. butterfly biologists (for further biographical information, see Bethune 1909, Essig 1931, Clench 1947, Remington 1947 and Mallis 1971). While the word "migration" is conspicuously

absent from the proceedings, this 1875 meeting was historically significant because it instigated an international interest in monarch travels.

In early October 1876, William H. Edwards (1877) observed a line of butterflies flying southward continuously for an hour near Boston (Edwards, another prominent 19th century lepidopterist, is best known for his beautiful *The Butterflies of North America*, 1868–1897). On reading the October report, Scudder (1877) speculated that the butterflies must have been monarchs, and interpreted the observation as migration per se. Both Edwards and Scudder subsequently maintained a long-term interest in the monarch and were frequently at odds over interpreting the most current data.

The accumulation of anecdotal notes of monarch swarms from the prairie across the Great Lake States to New England, supplemented by frequent newspaper and signal officer reports of swarms passing over Iowa, Kansas, Missouri, and Texas, finally convinced Riley (1878a:273–274, republished in 1878b) that the monarch indeed performs a bird-like fall migration. While still maintaining that a few individuals hibernate in the north, he now proposed that, following the deterioration of milkweeds, most of the monarchs instinctively congregate in masses and migrate southward to find nectar sources and “to reach a warmer country in which to hibernate.” With great prescience, he contended that “Southerly timber regions offer most favorable conditions for such hibernation” (pp. 273–274).

Stroop’s (in Stroop & Riley 1870, see also Riley 1871:151) springtime observation of a “bevy” of about 30 worn monarchs south of Dallas, Texas on 31 March 1870 appears to have been a key piece of the puzzle: Riley now (1878a:274) proposed that the few females that survived hibernation “upon waking from their winter torpor, make at once for the prairies, where the milkweeds most abound. Faded and often tattered, they may be seen flying swiftly over such prairies. . . I have no doubt but that they travel thus for many hundreds of miles, keeping principally to the north, and, ere they perish, supplying the milkweeds here and there with eggs. . . . In short, these migrations find their readiest explanation in the instinct of the species to lengthen the breeding season and to extend its range. . . . There is a southward migration late in the growing season in congregated masses [i.e. a fall migration], and a northward dispersion [i.e. a spring remigration] early in the season through isolated individuals.”

The next piece of the puzzle bore out Riley’s (1878a, 1878b) hunch about where monarchs must spend the winter. Roland Thaxter (1880, republished in 1881), who would become a professor of botany at Harvard University (Clark 1941), in January 1873 observed huge numbers of monarchs densely aggregated across an acre of pine trees along the Gulf Coast in Apalachicola, Florida, about 100 km southwest of

Tallahassee. Riley (1880b) seized upon Thaxter's discovery as proving that the bird-like migration of the monarch involved a fall migration to the south, hibernation there during the winter months, and a return migration the following spring. However, he still maintained that most of the hibernating individuals comprising the overwintering swarms must perish. In what may have been his final view on overwintering, Riley (in Riley et al. 1893:270) published an observation of monarchs having been eaten by mice along the Gulf Coast in Texas, while "hidden away in their hibernating quarters in the south."

Riley's increasingly sophisticated understanding of monarch biology was cut short on 14 September 1895, when he died at the age of 52 as a result of a bicycle accident (Remington 1947a, Mallis 1971). It was indeed ironic that, 25 years before his own accidental death, Riley (1870) had described the loss of his co-editor and mentor Benjamin Walsh, who died from internal injuries sustained while jumping out of the way of a locomotive in his hometown in Rock Island, Illinois.

TUTT'S CHALLENGE AND MOFFAT'S REBUTTAL

By the end of the 19th century, J. W. Tutt, editor of the British *Entomologist's Record and Journal of Variation*, was drawn into the fray, thus initiating overseas interest in monarch migration. Tutt (1898, 1899, 1900) rejected Riley's two-way migration hypothesis and held that the monarch was no different from the known one-way migrants (=emigrants) such as *Vanessa atalanta* (L.) (Nymphalidae) or *Colias croceus* Geoffroy (Pieridae), which breed continuously in their native habitats in southern Europe and north Africa. Periodically over-reproducing there, they emigrate to England where they produce one or more generations, which then die during the winter without a return migration (cf. Carter & Hargreaves 1986).

Tutt (1902:262–263) finally argued that the purported fall migration of monarchs had been misinterpreted; rather, he maintained that they were dispersing at random in the fall, perishing without overwintering and without hibernating. Recolonization of the north would periodically occur when the monarchs, analogous to *Vanessa* and *Colias*, again overbred in their southern range and spread northward, breeding through the summer on the milkweeds, and then all dying (see also Tutt 1900: 185, 208, 254).

Tutt's challenge was summarily rejected by Scudder (1898) and then rebutted by John Alston Moffat (1901b), an amateur entomologist who was secretary of the Entomological Society of Ontario (Bethune 1905). Moffat's prior papers on the monarch (1880–1900) had been largely observational, but he now combined facts and hypotheses in a thought-

ful review of the literature. In his words, the monarch "is a southern butterfly, which has inherited a powerful migratory instinct, and is endowed with a capacity to indulge it to the utmost limit. . . . The northern portion of the American Continent . . . is where it finds the conditions most favorable for . . . multiplying . . . to an unlimited extent. But it cannot endure frost, therefore goes southerly in autumn, and . . . gathers in immense swarms before it starts out. It makes the journey in easy stages, spending months on the way. As it does not hibernate, it keeps on the move south-west until its breeding season comes around, when these, or more southerly bred specimens, start the northerly movement" (Moffat 1901b:50).

Moffat (1902b) urged Thaxter to fill in the details of the behavior of the butterflies he had seen overwintering along the Florida Gulf Coast in the winter of 1873. Thaxter (in Moffat 1902b) replied that the butterflies had begun to scatter and mate in February. This now fully convinced Moffat that monarchs were not hibernating *per se* along the Gulf Coast, but were passing the winter in an active but reproductively repressed state. Moffat deduced that a northward spring remigration of these monarchs in February would be too early for them to exploit the spring milkweed resurgence in the north. He then proposed a new, complex hypothesis: the Florida butterflies must fly farther southward in search of milkweeds, while those that had flown even farther south in the fall would fly northward, also in search of milkweeds.

Lugger (in Riley et al. 1890) noted that numerous monarchs migrating through Baltimore in October had frozen. Moffat had reviewed freezing resistance in insects (1893), and with considerable insight, he was dubious that Florida and the Gulf Coast could be successful overwintering areas. He had noted an adult monarch that froze to death on his windowsill (1901a) and mentioned (1901b) having seen dead chrysalids after frosts. Citing occasional northern cold fronts which had been reported to destroy orange groves and even to have killed overwintering bluebirds in Florida, he (1902b) proposed that such frosts would kill all the overwintering monarchs along the south Atlantic states. Noting that the northern region had been recolonized successfully by monarchs but not by bluebirds after a big freeze, Moffat astutely reasoned that the recolonizing monarchs must have originated, not from Florida, but from their "tropical home" (p. 81). Thus, while not explicitly stating it, Moffat proposed a frost-free winter breeding range for the monarch south of the continental United States which would be the source of the spring remigrants. This would have to be Mexico, the Caribbean, Central America or South America. As far as I can ascertain, he has never been credited for this important deduction, probably because Tutt (1902: 292-295) regarded the collective evidence as inadequate.

EARLY SPECULATIONS AND OBSERVATIONS ON THE
FALL MIGRATION TO MEXICO

The first suggestion that monarchs migrate to Mexico per se apparently was made by Jennie Brooks (1907, 1911), a naturalist who for several years had observed them migrating through Lawrence, Kansas during the autumn. In her words, "From the north they came . . . to the south they swept away . . . as far as I could see them—to Texas, to Louisiana, to Mexico" (1907:111), and "all along the Canada line east and west the mighty winged host of monarchs advances, when instinct stirs, straight down across the states to Mexico" (1911:48). Brooks' 1907 essay also was the first detailed description of the monarch's clustering behavior during the fall migration. She combined elegant prose, high quality observation, counts of monarchs in the clusters, and actual experimental manipulation. No one before or since has so fully documented watching the quiescent monarchs all night long, their reaction to the rising sun, cluster break-up, and resumption of the southward migration. Her 1911 essay, published in the beautiful magazine *Country Life in America*, included the very first photograph—taken by flashlight—of "sleeping monarchs on the twigs of a cedar tree." In an article adjacent to Brooks', Thoms (1911) provided further quantitative data: during August 1910 at Green Lake, Minnesota, one cluster contained 300 individuals, another 500. His note included a photograph of disturbed monarchs flying against the sky in which he counted 1,300 individuals.

There are remarkably few records of the fall migration through Mexico (Urquhart 1960:261–262). The first was made in 1890 by Sir Rider Haggard (in Williams et al. 1942:171) who reported thousands of monarchs flying southward in Orizaba, an area east of Mexico City along the easternmost peak of the Transverse Neovolcanic Belt. The most substantive observation was Rzedowski's (1957) on 27–28 October 1956 along the Sierra Madre Oriental, near Ciudad del Maiz in the State of San Luis Potosi at about 1100–1500 m elevation. He and an assistant saw small numbers of monarchs flying over the vegetation through a xeric habitat 2–6 m above the ground in a sustained southeasterly direction. Later in the afternoon, they also observed the formation of an aggregation: hundreds of monarchs zeroed in and vied for position (=assembling behavior) on one of several mesquite trees (*Prosopis juliflora* D.C., Leguminosae). Speculating on the southeasterly direction of the migration, Rzedowski offered two hypotheses: the monarchs were following the southeasterly trajectory of the Sierra Madre Oriental, or they were actively crossing these mountains to reach the humid tropical regions along eastern Mexico (I interpret Rzedowski's comments as implying that the monarchs were either headed (a) to an unknown overwintering area, or (b) to a lowland area where they could

breed). In the same paper, Rzedowski also reported that Pelaz had observed a migration through the same area in December 1951. The southeasterly direction of the migration through this area subsequently was verified by Calvert in the late 1970s (unpublished observations, summary in Calvert & Brower 1986).

The apparent absence of representations of monarch butterflies in the art and pottery of prehispanic Mexico (Beutelspacher 1980, 1988) is curious, but may be related to the fact that the principal overwintering area was in a "no man's land" between the Aztec culture to the east and the Tarascan culture to the west (Arbingast et al. 1975:24, 73). It could be profitable to search the early Mexican literature in more detail for records on the overwintering and migrations, e.g., the late 18th century writings of botanist-explorer Don Martin de Sesé and the renaissance Mexican, José Antonio Alzate, who reported on many scientific and natural history topics (see Motten 1950, Leopold 1959).

Monarchs migrate in great numbers through Angangueo in north-eastern Michoacan (Brower & Calvert, personal observations 1977–1995). This town is near the center of the major overwintering areas, including the Sierra Campanario, Sierra Chincua, Sierra Chivati and Sierra Pelon (see Fig. 1 in Calvert & Brower 1986). In 1909 Angangueo's rich silver mines came under the control of the American Smelting and Refining Corporation (ASARCO), part of the Guggenheim family empire (Carreño 1983). More than 3,000 workers shipped 200 tons of high grade silver ore every day to the ASARCO smelters in Aguascalientes (Bernstein 1964:56, O'Connor 1932). In their quest for riches, apparently no one ever took the time to record the incredible numbers of migrants swirling around them on the way to overwintering valleys, less than 15 km from the center of town.

YEARS OF MUDDLING: THE HIBERNATION HYPOTHESIS

Nineteenth century lepidopterists knew that several species of Holarctic nymphalid butterflies in the genera *Gonepteryx*, *Nymphalis*, *Polygonia*, and *Vanessa* survive winter freezing in the north temperate region as adults inside of tree holes and hollow logs, and this they called "hibernation" (see Holland 1898, Ford 1945, Urquhart 1978, Young 1980, Scott, 1986). Riley had described hibernating larvae in Nymphalid butterflies, including *Limenitis archippus* (Cramer) (1871) and *Asterocampa* (Riley 1874), and apparently assumed (1871:144) that "impregnated" monarch females can survive the winter in the north by hibernating in the adult stage. The facts that trickled in did little to settle the issue. For example, in Amherst, Massachusetts, Parker (1872: 115) reported "an interesting capture of a much worn and faded female *Archippus*" on 12 May 1871 . . . as "bearing on the winter history of the species" (nineteenth century monarch nomenclature varied, and

included the generic names *Anosia*, *Danais* and *Danaus*, and the specific names *archippus*, *menippe* and *plexippus*; see Scudder 1889:726, Ackery & Vane Wright 1984:202.)

The hibernation hypothesis had been accepted uncritically by Saunders (1873), Scudder and Gulick (1875), Edwards (1876a, 1876b, 1878), Weir (1876), Distant (1877) and Bowles (1880). Riley (1878b:273–274) firmly restated that “The *archippus* butterfly hibernates.” However he now rejected “Saskatchewan country” as a place of hibernation, implying that they would freeze to death in the far north. He still maintained that they hibernated in “the temperate belt . . . within hollow trees and in other sheltered situations,” and he speculated that the major hibernation range would prove to be in “the southerly timbered regions.” Thaxter’s (1880) discovery of overwintering butterflies along the Florida Gulf Coast led Riley (1880b:101) to place even more emphasis on the south as the place of hibernation, and Riley was now dubious about the prairies where “there is a want of protecting forest as will permit hibernation . . . even if the butterflies could withstand the severe winter” (see also Riley et al. 1890). Scudder (1889:727–748) struggled with the evidence for and against hibernation in the north, and appears to have concluded that a few do survive winters as adults, at least as far north as New England. This view subsequently prevailed in his popular book *Frail Children of the Air* (1895:141) as indicated by his statement that “woodsmen sometimes, in cleaving open a tree, will discover a little colony of hibernating butterflies, as has been done in the case of the monarch.”

Moffat (1888) doubted that monarchs quiescently hibernate inside trees. He had observed that the first individuals appeared in Ontario in late May, and, noting their wing wear, deduced that they were too fresh to have hibernated. Further doubt was generated by Emily Morton (1888:226–227) in lower New York state. “Having been requested by my friend, Mr. Wm. H. Edwards, to make observations on *Danais Archippus*,” Morton reported that she had peeled and split “many and many a stump” in search of hibernating monarchs, without success. She did, however, discover a mourning cloak (*Nymphalis antiopa* (L.) Nymphalidae) “torpid, though still alive . . . in the very center of a stump cosily mixed up with the damp saw-dust left by the ants and other borers.” Holland (1898:82), in the first edition of his popular and influential *The Butterfly Book* (see Remington 1947b), apparently accepted Moffat’s deduction, stating that monarchs do not hibernate in “any stage of their existence.” Moffat (1901b:49), reflecting on Thaxter’s observation that monarchs were copulating during their sojourn along the Gulf Coast of Florida, concluded that “we have not the slightest reason to believe that they hibernate (sic) at all, anywhere.”

Moffat (1902b:79), now intent on rejecting the hibernation hypothesis, asked Thaxter to provide the exact dates of his observations. Thaxter replied that he had first sketched the clustering butterflies on 3 January 1873 and that the swarms did not begin to scatter until February, at which time many were seen "*in coitu*" (these dates had been confirmed by Scudder 1889:743, who also had written to Thaxter). Armed with this supplemental evidence, Moffat concluded that the flocks of monarchs "were not there in search of a place to hibernate, but with the intention of passing the time in an active state until their season of breeding had arrived" (p. 79). He confidently entitled this paper: "*Anosia archippus* does not hibernate."

Early workers recognized that courtship, oviposition and egg maturation were repressed in monarchs immediately prior to the fall migration (Edwards 1878, Riley 1878b, Moffat 1901b). However, they lacked sufficient knowledge to associate these changes with the day-length and hormonally mediated syndrome (Johnson 1969, Barker & Herman 1976b) that we now know controls several aspects of monarch physiology and behavior. These include the onset and breaking of reproductive diapause, the associated repression and stimulation of sexual activity, the fall and spring migrations, and the aggregations along the fall migratory routes and at the overwintering sites (Brower 1985a, Rankin et al. 1986, Scoble 1992, Herman 1993, James 1993, McNeil et al. 1995).

Moffat's ultimate rejection of hibernating in the north was embraced by the lepidopterists' community well into the 20th century (e.g., Ricker 1906, Inkersley 1911, Shannon 1916, Comstock 1927, Shepardson 1939: 26, Holland 1940, 1945:101, Shannon 1954). However, Williams' (1930: 152-153) seminal review of butterfly migration apparently ignored the rejection because of the discovery of quiescent overwintering colonies of monarchs in California (see below). This clearly indicated that monarch adults do hibernate in some parts of their annual range, as Riley had realized (Riley & Bush 1882). Failure to locate consistent overwintering areas east of the Rockies, together with the deductive rather than empirical evidence against hibernation adduced by Moffat, led several authors (e.g., Clark 1941:534, Klots 1951, Baker 1978, Shull 1987) to speculate that monarch adults and perhaps even pupae can withstand freezing temperatures. They thus resurrected the idea that monarchs hibernate in the north!

In retrospect, Riley's intellectual intermingling of the physiological phenomenon of hibernation with the geographic location of hibernation proved a major distraction in understanding the migration of the monarch (Ackery & Vane-Wright 1984). The discovery of monarchs overwintering in Mexico, together with our modern understanding of insect

diapause, would seem to provide the necessary coup de grâce to the recurrent hypothesis that monarchs hibernate in their summer breeding range.

DID THE MIGRATION EXPAND EASTWARDS DURING THE LATTER PART OF THE 19TH CENTURY?

Prior to the 1880s, as we have seen, the majority of reports of fall "swarming behavior" were from the Great Plains states. Riley (1880b: 101) had described monarchs flourishing on "the vast plains and prairies lying to the north between the Mississippi River and the Rocky Mountains" where "milk-weeds abound." While this may have reflected his living in the midwest as Missouri State Entomologist, it also is possible that the Great Plains were where most monarch breeding did naturally occur. Perhaps significantly, Doubleday and Westwood (1846-1852:90) stated that "*Danais Archippus*" is abundant even in "the largest towns of the Middle and Northern states." Shannon's (1916:229-230) description of monarchs migrating through Minnesota, Iowa, Kansas, Oklahoma and eastern Texas is certainly consistent with the early observations. Contrasting these numbers with the smaller migrations through Illinois and the states to the east, he stated that the "wide highways of the Great Plains and West Central States offer the most frequent reports of remarkable butterfly spectacles . . . gatherings of almost unbelievable magnitude . . . move forward in . . . congregations . . . miles in width . . . forming veritable crimson clouds."

I feel it is significant that it was not until the 1880s that large fall migrations and aggregations were reported farther east and along the Atlantic coast. Abbott (1887:80) described a migration of monarchs extending 40 km in length through New Jersey in September 1881 and stated that "several such migrations occurred at about this time in the New England and Middle States." Wintle (1885:179-180) noted large numbers of clustering monarchs in the Montreal area on 22 August 1885 and said "I don't remember having seen this species so abundant here for several years" (whether they were as abundant at an earlier date is implied, but moot). The build-up throughout the east must have been widespread in 1885, because Hamilton (1885) recounted accumulations along the New Jersey coast during the first week of September as "almost past belief . . . millions is but feebly expressive . . . miles of them is no exaggeration." Ellzey's (1888) report on the 23 September 1886 migration through southern Maryland along the Chesapeake Bay was equally vivid: "The whole heavens were swarming with butterflies . . . an innumerable multitude of them." Another large migration was reported (Anon. 1896) along the Atlantic Coast over Ocean City, Maryland on 13 September 1896: a northeasterly wind was blowing and the

"heavens became almost black with swarms of huge red-winged butterflies" moving in a southerly direction for at least an hour.

I propose that Riley's emphasis on the prairie states as the original center of summer breeding was not biased and that monarchs actually expanded their area of intensive breeding from the midwestern to the eastern states during the latter part of the 19th century. This would have been caused by plowing and deforestation greatly altering milkweed distributions and abundances in both the prairie and the northern forest ecosystems (Marks 1983). Plowing virtually destroyed the 433 million acres of the original midwestern prairie (Sims 1988) which was host to about 22 habitat-specific and non-weedy *Asclepias* species (Rydberg 1932, Woodson 1954, Wilbur 1976, Barkley 1977). Even Minnesota, one of the northernmost prairie states, has 16 milkweed species, several of which were abundant (Upham 1884). With the introduction of the John Deere steel plow in 1837 and the twenty mule combine harvesters by the 1880s, diminution of the native prairie flora proceeded at an astonishing rate (Weaver 1954, Vankat 1979, Petulla 1988). Heavy grazing by cattle and sheep began in the 1860s and by 1910 most of the grasslands had been plowed and replaced with grain fields (McAndrews 1988). The extent of ruination of this magnificent native North American environment is staggering: for example, less than 0.5% of Missouri's original 15 million prairie acres (Robbins & Esterla 1992) and less than 1% of Wisconsin's 2 million prairie acres are still intact (Curtis 1959). The resultant changes in relative abundance of the various herbaceous species would have dramatically altered not only the monarchs' larval menu, but also the nectar bonanza provided by the rich diversity of the Compositae and other herbaceous plants amongst the original prairie grasses (see Conrad 1952:66, Risser et al. 1981).

Ironically, while milkweed habitat was drastically altered in the midwest, newly habitable areas were being generated in the northeast. By 1860 most of the northeastern deciduous forest had been cut, and between 1860 and 1890, 50 million more acres of forest were cleared across the Great Lake region (Cronin 1983, Williams 1989). As Urquhart and Urquhart pointed out (1979:41-42), there is little doubt that clearing the forest vastly increased the abundance of a single species of milkweed, *Asclepias syriaca* L. Thus, Haley (1887:80) had reported the monarch as beneficial in Brownfield, Maine because "Its foodplant (*Asclepias*) is very troublesome to farmers," and Scudder (1888:66) implied that milkweeds had become extremely abundant in hayfields. Seitz (1924:113) stated that the monarch accompanies "cultivation further and further into the primeval forest as soon as a few clearings have been formed where foodplants of the larvae, species of *Asclepias*, can get a foothold." This spread of *A. syriaca* into the opened forest areas

was consistent with the fact that it is the one truly weedy species of the 29 native milkweeds in the monarch's summer breeding range east of the Rocky Mountains (Whiting 1943, Woodson 1954:28).

The combined destruction of the prairie flora and the opening of the eastern forest thus caused an increase in the abundance of *Asclepias syriaca* that undoubtedly caused monarchs to expand their summer breeding from the Grass Land Province into the Eastern Deciduous Forest Province, as delineated in Gleason and Cronquist (1964:174, Fig. 1). This Eastern Deciduous Forest Province is virtually congruent with the distribution of *Asclepias syriaca* and with the summer breeding area currently considered most important for monarchs (Urquhart 1960: 66, 298, Urquhart & Urquhart 1976b:80, 1980:722). Whether a net increase in milkweed biomass in eastern North America resulted from these changes—as opposed to a shift onto the geographically expanded *A. syriaca* resource—is an important question that may be unanswerable (see “Columbus hypothesis” below).

We have confirmed the overwhelming predominance of *A. syriaca* as the current foodplant of the fall generation of monarchs of the eastern North American population by means of cardiac glycoside fingerprinting. This is a chemical technique developed by James Seiber, Carolyn (Roeske) Nelson, and me in the 1970s (Roeske et al. 1976, Brower et al. 1982, reviewed in Brower 1984). It utilizes the fact that monarch larvae ingest toxic chemicals called cardiac glycosides (also known as cardenolides) from milkweed plants that they eat in the wild. We showed that many species of North American milkweeds have different arrays of these poisons, and that the specific array sequestered by larvae feeding on different milkweed species remains intact through to the adult stage. By extracting the poisons from individual butterflies and visualizing the poison array on a thin layer chromatography plate, we can determine a specific “cardiac glycoside fingerprint” for each wild captured monarch. Adults originating from different geographic regions, that have eaten different species of milkweeds, consequently have different cardiac glycoside fingerprints. The technique has limitations: some milkweed species have similar arrays of poisons and some have none or very low concentrations of them. However, we were able to determine that more than 90% of 386 monarchs collected at the overwintering sites in Mexico had fed on *A. syriaca*, and thus quantitatively confirmed the Urquharts' hypothesis (Seiber et al. 1986, Malcolm et al. 1989, Malcolm et al. 1993, Table 5).

So far, monarchs have been recorded feeding on only 27 of the known 108 North American *Asclepias* species (Ackery & Vane-Wright 1984, Malcolm and Brower 1986). These 27 species include 12 that are native to the Great Plains (Barkley 1977). However, I predict that most, if not all, *Asclepias* species (as well as several Asclepiadaceous species in other

native milkweed genera; Ackery & Vane-Wright 1984:202) will eventually prove to be monarch foodplants in the wild. If it were possible to locate an intact collection of monarchs made in the midwest between 1860–1880, the butterflies could be fingerprinted and compared to monarchs reared on the native *Asclepias* species of the area. This would permit a test of the hypothesis that the butterflies switched from a diverse milkweed menu largely to *A. syriaca* as the prairies were plowed and the forests cut.

MIGRATION OF THE WESTERN POPULATION

Jennie Bush (in Riley & Bush 1881, 1882) reported three Monterey pines (*Pinus insignis* Dougl. = *P. radiata*, Pinaceae) completely covered with monarchs in Monterey, California on 27 February 1881. She also stated that “A lady resident informed me that for the 12 years she had lived there the appearance had been the same” i.e., back to 1869 (1881: 572). Kellog (1904) noted similar behavior on Point Pinos in nearby Pacific Grove, also on the Monterey Peninsula. Citing the rarity of milkweeds within 50 miles of the Monterey area, his own observations of extensive breeding 80 km to the north, and his knowledge of the eastern migration, Kellog was the first person to infer that monarchs also migrate in California. Inkersly (1911:283) provided the first detailed description of monarchs overwintering in Pacific Grove, and speculated that they probably originated in “the country west of the Rocky Mountains.”

Three years later Lucia Shepardson (1914) published a remarkable pamphlet on the Pacific Grove monarchs. Although she cited no published reports, her writing indicates that she was aware of the then-current monarch literature. It is unfortunate that she has been largely ignored by subsequent monarch researchers because she had an impressive grasp of the larger picture of the monarch’s “annual migration . . . phenomenon” (p. 12). As verbatim (p. 28, italicized parenthetical phrases added by LPB): “One of their most noted characteristics, mentioned by all authorities on butterflies, is their tendency at the end of summer to gather in great swarms, as if preparing for a long flight. At such times they are found clinging in masses upon low trees and shrubs (*aggregation behavior*), just as they cling to the pines during their long sojourn (*the overwintering period*) in the Monterey woods, but as yet the latter place is the only known spot where they remain thus assembled for any length of time, their gatherings which have been observed elsewhere (*i.e., presumably the eastern population*) being only temporary, a day or two in duration at the longest.” Her own observations indicated that the monarchs had returned (*migrated*) to the Pacific Grove trees back to 1898, and that the “earliest authentic information” (p. 12) dated their having been seen there back to 1864. Her revised

edition (Shepardson 1939) provided an astonishing wealth of new information, including a wonderful description of the fall migration across the Monterey Bay from the Salinas and Santa Clara Valleys, bivouacking (i.e., late afternoon cluster formation), site fidelity, frost resistance (but see Teale 1956:343), rapid breakup of the colony in the spring, and annual variation in the numbers of overwintering butterflies.

Shepardson was the first person who clearly distinguished the eastern and western migratory populations of the monarch. She wrote: "It is presumed that those which are in the eastern and middle-western states go to the south during the cold weather, while those which winter near Pacific Grove come from a large part of the country lying west of the Rocky Mountains" (p. 29). She supported her implied fall migration hypothesis by citing observations made by forest rangers "every year" at the end of September in the Siskiyou Mountains of north central California. In her words "a long stream of them travels down through the hills from the north. . . . They fly a little below the tree tops, a thin and fluttering band about fifty feet wide . . . unwavering . . . they keep to an unerring course evidently with a fixed destination in view". . . . This destination—the Pacific Grove butterfly trees—would constitute a southward journey of 725 km.

Shepardson's second-hand account of the southward flight through the Siskiyou was the first accepted documentation of a fall migration of the western population. Williams et al. (1942:167) appear to have unearthed the original observation, which had been made by Alan Forbes. "In August 1912, at Marble Mts., Siskiyou County . . . an observer at the summit of the pass, much lower than the surrounding mountains, suddenly came upon an amazing line of butterflies. They were coming up the slope as far as could be seen, then crossing the summit, and immediately descending . . . the flight was watched for half an hour and was . . . passing 'in countless millions' . . . 10 to 20 feet above the ground."

However, John Lane (pers. comm., 1994) has suggested that the butterflies may not have been monarchs because *Nymphalis californica* Bdv. (Nymphalidae) is known to have colossal migrations through this region (e.g., Whittaker 1953) and the two butterflies have somewhat similar color patterns. This possibility of confusion is lessened by additional observations. Mary Barber (1918:5–6), in another overlooked and informative booklet, *Winter Butterflies in Bolinas*, stated that Bolinas (immediately north of San Francisco) "is the winter home of the Monarch butterfly which comes not only from the Sierra Nevada mountains but also from the western ranges of the Rockies." In describing the fall migration, she wrote "Thousands of these frail butterflies start on their long journey toward the Pacific, in search of a mild climate, free from frost and snow, in which they can live all winter.

In Nevada County (California) great flocks of them have been seen, following the course of a stream downwards from the mountains towards the sea." These were unlikely to be *Nymphalis* because monarchs breed extensively along the forks of the Yuba and American Rivers that drain the western slope of the Sierra Nevadas in Nevada and Placer Counties (Brower et al. 1982, 1984b). Orr's (1970:91) description lends further credence to huge fall migrations in the Pacific states: "In Washington in 1928 a flock of monarchs estimated to be several miles wide and ten to fifteen miles long was observed in the Cascade Mountains. The number of individuals in this flock was believed to be in the billions."

In her revised edition, Shepardson (1939) added that the monarchs migrate into Pacific Grove from as far north as British Columbia, are seen in vast numbers each autumn in the Santa Cruz Mountains, and fly in from east of Pacific Grove, from the Santa Clara Valley and Santa Lucia Mountains, where they had bred. However, the absence of hard data on the routes of the fall migration in the West apparently led Essig (1926:639) simply to state that monarchs are "migratory in habits and their great numbers in many parts of Southern California during the winters are probably the result of a southern migration from the north Pacific states." Essig (in Williams 1930) later extended the geographic extent of the overwintering sites from Monterey to San Diego. I find it curious that Essig did not refer to the observations either of Ms. Shepardson or Ms. Baker.

More than 50 years after Downes reviewed the Pacific Coast data (in Williams et al. 1942:160), his conclusion is still true, that "the precise point of origin of the autumn migration, and the course of both the autumn and spring flights, seems largely to be unknown." Recent research by Lane (1984, 1985) and Nagano and Lane (1985) has documented at least 200 overwintering colonies along the Pacific Coast, from northern Baja California, Mexico to north of San Francisco, in Mendocino County (see also Nagano & Sakai 1988, Sakai et al. 1989, Sakai & Calvert 1991). As Wenner and Harris (1993) pointed out, however, the numerous winter aggregations in California imply but do not prove that there is a fall migration in the West comparable to that of the eastern population. Unfortunately, as Wenner and Harris also observed, the Urquharts' release and recapture data have never been published with sufficient detail to document the western fall migration unequivocally (Urquhart 1960:320, 1965a, Urquhart et al. 1970, Urquhart & Urquhart 1977a, Urquhart 1987:169 and Plate 12).

In contrast to the inadequacy of the data supporting the fall migration in the West, data obtained from tagging butterflies at the coastal overwintering sites in California definitely have established a long distance spring remigration eastwards across the Coast Range. Thus Urquhart

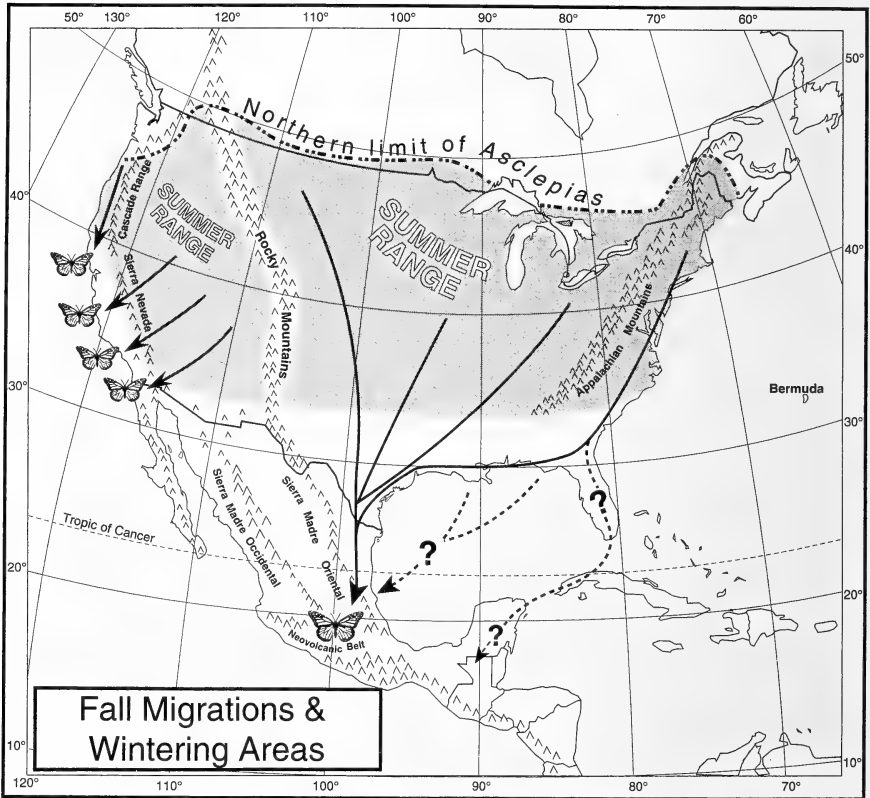


FIG. 1A. Fall migrations of the monarch butterfly in North America. Two migratory populations of the monarch occur in North America. The *western population* breeds west of the Rocky Mountains during the spring and summer and migrates to numerous overwintering sites, mainly along the California Coast, from north of San Francisco to south of Los Angeles. The second, much larger *eastern population* breeds east of the Rocky Mountains and migrates south to about twelve overwintering sites in the high peaks of the Transverse Neovolcanic Belt, south of the Tropic of Cancer in central Mexico. The last summer generation of monarchs in the East breeds principally on the abundant *Asclepias syriaca* milkweed which grows in an area of at least 2.6 million square km. The occasionally reported overwintering sites along the Gulf Coast are unstable because of periodic freezing, and migration across the Gulf of Mexico and Cuba remains hypothetical. The demarcation between the eastern and western populations is also hypothetical, and the degree of natural interchange between them is unknown, but probably minimal (revised, originally from Brower & Malcolm 1991).

(1960, Table 11) reported that 9 butterflies tagged at several overwintering sites near Monterey were recaptured in the Central Valley, and Beard (in Zahl 1963), who released more than 4,000 tagged monarchs in the same general area, reported 6 recaptures in the Sierra Nevada foothills. During 1985 and 1986, Nagano et al. (1993) marked 57,771 butterflies at 14 overwintering sites further south in California. The authors analyzed 100 recaptures that had flown from 10 to 465 km

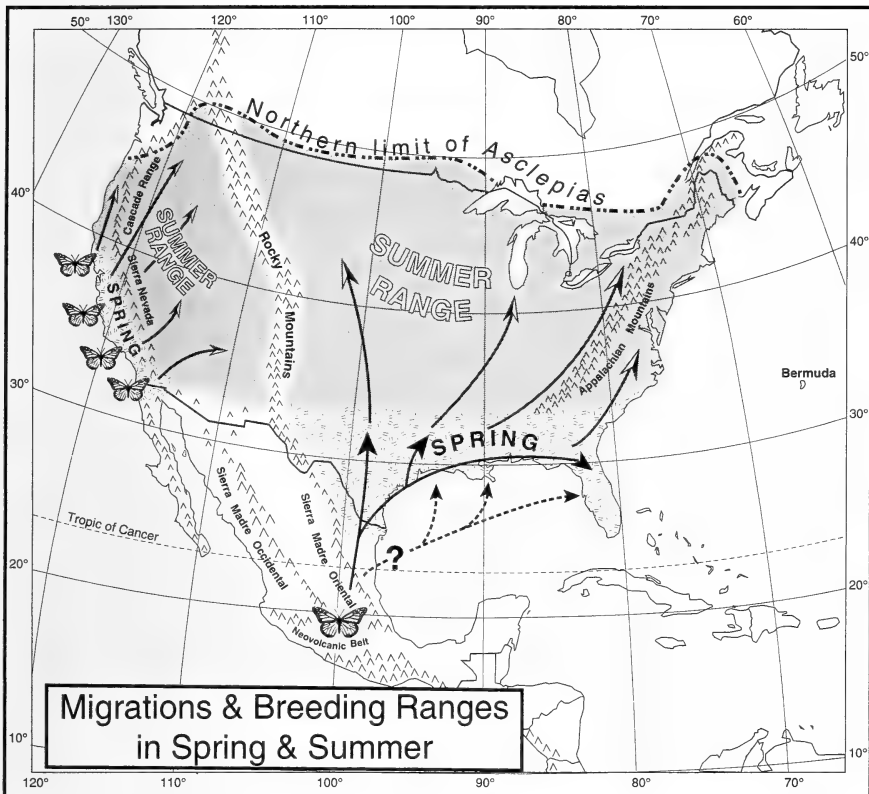


FIG. 1B. Spring remigrations of the monarch butterfly in North America. Overwintered individuals of the western population remigrate in early spring into the Coast Ranges, the Central Valley, and the Sierra Nevadas where they lay their eggs on the resurgent milkweed flora and produce a spring generation. The extent to which they, or later generations, migrate over the Sierra Nevadas and eastwards to the Rocky Mountains is poorly understood. Monarchs that overwintered in Mexico remigrate at the end of March and early April to the Gulf Coast states where they produce a new spring generation on the southern milkweeds. A few of the overwintered monarchs probably migrate as far north as Canada. The large new generation produced in the south in April and early May flies northwards to southern Canada, laying eggs along the migration routes. After the first spring and two or three subsequent summer generations, the monarchs enter reproductive diapause and begin migrating southward to their respective overwintering sites. Spring remigrations of the eastern population over the Gulf of Mexico and through Cuba remain open to question (revised, originally from Brower & Malcolm 1991).

from the points of release and concluded that there is a bi-directional spring migration away from the southern California coastal overwintering sites: one northwesterly, the other easterly. Wenner (1994) reanalyzed these data and convincingly argued that the purported bidirectional distribution can not be statistically differentiated from random headings (letter from A. Wenner to W. Sakai, copy to LPB, 15–23 November 1994; LPB letter to Wenner, 15 January 1995). Nevertheless,

the data established that 37 monarchs flew distances of 100 to 465 km from their overwintering sites, including flights northward through the Coast Ranges, over the Coast Ranges both to the Sierras and northward through the Central Valley, and eastwards into the San Gabriel and San Bernadino Mountains. Until it is technically possible to follow the tracks of large numbers of individual monarchs, we may be unable to distinguish a directional spring remigration from a random spring dispersal in California (the same criticism, in fact, applies to the spring remigration from Mexico).

Based on the information now available, the fall and spring migration patterns of the western population of the monarch are assumed to be as shown in Figs. 1A and 1B. Future tagging studies of the western population should concentrate on better understanding the fall migration throughout the western states to the numerous California overwintering sites.

EARLY SPECULATIONS ON THE OVERWINTERING AREAS OF THE EASTERN MIGRATION

Williams' (1930) collation of the literature through 1924 established that a fall migration of the monarch occurs east of the Rocky Mountains from Alberta to Maine, and southward to the Gulf Coast states from Texas to Florida, an area of about 8.3 million square km. Continuing to piece together the accumulating reports, Williams' subsequent summary maps (1938, Fig. 1, p. 218; Williams et al. 1942, Fig. 20, p. 172) supported the initial hypothesis that there are two migratory populations of the monarch in North America, one east and the other west of the Rocky Mountains, with overwintering areas in Florida and California, respectively. In the *Lepidopterists' News* of the newly founded Lepidopterists' Society, Williams (1949:18) called for more information on the overwintering sites: "In the south the butterflies hibernate in masses on trees. Such locations are known in southern California and in Florida, usually very close to the sea. What other areas are there? Are there hibernating areas along the Gulf Coast in Alabama, Mississippi, Louisiana or Texas? Are there any inland localities? What happens to the butterflies that fly south through Texas in the fall? Do they go into Mexico? If so, do they hibernate there, or remain active, or breed?"

The ensuing failure to confirm any overwintering sites along the Gulf Coast west of Florida led Williams (1958:13) to raise the possibility of three separate North American migrant populations: a western one overwintering in California, a second one overwintering along the Florida Gulf Coast (perhaps including Louisiana), and, as originally suggested by Brooks (1907, 1911), a third one migrating through Texas to overwinter in Mexico (see also Zahl 1963).

Early in his career, Urquhart (1949) proposed an even more complex

hypothesis involving four overwintering areas for the eastern monarchs: (1) some overwinter in aggregations in Florida; (2) others overwinter as scattered individuals across the Gulf Coast States; (3) others must migrate to overwinter in Mexico and beyond; (4) while still others migrate westwards across the southern states to join the overwintering clusters in California.

The idea that eastern monarchs might migrate to California was potentially important because it departed from Williams' hypothesis of separate eastern and western populations and effectively considered *all* North American monarchs to be part of a single population. Urquhart kept the idea alive for the next 24 years (1965a, 1965b, 1966a, 1973a, 1973b), but recaptures of tagged butterflies did not provide evidence one way or the other. The idea thus stagnated until given a novel twist by Malcolm and Zalucki (1993b) in the general conclusions to their book (1993a:398): "Monarchs in California could be a sink population, continuously maintained by eastern monarchs as a source population." This seems unlikely because monarchs breed extensively at the lower elevations in the Coastal Range, the Sierra Nevada, the Cascade Range and in the Central Valley in California (Brower et al. 1982, 1984a, 1984b).

Given the fact that it is still unresolved whether any monarchs from the eastern population fly to the overwintering colonies in California, it seems prudent to cease making experimental transfers of monarchs between the eastern and western populations (Urquhart & Urquhart 1964, Cherubini in Anon. 1992). The fact that several of the transfers survived and were recaptured suggests that the releases probably already have resulted in interbreeding. This could confuse interpretations of classical morphological analyses as well as the new molecular and biochemical techniques that could be used to resolve this important biogeographical problem. My colleagues and I have recently written on the potential dangers of making such transfers (Brower et al. 1995).

DOES OVERWINTERING OCCUR IN PENINSULAR FLORIDA AND ALONG THE GULF COAST?

Thaxter's (1880) report of overwintering butterflies along the Gulf Coast of Florida together with Bush's discovery of well defined overwintering colonies in California (in Riley & Bush 1881, 1882) biased subsequent workers into thinking that the eastern monarchs overwinter in the Gulf Coast states (Williams 1930, 1938, 1949, 1958, Urquhart 1960). Attempts over the years to obtain further evidence proved confusing and, at best, weakly confirmed the hypothesis. Thus Bromley (1928) reported great numbers of monarchs during January 1924 flying about, nectaring, and mating in the northern Everglades near Lake Okeechobee, and speculated that they represented an active overwin-

tering population rather than resident breeders. While a lighthouse keeper reported "large numbers" of monarchs clustering on pines every winter from 1931–1937 on St. George Island (south of Apalachicola), other records between 1924–1937 only vaguely supported the idea that monarchs overwinter in Florida (Williams 1938:216–218). Fernald's (1939) discussion of the fall migrations southward through the Florida peninsula (rather than westwards along the Gulf Coast) stated that monarchs generally arrive in the Orlando area early in November. They then disperse, effectively disappearing by February, and reappear at the end of March or early April. The Hodges' data in Beall (1952) on migrations along the Atlantic Coast through Indialantic (about half way down the Florida peninsula) corroborated this timing. Fernald (1937) earlier had reported monarchs breeding in the Orlando area during January, and was clearly struggling in his 1939 paper to understand exactly when and where these migrants overwinter. He suggested that they may continue to Key West and even possibly to Cuba. What little is known of the phenology of monarchs in the Florida Keys weakly supports this hypothesis (Leston et al. 1982).

In an attempt to clarify the Florida situation, in January 1956 Urquhart (1960:302–307) searched for clusters from the Atlantic to the Gulf Coast near Tampa, without success. Correspondents' information, gathered during the 1950s, but frequently presented without definite dates by Urquhart, provided conflicting evidence. Thus Kimball reported few monarchs in Sarasota; Smith recounted large but abruptly disappearing clusters on oaks south of Tampa; Stiles traveled from the island of Captiva, south of Tampa, to Houston, Texas looking for clusters but found none. In contrast, Harris noted large numbers of monarchs forming loose aggregations on pines on Captiva on 5 November; and Stoddard reported several aggregations in a ten acre tract of young pines on Bald and Alligator Points on 4 November 1954 (these two Gulf Coast points are 56 km southwest of Tallahassee, about one mile west of Lighthouse Point in Franklin County). During the first week of February 1956, Harris and Stoddard returned to Alligator Point (Urquhart 1957:25–26) and tagged 1,000 of 1,500 clustering butterflies that they found clinging to the branches of the pine trees in four separate groups. Baker (1978:428) apparently interpreted these fragmentary observations to indicate extensive overwintering along the Gulf Coast and in Florida. It seems likely that he also was influenced by Williams' maps (1938:218, and Williams et al. 1942:172) showing five Gulf Coast overwintering sites.

Between 27 November 1981 and 20 February 1982, Brower and Calvert (Brower 1985a) monitored wintering clusters of an estimated 2,000 monarchs in a dense grove of pines on the northern part of Honeymoon Island, off the Gulf Coast west of Tampa. Other reports

(including Urquhart 1966a) provided no further evidence of extensive overwintering aggregations in Florida, and a recent study suggests that the Brower-Calvert observations may have been made during an exceptional season (Cherubini 1994).

As far as I can glean from the literature, no winter aggregations have been reported along the Gulf Coast in Alabama, Mississippi, Louisiana or Texas (Bromley 1928, Williams 1938:218, 1949, Lambremont 1954, Teale 1954, Mather 1955, Mather & Mather 1958, Urquhart 1957, 1958, 1960, 1966a, Kimball 1965). Urquhart (1960), and numerous authors who subsequently cited him, clearly confused temporary bivouac clusters made by the fall migrants with true overwintering clusters. Other examples of this confusion included clusters seen at Lake Pontchartrain in Louisiana in October 1938 and November 1941 (Beall 1946), and clusters reported along the coast of western Mississippi at the end of October 1923 (Lyle, in Williams et al. 1942:169).

CAN OVERWINTERING OCCUR IN PENINSULAR FLORIDA AND ALONG THE GULF COAST?

Many monarch adults are killed by freezing during winter storms at the Mexican overwintering sites (Calvert & Brower 1981, Calvert & Cohen 1983, Calvert et al. 1982a, 1982b, 1983, 1984, 1986, Alonso et al. 1992). Following up on these studies, Anderson (in Brower 1987, 1990), and Anderson and Brower (1993) experimentally determined the temperature at which adult monarchs freeze to death. When there was no surface water on their bodies, 50% of the butterflies were killed at approximately -8°C , and 100% were killed at -14°C . If, on the other hand, their wings and bodies were wet, they lost at least half of this freezing resistance i.e., 50% died at -4°C and 100% died at -8°C . If the forest canopy above the butterflies has been thinned by wood harvesting, further heat is lost due to thermal radiation from the monarchs' bodies to the cold night sky, and even more freeze (Alonso et al. 1992). This is because the monarchs' body temperatures under open clear sky actually fall below the ambient temperature (Anderson & Brower, in press). A recent study by Larsen and Lee (1994) discovered that wet monarchs freeze faster than dry ones, adding to the importance of the sheltering effect of the intact Oyamel fir forest. The lowest temperature we have recorded in Mexico was in a treeless area near a Sierra Chincua colony on a clear night, when the temperature on the ground reached -8°C (Alonso et al. 1992).

What is the frequency and intensity of freezing during the winters along the Gulf Coast states, including Florida? The extreme one-time minimum temperatures recorded for at least 73 years through 1964 (except for Mobile, circa 25 years through 1963) were: Tallahassee, Florida, -16.7°C ; Mobile, Alabama, -11.7°C ; New Orleans, Louisiana,

-13.9°C; Houston, Texas, -15.0°C; and Brownsville, Texas, -11.1°C (Conway et. al. 1963, Bair 1992). A more detailed analysis of Jacksonville data for 150 years through 1985 indicated 24 winter freezes exceeding -6°C, 12 exceeding -8°C, and two exceeding -12°C (Chen and Gerber 1985). The all-time historical low was -15°C in January 1985. Indeed, Florida winters are characterized by frequent intrusions of Arctic air masses that are forced into the peninsula by southerly loops in the jet stream. Equally important is the fact that the leading edges of these cold fronts are generally preceded by rain (Johnson 1963, Chen & Gerber 1990).

Combining freezing records from Jacksonville with the monarch freezing point data leads me to conclude that about once each decade weather conditions in northern Florida would result in 50% mortality if the butterflies remained dry, or 100% mortality if they were previously wetted by rain. Severe freezes also occur farther south in the Florida peninsula. Thus, in Tampa the 75 year low through 1964 was -7.8°C. Such a winter freeze apparently killed monarchs at Davenport in central Florida during the 1937-1938 season (Colvin, in Williams et al. 1942:167). These data indicate that overwintering along the Gulf Coast from Northern Florida to Texas would be precarious, and in the long term, stable overwintering in this region probably can not be favored by natural selection.

The probability and severity of freezing is less in the areas south of Tampa, including the Everglades (Chen & Gerber 1985, 1990, Fig. 2.4). It therefore might be assumed that overwintering is possible in south Florida. However, here monarchs are confronted with a different problem: most of the time the weather is warm, with the consequence that the butterflies must become reproductively active (evidence in Brower 1985a, Table 1). When this occurs, the hormonal balance is shifted and the ability to migrate northwards almost certainly would be lost (see below). Thus, any monarchs that terminate their migration this far south will probably be incorporated into the local breeding populations. This appears to be occurring in a monarch population immediately northwest of the Miami airport, as described in Brower (1985a) and Malcolm and Brower (1986). Overwintering per se in southern Florida thus seems impossible.

I conclude that the sporadic observations made of monarch clusters over the past 150 years from Florida to Texas, together with the periodic freezes that must decimate them, provide very strong evidence that the southern Atlantic and Gulf Coastal states, including northern Florida, cannot and do not serve as safe, long term overwintering areas for the monarch.

FURTHER CONFUSION: WINTER BREEDING IN FLORIDA, ARIZONA,
CALIFORNIA—AND THEREFORE MEXICO AS WELL?

Although Williams (1949) began questioning whether monarchs that migrate through Texas to overwinter in Mexico might possibly breed there, he subsequently (1958:108, 176) returned to his earlier position that they do not. Urquhart's data (1960:174 vs. 299–305) remained ambiguous. Soon thereafter, Brower (1961, 1962) reported monarch larvae in south central Florida during January as well as extensive breeding in the same area during the last week of March through mid April. Funk (1968) then reported winter breeding in southwestern Arizona, and Urquhart, Urquhart and Munger (1970) stated that they had found another continuously breeding population in southern California. These observations clearly challenged Williams' (1958) contention that monarchs do not breed in their purported overwintering range.

During January and February 1969, the Urquharts traveled in search of monarchs from Texas southward to the Chapala Lake area near Guadalajara in Jalisco, Mexico (Urquhart & Urquhart 1976e). This area is considerably west and north of where the overwintering sites would eventually be discovered. They reported that "during the months of January and February there were no monarch butterflies throughout southwestern Texas and Mexico north of Mexico City" (p. 439). Although suggesting that the butterflies might "remain in some obscure area of Mexico," it is clear from their new map and its caption that the discoveries of populations breeding during the winter in Florida, Arizona, and in southern California had begun to shift their thinking. Instead of envisioning passive overwintering colonies similar to those in Pacific Grove or Apalachicola, they now speculated that the fall migrants of the eastern population might end up breeding as far south as the Gulf of Tehuantepec in Mexico or even in Central America, while the western population might end up breeding as far south as Baja California.

Based on the recapture of one tagged monarch in San Luis Potosi (about 275 km north of the overwintering sites), and another near Mexico City, the Urquharts (Urquhart 1973a, 1973b) appear to have settled on the hypothesis that the terminus of the fall migration of the eastern population of monarchs must be southern Mexico or Central America. Speculating on the spring remigration, Urquhart said "we are of the opinion that the same individuals do not return, but their progeny do" (Urquhart 1973b:14). He then proposed that a new generation of monarchs born in Mexico and Central America flies north to Texas, there to produce a second, new generation in the spring, which in turn

recolonizes the northern range. The Urquharts appear to have maintained this position even after the overwintering sites had been discovered. Thus, a 30 September 1975 newspaper article describing their research stated: "Few if any of the monarch butterflies which migrate south in the fall ever return. Most of those which come north in the spring are the children, or even the grandchildren of those who left the previous autumn" (del Vecchio 1975:20). Ordish (1977), a popularizer of science, wrote a semi-fictional account of monarch migration in eastern North America (see Brower 1977b), and stated that the butterflies overwinter south of the tropic of Cancer in the eastern Sierra Madre Oriental mountains. His statement appears to have been based on Rzedowski's (1957) earlier report of monarchs migrating along these mountains (see above).

The Urquharts' calls for help in locating the monarchs were published in Mexico City during February 1973 in English (Urquhart 1973a, 1973b) and Spanish (according to Urquhart 1987:155; see also de Montes 1975). Most significantly, Urquhart concluded each article with a request to naturalists in southern Mexico and Central America to join their tagging team "in order to obtain data to solve . . . (this) most interesting yet perplexing problem." The Urquharts' emphasis was on solving the spring remigration and clearly no one, including me (e.g., Brower and Huberth 1977), had any inkling of the incredible nature of the overwintering sites before November 1973.

DISCOVERY OF THE SIERRA PELON AND SIERRA CHINCUA OVERWINTERING SITES IN MEXICO

Although the well known Mexican poet, Homero Aridjis (1971), mentioned monarchs flying out of what we now know is an overwintering site on Cerro Altamirano in northern Michoacan (described in Calvert & Brower 1986), scientific resolution of the major eastern overwintering sites was achieved by two research associates of the Urquharts, Kenneth and Cathy Brugger. Because it is not clear from any of the Urquharts' publications (through Urquhart 1987) or from press releases (e.g., Del Vecchio 1975, Rensberger 1976) exactly when or where the Bruggers discovered the butterflies, I here attempt to reconstruct the sequence of events.

Kenneth Brugger, an American citizen working in Mexico, read one of the Urquharts' research notices and, according to Urquhart (1976b), volunteered to help in a letter to Urquhart dated 26 February 1973. On 6 November 1973, while Brugger was driving through the mountains west of Mexico City, he saw monarchs being pelted out of the sky by hail (Herberman 1990). In their annual newsletter summarizing the 1973 observations, Urquhart and Urquhart (1974:2) tantalized their readers with the statement that Ken Brugger of Mexico City was in-

vestigating the presence of monarch butterflies west of Mexico City and that “we are assured that somewhere in this general area the monarchs from the eastern United States and Canada spend the winter months.” This finding also was referred to by de Montes (1975).

With the Urquharts’ support and encouragement, Brugger and his Mexican wife, Cathy Aguado, finally discovered the first overwintering colony in January 1975. The Urquharts briefly reported the discovery in their 1975 annual newsletter, which in turn was quoted in a New Jersey newspaper by del Vecchio on 30 September 1975. Given the *New York Times*’ frequent editorials and articles on the monarch (Anon. 1973, 1975, 1976, Sullivan 1973, Panzer 1975), I find it enigmatic that this newspaper, in particular, did not pick up on the discovery. The real impact of the Mexico findings came only after release of the August 1976 issue of the *National Geographic* magazine (Urquhart 1976b), followed by two scientific publications (Urquhart & Urquhart 1976c, 1976d).

Although Urquhart and Urquhart (1977a) gave 9 January 1975 as the discovery date, Herberman (1990:30) interviewed the Bruggers and determined that they had located the colony on 2 January 1975 (phone conversation, E. Herberman to LPB). According to Herberman, the initial colony was on Cerro Pelon, a 3,500 m high mountain in the Transverse Neovolcanic Belt, about 120 km west of Mexico City (see Calvert & Brower 1986 for the exact location of this site that we called *Sierra Pelon*).

Urquhart (1976b:173) wrote that “on their 1975 discovery trip, the Bruggers found two nearly equal concentrations a few miles apart.” By piecing together information from Calvert’s and my research and from the Urquharts’ publications, I have deduced that this second site was the *Sierra Chincua* colony. Urquhart and Urquhart (1976c:157) stated that two butterflies were recaptured “at the overwintering sites” in January 1975. One of these recaptures, of a monarch tagged by Mrs. C. Emery in Nevada, Missouri on 9 September 1974, was made at “Monera Alta, Michoacan, Mexico” (Urquhart & Urquhart 1975:10; 1976c:157). Calvert and Brower (1986) determined that the *Mojonera Alta* is a large stone boundary marker near the summit of the Sierra Chincua, a separate mountain range about 30 km NNW of Sierra Pelon. In both the 1976–1977 and the 1977–1978 overwintering seasons, we found a large monarch colony about 2 km west of the Sierra Chincua marker, on the north facing slope of the Arroyo Zapatero (Calvert & Brower 1986). The *Mojonera Alta* is located at the intersection of the N–S coordinate 76 and E–W coordinate 64 as shown in Anonymous (1987). Thus the Emery butterfly had to have been recaptured by Brugger, in January 1975, near the *Mojonera Alta*, in the Sierra Chincua.

Further light can be shed on the history of the discovery by weaving

together information in the Urquharts' 1975 annual newsletter, in the August 1976 *National Geographic*, and in a richly illustrated article by photographer Albert Moldvay, published nearly 6 years later in *Westways* magazine (Moldvay 1982). The Urquharts (1975:3) stated, after the Bruggers' discovery in January 1975, that "The National Geographic Society sent one of their official photographers to the site." According to Moldvay (1982:22), Bob Gilka (then Director of Photography of the magazine) telephoned him in Mexico in January and said "The wintering grounds of the Monarchs have been discovered." Moldvay's assignment was "to picture this sensational discovery of a mountaintop covered with migrating monarchs." Joining up with Ken and Cathy Brugger, and a guide named "Juan Sanchez," the four ascended the mountain. At the top, Moldvay "discovered a grove so thick with butterflies that I shouted for Cathy to come and pose among them. Soon she was as thickly covered in orange as the surrounding tree trunks."

Comparing the two articles, it is clear that two photographs in *National Geographic* and one in *Westways* are similar shots of Cathy posing amongst the monarchs on the Sierra Pelon (verified in Herberman 1990:30-31). That the mountain was the Sierra Pelon, and not the Sierra Chincua, is certain because another of the photographs in the *Westways* article (p. 22) is the valley below Pelon's western slope which I have ascended on two separate expeditions. To avoid future confusion, it should be noted that the guide "Juan Sanchez" in *National Geographic*, photographed by Bianca Lavies, is a different person than the guide "Juan Sanchez" shown in Moldvay's article. While Moldvay's "Juan Sanchez" presumably lives at the foot of Sierra Pelon, the man depicted in *National Geographic* is actually Raphael Sanchez who lives in Angangueo, the town below the Sierra Chincua colony. The Angangueo "Juan Sanchez" subsequently worked with Monarca AC of Mexico City, as well as with our research group. Because of his long commitment to the monarchs, Raphael Sanchez was awarded a citation by His Royal Highness Prince Philip, Honorary President of the World Wildlife Fund, in a ceremony that I attended in February 1988 in the Sierra Chincua.

From the above, it is now clear that the Moldvay photographs in the original 1976 *National Geographic* article were taken in the Sierra Pelon Colony during January 1975 with the Bruggers, while the Lavies photographs were taken at the Sierra Chincua Colony in January 1976 during the Urquharts' first expedition to the overwintering sites. Obfuscation of the facts surrounding the discovery of the overwintering sites, as we shall now see, was an unfortunate consequence of a policy decision made by the National Geographic Society.

THE URQUHART-BROWER SAGA

During the early 1970s I began a collaboration with James Seiber and Carolyn Nelson at the University of California in Davis to develop our previously described cardiac glycoside fingerprinting technique. In January 1973 I sent Urquhart a reprint of our study (Brower et al. 1972) comparing the cardiac glycoside content of various monarch populations in the east. In my letter I asked: "... do you know of any clustering sites in Mexico?" (LPB letter to Urquhart, 22 January 1973). He replied, "If we do find the areas of concentration we will certainly be able to arrange for specimens to be sent to you, or, if you wish, give you exact locations and names of the persons to contact" (FAU letter to LPB, 9 May 1973).

Because the thought of monarchs overwintering in Mexico had begun to tantalize me, I had also written to Dr. Eduardo Welling in Mexico about the migration, saying, "It really seems as if the migration is to a large extent a North American phenomenon in the Monarch butterfly. It seems likely that there must be some vast overwintering areas in Northern Mexico and that they do not just keep going southward" (LPB letter to Eduardo Welling, 9 September 1973). During the fall of 1973 and the spring of 1974 while on sabbatical at U. C. Davis, I began observing monarchs in their overwintering groves in California, and I decided to produce a film that would tie together the migration biology with our chemical studies (Brower & Huberth 1977).

In late 1974 Urquhart kindly sent me *Asclepias* seeds from Mexico (apparently that Brugger had collected, see Urquhart & Urquhart 1974). Without knowledge of the Bruggers' 2 January 1975 discovery, I wrote to thank Urquhart for the seeds and asked: "Have you found where the Monarch butterfly overwinters in Mexico yet? It must be a spectacular sight to see" (LPB letter to FAU, 8 January 1975). Because he did not answer this letter, and because his Annual Newsletter (Urquhart & Urquhart 1975) had announced the discovery, I again called him on 8 September 1975 and asked him to share the location of the site with me. He indicated that he could not divulge its location prior to publishing the *National Geographic* article, but that he would be able to do so after the discovery was in print (LPB record of phone conversation, and LPB letter to FAU, 11 October 1976).

Increasingly frustrated, I phoned the National Geographic Society in December 1975 and spoke to Mary Smith about whether they would share the location of the site. In a gracious letter (M. Smith letter to LPB, 10 December 1975), she indicated that the Society had adopted a policy not to divulge the location of the colonies prior to the publication

of the discovery in their journal. I replied to her letter (LPB to M. Smith, 18 December 1975) that "I would trust that the National Geographic Society would, after having obtained . . . priority upon the article, disclose to bona fide scientists the information to pursue studies which might in fact make it easier to result in the ultimate protection . . . of the . . . monarch."

Following the Urquharts' (1976c) publication in the 22 September 1976 issue of the *Journal of the Lepidopterists' Society*, I wrote Urquhart (LPB letter to FAU, 11 October 1976) congratulating him on discovering the overwintering monarchs in Mexico, reminding him of our 8 September 1975 conversation, and again asking him to share the location of the colonies. I also invited him to Amherst College to present a lecture to us on his discovery. Since he did not immediately reply, and because neither the *National Geographic* nor the *Journal of the Lepidopterists' Society* articles gave details on the locations of the colonies, I began discussing the possibility of independently locating the sites with William H. Calvert, then a postdoctoral associate at the University of Massachusetts.

During the fall of 1976, Calvert and I attempted to deduce the general location of the sites from two crucial bits of information in the two Urquhart articles: (1) "At 10,000 feet, as we walked along the mountain crest, our hearts pounded" (Urquhart 1976b:166); and (2) "The overwintering colony . . . was located . . . in the northern part of the State of Michoacan, Mexico" (Urquhart and Urquhart (1976c:153).

In early December, Urquhart replied to my October letter (FAU letter to LPB, 3 December 1976) indicating that he had met with the National Geographic Society in August 1976 and that members of the editorial staff, President Payne, and others had "agreed that the site should not be divulged since it was anticipated that many people, collectors, film makers, etc. would wish to visit and, as happened in other similar situations, destroy it . . . I would suggest to you, since the Mexican site is not available, that you examine the . . . monarchs that pass along the . . . Gulf Coast . . . during October and November. These monarchs will eventually reach Mexico and you would accomplish the same results as visiting the area" (see also Urquhart & Urquhart 1977c, Urquhart 1978).

I replied (LPB letter to FAU, 14 December 1976) that I was "greatly distressed" by his letter. I explained that I was keen to visit the overwintering site to complete my 30-minute documentary film (Brower & Huberth 1977) which I had begun in California, and that I wanted the animated migration map to depict the migration to Mexico accurately. In addition, samples from the newly discovered overwintering sites would be of great interest for the fingerprinting analyses that I was

pursuing with my honors students at Amherst College. I ended my letter as follows: "Perhaps in view of this letter, you might review your position and consider sharing the location of the site with a fellow scientist, who, like you, is equally keen in conserving the site from modern depredations of human society. Again, I congratulate you upon your discovery."

Motivated even more strongly by Urquhart's 3 December letter, Calvert and I obtained a copy of a 1:1,000,000 topographic map (Anon. 1959) that included the Michoacan region of Mexico. We circled all the areas on the map above 10,000 feet in the general area suggested by the Urquharts' two articles. Then, armed with copies of the map, Calvert, accompanied by John Christian, Victoria Foe, and Michael Dennis, left Austin, Texas for Mexico on 26 December 1976. On New Year's Eve, Calvert telephoned me from Mexico at my home in Amherst, Massachusetts: with the help of a local guide who was a nephew of Municipal President Manuel Arriaga Nava from the town of Anganguero, they had located the Sierra Chincua colony on 30 December 1976. Earlier that day, Mayor Nava had given Calvert written authorization to visit the area (copy in Brower files). According to Urquhart and Urquhart (1977c:3), Brugger had located this same site two days before Calvert and his colleagues had found it.

Following Calvert's return to Amherst, he, my technician Lee Hedrick and I mounted a second expedition and arrived at the Sierra Chincua site about 1500 hr on 22 January 1977. I summarized our observations in the May/June issue of *Natural History* (Brower 1977a) and later in the *Journal of the Lepidopterists' Society* (Brower et al. 1977). As fate would have it, we encountered the Urquharts and Brugger tagging monarchs inside the colony. The Urquharts were bewildered by our arrival and initially treated us rudely, and then with hostility. After returning to Toronto, the Urquharts mailed a letter to their research associates dated (according to Anne Neale, in a letter to Robert Dirig) 3 February 1977. This letter incorrectly accused us of impropriety at the overwintering site, and subsequently generated vitriolic correspondence from some of the Urquharts' associates (including a letter to then-President John Ward of Amherst College).

Bayard Webster, a science writer for the *New York Times*, was aware of the brouhaha, and attended the annual banquet of The Xerces Society in New York City on 30 April 1977, hosted by Joan DeWind. After my invited talk and slide show, Webster and I discussed the allegations and I informed him of my forthcoming article in *Natural History* (published in June 1977). I subsequently provided him with several of my publications, a copy of field notes made at the Sierra Chincua, and copies of most of the aforementioned correspondence. In reviewing my *Nat-*

ural History article in the *New York Times* on 29 May 1977, Webster downplayed the rancor, stating that my article had "brought attention to a smoldering rivalry between two internationally known scientists."

Unfortunately, the *New York Times* index for 1977 embellished this: "Profs are keen rivals in longtime search for species' habitat" (Anon. 1977d:199–200). The negative aspects were amplified by Richard Barthelemy (1978), who had independently discovered the Sierra Chincua site in March 1977 (Barthelemy 1977; Barthelemy later joined our expeditions to the Sierra Chincua and we became good friends before he died from cancer in 1988). In early June, the world press succeeded admirably in turning the "rivalry" into a major conflagration (see for example: Anon. 1977a–c, Michelmores 1977, Hough 1977, Saenger 1977). Among the more inflammatory journalistic statements were those by Peter Wood (1977:56) in *Time-Life's Nature Science Annual* e.g., "The dispute may be settled by the Mexican government, which is now considering setting aside the area as a sanctuary, safe from the biologists' squabbles and other ecological perils." This was published after I was interviewed by phone, and over my objections to the draft statement (Charlie Clark letter to LPB, 24 June 1977; LPB letter to C. Clark, 13 July 1977).

In September 1977, the Urquharts mailed a letter and an eight page mimeographed "special report" to their research associates (Urquhart & Urquhart 1977c). The document bitterly attacked the *Natural History* article and falsely accused us of having followed Brugger into the site, and of purposefully starting a fire under the butterflies "to dislodge monarchs from their roosting trees to provide material for dramatic photographic shots. . . ." Calvert, Hedrick and I wrote Urquhart on 28 September 1977 explaining in detail how we had found the Sierra Chincua overwintering site, and that we felt he had misinterpreted our research activities. The Urquharts never replied either to this or to any of several other attempts to reconcile the situation.

In spite of initial urging from President Ward of Amherst, I chose not to respond in print to the Urquharts' accusations. In retrospect, this was a mistake, because the unrefuted allegations polarized the monarch community—the very group of people who, had they adopted a unified front, could have been far more effective at promoting conservation of the overwintering sites.

MONARCHS OVERWINTER IN THE OYAMEL FIR FOREST ECOSYSTEM LOCATED IN THE TRANSVERSE NEOVOLCANIC BELT OF MEXICO

Following our January 1977 expedition to the Sierra Chincua, Calvert joined my Amherst College research group and subsequently led several expeditions to determine the extent of monarch overwintering in Mexico. Calvert teamed up with Javier de la Maza, a prominent member

of the Mexican Lepidopterists' Society, and they and others searched widely in central, eastern, and southern Mexico (de la Maza et al. 1977, de la Maza & Calvert 1993). By 1986 they had located a total of approximately 30 overwintering colonies on 9 separate mountain massifs, all between 70 and 170 km west of Mexico City in the states of Mexico and Michoacan (Calvert & Brower 1986, de la Maza & Calvert 1993). Their work confirmed that the overwintering phenomenon is intimately associated with Oyamel fir forests, *Abies religiosa* (H.B.K.) Schl. & Cham. (Pinaceae) (reviews in Brower 1985, Calvert et al. 1989, Brower & Malcolm 1991, Snook 1993a, Núñez and García 1993, see also Urquhart & Urquhart 1978a, 1978b, 1980, and Anon. 1981).

All of the sites known to us occur in a small area of *The Transverse Neovolcanic Belt*, a 50 to 100 km wide belt of volcanic mountains and valleys that extends for 800 km across Mexico between latitudes 19°N and 20°N. This is a rugged, beautiful and topographically complex region averaging about 2,500 m in altitude. It contains hundreds of volcanic cones projecting into rich elevated valleys, including 13 of the highest peaks in Mexico, three of which exceed 3,650 m (Moore 1945, Goldman & Moore 1946, Raisz 1964, Arbingast et al. 1975). According to Thayer (1916), Garfias and Chapin (1949) and Duellman (1965), the Transverse Neovolcanic Belt originated during two periods of volcanism that accounted for most of the uplift as well as the volcanic peaks. The first period of volcanism occurred during the Miocene and affected all of Mexico, while the second began in the Pliocene and is still occurring in the Transverse Neovolcanic Belt.

The Oyamel forest is a specialized high altitude ecosystem that occurs as 13 vegetational islands on the higher peaks in Mexico and constitutes less than one half of one percent of Mexico's land area. Nine of these montane islands occur in the Transverse Neovolcanic Belt, three in the Sierra Madre Oriental, and one in northern Baja California (Leopold 1950, 1959, Arbingast et al. 1975, Anon. 1981). Because the Oyamel forest's general physiognomy is like that of northern Canadian forests, it is called a boreal forest ecosystem. According to Rzedowski (1978) and Manzanilla (1974), as summarized in Snook (1993a:365): "Today's fir forests in Mexico are relicts of extensive boreal forests that advanced southward as the cold climates descended to tropical latitudes during the periods of glaciation. . . In the 10,000 yr since the glaciers retreated, these forests have been displaced by temperate and tropical floras adapted to the warmer climatic conditions of today. Now only 40,000 to 50,000 ha of fir forests remain in Mexico. . . , distributed as isolated islands at elevations between 2,400 and 3,600 m. . . , where the cold climate excludes most other genera and permits the firs to dominate. This reduced area and patchy distribution pattern make the fir forest perhaps the most vulnerable to deforestation pressures of any type of

forest in Mexico." Below the fir belt, various species of oaks and pines are abundant, whereas above the firs several other species of pines dominate up to the snow line (Loock 1950:32). The fir forest coincides with a summer fog belt and is damp, with mosses and lichens on the forest floor, and a rich herbaceous and shrub understory growing in partly opened areas beneath the forest. On clear days throughout most of the winter, hummingbirds are commonly seen feeding on crimson flowers. For a wealth of new information on the vegetation associated with the monarch's overwintering areas in this fir forest ecosystem, see Snook (1993a) and Núñez and García (1993).

Survival of the monarchs from November through March depends on a balance of macro and microclimatic factors, such that the weather is: (1) cold enough to maintain the butterflies in a state of reproductive torpor, but not so cold as to kill them; (2) warm enough to maintain the integrity of their clusters, but not so warm as to result in excessive activity; and (3) wet enough to prevent desiccation and forest fires, but not so wet and cold as to preclude all activity (Brower 1985, Masters et al. 1988). The microclimate of these Oyamel forests shares many characteristics with the sea-level Monterey pine and *Eucalyptus* forests along the coast of California where the western population overwinters (Leong 1990, Weiss et al. 1991).

Contrary to expectation based on the aggregation behavior and sophisticated chemical defense of the monarch (Brower 1985), we discovered that two species of birds and one species of mouse are killing as many as one million butterflies in the overwintering colonies (Calvert et al. 1979, Fink & Brower 1981, Brower & Calvert 1985, Brower & Fink 1985; Brower et al. 1985, 1988, Glendinning & Brower 1990, Arrellano et al. 1993). We have hypothesized that these current high predation rates are due to the historical shift of larval feeding from the more toxic prairie milkweeds to *Asclepias syriaca*. As noted above, this milkweed increased in abundance following the plowing of the prairies and cutting of the eastern forests. *Asclepias syriaca* contains variable amounts of weakly emetic cardiac glycosides. Monarchs that feed upon it as larvae in the wild reflect this low toxicity and gradually lose the poisons as they age (Alonso-Mejia & Brower 1994). This presumably results in the ability of the birds and mice to feast on the butterflies.

As summarized by Calvert and Brower (1986, Fig. 1) and de la Maza and Calvert (1993), the principal overwintering sites are limited to perilously few mountain ranges in the center of the Transverse Neovolcanic Belt, overlapping the northern state borders of Michoacan and Mexico, between latitudes 19°20' and 19°45'N and longitudes 100°10' and 100°20'W. Within this tiny area of about 800 square km, five mountain ranges—the Sierra Chincua, Sierra Campanario, Sierra Chi-

vati, Sierra Picacho and Sierra Pelon—have consistently harbored one or more overwintering colonies. Four smaller and less predictable overwintering areas also occur within a radius of 50 km of the main area: Contapeac and San Andreas occur to the North, and Las Palomas and Herrada occur to the southeast, on the southwestern slope of Volcan Toluca (Xinantecatl = The Nude Man, Melgareio 1910; after major snowstorms and the passage of cold fronts, this 4,558 m high volcano is a magnificent spectacle.) De la Maza and Calvert (1993) discuss weak evidence for other colonies and migrations in southern Mexico and in northern Guatemala which may result from monarchs migrating across the Gulf of Mexico, or from Florida across Yucatan (see below).

NOMENCLATURE OF THE TRANSVERSE NEOVOLCANIC BELT

The nomenclature of the geographic location of the overwintering area in the volcanic highlands of central Mexico has been historically fluid (partly, I must confess, through my own writings). A serious error was made in the original *National Geographic* article which referred five times to the area as the “Sierra Madre” (Urquhart 1976b, see also Urquhart & Urquhart 1977a, 1977b). The eastern Sierra Madre Oriental and the western Sierra Madre Occidental (Figs. 1A and B), are two distinct mountain complexes which are much older than the volcanic highlands, having originated during the Laramide (Rocky Mountain) and Sierra Nevadan orogenies, respectively (see Arbingast et al. 1975 and Garver 1981 for maps that clearly depict the major mountain ranges of Mexico.) Although the Urquharts subsequently corrected their error, referring to the area as the “Neo-Volcanic Plateau of Mexico” (1978b: 1760, 1978c:134), the Hollywood-like ring of “The Sierra Madre” has proven difficult to expunge from the popular literature (e.g., Wood 1977, Pyle 1981, Ellis 1984, Shull 1987, Peach 1988, Anon. 1991, Dalrymple & Gottfried 1995).

In my original description of the Sierra Chincua overwintering site, I referred to its location as *The Trans-Mexico Volcanic Belt* (Brower 1977a), which we changed to the etymologically incorrect *Trans-Volcanic Belt of Mexico* in Brower et al. (1977); to *The Volcanic Highlands of Central Mexico*, *The Sierra Volcanic Transversal* and *The Transvolcanic Range of Mexico*, all in Brower (1985); and, finally, to the *The Transvolcanic Belt of Central Mexico* in Calvert and Brower (1986). Other authors' names for the region include *The Cordillera de Anahuac*, rejected in favor of *The Volcanic Province* (Thayer 1916), *The Transverse Volcanic Biotic Province* (Moore 1945, Goldman & Moore 1946), the *Sierra de los Volcanes* (Garfias & Chapin 1949), *The Great Cross Range* (Loock 1950), *The Neovolcanic Plateau* (Raisz 1964), *The Cordillera Volcánica* (Duellman 1965), *The Cordillera Neo-*

volcánica (Arbingast et al. 1975), *The Provincia Eje Neovolcánico* (Anon. 1981), *The Eje Neovolcánico Transversal* (de la Maza & Calvert 1993), and *The Transverse Neovolcanic Belt* (Núñez & García 1993). In honor of Dr. Leonilla Vasquez García who was one of the first Mexican scientists to visit the Sierra Chincua overwintering area, I propose that Lepidopterists settle on *The Transverse Neovolcanic Belt*.

HISTORICAL AND CURRENT ABUSE OF THE OYAMEL FORESTS

As Leopold (1950:511) pointed out, the land below these Oyamel forests has been abused by humanity since prehistoric times: "... the greatest part of the Mexican population has lived in the pine-oak zone with its healthy, temperate climate suitable for the cultivation of corn. As a result ... natural resources of the southern uplands have been severely taxed and in some localities largely destroyed."

According to Loock (1950:29-32), the original *Abies religiosa* forests consisted of trees nearly 2 m in diameter and 50 m in height, far larger than trees we have observed in all the current overwintering sites. When these forests were less disturbed by humans, it is likely that monarchs overwintered in them more widely in the Transverse Neovolcanic Belt. In 1984, Monarca AC, a Mexico City non-governmental conservation organization largely supported by the World Wildlife Fund (Ogarrio 1993, Gottfried 1993, Monasterio 1993, Camus 1993) sponsored an extensive search of more than 60 oyamel forests across the entire Transverse Neovolcanic Belt. More than 60 potential overwintering sites were found "located in areas where intense commercial lumbering has resulted in the destruction of much of the original vegetation" (de la Maza & Calvert 1993:296).

A detailed documentation of the current pressures on the Oyamel forests, as well as suggestions for coping with them, are in Snook (1993a). Wood is being harvested in and adjacent to the current overwintering areas by local inhabitants for building their homes and sheds, for heating, and for cooking; commercial logging that is both legal and illegal is being conducted on a large scale, apparently at ever-increasing rates; and a cottage charcoal industry is developing.

The Decree issued by President Miguel de la Madrid in October 1986 (de Castro 1993) that supposedly protected five of the nine known Mexico overwintering sites has been violated at most sites. The Sierra Chivati was clear cut in 1986, the very year the decree was declared. Wood cutting is now focusing on the so-called buffer areas around virtually all of the colony core areas (Brower 1987, Calvert et al. 1989, Stevens 1990, Homero Aridjis in Nusser 1992, de Castro 1993, de Castilla 1993, Snook 1993a, Brower, Calvert & Alonso M., current observations through January 1995).

It is possible that these extensive forest disturbances are disorienting current generations of fall migrants. This may explain the temporary clustering sites and enigmatic migratory movements reported by de la Maza et al. (1977). I also have an uneasy impression, based on my observations of the spring remigration into north central Florida since 1981, that monarchs left the overwintering sites in Mexico abnormally early in the springs of 1994 and 1995.

Overwintering of the monarch butterfly in Mexico is clearly threatened (see below). Current statements in the popular press that the overwintering monarch numbers are "normal" in Mexico (e.g., Marriott 1995) are not cognizant that the outlying sites, to which tourists do not have access, may be collapsing. Bereft monarchs may well be aggregating at the few protected sites, giving a false impression of the total numbers that are actually overwintering.

SPRING RECOLONIZATION OF THE EASTERN BREEDING RANGE

The *modus operandi* of the spring remigration of the eastern population was debated vigorously in the 19th century. Observations made by Edwards (1878) in West Virginia led him to suggest that the overwintered individuals produce a succession of generations that move north over the spring and summer, while Scudder (1881) speculated that individual winter survivors move northward and recolonize the entire breeding range. Urquhart's (1960, 1965a, 1966a) summaries of his tagging program did not resolve the issue (Roer 1967:197), and by early 1973 Urquhart (1973b) proposed that the fall migrants themselves probably do not return from the south, but that their progeny do.

The discovery of the overwintering sites in Mexico effectively jettisoned the hypothesis that a fresh generation of monarchs reinvades the United States each spring and stimulated my research group to investigate the spring remigration (Brower 1985, Malcolm et al. 1993, Brower 1993). We formalized the two 19th century alternatives as: (1) Scudder's modified "single sweep hypothesis," in which winter survivors from Mexico fly to the southern United States, oviposit on the newly emergent *Asclepias* flora, and continue to fly northward to southern Canada ovipositing along the way; and 2) Edwards' modified "successive brood hypothesis," in which the winter survivors fly to the Gulf Coast where they oviposit extensively on the milkweeds, and then die. A new spring generation produced in the south then continues the migration northward to southern Canada, laying eggs along the way.

The departure of monarchs from the overwintering sites in Mexico occurs towards the end of March and early in April (Brower 1985, Calvert & Brower 1986). This timing is consistent with an earlier report

of the spring remigration in eastern Mexico. On 22 March 1962 while driving along the eastern slope of the Sierra Madre Oriental in Mexico, Heitzman (1962) encountered large numbers of monarchs flying northward through the town of Ciudad Mante, in the State of Tamaulipas. The butterflies were drinking nectar from roadside flowers, and roosting was observed as early as 14:30 hr.

Malcolm, Cockrell and Brower (1993) determined that Edwards' successive brood hypotheses prevails, by comparing the cardiac glycoside fingerprints in four groups of monarchs: (1) fall migrants of the last summer generation, most of which we predicted had fed on *Asclepias syriaca*; (2) monarchs collected at their overwintering sites in Mexico; (3) monarchs that had flown back from Mexico in April to the Gulf Coast states of Texas, Louisiana, Mississippi, Alabama and Florida; and, crucially, (4) monarchs collected in early June across the northern tier of states, from Massachusetts through Wisconsin to North Dakota. We found that over 80% of several hundred fall migrant, overwintering, and returning coastal monarchs had the *A. syriaca* foodplant pattern. In contrast, only 6% of 629 butterflies collected along the northern tier in June had the *A. syriaca* pattern; 90% of them had fingerprints derived from southern milkweeds, including *A. viridis* and *A. humistrata*. These data clearly indicate that the majority of migrants returning from Mexico lay their eggs on the southern milkweed species and then die. Their children, imbued with the distinctive *A. viridis* or *A. humistrata* fingerprints, then continue the migration to the northern states. Thus Edwards' perspicacity of 1881 proved to be largely correct: monarchs recolonize eastern North America each spring by successive brood remigration (Fig. 1B).

I say *largely*, because fragments of data in the older literature have swayed me to believe that Scudder's single sweep remigration hypothesis should not be completely discarded. Shannon (1915) reported seeing old, faded monarchs on Long Island, New York in June and later (1954) reported several worn and faded monarchs of both sexes in Port Monmouth, New Jersey on 12 May 1916. If these butterflies were of the new spring generation produced in the Gulf states, they should have looked fresher, as were most of the monarchs collected in the Great Lakes region in early June as reported in Malcolm, Cockrell and Brower (1993).

Two of the earliest observations of spring swarming behavior (reported in Riley 1871:151) add credence to the single sweep hypothesis. The first was Stroop's observation of about 30 individuals on 31 March 1870 near Dallas, Texas (see also Stroop & Riley 1870). The second was made the very same spring in Manhattan, Kansas, where in mid-April

Wells saw large numbers of monarchs in a swarm coming "rapidly with a strong wind from the (sic) N.W. . . filled the atmosphere all around for more than an hour, sometimes as to eclipse the light." Riley accepted both reports on face value and made two critical assumptions: it was too early for milkweeds to have flushed out either in Texas or in Kansas, and the "bevies" in both areas were moving southwards. Tutt (1900: 209) questioned the direction of flight of the Kansas butterflies saying "surely at this time of the year the flight should have been going to the north-west, not coming 'from' the north-west." Moffat (1901b:50) later reasoned that both of these groups were actually migrating northward in the spring, interpreting the seemingly incorrect direction as a consequence of the swarms having been caught up in a wind too heavy to fly against. He based this deduction on having personally observed individual monarchs in a gale that were being blown along with the wind.

We now know that the milkweeds would have flushed out by this time in Texas and Louisiana (Lynch & Martin 1993, Malcolm et al. 1993, Riley 1993), and that by mid April very early shoots would probably also have been available in Kansas (Orley Taylor, pers. comm. 1995). I think it likely that there may have been a large migration of monarchs returning to Texas from Mexico in the spring of 1870, and that some of the butterflies were blown northward just as the milkweeds were sprouting in Kansas. If the offspring of these early migrants survived, then a single sweep also would be indicated.

Three other reports of early spring remigrations in the north that also supported the single sweep hypothesis were as follows: during 1889 in the Red River Valley of Minnesota, monarchs arrived as early as 2 May (Lugger 1990); a more or less constant low flow of monarchs passed north or northwestward along Virginia Beach, Virginia from 18–30 April 1906 (Jones, in Clark 1941); and a large flock of hundreds of presumed monarchs were seen flying northward over Oklahoma on 9 March 1928 (Cleveland, in Clark 1941).

I predict that future research will establish that the successive brood recolonization is the major strategy employed by the monarch, but that a few individuals do manage a single sweep recolonization to the north. Many of these latter monarchs may overshoot the expanding northward wave of sprouting milkweeds and freeze to death. On the other hand, if they survive until the milkweeds have sprouted, they could gain a substantial temporal advantage. Both strategies may contribute to establishing many breeding colonies throughout the expanding spring range of the monarch. Long-term quantitative studies that monitor the timing and magnitudes of the spring movements of monarchs through

key areas are needed to gain a fuller understanding of the spring remigration (e.g., see Fales 1977, 1984).

HOW MANY GENERATIONS ARE THERE IN THE BREEDING RANGE?

The number of broods of monarchs produced at various latitudes was vigorously debated in the 19th century. Edwards (1876a, 1876b, 1878, 1881, 1888), Morton (1888) and Marsh (1888) provided strong evidence for multiple broods from West Virginia to southern Canada while Scudder (Scudder & Gulick 1875, Scudder 1881, 1889:741-742) stubbornly argued for a single brood throughout the monarch's range (see Tutt 1900:183-184). Riley (1878a, 1878b) believed there were three or more broods in the south, but only one towards Canada (see also Riley 1880b, 1890). It is curious that Scudder did not deduce that several generations were possible from Harris' early 19th century data, which Scudder himself had spent an enormous effort to collate and publish (Scudder & Harris 1869). Harris, a sadly frustrated Harvard librarian who had quit his medical profession in order, he hoped, to pursue entomology (Evans 1985), produced the first data on monarch development rates (Harris 1863, given in detail in Scudder & Harris 1869). If four days for egg development and four days for adult maturation following eclosion are added to Harris' recorded minimum of 23 days for larval and chrysalid development, a total of 31 days is obtained. It should therefore have been obvious to Scudder that more than one summer generation was possible in New England.

Moffat (1900a, 1901b, 1902b), who lived in southern Ontario, provided concrete evidence for more than one brood in the north, but also suggested an important alternative: because there may be more than a single wave of migrants returning from the south, there may be an overlapping of generations. In their highly influential book, *How to Know the Butterflies* (1904), John Henry Comstock, the first professor of entomology at Cornell University, and his wife Anna Botsford Comstock accepted that there are multiple broods: "The mother butterfly follows the spring northward as it advances as far as she finds milkweeds sprouting [and] generation after generation pushes on . . . as far north as Hudson Bay" (p. 205). Seitz (1924) also endorsed multiple broods, stating that there were up to four each year.

The emerging idea of a relay race involving successive generations was embraced by Ricker (1906:48) and Julia Rogers (1911), editor of the Nature Club Column of *Country Life in America*. However, lack of definitive evidence apparently was responsible for J. A. Comstock's (1927:58-59, 127-130) vague description of the spring recolonization (J. A. Comstock, no relation to Cornell's John Henry Comstock, was Director of Science at the Los Angeles County Museum and author of

Butterflies of California; Kendall et al. 1977:83–84). Clark and Clark (1951) again implied that there is a relay race and stated that there are four to six summer generations in Virginia. Urquhart (1960:60–62) attempted to deduce the number of generations at various latitudes and longitudes as well as the degree to which they overlap. Based on new development rate data (Rawlins & Lederhouse 1981, Zalucki 1982), Cockrell, Malcolm, and Brower (1993) calculated that there is probably a maximum of five generations in the eastern population, which would include two generations in the southern U.S.A. and three northward to Canada over the late spring and summer. More quantitative data are needed to establish the number of broods and the degree to which they overlap throughout the range of the monarch in eastern and western North America.

FLUCTUATIONS IN THE NUMBERS OF FALL MIGRANTS

The accumulated anecdotal evidence on the eastern population over the past 125 years indicates variability in the numbers of monarchs migrating southward. Examples included a large migration in the fall of 1872 over Cleveland where no migrations were reported during the next three years (Ison, in Anon. 1875), and another large migration through Hamilton, Ontario in 1899 that had been preceded by three autumns when the monarchs in the same area were comparatively scarce (Moffat 1900a, 1900b, Bethune 1900:101). Other instances of year to year variability, or years of notably large numbers, were reported by Reed (1869), Scudder and Allen (1869), Saunders (in Riley et al. 1875), Lugger (1890), Brooks (1911), Thoms (1911), Stoner (1919), Webster (1892, 1912, 1914, 1915), Hutchings (1923, in Felt 1928:101), Williams (1930, 1938), Clark (1941), Williams et al. (1942), Brown (1950), Ferguson (1955), Urquhart (1960, 1974), Hoying (1972), Anon. (1973), Sullivan (1973), Brewer (1974), Jackson (1974), and Yeager (1974).

We therefore have a substantial but completely anecdotal literature that the numbers of butterflies in the fall migration of the eastern population fluctuate from enormity to rarity, without understanding why this is so. Reconstruction of at least a crude picture of the fluctuations back to the 1880s could probably be done by systematically organizing records from the literature (including the annual field season summaries in the *News of the Lepidopterists' Society*), gleaning information from local newspapers, scouring unpublished records of various state parks and wildlife sanctuaries, interviewing naturalists who keep accurate records, and computerizing the Urquharts' extensive files.

Urquhart (1960:69) had interpreted the available data as indicating

a 6–7 year cycle which he initially attributed to weather, and later to a virus (1966b:1970, see also Sullivan 1973), which another author suggested may have been a bacterium (Anon 1971). Urquhart (1987: 95) recently concluded that “there is no true cycle, but rather the fluctuation in population is irregular, and periods of scarcity and abundance occur in any year.” He vaguely attributed the fluctuations to a dynamic interaction of the monarch with summer temperatures, storms, and the waxing and waning of polyhedrosis virus resistance.

My field studies in the eastern breeding range over the past 38 years and at the overwintering sites in Mexico over the past 17 years lead me to conclude that monarchs are not often subjected to heavy disease and parasitism in wild populations. I hypothesize that this is because the almost continuous migratory movement of the adult butterflies from March through October allows them to escape the build-up of viral and bacterial pathogens and hymenopteran and dipteran parasitoids. There is, however, a severe protozoan pathogen in the California population that may currently be decimating the colonies (Brower et al. 1995).

I propose that years of small autumn migrations are principally a consequence of storm-caused mortality at the Mexican sites the previous winter followed by overcast, wet and cold weather during the spring and summer breeding in the U.S.A. and Canada. Since the 1976–1977 overwintering season in Mexico, we have witnessed two winter storm systems that caused severe mortality. During the 1980–1981 season, approximately 42% of the monarchs were killed in the Sierra Chincua colony during a period with snow, rain and freezing temperatures (Calvert et al. 1983, Calvert & Brower 1986). In February 1992, prolonged rainy weather during January and February was followed by a severe freeze that killed more than 80% of the butterflies at the Herreda overwintering site (Brower in Culotta 1992, Brower et al. unpublished data).

Variations in temperature, cloud cover and rainfall throughout the monarch's breeding range will affect both the milkweed and nectar sources. Climate, therefore, is probably the major determinant of both the success of breeding in each generation as well as the number of generations produced. If severe freezing at the Mexican overwintering sites were followed by wet and cold weather in the spring and summer breeding ranges, then I would predict fewer and smaller generations and a reduced fall migration. Dry, hot summers also would be detrimental. If, on the other hand, a mild winter in Mexico were followed by warm and clear weather across the eastern U.S.A. and southern Canada, with sufficient rainfall to optimize the growth of milkweeds and nectar resources, I would predict a large fall migration.

Correlating past and future annual variation in the abundance of fall

migrants with historical weather data will undoubtedly prove informative. Standardized, quantitative estimates both of the colony sizes in Mexico and the numbers of butterflies migrating in the spring and fall are greatly needed to monitor the impact of humans on the monarch's breeding and overwintering habitats, as will be discussed below.

Over the next few years, I predict that the size of the monarch's fall migration will dwindle because of the increasing use of herbicides across North America (Lever 1990). These chemicals kill both the milkweed larval foodplants and other herbaceous plants that serve as nectar sources throughout the monarch's annual cycle. In 1993, an estimated 4.6 billion dollars were spent on 620 million pounds of herbicides in the U.S.A., and usage of these chemicals exceeded the combined use of all other pesticides, including insecticides, fungicides and other undesigned biocides (Aspelin 1994). The intended goal of herbicide use (now sprayed by over one million "certified applicators") is to kill all competing plants over tens of millions of hectares of croplands.

EVALUATION OF THE "ABERRANT EAST COAST MIGRATION" HYPOTHESIS

Prior to announcing the discovery of the Mexican overwintering sites (Urquhart 1976b, Urquhart & Urquhart 1976c), Urquhart and Urquhart (1976b) had proposed that the fall migration along the eastern coast of the United States is "aberrant." By this they meant that the migration was off of the direct southwesterly route to Mexico. While this hypothesis seems to have crystallized as a result of the Mexico discovery, they attributed it to tagging recoveries, personal observations, and collaborators' reports.

According to the initial hypothesis (Urquhart & Urquhart 1976b), there is only a meager migration through Florida, largely along the western side of the peninsula. Developing the idea further, Urquhart and Urquhart (1976d, Fig. 3) presented a map showing two fall migratory routes for the entire eastern population. The route flown by the majority of monarchs produced in the Great Lakes region is on a southwesterly course to the central Mexican overwintering sites (see also the extensive new directional data in Schmidt-Koenig 1985, 1993). The second route, which they now called "the migration route of the aberrant population" was hypothesized to be a subgroup of these butterflies flying southward over the Appalachians into Florida, thence to Cuba, the Yucatan, and Guatemala. In their next publication, the Urquharts re-drew their 1976b map (see Fig. 2, p. 1586 in Urquhart & Urquhart 1977a) to include a western Great Plains component of monarchs flying southeasterly to join with the main group migrating into central Mexico.

Two years later Urquhart and Urquhart (1979b, see also Urquhart, 1987:138–143) published a new set of recapture records and elaborately developed the hypothesis. Strong winds out of the west during the fall migration, they proposed, blow many monarchs off their main southwesterly course and drive them eastwards towards the Atlantic Coast (see also Gibo, 1986:178). Presumably, most of these monarchs recover their southwesterly flight orientation and eventually fly through Texas to Mexico. The rest of the butterflies, however, accumulate along the east coast and may then perform three possible so-called “aberrant migrations” across the open ocean. While the Urquharts’ recapture data at best weakly supported their hypothesis, I believe that they were largely correct in postulating these three movements. However, I contend that what they called “aberrant migrations” should be called “eastern dispersal routes” for reasons that will become clear. The Urquharts’ three dispersal routes are as follows.

Eastern Dispersal Route 1: Florida to the Yucatan and Central America. These butterflies are held to fly along the Atlantic coastline southward into the Florida Peninsula and Keys, across about 50 km of open ocean to northwestern Cuba, and thence southwestwards across the 200 km Yucatan Channel to the Yucatan Peninsula in Mexico. In addition to the evidence provided by a single recapture in Cuba, (Fig. 2 in Urquhart & Urquhart 1978a), Urquhart and Urquhart (1979b, 1979c) and Urquhart (1987:138–143) supported their contention by stating that (1) they had observed monarchs flying with a strong onshore wind into the Yucatan during October 1978, (2) overnight roosts had been seen in Cuba, and (3) their field assistant had made numerous observations of overnight roosting clusters in eastern Yucatan. The Urquharts held that these monarchs continue flying westwards across the Yucatan Peninsula to hypothetical overwintering sites in Guatemala or Honduras.

Possible direct evidence for a southerly migration during November 1985 along the eastern coast of the state of Quintana Roo in the Yucatan was cited in de la Maza and Calvert (1993). Deductive reasoning that supports the hypothesis is in Baker’s (1978:424) analysis of Urquhart’s (1960) speed of flight data which gave a maximum daytime flight distance for individual monarchs of 130 km. Assuming moderate wind assistance, the distances are short enough that hopscotching from the Florida Keys across Cuba to the Yucatan seems a viable possibility. That wind assistance is possible is supported by observations of monarchs scudding along with cold fronts at several hundred meters above the ground during the fall migration in Minnesota (Luggar 1890), during October in Arkansas (Merrill, in Williams et al. 1942:166), and on 9 October 1994 in central Texas (Brower et al. unpublished data).

Biogeographic evidence may also support this dispersal route. The lighter colored *Danaus plexippus plexippus* from North America shows clinal intergradation in southern Mexico and in Central America with the darker *Danaus plexippus megalippe* (Hübner) from northern South America. The intergradation could result from the invasion of northern monarchs westwards across the Yucatan and Guatemala, followed by interbreeding with *megalippe* (see Godman & Salvin 1879–1901, Clark 1941, Williams et al. 1942:158–159, Figs. 18A–C). However, a southward over-shooting of the Mexican overwintering sites in the fall, or dispersal southward from the overwintering sites in the spring, could have the same effect. More research is needed to resolve the issue.

Eastern Dispersal Route 2: Cross-Atlantic to Bermuda. Even though the Bermuda island group is 1040 km from Cape Hatteras, a dispersal route eastwards over the Atlantic ocean to Bermuda is supported by the older literature. Monarchs were first recorded in Bermuda in November 1847, and by 1859 were common and breeding throughout the year (Hurdis, in Jones 1859, Hurdis & Hurdis 1897, Tutt 1900:237, Verrill 1902:763). Since there were no native asclepiads in Bermuda, monarchs could not have become established prior to the introduction of *Asclepias curassavica* L. or *A. physocarpa* Schlechter (Asclepiadaceae) (Hilburn 1989, Ferguson et al. 1991).

Migrating individuals, thought to be riding eastward on cold fronts or hurricanes, arrive in Bermuda from the mainland in September and October. For example, on 4 September 1970 several thousand monarchs were reported flying in from the ocean and clustering on the imported Australian “pine,” (*Casuarina equisetifolia* L. Casuarinaceae) (Ferguson et al. 1993). The arrival of other butterfly species on Bermuda support this windborne hypothesis: Jones (in Scudder 1876) had noted large numbers of *Terias lisa* (Pieridae) suddenly arriving in Bermuda in 1875 and attributed their arrival to having “been caught up by the winds in a period of great atmospheric disturbance, and whirled over the sea to this island” (p.395).

Other supporting evidence for dispersal to Bermuda was presented in Urquhart (1976a): Sabo reported from an oceanographic expedition that he had seen more than a thousand monarchs flying over the Atlantic near Bermuda during an 8 day period in September, 1973. An earlier observation at sea, associated with a hurricane, was made in September 1944 by Varey (quoted in Urquhart 1987:140–141): “we ran through a massive swarm of monarch butterflies. . . . I remember standing on deck watching this mass of colorful creatures fluttering around the ship’s rigging.” This encounter occurred immediately *after* the ship steamed westward through the eastern edge of the hurricane, about 1600 km east of New York. Brewer (1967:167) had earlier documented the land-

ing of large numbers of monarchs on a Coast Guard vessel in the Atlantic Ocean in the fall of 1941; these butterflies presumably were blown out over the Atlantic Ocean by a hurricane.

The eastern dispersal route to Bermuda is thus supported by direct observations of monarchs at sea, witnessed arrivals, and the breeding populations that have been established there for well over a century. However, cross-oceanic dispersal to islands could not have been an adaptive behavior prior to the introduction of milkweeds. Thus monarchs migrating to such places as Bermuda would have died without issue unless they could return to the mainland. To date, there is no evidence for a return migration to the U.S.A. from Bermuda, Cuba, or any of the other marginal southern destinations of the dispersing fall migrants.

Eastern Dispersal Route 3. A subset of the monarchs that are blown towards Bermuda constitutes the Urquharts' third hypothetical group. The authors postulate (supported by minimal data in Urquhart & Urquhart 1978a, Fig. 2, p. 614) and Urquhart 1987:142-143) that these monarchs somehow recover a southerly orientation and pass through the Bahamas and the Antilles to Central or South America, ultimately to winter in the mountains of Guatemala, Colombia, or Venezuela.

Synthesis: (a) The Trans-Oceanic Dispersals. To accept these three trans-oceanic dispersal routes as fall migration routes requires that monarchs succeed in reaching overwintering sites and then return to the southern U.S.A. the following spring, as is now proven for the main cohort that overwinters in Mexico (Malcolm et al. 1993). The extensive tropical lowlands through which the reproductively-repressed adults would have to fly during the September-November migration period are hot. For example, mean monthly temperatures during October through December in Quintana Roo (southeastern Yucatan) exceed 23°C (Snook 1993b). Consequently, any butterflies reaching mainland Central or South America would almost certainly undergo rapid gonadal maturation (Johnson 1963), mate with the local non-migratory populations, reproduce, and die before ever reaching the hypothetical mountain overwintering sites (Brower 1985a:757). Peter Hubbel (pers. comm. 1994), an entomologist who has collected extensively in Guatemala, has never observed any clustering in the mountains, and there are no solid records of overwintering sites in any of the Urquharts' postulated Central or South American areas (de la Maza & Calvert 1993).

I therefore tentatively conclude that the Urquharts' "aberrant migration" routes over the Atlantic Ocean to hypothetical Central and South American overwintering sites are best considered as failures of the fall migration to Mexico. Rather, they, as well as the chance arrivals in Bermuda, probably constitute emigration and dispersal routes, with

only a remote possibility that these individual monarchs or their offspring can ever complete a spring remigration to the northern breeding grounds in the U.S.A. or Canada.

Let me inject a caveat, however. It took more than 100 years for scientists to find the Pelon and Chincua Mexican overwintering sites that are less than 125 km from Mexico City. Rais (1964) referred to the Neovolcanic Plateau as the "the cultural-historical center of Mexico." Lack of interest in recording local natural history phenomena may well be a parsimonious explanation of our ignorance of other overwintering areas in Central America, or even elsewhere in Mexico. Thus, although the broader biological picture of the monarch argues against the existence of other overwintering sites in Central and South America, it seems worthwhile to continue looking for them.

Synthesis. (b) East of the Appalachians: what happens to the Atlantic Coastal and Florida fall migrants? Focusing on the aberrant dispersal routes ignores the importance of the monarch migration east of the Appalachians. As seen above, the historical anecdotal evidence indicated a predictable annual fall migration along the Atlantic Coast with occasional spectacular years. My colleagues and I have initiated a new program that is providing a long term data base on the fall migration through Cape May, New Jersey. We have so far recorded a regular migration through the area for four years during September and October (see Walton 1993, 1994). This research also determined that there is a high correlation between our Cape May migration data and the previous Fourth of July monarch counts taken annually east of the Appalachians during the monarch's summer breeding period (Swengel 1990, Opler & Swengel 1992). This correlation strongly argues that it is incorrect to consider the migration along the east coast of the U.S.A. as aberrant (Walton & Brower 1995).

The major clue to the fate of the migrants east of the Appalachians is the lack of recurrent literature reports of migrations southward through the Florida peninsula (see above for the frustrating searches for overwintering populations in Florida; see also Urquhart 1960, 1987:100-101, 138). I am led to conclude that the majority of monarchs breeding east of the Appalachians either migrate southwestward through these mountains, or, if they migrate along the coast to southern Georgia and Northern Florida, they turn westward and fly towards the Gulf Coast. Eventually these butterflies probably join the major southwesterly migration to Mexico. Those that get blown out over the Atlantic by westerly winds and storms have lost control of their destiny. Prior to the spread of milkweeds by humans (see below), these butterflies would have perished.

Systematic, quantitative research on the fall migrations in relation

to weather patterns is clearly needed, as has been done for bird migrations (e.g., Alerstam 1990). The periodic appearance of large numbers of fall migrants on and near Nova Scotia and Newfoundland (e.g., Brown 1950, Ferguson 1955, Jackson 1974, Urquhart 1974, Maddox & Cannel 1982), where native milkweeds do not occur, probably also represent monarchs that are blown off course. It would be interesting to search old newspaper records of Atlantic coastal towns from Quebec and Newfoundland to Florida, and correlate reports of migrations with weather patterns over the years.

LONG DISTANCE DISPERSAL ACROSS THE ATLANTIC AND PACIFIC OCEANS

Nineteenth century biologists witnessed a rapid expansion of the geographic distribution of the monarch butterfly from North America across both the Atlantic and Pacific Oceans, distances of 5,000 km and more. According to Ackery and Vane-Wright (1984), the first sighting in Europe was by Llewelyn (1876). A "fine fresh specimen" (p. 108) was captured in southern Wales on 6 September 1876, which Llewelyn and the editor suggested could have been transported as a chrysalid "or even . . . a perfect insect" on one of the many ships from America sailing into the Bristol Channel. Distant (1877:94) formalized the first hypotheses to explain these long distance dispersals and island colonizations: "We are justified in considering the principal and only factors, as winds, [ocean] currents, and the agency of man. . . and whether the dispersals are. . . voluntary or involuntary migration." Distant was aware of bird migrations to England as well as many sightings of butterflies from ships at sea, and suggested that riding wind currents, landing on ships, and possibly even riding on terrestrial vegetation carried along by the Gulf Stream were ways monarchs might cross the Atlantic.

In reviewing cross-Pacific flights, Gulick (in Scudder 1875, and elaborated in Scudder 1889:730-731) noted that monarchs were found in the Sandwich (=Hawaiian) Islands after a neotropical *Asclepias* (presumably *A. curassavica*) had been introduced. Gulick moved from Hawaii to the western Pacific and recounted how he had accidentally naturalized *Asclepias* seeds in the Caroline Islands (NW of New Guinea). He reasoned that the milkweed seeds must have been in the soil accompanying a tightly packed shipment of plants that he had brought from Hawaii to introduce and cultivate. To his astonishment, monarch larvae appeared on the young milkweeds shortly thereafter (an alternative possibility is that *A. curassavica* had already become established prior to his arrival; because of its ornamental properties, this neotropical milkweed was widely disseminated through the old world tropics and Oceania, including Tahiti; Pickering 1879:983). With the details pro-

vided by Gulick, Scudder deduced that the larvae must have been the progeny of one or more monarch adults that had arrived on the same ship. Bowles (1880) bolstered Scudder's argument by documenting a monarch that had been captured on shipboard in the Atlantic hundreds of kilometers from shore. By 1886, Scudder was firmly convinced that the transoceanic dispersal of monarchs was a consequence of the serendipitous transport of adults on commercial ships.

In contrast, Walker (1886:222), in thoroughly documenting the rapid monarch colonization of the south Pacific Islands, Australia, and New Zealand, presented an alternative hypothesis: both the *A. curassavica* seeds and the monarch adults had been naturally transported to the islands by winds: "It is . . . not difficult to imagine one of the great migrating swarms of *Anosia plexippus* being blown out to sea from the Californian or Mexican coast, and traveling with the NE trade wind; the greater number by far perishing en route, but a few stragglers . . . would reach the . . . islands . . . I should imagine . . . the light and downy seeds of the *Asclepias* could be carried by the agency of the winds . . . alone." He viewed crossing the "much more stormy" Atlantic with its "less steady winds" as more difficult, and suggested that monarchs complete the trip by "resting . . . on the numerous vessels constantly crossing the Atlantic." Meanwhile, Webster (1902:797) had written a general review of the role of wind in dispersing insects and stated that "The influence of high winds on insects is illustrated . . . by the great number of butterflies that are sometimes encountered by ships at sea, long distances from land."

Comstock and Comstock (1904) promulgated the hypotheses that the transoceanic colonists had arrived "Either by flight or as stowaways in vessels" (p. 206). Walker (1914) subsequently concluded that natural wind dispersal across the oceans was more important than human-caused dispersal. An additional possibility raised for the trans-Pacific dispersals was the purposeful human distribution of monarchs to control the exotic asclepiads which had become troublesome weeds (Scudder & Gulick 1875, Walker 1886:219). Felt's (1928) extensive review of insect dispersal in relation to global wind patterns considered the monarch a prime candidate for dispersal across the Pacific and Atlantic Oceans by normal wind currents and storms, and minimized the importance of ships. Williams (1930) agreed with the wind dispersal hypothesis, but also cited an additional observation (in Barrett 1893) of several monarchs flying amongst the rigging of a ship 320–480 km from the British shore. Another sighting of a monarch in the Atlantic 97 km off of Portugal was made by Harker (1883), and a century later two monarchs were captured on the deck of an oceanographic vessel in the Gulf of Mexico, 800 km off the coast of Florida (Wolf et al. 1986). Ford

(1945:160) favored the hitch-hiking hypothesis, but, like Walker, was baffled by the simultaneous arrival of several monarchs in southern England in some years e.g., 38 records in 1933 (Williams et al. 1942: 181) and 12 citations in 1983 (Bretherton 1984). Urquhart (1960:192-195, 1987:145), citing an additional observation of fall migrants taking refuge on a small sailing vessel in Lake Ontario during a strong wind, also endorsed the hitch-hiking hypothesis, as did Scott (1986:230).

In my judgment, Sabo's observation (in Urquhart 1976a) of more than a thousand monarchs flying over the Atlantic near Bermuda, with some landing on the oceanographic vessel, provides the solution to this long-standing debate: wind dispersal and hitch-hiking are complementary, not competing, explanations of long distance dispersal of monarchs to the Atlantic and Pacific islands, mainland Europe and Australia (Anon. 1871, Miskin 1871, Anon. 1898, Tutt 1902:318, Owen & Smith 1989). Since monarchs easily find isolated milkweed patches (Shapiro 1981, Brower 1985a, Malcolm & Brower 1987), the successful establishment of a breeding population by the dispersed butterflies is virtually inevitable if they make a successful landfall where one or more exotic milkweed species had already become naturalized. However, the few dispersers that make it across oceans for very long distances to landfall on any of the Atlantic or Pacific Islands, Australia, New Zealand or Europe will have no possibility of a return migration to North America. I conclude that a combination of wind dispersal and hitch-hiking on ships is the most reasonable hypothesis to explain the dispersal of monarchs across the Atlantic and Pacific Oceans during the 19th century.

THE "COLUMBUS HYPOTHESIS" AND THE EVOLUTION OF MONARCH MIGRATION IN NORTH AMERICA

In distilling the ideas about the rapid transoceanic colonizations, Richard Vane-Wright of the British Museum of Natural History (1986, 1987, 1993) rejected both the hitch-hiking and wind dispersal hypotheses in favor of his novel "Columbus hypothesis." There are two major parts of this hypothesis. First, early deforestation of both northeastern and western North America are held to have resulted in a massive increase of milkweed biomass that caused monarch populations to explode in the 19th century. In effect, monarch 'shrapnel' from the explosion is held to explain the rapid transoceanic colonizations, which were essentially completed by 1880. Secondly, the current coordinated migration and overwintering cycle in North America, including the large monarch roosts in Mexico, is held to be less than 200 years old.

At least three critical assumptions lie behind Vane-Wright's Colum-

bus hypothesis: (1) prior to clearing the American forests, the monarch had not yet evolved its current patterns of migrating and overwintering. In his words: "... the annual coordinated migration and massed overwintering cycle is a very recent phenomenon." (1993:179); (2) lacking a well developed southwesterly orientation, the vast numbers of individuals produced on the new milkweed supply growing in the cleared forests would, in addition to flying south, disperse in westerly or easterly directions towards the oceans, and a few would succeed in colonizing the Pacific and/or Atlantic islands; (3) flying out over the oceans would result in enormous mortality. As a consequence, strong selection over the 200 year period would have resulted in the rapid evolution of unidirectional migrations, the complex swarming and bivouacking behavior that occurs during the fall migration, and the highly organized overwintering behavior that involves dense clustering of thousands to millions of individuals, as currently occurs in California and Mexico.

Malcolm and Zalucki's (1993b) critique of the Columbus hypothesis emphasized that Vane-Wright made an additional key assumption: deforestation resulted in a net increase of milkweed biomass in the northern breeding range of the monarch. I agree with Vane-Wright that breeding monarchs probably did shift eastwards from the prairie milkweeds to take advantage of the increasingly abundant *Asclepias syriaca* that was colonizing the newly cleared northeastern forest. While a net increase in milkweed biomass probably did occur, certainly the biomass of more than 20 species of milkweeds growing naturally in the nearly half billion acres of the original prairie also must have been enormous (see above, "Did the migration expand eastwards during the latter part of the 19th century?").

A major weakness of the Columbus hypothesis is Vane-Wright's assumption that because monarch overwintering clusters in California were not reported in the early literature, the complex migration-aggregation-overwintering behavior did not evolve until late in the 19th century. This seems highly unlikely given the fact that migration and aggregation behaviors occur not only in numerous Old World danaid species in five genera (*Euploea*, *Tirumala*, *Ideopsis*, *Parantica*, and *Danaus* (*Salatura*)) (Wang & Emmel 1990, Scheermeyer 1993), but also in *Anetia briarea* in the Dominican Republic (Ivie et al. 1990, Brower et al. 1993). The common behavioral attributes in these divergent species groups of the Danainae suggests that features of the migration-aggregation syndrome are ancient characters of the subfamily.

Lane (1993) uncovered an early report of clusters in the fall of 1873 in California, probably in Pacific Grove (Anon. 1874). This predated Bush's (in Riley & Bush 1881, 1882) observation, and is important, not for pushing back the discovery date of California overwintering, but

rather because the report had been overlooked by the scientific community until 1993. I submit that the nine year hiatus between this and Bush's report indicates that 19th century residents of the Monterey region had probably long known of the overwintering phenomenon, but were so involved in their own individual pursuits (e.g., Steinbeck 1954:258–262) that they either ignored the butterfly clusters or took them for granted. Shepardson (1939:18) pondered the same question and concluded that “nothing smaller than a bear would have attracted the. . . [early settlers'] attention.” Lucia Shepardson's hypothesis that residents simply ignored the phenomenon is supported by the fact that, despite the existence of numerous overwintering colonies near several University of California campuses, remarkably few research papers were published on the biology of California monarchs before 1969 (e.g., Kammer 1970).

In my judgment, the rapid rate of evolution (200 years) required by Vane-Wright's Columbus hypothesis to account for the complex of monarch behaviors involved in the current Mexican and Californian migrations is impossible. The short time is also at odds with Kitching et al.'s discussion (1993) of the likelihood that the monarch's clade (i.e. the subgenus *Danaus*) evolved in South America during the Pliocene from Old World stock that had arrived in the New World at an earlier time (see also Grehan 1991). According to this hypothesis, a progenitor of *Danaus plexippus* crossed the land bridge from South to Central America that had formed towards the end of the Pliocene, about 3 million years ago (timing from Delcourt & Delcourt 1993:71). The Great Plains and prairie environment had begun expanding by this time (Graham 1993:69), so that the monarchs must have been increasingly able to extend their breeding range northward with the expanding milkweed flora (Woodson 1954). However, because of their tropical origins, the butterflies would have had to retreat southwards each fall to avoid freezing.

With the arrival of the Pleistocene, the alternating glacials and interglacials would have caused major contractions and expansions of the geographic ranges both of the Oyamel forests in Mexico and the milkweeds in northern Mexico, the United States and southern Canada. The necessity of retreating southwards each year, together with these longer term movements of the evolving flora, must have been powerful selective forces affecting the evolution of the monarch's current migration biology (see also Brower 1977a, 1986, Young 1982).

If this scenario is correct, the monarch's current migration in North America could have evolved gradually over the approximately 1.75 million years of the Pleistocene, rather than almost instantaneously as postulated by the Columbus hypothesis. As McNeil et al. (1994:13)

concluded in a recent review of insect migration: "Migration is not a random act of 'casting one's fate to the winds' but rather a physiologically coordinated sequence of behaviors, determined by both genetic and environmental factors." Wind dispersal combined with hitch-hiking on ships seems a completely adequate hypothesis to explain the 19th century transoceanic colonizations. Unless compelling new evidence is forthcoming, the Columbus hypothesis seems untenable.

CAN MONARCHS MIGRATE BACK AND FORTH ACROSS THE GULF OF MEXICO?

Evidence that monarchs fly across the Gulf of Mexico is indirect and weak. For several years between 1981 and 1993 monarchs have arrived almost synchronously in late March and early April in eastern Texas, Louisiana (Lynch & Martin 1993, Riley 1993), and north central Florida (Cohen & Brower 1982, Malcolm et al. 1987, 1993, Zalucki & Brower 1993). If returning migrants follow the Gulf Coast northward and then eastward, they should arrive in Texas earlier than in Florida. The nearly simultaneous arrivals suggest, but do not prove, that a broad wave of butterflies could be crossing the open water. Indirect evidence for a fall migration over the Gulf is a report of large numbers of monarchs flying ashore near Veracruz, Mexico (de la Masa & Calvert 1993).

Recent observations of monarchs and other insects landing on oil rigs in the Gulf of Mexico have been cited as evidence of cross-Gulf migrations (Baust et al. 1981, Wolf et al. 1986, Mather 1990). More than 3,000 oil and gas production platforms have been installed in the Gulf at various distances from the Louisiana shore, and Ross and Behler (1993) and Ross (in Stutz 1993) reported monarchs landing on more than 20 platforms during March and October of 1991 and 1992. Hundreds, if not thousands, were said to have landed on at least one platform in both years. The authors interpreted their observations as indicative of a 145–160 km wide flyway from the U.S.A. Gulf Coast to Tamaulipas, Mexico, as Mather's (1990) hypothetical map had suggested.

The conclusions drawn from the oil rig observations did not consider alternatives, and reflect the speculative nature of much of the literature on transoceanic butterfly migrations (e.g., Larsen 1993). For example, the oil platforms could be serving as artificial islands that permit chance interceptions of monarchs that have flown, or have been blown, off of a land course to or from Mexico. Landing on the oil platforms is analogous to the many observations of monarchs landing on ships at sea, as discussed above.

Since the distance from the Mississippi Delta to one suggested landfall in Mexico i.e., Tampico (Mather 1990) is greater than 1,000 km, migration across the Gulf of Mexico could only be achieved if monarchs

(1) do not avoid flying over water, (2) continue flying at night, (3) rest on the ocean surface, or (4) exploit tailwinds.

Are monarchs reluctant to cross large bodies of water? In noting the great fall swarms of monarchs seen in New Jersey, Holland (1898: 82–83) stated that “The swarms pressing southward are arrested by the ocean.” From observations on Long Island, New York, Shannon (1915, 1916:229) maintained that fall migrants generally followed the shore rather than heading out over open ocean. Holding to this position, he later speculated (Shannon 1954:237) about a group that had been reported 24 km at sea: “it is likely . . . that few of these venturers ever regain the land.” Urquhart (1960:86) and Urquhart and Urquhart (1979c: 44) agreed with Shannon’s position, stating that monarchs have an “antipathy” to flying across the Great Lakes, instead moving along the shores. In contrast, Alexander (in Moffat 1901b:48) reported sailing on Lake Erie “for hours through a flock of *Archippus*” flying southward. Teale (1954:59–61) similarly observed 64 monarchs flying southwards from Point Pelee into a headwind and across Lake Erie during the fall migration. Jackson (1974), reporting the largest number of monarchs ever seen in Newfoundland during September 1973, stated that fisherman had also seen monarchs flying past their boats while three miles out at sea.

Later, in discussing the westerly rather than the usual southwesterly heading of fall migrants along the Florida Gulf Coast, Urquhart and Urquhart (1980:722) maintained that “the change of direction from a southward to a westward movement is due to an apparent antipathy on the part of the migrants to travel over large bodies of water where distant land masses are beyond the optical range of the butterflies. . . . The occasional migrant would fly out over the water only to return again to land.” Three recent studies support the Urquharts’ contention that individual monarchs flying out over the Gulf of Mexico tend to turn back towards land (Schmidt-Koenig 1985, 1993, Ishii et al. 1992).

Do monarchs fly at night? Whether monarchs can fly at night is controversial. In the only published nocturnal observations of which I am aware, Jennie Brooks (1907:110) stayed up all night watching clusters of monarchs during their fall migration through Lawrence, Kansas: “The night was cloudless and absolutely without wind . . . the butterflies slept on, and on, and on, with wings tightly folded together” until the rays of the sun fell upon them the following morning, and then . . . “as if touched with a magic wand, the mighty colony . . . wafted into the air.” A less poetic description of nocturnal inactivity during a large fall migration through the Blue Ridge Mountains of Central Virginia in October 1935 was reported by Walton (in Clark 1941:536): “when night came they would all rest just where darkness caught them.”

These observations of total quiescence through the night are in disagreement with several other reports. Thus, in describing monarchs overwintering in California, Inkersley (1911:283) stated "During their stay in Pacific Grove the monarchs set out daily at an early hour, often before sunrise, to gather honey . . . frequently not flying homewards till some time after sundown." Likewise, in reporting a migration over Chicago on 16 September 1952, Fulton (1953) said that a few stragglers continued to pass "as late as the time of the sunset." The most dramatic evidence for nocturnal activity was that of Merrill (in Williams 1942:166, Williams 1958:105) who reported seeing thousands of monarchs through a telescope trained on the moon in Arkansas on 21 October 1921. How he identified the butterflies as monarchs was not described.

Some authors have taken firm positions on nocturnal behavior without presenting any evidence. Thus in Shepardson's (1939:28) description of Pacific Grove, she said: "One indisputable fact is that butterflies are in no way nocturnal . . . they can not travel after dark." Park (1948) also stated that monarchs do not fly at night. Urquhart (1965a:31) claimed that caged monarchs did not fly in the dark and therefore concluded that free flight at night was "improbable." His position against nocturnal flight subsequently was elevated to fact, without additional experimentation or observations (Urquhart & Urquhart 1979c, Urquhart 1987:142, 145, see also Moffet 1985). In his review, Johnson (1969:538) interpreted the available literature differently, and stated that monarchs "proceed alone by night as well as by day" during their northward spring migration. This, in turn, appears to have been the basis for Rankin's (1978:11) statement that there is nocturnal flight during the monarch's spring remigration.

Other authors reiterated previously-published ambiguous reports (e.g., Tutt 1900:69, Williams 1930:342) and in some accounts it is impossible to determine whether authors saw monarchs flying at night, or whether they saw monarchs roosting at night (e.g., Pribble, in Scudder 1899). It may be that monarchs flying in to aggregate on trees or other vegetation at dusk (Lugger 1890, Dernehl 1900, Shannon 1915) have been mistakenly interpreted as butterflies migrating at night. Some reports of nocturnal flight may be artifacts of monarchs being attracted to bright lights, such as lighthouses, sports arenas, and vehicle headlights, from nearby roosting clusters (e.g., Merriam, in Felt 1928:101, Heitzman 1962, Shields 1974:236). Heitzman (1962), Neck (1965), and Kendall and Glick (1972) reported monarchs and other butterflies being attracted to lighted moth traps, and suggested that these butterflies had been disturbed from their roosts by the investigators, other insects, or predators. While Ross and Behler (1993) and Ross (in Stutz 1993) reported that the monarchs landing on oil platforms in the Gulf of Mexico

remained there through the night, Ross (1993:3) also wrote that "many of the offshore migrants continue to fly long after dark." A possible explanation of the latter observation is that the butterflies had settled on the oil rigs in late afternoon but became activated by bright lights on the oil rigs after dark. Kingdon's (1932) report of *Pyrameis cardui* L. (Nymphalidae) flying at midnight around a ship's light 140 km at sea may have been a similar artifact.

A final ambiguous report is of a male monarch nectaring on a flowering *Eupatorium* late at night (Neck 1976b). It is possible that this could have been a dead butterfly which had been ambushed by a predator such as a crab spider (Thomisidae), e.g., Larsen (1992).

In addition to all the conflicting reports, no one has attempted to sort out how the flight behavior of monarchs in the late afternoon is influenced by diminishing light *and* lowering ambient temperatures. Our thermoregulatory studies in Mexico (Masters et al. 1988, Calvert & Brower 1992) indicate that sudden shadowing by a cloud can cause monarch body temperatures to fall below flight threshold, even in flying butterflies. This raises the possibility that migrating butterflies may be forced to land early on days when they are overtaken by a cold front. What happens to the migrating butterflies as night approaches if the ambient temperature remains high or suddenly shifts upwards remains moot. Moreover, does moonlight play any role? While the evidence summarized above is clearly inconclusive, I believe that long distance powered flight by monarchs at night is unlikely. However, it remains possible that they may be able to continue to fly on warm nights during favorable weather conditions.

Is resting on the ocean surface possible? If monarchs cannot fly at night, flight across the Gulf of Mexico could still be possible if the butterflies alighted on the ocean surface for the night and flew off again the next morning. Although this behavior was suggested by Williams (1930:342), most evidence indicates that landing on water for more than a few minutes is lethal. Monarchs do seem able to land on the water surface for short periods of time. Sabo (in Urquhart 1976a) observed monarchs alighting on the ocean surface for about 20 seconds and then flying off again. Seitz (1909:77) had noted similar behavior: "I very often saw *plexippus* at sea flying at a very considerable height, and observed that it could settle on the surface of the water with the wings expanded and rise again without difficulty into the air."

Tutt (1900:257) argued that butterflies, including monarchs, landing on the ocean surface would become waterlogged rapidly, particularly if they repeatedly landed and flew off. One of Urquhart's (1965a) experiments supported this conclusion: monarchs downed on the surface of water became waterlogged and incapable of flying off again after

about 20 minutes. Another hazard of flying across large bodies of water was noted off the coast of Jamaica during one of Christopher Columbus' voyages: huge numbers of butterflies were said to have perished as a result of a heavy rainstorm (Riley 1880a).

Numerous reports made during the fall migrations indicate that monarchs are at risk of becoming trapped in water. Rogers (1872), Bowles (1880), Moffat (1901b:48), Beall (1946), Teale (1956:59) and Brown (1992) reported dead or dying monarchs beached along the shores of the Great Lakes, and Webster (1914) reported similar fall mortality along the Atlantic Coast in South Carolina. During the spring remigration in April 1906, Jones (in Clark 1941:535) noted many dead monarchs "washed up by the waves" along the shore in Virginia Beach. William Beebe (in Hutchings 1923) was reported to have observed millions of monarchs drowned at sea. Mortality during the spring was also observed along the Gulf Coast at Padre Island, Texas on 26 March 1962 by Heitzman (1962). The chain of events leading to the presumed drowning of these butterflies is unknown. Possible causes of landing on the water surface include: (1) exhaustion due to running out of lipid energy reserves; (2) being overtaken by advancing darkness; (3) being cooled below flight threshold by advancing cold temperatures; or (4) being pelted out of the sky by heavy rain.

The combined evidence thus supports the hypothesis that migrating or dispersing monarchs can land on water for short periods of time, but it is highly unlikely that they could rest there for more than a few minutes, and virtually certain that they could not spend the night resting on any body of water, including the Great Lakes, the Gulf of Mexico, or the Atlantic or Pacific Oceans.

Monarchs may fly across the Gulf of Mexico on strong tailwinds. Winds across the Gulf of Mexico apparently do blow predominantly southward in the fall and northward in the spring (Rankin & Singer 1984, 1986, Wolf et al. 1986). Strong fronts, combined with powered and soaring flight, could conceivably increase the monarchs' flight speed sufficiently to make the 1,000 km crossing during a single day (Gibo & Pallet 1979, Gibo 1981, 1986, Buskirk 1980, Drake 1985).

Synthesis. The inconclusive nature of the evidence pertaining to each question raised in this section is, to say the least, frustrating: we lack sufficient critical data to determine if monarchs regularly fly across the Gulf, or whether they fly at night, land and survive on the water surface, or use tailwinds for rapid long distance migration. My own assessment of the historical data base is that monarchs are reluctant to fly out over large bodies of water when an alternative land route is possible; that they probably cannot utilize powered flight at night; that they probably cannot survive for more than a few minutes on any water

surface; but that they may be able to migrate across the Gulf of Mexico by exploiting strong tailwinds during the daytime, and perhaps also at night. It seems worth emphasizing that the elaborate aggregation ("swarming") behavior that occurs at dusk as monarchs settle on trees and bushes along the fall migration routes is consistent with the hypothesis that normal monarch migration evolved as a means of flying over land during daylight hours. Novel quantitative methods need to be devised to solve these problems. Current radar technology that can indicate the size and altitude of individual migrating insects (e.g., Reynolds 1988) may provide a key to exploring the extent to which monarchs cross the Gulf of Mexico.

IS THERE AN INTERMINGLING OF THE EASTERN AND WESTERN POPULATIONS?

Substantive evidence on the degree to which eastern and western populations intermingle along their Rocky Mountain interface is lacking (Malcolm & Zalucki 1993b). Williams' review maps and tentative conclusions (Williams 1938, 1958, Williams et al. 1942) suggested that the two populations are almost completely isolated. While the Urquharts have never provided convincing data bearing on the issue, they have for years stated that there is substantial interchange between the two populations (Urquhart 1966a, 1987, Urquhart & Urquhart 1977a). Most recently, Urquhart (1995:6) summarized his position as follows: "There is definitely gene-flow in the north in the area of the Snake River and in the south along the Gulf Coast to Mexico ensuring a uniform physiological species" i.e., throughout North America. Currently available distribution records shed little light on the question (e.g. Ferris & Brown 1981:407).

A recent study attempted to address this issue by analyzing the extent of mitochondrial DNA divergence between two samples of 12 monarch adults collected from eastern and western overwintering populations (Brower & Boyce 1991). The authors found virtually no differences between the two and argued that a population bottleneck probably occurred prior to the differentiation of the eastern and western migrations. Thus, the mitochondrial DNA data do not appear able to address the degree to which interchange may be occurring currently, and the question remains moot. Allozyme comparisons of individuals collected from the eastern and western populations might show differences, but have not been done to date.

IS THE EASTERN POPULATION GENETICALLY HOMOGENEOUS?

Is the eastern population of the monarch genetically homogeneous, or are there distinct subpopulations? Shannon (1916), drawing parallels

between monarch and bird migration, speculated that the butterfly has four major autumn flyways: an Atlantic coast flyway, two midwestern Great Lakes flyways, and a western central states flyway (see also Williams 1938, Fig. 1, Teale 1956:90). Our 1991–1994 data indicated regular fall migrations along the Atlantic Coast at Cape May, New Jersey that strongly correlated with the previous Fourth of July summer breeding censuses in the northern Appalachian region. The correlation is consistent with the idea of a separate Atlantic flyway. Further data are needed to define the purported separate flyways west of the Appalachians, as well as the degree to which the migrations along the different flyways may or may not be synchronized (Beall 1951).

If the routes of distinct flyways led to geographically distinct overwintering areas, then we might expect genetic differentiation to occur. Based on recaptures of a few tagged monarchs in Mexico, Urquhart and Urquhart (1978b, 1980, see Urquhart 1987) proposed that subgroups of the eastern population do overwinter in geographically separated mountain enclaves in Mexico, with the implication that they return to their respective breeding areas the following spring. Thus the Urquharts proposed a sorting of monarchs with the western, central, and eastern overwintering sites representing concentrations from the Great Plains to more easterly populations.

Too few tagged butterflies have been recovered to support or reject the hypothesis (Urquhart & Urquhart 1978b, 1978c, 1979a, 1979c, Urquhart 1987:160–161), and several facts strongly challenge it. First, the geography of the overwintering sites makes such sorting unlikely: the five major sites (Chincua to Pelon) are within 30 km of each other and occur in a north to south orientation rather than the east to west orientation depicted by the Urquharts (compare Urquhart's 1987 figure on p. 160 with Fig. 1 in Calvert & Brower 1986). It therefore seems likely that butterflies from the different regions mix before and during their arrival at the different overwintering sites. Second, when the monarchs reach the overwintering sites at the end of November and in early December, most are in reproductive diapause: only 19% of 353 females from the Sierra Chincua contained one or more spermatophores during January–February 1978. In contrast, by 1 April 1978, the time of the spring remigration, 62% of the females had spermatophores (Brower 1985a, Table 1, Herman et al. 1989). Thus any potential differentiation within the fall flyways would be canceled out as the mostly virginal male and female monarchs from the entire northern breeding range intermingle over at least a two month period before mating and leaving (see also Van Hook 1993). These facts argue that the monarchs become an effectively panmictic population at the overwintering sites.

Genetic evidence derived from summer breeding and fall migratory

populations supports this genetic mixing scenario. Eanes and Koehn (1978) and Eanes (1979) found that differentiation developed at several electrophoretic loci in local samples collected over the summer, but the differences were homogenized in samples from the fall migratory populations collected in the U.S.A. Even further mixing must occur as the butterflies funnel through Texas, migrate southwards along the Sierra Madre mountains, and thence westwards into the overwintering sites (Brower 1985a).

Finally (and this Eanes and Koehn did not know at the time of their study), monarchs largely recolonize the U.S.A. and Canada by the successive brood strategy shown in Fig. 1B (Malcolm et al. 1993). Following spring breeding in the Gulf Coastal states, butterflies of the new generation move northward to the central and northeastern United States and southern Canada and multiple overlapping generations are produced over the summer (Cockrell et al. 1993). Thus, the annual reproductive cycle of the monarch seems perfectly suited to explain Eanes and Koehn's summer genetic differentiation, followed by effective panmixis during the fall migration, the overwintering period and the spring remigration. Clark's (1941:534) evidence that the color pattern of the monarch "is extraordinarily constant throughout its enormous range" is consistent with this mixing hypothesis.

In conclusion, the combined evidence argues for a general lack of genetic differentiation of monarchs of the eastern population. Electrophoretic comparisons of samples from the various Mexican overwintering colonies should definitively resolve this question.

IMPLICATIONS OF THE SALINE VALLEY OVERWINTERING POPULATION IN CALIFORNIA

One mystery of the western population is the occurrence of overwintering colonies in the Saline Valley, an interior drainage basin immediately west of Death Valley in California. These were first reported by Giuliani (1977-1984). In November 1986, I visited several of these sites with John Lane in an adventure yet to be told. Recent data indicating the annual recurrence of these colonies are in Cherubini (1993) and Sakai (1994).

Overwintering in this environmentally hostile desert area that is nearly 320 km inland from the coast of California raises the possibility that other unknown overwintering sites of the western monarch population may exist in the western U.S.A. or in western Mexico, perhaps in the Sierra Tarahumara or in the Sierra Madre Occidental. A tantalizing but incomplete description of monarchs possibly migrating through this latter region (near Culiacan in the state of Sinaloa) was given by Gluecker (in Urquhart 1960:262).

MONARCH MIGRATION: AN ENDANGERED BIOLOGICAL PHENOMENON

Because the winter aggregations in California and Mexico concentrate virtually the entire breeding stock of monarchs in a few vulnerable locations, various authors have regrettably concluded that the monarch's migration in North America is an endangered biological phenomenon (Brower & Pyle 1980, Wells et al. 1983:xxi, Pyle 1983, 1983b, 1983c, Brower & Malcolm 1989, 1991).

While most of the California overwintering sites are threatened by real estate development, several are protected within state, county and town parks (Nagano & Lane 1985, Vaccaro 1992). The numbers of monarchs overwintering in California during the 1994–1995 season appeared to be the lowest ever recorded, and may be an ominous sign (Sakai 1995). The reasons for this decline are unknown, but one possible explanation is a protozoan disease (McLaughlin & Myers 1970) introduced into the western population by experimental transfers of monarchs from the eastern population. Brower et al. (1995) reviewed the history of these interchanges and presented a series of reasons why transfers between different monarch butterfly populations should cease. A long term strategy is needed to conserve the existing California overwintering sites, as well as to restore some of the historical ones, as is being attempted in Pacific Grove (Vaccaro 1994).

In contrast to the partially protected western population, the eastern population that overwinters in Mexico is in dire straits (Brower & Malcolm 1989, 1991). The butterfly assemblages are largely restricted to the Oyamel fir forests on four mountain ranges in the Transverse Neovolcanic Belt, with the result that virtually the entire gene pool of the eastern population is dependent upon the integrity of these remaining forests. As discussed above, this frighteningly small area—800 square km—is undergoing rapid degradation due to legal and illegal wood harvesting. Such rapidly increasing forest exploitation portends International cooperation between Canada, the United States and Mexico in protecting the milkweed breeding habitats, the wild nectar sources along the migration routes as well as the overwintering sites in Mexico is a *sine qua non*.

I consider that the economic benefits that could be realized from the long term preservation of the overwintering areas would far exceed the short term income gained by cutting them down. One clear benefit is the maintenance of high quality watersheds upon which all the surrounding villages depend (Leopold 1950, 1959, Loock 1950:55). A second is the potential for lucrative tourism that is beginning to be realized at the "Rosario" site in the Sierra Campanario (de Castilla 1993, Howell & Marriott 1994). A third is the restoration of the original wildlife to

the area (Leopold 1950), which in turn might contribute to tourism income over a longer portion of the year.

While allocating resources to humans versus wildlife is a contentious problem in implementing conservation everywhere, if protection of the few relatively intact montane islands of fir forests, comparable to the level of protection provided by the U.S. National Park systems, is not instigated within this decade, the eastern migratory population of the monarch butterfly will not survive long into the next century. Monarchs overwintering in Mexico are a treasure comparable to the finest works of art that our collective world culture has produced over the past 4,000 years. If we do not succeed in conserving their overwintering grounds, the eastern populations of the monarch butterfly will soon become a remnant of history, and humanity will be deprived of one of the most magnificent natural spectacles on our planet.

ACKNOWLEDGMENTS

In writing this review, I became fascinated by the often overlooked findings of early workers. Charles Valentine Riley's contributions to monarch butterfly biology have been largely forgotten, yet he was one of the great insect biologists who established a strong foundation for most subsequent research on the monarch. John Alston Moffat was a master at deduction, and a more careful notice of his 1902b paper might have compelled an earlier search for overwintering monarchs in Mexico. Jennie Brooks' (1911) insight that monarchs must migrate to Mexico was never acknowledged, nor was her all night watch of clustering monarchs in Kansas (1907), demonstrating that the butterflies were inactive at night. Likewise, Lucia Shepardson's two pamphlets (1914, 1939) on the monarchs of Monterey are biology classics that have been largely ignored. A recent researcher whose contributions should not be lost simply because of his iconoclastic approach is Adrian Wenner. His conclusion (Wenner & Harris 1993) that the fall migration in California lacks adequate documentation is correct. Uncritical acceptance of the fall migration of the western monarch population has a historical counterpart: just as overwintering of the eastern population was assumed to occur regularly along the Gulf Coast by analogy with the undisputed overwintering aggregations in California, so the existence of a definite fall migration in the West has been assumed through analogy with the undisputed fall migration of the eastern population.

It was difficult to complete this review because of the many recondite references in the literature. I apologize to those whose works I may have missed. I also implore those who publish their findings in any format—from letters, to the electronic media—to document each observation with localities that can be found in atlases, dates that include the year, weather conditions, and estimates of the speed and direction from which the wind is blowing, the direction in which the monarchs are flying, their altitude, and the numbers of monarchs seen per person per unit time. Many anecdotes in the literature might have better fit into the puzzle had they contained greater detail and had they been carried out in a more organized manner.

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APOSEMATISM AND MIMICRY IN CATERPILLARS

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ABSTRACT. In the Lepidoptera, described instances of larval mimicry are vastly and curiously fewer in number than those tabulated for adults. This disparity may arise in large part from a lack of pertinent research, rather than actual differences between the two life stages. The evolution of larval coloration and its role in the development of possible larval mimicry complexes represents largely unbroken and fertile ground for study.

Aposematic coloration is a conspicuous characteristic of many larval lepidopterans—so conspicuous, in fact, that Darwin (1871:326) was prompted to remark:

“... distastefulness alone would be insufficient to protect a caterpillar unless some outward sign indicated to its would-be destroyer that its prey was a disgusting morsel. . . . Under these circumstances it would be highly advantageous to a caterpillar to be instantaneously and certainly recognized as unpalatable by all birds and other animals. Thus the most gaudy colors would be serviceable and might have been gained by variation and the survival of the most easily-recognized individual.”

Conspicuous in their absence, however, are the mimicry complexes that are associated so frequently with aposematic adult Lepidoptera. Virtually all of mimicry theory as it relates to Lepidoptera revolves around discussions of wing patterns in adults and has done so for over a hundred years (Remington 1963). This bizarre apparent asymmetry in the frequency of mimetic resemblance in larval versus adult stages has been remarked upon, but not satisfactorily accounted for, by several authors (e.g., Sillen-Tullberg 1988, Turner 1984). Recently, Bowers (1993), accepting the notion that this paucity of mimicry complexes among larval lepidopterans was a biologically “real phenomenon” and not a sampling artifact, offered several possible explanations. First, she suggested that visual cues are in general more important to adults than to larvae in that adults rely upon such cues for species recognition during courtship and mating. She also suggested that, while visually orienting vertebrate predators are most important for adult Lepidoptera, larval stages may be more subject to selection by invertebrate predators such as parasitoids, which rely heavily on chemical, rather than visual, cues for host-finding.

Although having at least some theoretical bases from which to draw is advantageous, neither of the explanations offered by Bowers (1993) is wholly satisfying. The reliance by adults upon visual cues for conspecific recognition during courtship and mating would seem to argue against the evolution of mimicry in *adults*, rather than against the evolution of mimicry in *larvae*; mimetic patterns should reduce the

efficacy with which potential conspecific mates are recognized. Moreover, there are aposematic moths that apparently rely upon chemical, rather than visual, cues during courtship. Sesiids which resemble stinging hymenopterans rely principally upon long-range female-emitted pheromones in courtship (Greenfield & Karandinos 1979); conspicuously colored and unpalatable *Utetheisa* species (Arctiidae) utilize both long-range female-produced sex pheromones and short-range male-produced aphrodisiacs in a complex, chemically mediated courtship ritual (Conner et al. 1981). In such cases, external appearances appear to result from natural selection exerted by predators, rather than sexual selection exerted by potential mates. As for the relative impact of vertebrate predators, in comparison with invertebrate predators, it is certainly true that parasitoids inflict greater mortality on caterpillar populations than they do on adult Lepidoptera. However, volumes of literature document the enormous appetite of birds for lepidopterous larvae (Holmes 1990). At low insect population levels, birds are capable of reducing numbers of lepidopteran larvae by 80 to 90%; population densities of larval lepidopterans inside exclosures, protected from birds, were as much as 50 to 300% higher than densities outside exclosures, where caterpillars were subject to bird predation. In contrast, Kettlewell (1955) observed only a 40 to 50% reduction in numbers of adult peppered moths as a result of bird predation. Whether mortality due to birds is greater for larvae than for adults is difficult to prove (and in fact may differ among species)—but there are few quantitative studies to suggest that it is substantially lower.

As for the discriminative visual capabilities of invertebrate predators, while chemical cues may be important, there is little evidence to suggest that vision is altogether unimportant. Particularly in host habitat finding, many parasitoids orient to visible signs of caterpillar feeding, such as leaf damage, leaf rolls, or abnormal growths (such as galls) (Berenbaum 1990). There are even studies to suggest that certain invertebrate predators, such as the mantid *Tenodera aridifolia sinensis* (Saussure), use visual cues in establishing learned aversions to aposematic prey (Gelperin 1968, Berenbaum & Miliczky 1984, Bowdish & Bultman 1993). Laboratory studies with artificially painted distasteful prey (the large milkweed bug *Oncopeltus fasciatus* (Dallas)) showed that broken patterns elicited a longer strike delay than did solid color patterns; this response is consistent with previous work on insect vision demonstrating that figural intensity (“edginess”) has a substantial effect on insect discriminative abilities and preferences.

Irrespective of whether the major predators on lepidopteran larvae are invertebrate or vertebrate, that visually orienting predators are important selection agents on lepidopteran larval morphology is attested

by the plethora of eucryptic or homotypic forms. Twig and bird dropping mimics are encountered frequently (the latter in two families, the Papilionidae and Nymphalidae). It is difficult to conceive of selection pressure other than that exerted by a visually orienting predator that could give rise to such morphology. Other forms of Batesian mimicry also can be found: fifth instar *Papilio glaucus* L. and *P. troilus* L. larvae bear an uncanny resemblance to green tree snakes. Thus, caterpillars can evolve to match their background, or to resemble animate as well as inanimate components of their environments. Why, then, do they rarely if ever evolve to resemble other caterpillars?

There are at least three alternative explanations to account for the paucity of mimicry complexes in larvae. One explanation is that there are developmental constraints, due to the demands of metamerism (e.g., Zrzavy et al. 1993), on pattern and color formation in larvae. There is no scientific evidence available in support of this notion; rather, work by Turner (1984) with *Bombyx mori* L. mutants suggests that there is an abundance of genetic variability available to lead to the evolution of special resemblance, either to snakes or to toxic caterpillar models. Individuals carrying four mutations—*moricaud*, *zebra*, *multilunar*, and *quail*—according to Turner, turn the silkworm into “a snake mimic not unlike the Elephant Hawk moth caterpillar, with frontally placed eye spots, and an intricate cryptic pink and brown pattern with short diagonal lines along the back.” Similarly, individuals carrying two mutations, *multilunar* and *striped*, are aposematically colored: black with orange spots.

A second explanation is that there are differences in the relative advantages of aposematism accrued by caterpillars and adults. Caterpillars are less able than butterflies to tolerate mistakes by naive predators. Unlike butterflies or moths, which possess a large expanse of wing (not all of which is essential for flight), caterpillars have few if any expendable body parts; loss of even a small amount of tissue could be fatal. While they may possess tough cuticle and resist predator damage to some extent (Järvi et al. 1981), their options for escape are far more limited than are those of adults. Restricted to crawling or dropping to the ground as a means of escape, caterpillars are substantially less likely than butterflies or moths to outmaneuver or outdistance their enemies and thus escape. Although falling to the ground may be an effective short-term means of survival, it is a strategy that is not without its own risks; caterpillars must resort to their more labored form of locomotion to recolonize hostplants and risk starvation, desiccation, or discovery in the process. It is interesting to note that chemically protected species with aposematic larval and adult stages frequently have cryptic pupae,

presumably because even chemically protected pupae, due to their lack of mobility, rarely survive an encounter with a predator (Wiklund & Sillen-Tullberg 1985, reviewed in Brower 1984).

Butterflies of necessity make themselves conspicuous when they search for mates or for oviposition plants; because conspicuousness is part of their lifestyle, aposematic coloration, legitimately advertising distastefulness, may be of tremendous benefit in avoiding attacks, particularly if there are specific patterns or colors that are innately avoided by predators (e.g., Schuler 1982). Caterpillars, in contrast, do little other than take in food and find a pupation site; neither activity necessarily involves long periods of exposure. In fact, many larval lepidopterans lead a concealed lifestyle; sedentary to the point of immobility, some feed internally in stems, fruits, or roots of plants. In some cases, a concealed lifestyle is complemented by the relatively short period of time spent in the larval stage, as compared to the adult stage. For example, univoltine depressariine oecophorids may spend three to four weeks as larvae, one or two weeks as pupae, and as long as ten months or more as adults (Hodges 1974). The probability of encountering a predator during the larval life stages for such species may be reduced accordingly.

For those species that feed externally, there may be greater benefit in remaining undetected, rather than running the risk of not surviving an encounter with a naive predator. Thus, aposematic patterns in caterpillars may be optimally designed to be "dual signals" (Brown 1988)—cryptic at a distance and aposematic at close range. This apparently paradoxical situation was described by Papageorgis (1975) in relation to mimicry rings among Neotropical butterflies: patterns that at close inspection appear classically aposematic in their natural setting, with natural patterns of shadow, light, and vegetation, are actually cryptic. As Brown (1988) succinctly states, "for an unpalatable but not invulnerable butterfly, this must be a very efficient protection, strongly favored by natural selection." Due to the relatively greater vulnerability of larvae, this strategy logically would be favored even more strongly. The brightly marked green and black larvae of *Pieris brassicae* L., while conspicuous on foliage, are more cryptic on the soil surface than are their uniformly green congeners *Pieris rapae* (Baker 1970). Järvi et al. (1981) argue that the banding pattern of *Papilio machaon* L. larvae is "cryptic at a distance but aposematic at a close distance" and cite previous studies by Windecker documenting the same effect for the black and yellow banded larvae of the cinnabar moth *Tyria jacobaeae* L. (Arctiidae). There may be sufficient selection pressure on caterpillars to maintain dual-purpose markings that there are consid-

erable constraints on the diversity of patterns that are compatible with survival—thus limiting the frequency with which high-fidelity mimetic complexes form.

Although it is not altogether satisfying, the third explanation—that larval mimicry complexes abound but are simply not recognized as such—may turn out to be the most likely. First of all, an enormous number of larval stages, even of well-known Lepidoptera, remain undescribed. Rarely are caterpillars collected for which adult stages are unknown; the reverse is all too often true. Second, although human vision shares many similarities with avian vision, and even insect vision (Land 1992), there are fundamental differences. Humans are very large, very mobile animals and may perceive things in a manner unlike that of any other type of insect predator. It is hardly encouraging that there is not even widespread agreement on whether any particular pattern is cryptic or aposematic (viz., Gould's (1892) assessment of Cameron's (1880) suggestion that the red spots on poplar moth larvae resembled red galls on foliage and hence increased crypsis; see Grayson & Edmunds, 1989). Even when the visual targets are closer to our own body size, as is the case with other mammals, aposematism and crypsis are not so easily distinguished a priori. Godfrey et al. (1987) demonstrated by Fourier analysis of striping patterns that, surprisingly, tigers are cryptic whereas zebras are conspicuous when examined against their natural background. Very little is known about spatial frequency analyzers in birds and even less in insect predators—likely the selective agents that have brought about striping patterns in larvae in the first place. Classifying patterns as aposematic or cryptic may well depend on background (but see Sillen-Tullberg 1985); different plant hosts, with different leaf shapes, may influence the efficacy of background matching or background contrast. Because complete hostplant lists are lacking for most species, a comprehensive picture of the selection pressures leading to a particular pattern also is lacking for most species.

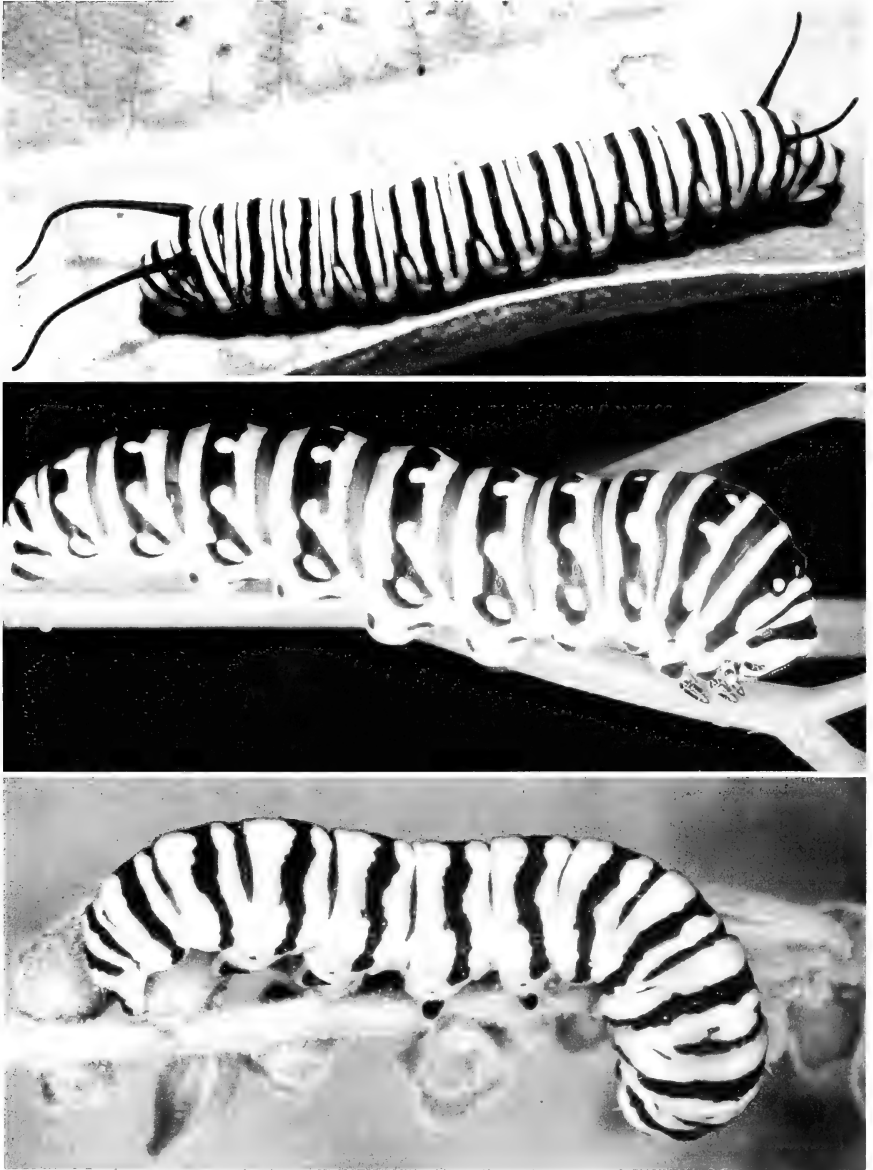
There are several suspected mimicry complexes that have been described in caterpillars; all involve aposematic models that sequester hostplant toxins. Bowers (1993) described several possible examples (Table 1) but for no case have extensive studies been conducted on the palatability of the larvae or on the responses of vertebrate or invertebrate predators to larval morphology under controlled conditions. Identifying additional mimicry complexes may prove difficult; one first step would be to identify aposematic unpalatable models that may serve as the focus for such a complex. One potential model throughout eastern North American oldfields is the aposematic unpalatable species, *Danaus plexippus* L., the monarch caterpillar (Fig. 1). The distastefulness of adult monarchs has been long known to be due to sequestration of

TABLE 1. Putative mimicry complexes involving caterpillars (after Bowers 1993). B = black, O = orange, W = white. See text for elaboration.

Species pair	Hostplants	Color	Mimetic system
<i>Euphydryas phaeton</i>	<i>Plantago</i> spp.	O/B striped	Batesian model
<i>Chlosyne harrisii</i>	<i>Aster umbellatus</i>	O/B striped	Batesian mimic
<i>Meris alticola</i>	<i>Penstemon</i> spp.	B/W/O	Mullerian mimic
<i>Neoterpes graefiaria</i>	<i>Penstemon</i> spp.	B/W/O	Mullerian mimic
<i>Papilio memnon heronus</i>	Rutaceae	.	Batesian model
<i>Cerura erminea menciara</i>	.	.	Batesian mimic

emetic cardiac glycosides from asclepiadaceous hostplants (e.g., Ritland & Brower 1991). Similarly, the distastefulness and protective value of the aposematic (black, white, and yellow banded) coloration of the larva have been documented in experimental studies with avian predators (e.g., Jarvi et al. 1981). Among potential mimics of this species is the black swallowtail caterpillar, *Papilio polyxenes* Fabr. (Fig. 2). These caterpillars, green with black bands and yellow spots, are strongly distasteful to Japanese quail; the basis for unpalatability is not known but it does not appear to involve osmeterial gland secretions, in that caterpillars with occluded osmeteria were rejected at frequencies equal to caterpillars with functional osmeteria (Leslie & Berenbaum 1990; see also Järvi et al. 1981). Their European relative, *P. machaon*, almost indistinguishable in larval appearance from *P. polyxenes*, is more distasteful to Japanese quail, *Coturnix coturnix* L., than is the monarch caterpillar *Danaus plexippus*, a species widely acknowledged to be aposematic as well as unpalatable, due to its ability to sequester hostplant cardenolides (Wiklund & Sillen-Tullberg 1985). Co-occurring caterpillars with more than a passing resemblance to the black swallowtail and monarch in northern North America include the clouded crimson *Schinia gaurae* J. E. Smith (Noctuidae), which feeds exclusively on the prairie plant *Gaura* (Fig. 1), a member of the Onagraceae, a plant family not known for toxic secondary metabolites. The three species are sympatric throughout the midwestern states in meadows and prairies. The resemblance between the black swallowtail and the clouded crimson is close but not perfect—they differ dramatically in size, for example, with *S. gaurae* only about half the length of *P. polyxenes* at maturity. Hinton (1974), however, suggested that, due to the “rapid peering” technique of foraging utilized by insectivorous birds, size differences may not necessarily be recognized immediately.

In general, the extent to which birds or other predators can generalize markings of aposematic caterpillar prey is unknown. Discriminative powers may vary among species. It may be that caterpillars are con-



FIGS. 1-2. Putative mimicry complexes involving caterpillars. 1. Top to bottom: monarch, *Danaus plexippus*; black swallowtail, *Papilio polyxenes*; noctuid, *Schinia gaurae*. 2. Top to bottom: pipevine swallowtail, *Battus philenor*; great spangled fritillary, *Speyeria cybele*. See text for elaboration.



FIGS. 1-2. Continued.

sumed by a greater diversity of bird species (they constitute an important part of the diet of flycatchers, warblers, vireos, chickadees, and a number of other passerines) whereas butterflies generally are consumed only by larger, more agile birds, so a more general resemblance

may be a more effective ploy. Because different birds forage using different cues, a generalized resemblance may work most efficiently at deluding the greatest number of birds. While at first glance it may seem that birds foraging for relatively slow-moving caterpillars should be able to discriminate between even subtly different prey items, such a view overlooks the fact that birds foraging for caterpillars do so against a highly heterogeneous background. Viewed against the comparatively uncomplicated background of the sky, adults may be easier to distinguish with precision. Moreover, different caterpillar patterns are more likely to be viewed against different backgrounds (e.g., hostplants) than are butterflies in flight, causing greater resolution problems for birds. Birds notwithstanding, naive freshman entomology students have been known to confuse black swallowtail caterpillars with the only vaguely similar monarch caterpillar *Danaus plexippus* in east central Illinois (personal observation); how representative naive college freshmen are of naive vertebrate predators in general is, though, anybody's guess.

The pipevine swallowtail butterfly, *Battus philenor* L., is the widely recognized model in a large Batesian mimicry complex involving as many as three families of Lepidoptera: Nymphalidae (*Limenitis astyanax* Fabr.), Saturniidae (*Callosamia promethea* Drury), and other Papilionidae (*Papilio polyxenes*, *Papilio troilus*, *Papilio glaucus*). As a larva, *Battus philenor* (Figure 2A) is aposematically colored: black with a series of red spots along the abdomen. Similar markings are found on the larva of the great spangled fritillary *Speyeria cybele* Fabr. (Nymphalidae) (Fig. 2). Both species frequent low-lying vegetation in forest understory throughout the eastern United States—*B. philenor* on *Aristolochia* species and *S. cybele* on *Viola* species. It is highly likely that birds or other predators foraging in this forest community could encounter both species (despite the fact that the nymphalid feeds nocturnally). Whether this resemblance represents Batesian or Muellierian mimicry (or, indeed, if it constitutes an example of mimicry at all) has yet to be demonstrated.

Experimental work has proceeded on mimicry in butterflies, yet the paradigms, even as they apply to the most familiar systems, are still being refined (e.g., Ritland & Brower 1991). Studies of caterpillar mimicry are a century behind. There is to date no system for which palatability of putative models and mimics has been assessed against even a single ecologically appropriate predator; for which predator responses to mimetic resemblances have been monitored; and for which there is a demonstrated selective advantage to mimetic pattern for larvae under field conditions. Until such studies are conducted, the differences in defense strategies of caterpillars and adults can never be fully understood.

ACKNOWLEDGMENTS

My interest in mimicry, in swallowtail caterpillars, and, for that matter, in insects in general can all be traced to the course I took from Professor Charles Remington during the second semester of my freshman year at Yale University. Although I entered the course as an entomophobe, I left with a newfound interest and affection for insects. In the years since that class, my appreciation for the astonishing achievements of arthropods has continued to grow, as has my deep appreciation for Charles—for his insights, his encouragement, his patience, and his tremendous ability to inspire and motivate.

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A HISTORY OF LEPIDOPTERA CONSERVATION, WITH SPECIAL REFERENCE TO ITS REMINGTONIAN DEBT

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ABSTRACT. In the past half century, the preservation of Lepidoptera and their habitats has risen from relative obscurity to become one of the most active subdisciplines in modern conservation biology. A wide appreciation and popularization of butterflies and moths has resulted. This paper presents an overview of the ascent, with emphasis on the intertwined roles played by scientific research, global growth in awareness of environmental issues, and political/legal action.

The conservation of uncommon species of butterflies and moths and their habitats has become a frequent topic of concern and discussion in the contemporary lepidopterological press. Such was not always the case. When, in 1967, a paper on the subject was first brought before the annual meeting of the Lepidopterists' Society, it was greeted with guarded interest. When the same paper was submitted to the *Journal of the Lepidopterists' Society*, it was rejected, doubtless due to its anecdotal nature and editorial shortcomings. But when it eventually appeared elsewhere in revised form (Pyle 1967) it was one of few citations available on the topic.

A different situation pertains today, when this and related journals routinely contain papers at least partly concerned with biodiversity conservation. Entire journals devoted to the subject, such as *Biological Conservation*, frequently contain papers related to butterflies, moths, and other insects. In just a quarter of a century, Lepidoptera conservation has grown from an arcane topic to a commonplace concern.

Several reasons for this growth suggest themselves. First, there is greater general recognition that the environmental crisis extends to small-scale life: through the writings of E. O. Wilson and others, insects have become respectable in public. Second, population growth has quickened habitat loss, such that no one who pays attention to insects can fail to notice. Third, the number of lepidopterists has grown as well, giving greater witness to these losses and concern for the protection of disappearing populations. Fourth, public interest in natural history and butterflies in particular has grown dramatically. Fifth, teachers and scientists who employ these animals in their research have produced students sophisticated in lepidopteran biology who are prepared to take part in conservation.

Perhaps the most influential of these teachers has been Charles Lee Remington. This paper aims to summarize the major historical developments in Lepidoptera conservation, while suggesting the Remingtonian contribution to the field and its impact.

THE EARLY STAGES

The earliest concern on behalf of insect conservation might have been that of Queen Cristina de Borbon of Spain, who asked Professor Graells to provide a plan for firefly protection around 1835 (Pyle 1976a, Pyle 1976b). Overt butterfly conservation can be thought of as beginning a decade or so later, when *Lycaena dispar dispar* Haw. became extinct in Great Britain due to the drainage of the East Anglian Fens (Ford 1945, Duffey 1968). British collectors mourned this and other losses from the changing landscape. Lord Walter Rothschild unilaterally established some of the earliest butterfly reserves, notably at Woodwalton Fen. In 1925, he was to chair the first butterfly conservation body, an arm of the Royal Entomological Society of London initially known as the Committee for the Protection of British Lepidoptera (this group subsequently became the Insect Protection Committee, and later the Joint Committee for Conservation of British Insects). While many notes of concern appeared in the European literature in the first half of the twentieth century, most of them consisted of allegations of overcollecting of *Parnassius apollo* L. and other rarities, rather than arguments for habitat conservation (Pyle 1976b).

Across the Atlantic, attention drew to the topic almost as early as in England. In a letter to Herman Strecker written on 26 September 1875, H. H. Behr lamented that *Glaucopsyche xerces* Boisduval "is now extinct as regards the neighborhood of San Francisco. The locality where it used to be found is converted into building lots, and between German chickens and Irish hogs no insect can exist besides louse and flea" (Pyle 1976b). *Glaucopsyche xerces* did not in fact become extinct until the early nineteen-forties (Downey & Lange 1956, Emmel & Emmel 1993), though it was preceded into extinction by the nominate subspecies of *Cercyonis sthenele* (Boisduval). Grote (1876) also called early on for protection of the White Mountain butterfly, *Oeneis melissa semidea* (Say), in New Hampshire. However, unlike in Great Britain, no formal committees arose in North America to address these early expressions of alarm.

In 1946, the Joint Committee for Conservation of British Insects (JCCBI) issued its first list of rare and endangered insects, surely the first such list anywhere. By this time there had long been a Committee for the Protection of the Large Blue in England, in recognition of the decline of *Maculinea arion* L. Its work of half a century would eventually prove in vain, due to inadequate knowledge of the insect's requirements (Thomas 1980). This need for solid autecological data upon which to base management was sounded by John Heath, whose studies on the moth *Eustroma reticulata* in the Lake District (Heath 1959)

opened the era of intensive study of threatened species with a view toward their conservation.

Charles Remington entered this rising climate of concern for the British biota when he went to Oxford to work with E. B. Ford on a Guggenheim Fellowship in 1958–59. Ford (1945) had summarized the changes in the British butterfly fauna that led to a general call for its conservation on behalf of lepidopterists. Although Remington's work with Ford primarily concerned ecological genetics, the Oxford don's knowledge of population decline was not lost on the young Remington. It was while Charles was in Britain those years that he acquired, in London auctions and by gift, the nucleus of Yale University's great collection of extinct and endangered insects, and further developed many of his ideas concerning the conservation ecology of rare insects. These concepts were to find expression in a series of papers published before and after Oxford (Remington & Pease 1955, Remington 1958a, 1958b) having to do with the general and specific ecological requirements of lepidopterans in nature.

LEPIDOPTERA CONSERVATION IN MID CENTURY

The 1960s saw a wave of environmental activism, culminating in the first Earth Day on 22 April 1970. During the decade, a number of suggestions appeared in print that lepidopterists should be paying close attention to disappearing habitats and the populations they supported (Rindge 1965, Sieker 1967, Pyle 1967). In 1961, George Rawson attempted a reintroduction of *Eumaeus atala florida* Rober into the Everglades in Florida, an effort defeated by Hurricane Donna. With future introductions of this sort in mind, as well as biological control, Remington (1968) reviewed the population genetics of insect introductions. At the 20th Annual Meeting (1967) of the Lepidopterists' Society in Corvallis, Oregon, at the suggestion of David McCorkle, a Conservation Committee was formed. McCorkle also promoted the establishment of The Nature Conservancy's first rare butterfly preserve for a disjunct population of *Boloria selene atrocostalis* Huard at Moxee Bog, Washington, in the late 1960s (Hendrix 1975). This fecund period saw the establishment of many environmental groups. Following publication of Society member Paul Ehrlich's influential book *The Population Bomb* (Ehrlich, 1968), Ehrlich and Remington co-founded Zero Population Growth (ZPG), in recognition of the fact that burgeoning human numbers underlie all other resource conservation problems, and, indeed, bias our own future.

By the late 1960s, Lepidoptera conservation activities in Great Britain had become numerous and sophisticated. The JCCBI, a new British Butterfly Conservation Society with revered naturalist Sir Peter Scott

as its President, and several other bodies were working on an array of habitat protection issues. The nerve center of this activity was Monks Wood Experimental Station, a field center of the British governmental agency known then as the Nature Conservancy. Monks Wood itself was an early, private insect reserve, and now is a National Nature Reserve (NNR), one of a number established after World War II in response to the Huxley Report, a biotic survey antecedent to our modern-day Natural Heritage Programs. The Experimental Station was set up in 1963 to conduct research to guide management of the NNRs (Steele & Welch 1973). A Nature Conservancy colloquium at Monks Wood (Duffey & Morris 1965) reviewed the state of invertebrate conservation and stressed the importance of further research and survey.

At Monks Wood in 1970, no fewer than eight biologists were employed on research and management projects substantially involving rare insects. Notable among these were Eric Duffey's research on the re-introduced population of *Lycaena dispar* at Woodwalton Fen; Jack Dempster's work on *Papilio machaon britannicus* Sietz; and Jeremy Thomas's investigations of the autecology of *Strymonidia pruni* L., and *Thecla betuli* L. Hall (1981) summarized these and related studies. Also based at Monks Wood were the Insect Recording Schemes of the Biological Records Centre. The late John Heath, one of the most active conservationists among the lepidopterists, had surveyed a century of change in British Lepidoptera (Heath 1974) and began producing atlases of species occurrence based on 10 km square dot maps (Heath et al. 1984). By updating these maps annually, through the efforts of many field volunteers and a professional staff, the Biological Records Centre was able to provide a dynamic picture of population expansion and contraction. Field research could then address the reasons for local extinctions and management needs. In this way both *S. pruni* and *Melitaea athalia* were brought back through a combination of mapping, research, and management (Thomas 1984, Warren 1987). The Butterfly Recording Scheme continues today, directed by Paul Harding at Monks Wood. Certain moth groups and other insects also have been mapped.

In 1971-72, I had the opportunity to pursue studies in Lepidoptera conservation at Monks Wood under the mentorship of John Heath and the other scientists in residence. This experience, and the example of the British large blue (*Maculinea arion*) as a symbol for Lepidoptera conservation, led directly to the founding of the Xerces Society on 9 December 1971. Jo Brewer voiced many parallel concerns in the United States (Brewer 1971) and lent her early support to the embryonic organization. Xerces' goals were to raise positive public awareness of butterflies and other beneficial insects, and to work for the conservation of rare species and their habitats.

The 25th Annual Meeting of the Lepidopterists' Society took place in San Antonio, Texas, in July, 1972. Under the leadership of then-President Charles Remington, a symposium was held on "Endangered and Extinct Lepidoptera." A series of papers outlined the present state of knowledge and action in the field, both in the United States and Great Britain. This meeting served as an effective launching pad for the Xerces Society, which subsequently situated itself at Yale University, in New Haven, Connecticut, at the invitation of Remington.

The first several years of the Society's activity saw the launch of the Fourth of July Butterfly Counts, the journal *Atala*, and the newsletter *Wings*, and involvement in several land-use issues. These included Forest Service management of the habitat of the New Mexico endemic, *Sandia macfarlandi* Ehrlich & Clench; Project Ponceanus on behalf of *Papilio aristodemus ponceanus* Schaus in Florida; conservation of the Karner blue in New York State; and conservation of several western fritillaries (summarized by Pyle 1976a, 1976b, and in early issues of *Atala*). At the same time, I was undertaking graduate studies at Yale with Charles Remington, with a view toward placing the activities of Xerces in an historic, worldwide, and scientific context. It was often said that if John Heath served as midwife to the Xerces Society, then Charles Remington was its godfather. This role was underscored when the first annual meeting of the Xerces Society was held at Yale University in April, 1974. Thanks to Charles' influence, distinguished guests such as Miriam Rothschild and Alexander Klots attended. This lent substance to the occasion and both encouragement and credibility to the young organization.

THE ENDANGERED SPECIES ACT AND BEYOND

The largest event in North American Lepidoptera conservation was the passage of the Endangered Species Act (ESA) in 1973. In 1974, society member Paul Opler was hired by the U.S. Fish & Wildlife Department as Staff Specialist in entomology. In 1975, 41 species and subspecies were proposed as candidates for listing under the ESA. Federal listing of six California lycaenids (*Apodemia mormo langei* J. A. Comstock, *Euphilotes battoides allyni* Shields, *E. enoptes smithi* (Mattoni), *Incisalia fotis bayensis* R. Brown, *Plebejus icarioides missionensis* Hovanitz, and *P. i. pheres* (Boisduval)), and two Florida swallowtails (*Papilio aristodemus ponceanus* Schaus and *P. andraemon bonhotei* (E. M. Sharpe)) soon followed, along with *Speyeria zerene hippolyta* (Edwards). Additional species were listed in later years, and numerous research projects undertaken toward the conservation of these and other endangered species, with a combination of federal, state, and private funding (see for example Arnold 1983, Gall 1984, Reid & Murphy 1986,

McCorkle & Hammond 1988, Powell & Parker 1993). One taxon, the Palos Verdes Blue (*Glaucopsyche lygdamus palosverdesensis* Perkins & Emmel) apparently became extinct in spite of protection from the ESA due to negligence of habitat development for a park (Mattoni 1993) but was subsequently rediscovered by Rudy Mattoni on naval land.

The Endangered Species Act was amended in 1983 in order to permit taking of listed taxa under certain conditions, including the preparation of a conservation plan for the survival and enhancement of the remaining population. This amendment was designed to remove the obstacle that the endangered Mission Blue and several other listed species presented to developers on San Bruno Mountain, south of San Francisco, in California. This was a divisive issue in Lepidoptera conservation circles. Xerces and The International Union for Conservation of Nature (IUCN) opposed it, contending that the expertise to re-create critical habitat did not exist, and the unknowns were too many. Others felt that the survival of the ESA lay in the balance, and supported the compromise. The outcome is as yet unclear, with both development and restoration underway (Bean et al. 1991, Cushman, 1993). Listings of invertebrates under the ESA ceased during the Reagan years until Paul Ehrlich et al. sued the U.S. Fish and Wildlife Service to list *Euphydryas editha bayensis* (Sternitzky) (Murphy & Weiss 1988).

The 1970s and 1980s saw vulnerable-species lists and red data books appear in several countries, including Britain, Spain, and Switzerland. Conservation activity in Europe became intense, chiefly through the offices of the European Invertebrate Survey and the Societas Europaeas Lepidopterologica, both co-founded by John Heath, who also performed a European butterfly conservation survey for the Council of Europe (Heath 1981). A spate of papers appeared during this stock-taking period, summarizing the initial wave of activity (Morris 1976, Thomas 1984, Pyle 1976b, Pyle et al. 1981). Kudrna (1986) summarized and analyzed the European Lepidoptera conservation scene in an important book, as did successive symposia held in Karlsruhe and Cambridge (see Heath 1982).

Sir Peter Scott, Chairman of the IUCN Species Survival Commission, created a Lepidoptera Specialist Group under my chairmanship, with Charles Remington as a key charter member. Meeting in Washington, D.C., in 1976, the Group designated the migratory phenomenon of the monarch butterfly as the highest priority in world butterfly conservation (see below). This and my work with the Wildlife Division of Papua New Guinea in 1983 convinced Scott of the need to include invertebrates in global monitoring procedures. The IUCN and World Wildlife Foundation (WWF) concurred, and work was begun in Cambridge at the Species Conservation Monitoring Unit (now World Conservation

Monitoring Centre) on an IUCN *Invertebrate Red Data Book*. The publication contained numerous lepidopteran entries (Wells et al. 1983), and was followed by a red data book devoted to swallowtails of the world (Collins & Morris 1985). Both tomes recognized *Ornithoptera alexandrae* (Rothschild), the largest butterfly in the world and a very narrow Papuan endemic facing powerful economic pressures, as a world conservation priority. IUCN and WWF, as well as the government of Papua New Guinea, subsequently treated it as such, though it is yet far from safe (Parsons 1992a, 1992b). New & Collins (1991) subsequently produced a worldwide Action Plan for swallowtail conservation.

One of the most significant elements of the IUCN *Invertebrate Red Data Book* was the listing of *Danaus plexippus* (L.) in the new category of Threatened Phenomenon, an idea jointly developed by myself and Lincoln Brower, Remington's first doctoral student and onetime E. B. Ford research fellow, and now the primary Monarch investigator in North America. In turn, this led to the founding of The Monarch Project as a unit of the Xerces Society, with myself as Chair, Brower as Scientific Chair, and Remington as an advisor. Xerces, always volunteer-run to this point, now hired Melody Mackey Allen as Executive Director of The Monarch Project and later of the Society as a whole. The Monarch Project sought to protect Monarch wintering grounds in Mexico and California, and migratory corridors throughout North America. These developments came about at the 11th annual Meeting of the Xerces Society, held at Yale University in June 1985, at Remington's invitation. Having overseen the group's early development, he now assisted it into a new era of professional activity.

Additional students and colleagues of Charles Remington carried the influence of Osborn Memorial Laboratory, the Peabody Museum of Natural History, and the Rocky Mountain Biological Laboratory into a variety of conservation arenas. Francie Chew (1977) demonstrated the relationship between introduced and native species of pierids. Larry Gall (1984) discovered a new and narrowly endemic species of North American butterfly, *Boloria acrocneuma* Gall & Sperling, and fostered its way to eventual Federal listing. Dale Schweitzer (1987) extended several state natural heritage and Nature Conservancy programs into a close examination of the butterfly and moth faunas within their bounds. Remington worked with Schweitzer and others to develop management criteria for the Karner blue (*Plebejus melissa samuelis* (Nabokov)) in upstate New York. The most recent candidate for Federal listing, the Karner blue's survival will owe much to these studies as well as to those of the Yale group's Cornell associates, Robert Dirig and John Cryan, who initially pursued this issue through Xerces. The long tradition of butterfly science at Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, continues to contribute basic ecological understand-

ing to a broad array of conservation settings, not the least in its own backyard. Many of the RMBL workers have been influenced by Remington's long, vital and ongoing association with the laboratory, whose new research facility bears his name.

THE PRESENT AND FUTURE OF CONSERVATION EFFORTS

Lepidoptera conservation has recently entered an era of expanded energy worldwide, at a time when environmental pressures have exacerbated and funding for protective measures has diminished. Private contracts, to a degree, have supplemented lost public funding, and non-governmental organizations also have assumed an increased role. Government activities in Great Britain contracted under the unsympathetic Thatcher regime. The Monks Wood collective of scientists already had broken up with the sundering of the Nature Conservancy into separate agencies for research and management. Much of the effort shifted to Furzebrook Research Station of the Institute of Terrestrial Ecology in Dorset, under the direction of M. G. Morris. This was the base for Jeremy Thomas's landmark studies of *Maculinea arion* leading to its effective reintroduction and management following extinction of the British race (Thomas 1980, 1989), and detailed studies of other rare British blues (Thomas 1984, 1985).

The British Butterfly Conservation Society (now called Butterfly Conservation) has grown dramatically, hired a professional director, and established a number of reserves and educational programs. The group celebrated its 25th anniversary by conducting a major symposium on Lepidoptera Conservation at Keele University in September 1993. This followed on the heels of a symposium on insect conservation hosted by the Royal Entomological Society in London, whose proceedings represent a seminal volume in the field. The Xerces Society has grown too, and has spread its influence into Jamaica, on behalf of *Papilio homerus* (Fab.) (Emmel & Garraway 1990), and Madagascar, whose jeopardized forests support many endemic butterflies and other invertebrates (Kremen, 1992). While its journal *Atala* has been suspended, the magazine *Wings* is published regularly in a popular color format that has widely raised interest in arthropods and their needs.

Increasingly, those needs are seen to lie in the tropics. Early efforts at developing butterfly ranching as an economic incentive for conservation in Papua New Guinea (Pyle & Hughes 1978) have been emulated in many tropical and subtropical countries, and a non-profit organization, Wings for the Earth, directed by Olaf Malver, now exists to encourage such projects. M. G. Morris explored prospects for butterfly farming in Oceania as a Churchill Fellow, and Angus Hutton and Mi-

chael Parsons have consulted on similar projects from India to China (Parsons 1992a, 1992b). Both Parsons and Larry Orsak (1993) have worked extensively in Papua New Guinea to strengthen the existing program and its ties to conservation of forest habitats while enhancing local economies. An international conference on butterfly conservation and local utilization was held in September 1993, in Ujung Padang, Indonesia.

Conservation involves more lepidopterists around the world each year. Many of the projects have been synopsized by the current IUCN Lepidoptera Specialist Group chairman, T. R. New (1990). He also has reviewed Australian insect conservation in depth, edited a volume on lycaenid conservation biology, and summarized the entire field of butterfly conservation in a volume sure to become the standard text in the field (see New 1991). New and his collaborators reviewed butterfly conservation management for the *Annual Review of Entomology* (New et al. 1995).

Pro Monarca, a Mexico City group, leads the campaign to save the Mexican monarchs, a challenging goal in the face of growing pressures from poverty and logging. The Xerces Society, the Lepidopterists' Society, and the Mexican Society of Lepidopterists held a joint symposium on Mexican and Californian Monarch Biology and Conservation in Cocoyoc, Mexico, in 1981. A second symposium was held in Los Angeles under the leadership of Julian Donahue; both led to published proceedings (Pyle 1984, Malcolm & Zalucki 1993). Another gathering was convened by The Monarch Project at the Esalen Center in California in January 1990, to review California monarch needs, research, management, and plans. Alternative income production through eco-tourism seems the most hopeful approach in Mexico, while California monarchs will depend largely on easements, reserves, and growth management. Pacific Grove, California, passed a bond issue in November 1990, to acquire and restore degraded but previously utilized monarch roosting habitat. This brings full-circle the American butterfly conservation movement, whose first official measure might have been a 1950s city ordinance to protect monarchs from public disturbance (but, fatefully, not from habitat loss) in Pacific Grove (Lane 1984). Monarch conservation science also underscores the Remingtonian legacy, in that the co-founders of The Monarch Project, Brower and Pyle, were both graduate students of Remington.

One area of growth in Lepidoptera conservation today is in awareness and education. Butterfly clubs have arisen in several regions, all of them involved to some extent with conservation. Butterfly houses and butterfly gardens are becoming popular wherever they appear. The forty or more butterfly houses in Britain (Collins 1987) have been emulated

by a dozen or more in North America (Emmel & Boender 1991). While few of these have yet taken direct action to breed and release rare species (a moot point, unless wild habitats are first addressed) they no doubt increase the public's lepidopteran literacy. Butterfly gardens, too, are making a major contribution to a heightened consciousness (Xerces Society 1990). When people create or take part in cultivating a butterfly garden, they come to appreciate the needs of individual species. These gardens help to maximize butterfly diversity and abundance in urban and suburban areas, conserving species that might otherwise become less common, while bringing the insects into public awareness.

A divisive issue throughout the history of Lepidoptera conservation has been collecting of specimens. From the earliest days, many of the published alarms have alleged overcollecting. However, most scientists and amateurs alike agree that collecting per se seldom has substantial impact on populations (Pyle et al. 1981, Morris 1976). Dangerously, collecting restrictions often distract attention from serious issues of habitat conservation. A most bizarre example occurred in Germany, where bureaucrats responded to a Council of Europe call for conservation action by banning collecting of almost all Lepidoptera. Rightly, some birdwings and other butterflies, including *Parnassius apollo*, have been placed on Appendix II of the Convention on International Trade in Endangered Species (CITES), in order to monitor trade in them. However, CITES has been misapplied in some instances, preventing trade designed to encourage responsible butterfly ranching and enhance habitat conservation efforts; and imposing unreasonable barriers to the orderly exchange of legally collected or reared specimens (Parsons 1992, New 1991).

Both the Xerces and Lepidopterists' Societies have adopted collecting policies to reinforce responsible collecting practices among their members (Pyle 1992). The British group Butterfly Conservation, however, has adopted an anti-collecting stance that has alienated and tarred many entomologists. I hope that this sort of needless polarization can be avoided among North American collectors and watchers. No instance of extinction by overcollecting has ever been shown unequivocally, although most lepidopterists can recite instances in which they think overcollecting has occurred at least locally. This is most likely where a highly restricted taxon has been ecologically stressed already. The most recent federal listing of a butterfly as endangered (*Euptychia mitchellii* French) for the first time named overcollecting as one of the causes of decline. This coincides with the rise of a general perception of collecting as depreciative and archaic, against which those who wish to continue collecting will have to resist.

At this writing, North American butterfly collectors are deeply con-

cerned over recent attempts by authorities of the U.S. Fish and Wildlife Service to implement the Lacey Act and other punitive laws and regulations in ways they see as arbitrary, unreasonable, or unrelated to conservation (see, for example, *News of the Lepidopterists' Society* from 1992 forward). This has chilled the very exchange of specimens and information that have given the Lepidopterists' Society much of its communicative function. It has also led to sharp debate over the Society's proper role with respect to conservation (Ziegler 1993, Wagner 1993). Clearly, it will be important for the officers of this and other biological societies to arbitrate among public resource agencies and their own memberships in order to arrive at an acceptable understanding; and to educate authorities to the ongoing importance of responsible collecting and the unlikelihood of its doing harm to the resource. Likewise, lepidopterists find themselves needing to become better informed about rules and regulations on public lands, and to be ambassadors for their hobby and science. Collectors will also need to monitor their own activities carefully if they are to avoid outside interference with activities they have long taken for granted. The same population pressures that squeeze wild habitats have also begun to diminish free access to the entomological resource, an unfortunate side effect that might have been predicted by Ehrlich and Remington when they founded Zero Population Growth.

Partly in response to changing attitudes about collecting, butterfly watching is growing dramatically as an outdoor activity (Pyle 1992, Glassberg 1993). The North American Butterfly Association has been formed to promote butterfly watching and butterfly counts, and tours to the tropics and elsewhere are now incorporating butterfly watching as one of their attractions. These developments will no doubt increase the clientele for butterfly appreciation and conservation. Tour participants have led efforts to protect rainforest remnants in Rondonia, Brazil, for example (K. Bagdonas and T. C. Emmel, pers. comm.).

Butterfly watching will augment but not replace collecting in research. Therefore, it is important that watchers be given an understanding of the paramount importance of habitat protection, and a parallel appreciation for the value of intelligent collecting as an activity that seldom harms populations and contributes greatly to biogeographical understanding. Charles Remington has long been an effective voice on this issue.

Perhaps the most active area in butterfly and moth conservation today is the application of ecogeographic data to regional ecosystem management plans. Lepidoptera conservation surveys are now well under way in North America. In some instances, basic survey is being combined with an ecogeographic approach, often employing Geographic

Information Systems (GIS) to define where maximum diversity and conservation planning can most effectively overlap. This "gap" analysis, as it is called, will not encompass every rare taxon, but it is the trend of the future in a climate of increasing need and diminishing resources (Pyle 1982, Scott et al. 1993). Recognizing this, the Xerces Society has entered into such projects in several U.S. states, integrating butterfly distributional data into the overall species data bases. The premiums from energetic survey work already are becoming apparent in increased butterfly and moth preserve activity on the part of The Nature Conservancy in many states, just as John Heath's Butterfly Recording Scheme led to direct on-the-ground conservation in Britain.

For ecogeographic analysis and natural heritage programs to work well, active and empathetic collaboration between watchers, collectors, gardeners and all other brands of butterfly and moth fanciers is necessary. It will require the continuing field work of lepidopterists—both amateurs and professionals, working together in the cooperative, inclusive manner envisioned by Remington and Clench when they launched the Lepidopterists' Society nearly fifty years ago.

Charles Remington's work in conservation carries on at Yale University, where for several years he has taught the graduate course on Biology of Endangered Species in the School of Forestry and Environmental Studies. He has also organized a new exhibit on endangered species at the Yale Peabody Museum, and Charles and I are currently pursuing a book on Lepidoptera conservation (Island Press). But the Remingtonian influence on conservation should not be considered solely in the context of entomology. Many graduate students in Forestry and Environmental Studies have gone on to influential careers with The Nature Conservancy and other conservation organizations (see the introduction to this *Journal* issue). Prominent among these is Spencer B. Beebe, long one of The Nature Conservancy's most effective professionals and later the founder of both Conservation International and Ecotrust. Beebe was among those influenced by the teachings of Remington in evolutionary and conservation biology. So was Thomas E. Lovejoy who is currently a science advisor to President Clinton, and formerly Vice-President for Science of the World Wildlife Fund.

Today one cannot peruse an issue of the *Journal of the Lepidopterists' Society* or the *News* of the Society without reading about habitat conservation needs, concerns, or activities. This owes partly to increased awareness, partly to a deepening crisis in ecosystem maintenance. But the fact that lepidopterists are widely, knowledgeably, and energetically responding to the challenge of Lepidoptera conservation clearly stems largely from the teachings, studies, and dedication of their fellow, Charles Lee Remington.

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PREDATORY AND PARASITIC LEPIDOPTERA: CARNIVORES LIVING ON PLANTS

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ABSTRACT. Moths and butterflies whose larvae do not feed on plants represent a decided minority slice of lepidopteran diversity, yet offer insights into the ecology and evolution of feeding habits. This paper summarizes the life histories of the known predatory and parasitic lepidopteran taxa, focusing in detail on current research in the butterfly family Lycaenidae, a group disproportionately rich in aphytophagous feeders and myrmecophilous habits.

More than 99 percent of the 160,000 species of Lepidoptera eat plants (Strong et al. 1984, Common 1990). Plant feeding is generally associated with high rates of evolutionary diversification—while only 9 of the 30 extant orders of insects (Kristensen 1991) feed on plants, these orders contain more than half of the total number of insect species (Ehrlich & Raven 1964, Southwood 1973, Mitter et al. 1988, cf. Labandiera & Sepkoski 1993). Phytophagous species are characterized by specialized diets, with fewer than 10 percent having host ranges of more than three plant families (Bernays 1988, 1989), and butterflies being particularly hostplant-specific (e.g., Remington & Pease 1955, Remington 1963, Ehrlich & Raven 1964).

This kind of life history specialization and its effects on population structure may have contributed to the diversification of phytophages by promoting population subdivision and isolation (Futuyma & Moreno 1988, Thompson 1994). Many studies have identified selective forces giving rise to differences in niche breadth (Berenbaum 1981, Scriber 1983, Rausher 1983, Denno & McClure 1983, Strong et al. 1984, Futuyma & Moreno 1988, Thompson 1994). In particular, research on the Lepidoptera has emphasized how host choice may be governed on the one hand by the distribution of toxic secondary compounds and/or "enemy free space," and on the other by the need to acquire adequate nutrients (e.g., Lawton & McNeill 1979, Atsatt 1981a, Strong et al. 1984, Bernays & Graham 1988, Stamp & Casey 1993).

Since most species of moths and butterflies consume plants, comparatively little research has focused on the ecology and evolution of predatory taxa. Cottrell (1984) conducted a comprehensive analysis of aphytophagy in butterflies, but did not include moths. Reviews and experimental treatments of cannibalism in the Lepidoptera and other insects (e.g., Fox 1975, Polis 1981, Schweitzer 1979a, 1979b, Elgar & Crespi 1992) contain useful discussions of the biology of carnivorous species. However, it has been more than fifty years since a full survey

of the life histories of predatory Lepidoptera has been published (Balduf 1931, 1938, 1939, Brues 1936, Clausen 1940). The great emphasis on phytophagous species overlooks the considerable dietary diversity exhibited by Lepidoptera as a whole, and yet a consideration of both the scope of this diversity and its limitations can provide valuable insight into the ecology and evolution of the group.

The rarity of carnivorous Lepidoptera is particularly striking considering the enormous dietary range exhibited by other holometabolous orders containing phytophages, such as Coleoptera, Hymenoptera and Diptera. Only about 200 species representing eight superfamilies are known to be obligate predators or parasites. Moreover, as predators, lepidopterans are remarkably unadventurous, feeding mostly on slow, soft-bodied scale insects, eggs of other insects or ant brood. The few parasitic species are primarily parasites of other insects.

In this review, I summarize what is currently known about the life histories of moths and butterflies with carnivorous larvae, and discuss outstanding features of their ecology and evolution. The review begins with a description of traits that appear to be associated with obligately carnivorous life styles, and then focuses on recent research into predatory species in the butterfly family Lycaenidae. It concludes with discussion intended to stimulate further inquiry into the evolution of carnivory in the group.

Balduf (1938) recognized four main types of entomophagous caterpillars: (1) cannibals, which largely represent diversions from otherwise phytophagous lifestyles; (2) occasional predators, which include species that sometimes attack non-conspecific caterpillars and scavengers that sometimes take prey living in the same habitat; (3) habitual predators, such as species that regularly feed on homopterans or insects such as ants; and (4) parasites/parasitoids, including the few species that undergo either part of, or their entire development feeding on a single host. This review primarily concerns species in categories 3 and 4, which together comprise the group of obligate carnivores, while the members of 1 and 2 are facultatively entomophagous. As a rule of thumb, I consider parasites/parasitoids to be those that consume their hosts in units of less than one, whereas true predators kill and consume more than one prey. I have not distinguished here between parasites and parasitoids (that ultimately kill their hosts), in part because relatively little is known about whether or not parasitic Lepidoptera eventually do kill their hosts. The term parasite is used hereafter in this collective sense.

The life histories of entomophagous Lepidoptera are summarized in three tables. Table 1 covers the life histories of carnivorous moths. Table 2 summarizes carnivorous groups within the butterfly family Lycaen-

idae other than Miletinae. Table 3 focuses on feeding specializations within the wholly carnivorous lycaenid subfamily Miletinae. I have attempted to include every record of obligate predatory or parasitic behavior I could find. Because of the lack of complete life history information for many groups, this summary is inevitably tentative, and will evolve as new information becomes available. I have not attempted to summarize the numerous records of scavenging, lichen feeding or cannibalism in the group, although I discuss their possible significance. Because a caterpillar is usually observed consuming only one prey item at the time of collection, inference and/or interpretation is sometimes necessary in designating species as predators or parasites. I have indicated in the Tables those instances where parasitism or predation have been strongly inferred for a particular species or group, rather than confirmed by direct observation.

The arrangement of taxa within the Tables follows the classification for the Lepidoptera put forward by Nielsen & Common (1991) and Scoble (1992). The broad outlines of this classification were provided by Kristensen & Nielsen (1983), Kristensen (1984a, 1984b), and Nielsen (1989), and more detailed information on the Australian taxa have been supplied by Common (1992). I refer here to "Homoptera" for clarity with respect to older literature, although "Hemiptera" is the appropriate designation for this group (their arrangement in Table 1 follows Carver et al. 1991). In the case of the Lycaenidae, controversy remains concerning the relationships among the main lineages, as well as relationships within each of the groups. I follow the classification proposed by Eliot (1973), which was modified by Fiedler (1991), and which Eliot revised in 1992 (Eliot in Corbet et al. 1992), as well as Eliot's revision of the Miletini (1988). In his 1992 revision, Eliot included the riodinines as a subfamily of the Lycaenidae (Ehrlich 1958, Kristensen 1976, cf. Harvey 1987, Robbins 1988, Scott & Wright 1990), and I will refer to them here as a subfamily, recognizing that their appropriate taxonomic rank remains uncertain.

I. OVERVIEW OF PREDATORY LEPIDOPTERA

Convergently derived origins. Fossil remains suggest that the larvae of the earliest Lepidoptera fed on mosses, while the adults possessed mandibulate mouthparts and fed on pollen (Kukalova-Peck 1991). The most "primitive" extant Lepidoptera are in the suborder Zeugloptera, containing the homoneurous family, the Micropterigidae, which are considered to be the sister group to all other Lepidoptera (Common 1990, Nielsen & Common 1991). Zeuglopteran larvae have been described (Kristenson 1991:140) as "'soil animals' occurring in moist situations (bryophyte growths, etc.) which would seem to be only a small

step away from genuine aquatic habitats" which characterize the larval habitats of their close relatives, the Trichoptera (see also Powell 1980, Tuskes & Smith 1984). In New Zealand, members of the genus *Sabatinca* feed on liverworts. In Australia, larvae have been collected from rotten logs in Queensland. Other species are known to feed on herbaceous plants, including grasses (Nielsen & Common 1991). From these accounts, we can conclude that the Micropterigidae are primarily plant or detritus feeders. Carnivory is therefore likely to represent a derived condition in the Lepidoptera, although without appropriate phylogenies in each case, the polarity of shifts in feeding specialization must remain speculative. Nevertheless, the occurrence of predatory habits in eight separate lepidopteran superfamilies (Table 1) suggests that the trait has arisen convergently several times.

A closer examination of the phylogenetic distribution of carnivory reveals further evidence of convergent origins. Within the butterflies, the family Lycaenidae (sensu Ehrlich 1958, Eliot in Corbet et al. 1992) contains about 5,455 described species, or close to 32% of all butterflies (Shields 1989). At least 80 species are known to be carnivorous or to feed on substances other than plants (Tables 2 & 3), and an additional circa 70 species are suspected to be aphytophagous. Cottrell (1984) argued that aphytophagy evolved independently at least eight times in the Lycaenidae (not including the riodinines), and DeVries et al. (1992) have recently added two instances of aphytophagy in the Riodininae that may well represent an independent origin.

Phylogenetic distribution of predatory and parasitic species. Obligately predatory and parasitic Lepidoptera occur in the Tineoidea, Gelechioidea, Tortricioidea, Zygaenoidea, Pyraloidea, Geometroidea, Noctuoidea and Papilionoidea (Tables 1, 2 & 3). The only entirely carnivorous families are the Epipyropidae and the Cyclotornidae in the Zygaenoidea. The Epipyropidae is a small family of perhaps as many as 40 species in 11 genera (Davis 1987 and pers. comm., Krampl & Dlabola 1983). The larvae are parasitic on Homoptera, primarily leafhoppers and also cicadas, and even on other Lepidoptera (Common 1990). The Cyclotornidae is a family containing five described species and at least seven undescribed species in the genus *Cyclotorna* that is endemic to Australia (Common 1990). The larvae of these species feed parasitically on Homoptera, and then switch to preying on ant brood (described below, Dodd 1912). With an estimated 120 species in four tribes (Eliot 1988, 1992), all of whose larvae are thought to be carnivorous, the subfamily Miletinae of the Lycaenidae is the most well-developed clade of predatory Lepidoptera (Table 2). The Lycaenidae also possesses the most diverse range of aphytophagous taxa, including representatives from 31 genera in 3 subfamilies (Tables 2 & 3).

Close relatives of entomophagous Lepidoptera commonly exhibit one or more of three ecological traits that may have been important in the evolution of carnivory: some are scavengers on insect remains or spider eggs; others are mycophages or feed on lichen; and still others associate intimately with ants. For example, most of the species in *Stathmopoda* in the Oecophoridae, *Batrachedra* in the Batrachedridae, *Blastobasis* in the Blastobasidae, *Pyroderces* in the Cosmopterigidae, and *Vitula* in the Phycitinae are specialized to feed on coccids, but each genus also contains one or two species that scavenge on droppings in bird nests, spider eggs and/or insect remains in spider webs, detritus in deserted paper wasp or bumblebee nests, insects trapped in pitcher plants, or galls (Common 1990). Scavengers on animal products or remains that occasionally prey on other insects are especially common in the Tineoidea, which also contains several obligately predatory species (Table 1). Since members of the basal group of Lepidoptera, the Micropterigidae, are plant and detritus feeders, it is unclear in these instances whether scavenging on detritus and dead insects is a precursor to the evolution of predatory behavior on groups such as Homoptera, or vice versa. Both feeding strategies may have arisen independently from phytophagy, although on intuitive grounds at least, this seems less parsimonious.

Lichen feeding is typical among the Liptenini in the Lycaenidae, and Balduf (1938) argued that lichen feeding may have been an important precursor to the homopterophagy found in the closely related Miletinae. This proposal awaits phylogenetic investigation. Lichen feeding and/or mycophagy have been recorded among the Hepialidae, Tineidae, Psychidae, Oecophoridae, Cosmopterigidae, Scythrididae, Pyralidae, Noctuidae, and Arctiidae (Common 1990, Powell et al. 1995), and, with one or two exceptions, these groups also contain entomophagous species. However, these families are also numerically large, and thus, again, further phylogenetic work will be necessary before we understand the relationship between lichenivory/fungivory and carnivory.

Finally, a clear relationship exists between larval associations with ants and all forms of aphytophagy in the Lycaenidae (Cottrell 1984), as is discussed at greater length below.

Phylogenetic distribution of prey. The great majority of carnivorous Lepidoptera feed on other arthropods as caterpillars. A striking exception can be found in the adults of the noctuid "vampire moth," *Calyptra eustrigata* Hampson, which have piercing mouthparts and suck the blood of ungulates. A number of other species are phoretic upon, or feed on the feces of vertebrate species, including *Cryptoces choloepi* Dyar, the "sloth moth," which rides on the backs of sloths, hopping off

to oviposit on their feces (Waage & Montgomery 1976, Davis et al. 1986). However, in contrast to orders such as Diptera and Hymenoptera, no species of Lepidoptera have been described that can inject venom or otherwise paralyze their prey.

Entomophagous Lepidoptera are largely specialized to feed on Homoptera (Table 1). Within the Homoptera, a wide variety of taxa are sampled, but the largely sessile, colonial and soft-bodied families of the Sternorrhyncha (which includes the psyllids, aphids, scale insects and mealybugs) are preferred to the hopping insects of the Auchenorrhyncha. Of the 112 homopterophagous species in Table 1, 83 (74%) feed on Sternorrhyncha. A notable exception to this general pattern is found among the Epipyropidae and Cyclotornidae. Most of the larvae of these taxa are parasitic, and tend to be associated with Auchenorrhyncha, especially the Fulgoridea.

Of the some 130 obligately predatory or parasitic moths listed in Table 1, only 9 are clearly documented to consume ants during at least some portion of their life cycle (although another 8 are suspected to be myrmecophagous, and many more species in the genera *Cyclotorna*, *Niphopyralis* and *Hypophrictis* may also feed on ants). Five species have been noted to feed on insect and spider eggs, and 15 ambush small insects. In the butterfly family Lycaenidae, myrmecophagy is considerably more common, with at least 55 species (68%) of the 81 listed in Tables 2 and 3 feeding on ant regurgitations or ant brood during at least some portion of their life cycle. As many as 34 species (42%) have been recorded feeding on Homoptera, and again, the majority of these are on members of the Sternorrhyncha (the percentages add to 110% because some species are both homopterophagous and myrmecophagous).

Degree of specialization. In many cases, we still know relatively little about the diet breadth of predatory species because prey are not always identified, with many of the homopteran species noted simply as "scales." However, sufficient examples exist to indicate that predatory Lepidoptera, like their herbivorous counterparts, vary considerably in the breadth of their trophic niche: some are specialists with respect to the taxa they attack, whereas others are generalists. Within the Noctuidae, apart from a species that feeds on insects trapped by pitcher plants (*Eublemma radda* Swinhoe), the entire genus *Eublemma* is carnivorous on scale insects. *Eublemma amabilis* Moore in India feeds only on *Kerria* (*Laccifer*), whereas *Eublemma scitula* Rambur feeds on *Kerria* (*Laccifer*), *Anomalococcus*, *Lecanium*, *Ceroplastes*, and *Pulvinaria* (Glover & Negi 1935, Hinton 1981). Within the Lycaenidae, females of the aphidophagous species, *Taraka hamada* Druce, lay eggs in response to bamboo grass infested by their customary woolly aphid prey, *Ceratovacuna*

japonica Takahashi but ignore bamboo grass infested by an alternative aphid, *Melanaphis bambusae* Fullaway (Pierce, unpubl. data).

In general, myrmecophages are highly specialized with respect to their hosts. For example, although species of European *Maculinea* in the Lycaenoidea can be adopted into the nests of a number of ant species, their survival is host specific (Thomas et al. 1989). In a complex interaction involving a miletine butterfly, *Miletus biggsii* Distant, that feeds on aphids and coccids, the females are thought to use ants (a species in the genus *Dolichoderus*) as cues in oviposition, so that in effect, the ants indirectly select the species of homopteran prey (Maschwitz et al. 1988).

Myrmecophagy in Lepidoptera other than Lycaenidae. In addition to the lycaenids (discussed below), species from several genera of moths consume ants, and again we see an intrageneric association of predation with other forms of aphytophagy. The tineid genus *Hypophrictis* contains about 25 species in the Old World tropics, many of which may be myrmecophagous (Robinson et al. 1994). The life histories of only two species have been documented: *Hypophrictis dolichoderella* Roepke feeds on the brood of the ant *Dolichoderus bituberculatus* Mayr (Robinson et al. 1994), while the larvae of *H. saprophaga* Diakinoff are scavengers in *Bombus* nests in Sumatra (Diakonoff 1948). The larvae of these species live in flattened cases, which may serve to protect them against prey. In the Pyralidae (Wurthiinae), Robinson et al. (1994) speculate that all 28 species of the Indo-Australian genus *Niphopyralis* are myrmecophagous. The larvae of *Niphopyralis aurivillii* Kemner appear to mimic ant recognition signals, which gains them favorable acceptance in nests of *Polyrachis bicolor* Fr. Smith, where they feed on the brood (Kemner 1923). The larvae of *Niphopyralis myrmecophila* Roepke consume the brood of weaver ants, *Oecophylla smaragdina* Fabr. (Roepke 1916), in Java.

The most specialized myrmecophages are found among the Australian endemic family Cyclotornidae, exemplified by *Cyclotorna monocentra* Meyr. The larvae of these moths begin life as parasites of leaf-hoppers in the Cicadellidae, and then move to the nests of meat ants, *Iridomyrmex purpureus* Smith, where they complete their development by feeding on the brood. Dodd (1912) observed that females of this species lay large numbers of eggs near the trails of ants attending the leaf-hoppers. The first instar larva spins a pad of silk on the abdomen of the host beneath the wings, with a small sac at the anterior end to protect the larval head. Once the larva leaves the leaf-hopper, it builds an oval, flat cocoon where it molts into a broad, dorsoventrally flattened larva with a small head that can retract into the prothorax. It adopts a particular posture when encountered by a meat ant, raising the anterior

half of the body and curling its posterior over its back to expose the anus. Following inspection, a meat ant will carry the larva into the nest, where it becomes a predator on the ant brood. In the nest, the larva continues to produce an anal secretion that is attractive to the ants. Its behavior is remarkably convergent with that of certain species of staphylinid beetles, whose larvae have specialized exocrine glands to ensure appeasement and adoption by the ants that they parasitize (Holldobler 1971). Once the larva has completed development, which may take weeks or possibly months, it emerges from the ant nest, and spins its cocoon in a protected spot nearby (Common 1990). In addition to *Cyclotorna monocentra*, the larvae of *C. egena* Meyr. have been reared in South Australia from larvae associated with *Eriococcus* scale insects on *Eucalyptus*, and it seems likely that additional species will share aspects of this unusual life history.

In the Miletinae, one species, *Allotinus apries* Fruhstorfer, appears to have a similarly complex life history. The first instar larva of this species feeds on coccids tended by ants in the genus *Myrmicaria*. The second instar has unusual lateral thoracic phlanges that are thought to be involved in eliciting the ants to pick up the larva and carry it into the brood chamber, where it feeds on ant brood and/or regurgitations until pupation (Maschwitz et al. 1988).

Ambush predators. The only ambush predators known among the Lepidoptera are Hawaiian members of the geometrid genus *Eupithecia* (Montgomery 1982). The genus *Eupithecia* is found in every faunal region, and the larvae of most *Eupithecia* species are flower or seed feeders. However, 15 species of *Eupithecia* found in Hawaii consume only live-caught insects and spiders. The "inchworm" caterpillars of these species, such as *Eupithecia orichloris* Meyr., perch on the edges of leaves and plant stems, waiting for prey. When a small insect touches the posterior abdomen of the caterpillar, within an instant (estimated at 1/12th of a second), it loops backwards and seizes the prey with its thoracic legs. It rights itself again to consume its prey. Montgomery (1982) suggests that this unique feeding specialization arose in the Hawaiian fauna in part because of the historical lack of entomophagous insect groups there such as ants, mantids, mantispids and ambush bugs (Zimmerman 1948). Moreover, like many members of the Lycaenidae (described below), the fact that most of the phytophagous members of *Eupithecia* prefer the nitrogen-rich parts of their host plants, such as flowers, pollen and seed pods, may have predisposed them physiologically to a concentrated protein diet.

Adaptations for consuming food other than plants. Aphytophagy in all its forms requires considerable specialization. Feeding on honeydew sources requires an ability to appease ants that are in competition for

those same resources (Malicky 1970, DeVries & Baker 1989). Consumption of homopterans requires not only the ability to appease ants that may be tending the homopterans, but adaptations for finding homopteran prey, some of which are both patchy and ephemeral in their distributions. Feeding on ants requires extreme chemical and morphological specialization to find and penetrate ant nests (Thomas et al. 1989, 1993, Elmes et al. 1991a, 1991b, 1994, Thomas & Wardlaw 1992, DeVries et al. 1993). Lepidoptera consuming either Homoptera or ants must have the appropriate digestive physiology to develop upon only one or two prey types (e.g., Stanley-Samuelson et al. 1990, Dadd 1983). Those caterpillars that feed on ant regurgitations must not only be able to penetrate the ant nest by means of chemical camouflage (as in the genus *Maculinea*) or brute force (as in the genus *Liphya*), but they must also be able to mimic the appropriate behavioral cues to solicit regurgitations from their host ants (e.g., Holldobler 1971).

Larvae of many of the species listed in Tables 1, 2 & 3 protect themselves in similar ways, suggesting that trophic convergence can result in concomitant defensive convergence. The most common behavior is to spin a silken web that functions as a shelter while the larva feeds on homopteran prey. For example, the larvae of both *Taraka hamada* (Lycaenidae) and *Oedematopoda semirubra* Meyr. (Helioidinidae) feed on the woolly aphid, *Ceratovacuna japonica* in Japan, and the larvae of both species weave silken shelters which protect them against the soldier caste produced by these aphids. Some species act as wolves in sheeps' clothing by accumulating wax and/or other homopteran camouflage which they carry on their backs. Whether homopterophagous lepidopterans can respond to the alarm pheromones and/or other chemical signals of their homopteran prey remains to be demonstrated.

The adults of many species of homopterophagous Lycaenidae have unusually long and sclerotized legs and abdomens, which may protect them against attacks by ants when ovipositing near their homopteran prey (e.g., Cottrell 1984, Kitching 1987, Maschwitz et al. 1988). It is widely thought that these adults may also secrete volatile compounds that protect them against ant attacks, although none have as yet been identified. Finally, the adults of species that eclose within their host ants' nests are often cloaked in deciduous scales that aid them in safely exiting from the nest (e.g., Dodd 1912, Johnson & Valentine 1986).

The larvae of myrmecophilous lycaenids are well known for possessing unusually thick cuticles (Malicky 1969, 1970), although this can vary among species (Thomas et al. 1991). Most are chemically camouflaged to gain favorable recognition by their host ants (Henning 1983), although species such as *Liphya brassolis* Westw. are defended by

their tank-like morphology (Johnson & Valentine 1986). Chemically camouflaged species have specialized exocrine glands that secrete substances that mimic ant recognition signals (Malicky 1969, Cottrell 1984). They also can mimic ants behaviorally, possibly even imitating host ant acoustical communication signals (DeVries et al. 1993). Females of some species use ants and/or homopterans as cues in oviposition (Atsatt 1981, Pierce & Elgar 1985, Maschwitz et al. 1985).

Predatory Lepidoptera often are unusually variable in their development. Some species vary greatly in time taken to reach maturity (Henning 1984, Common 1990). Others vary with respect to the final adult size (Banno 1990). Some lay thousands of eggs that hatch over several months, thereby providing a wide time window for larvae to find suitable hosts (Kirkpatrick 1947). Others can withstand long periods of starvation or low moisture conditions (Hinton 1981, Banno 1990, Thomas & Wardlaw 1992). Presumably these are developmental responses to specializing on host distribution and phenology (e.g., Elmes et al. 1991b). Carnivorous species may also be physiologically better able to withstand periods of starvation and/or low moisture than their phytophagous relatives (Banno 1990).

Among the Lycaenidae, many species have been recorded to feed on the secretions of extra-floral nectaries (e.g., DeVries & Baker 1989). This behavior may enable larvae to withstand periods of time when food (either foliage or prey) is in short supply. The adults of homopterophagous butterflies often spend long hours feeding on the honeydew of their prey (Fukuda et al. 1984, Maschwitz et al. 1988, Banno 1990), and again, this behavior may enable adults to live for considerably longer periods, perhaps allowing them to wait until the density of their intended prey is appropriate for oviposition.

Possible insights from cannibalism. Many species of Lepidoptera are cannibalistic both in the laboratory and the field (Fox 1975, Polis 1981, Schweitzer 1979a, 1979b). In particular, pyralids and noctuids demonstrate numerous instances of cannibalism and incidental predatory behavior (Table 1, see Balduf 1938). Dethier (1937, 1939) found that different species vary with respect to conditions eliciting cannibalism, but that hunger, crowding and thirst are prime factors in influencing this behavior. Members of the Lycaenidae are particularly well-known for cannibalistic tendencies (Mattson 1980), and the question naturally arises as to whether factors giving rise to cannibalistic behavior also give rise to predatory behavior.

Diet breadth of phytophagous species may be associated with the likelihood of occasional cannibalism. In his discussion of cannibalism in the noctuid tribe Lithophanini, Schweitzer (1979b) found that of the 8 non-cannibalistic genera, 9 (50%) of the 18 species were polyphagous.

However, of the 6 cannibalistic genera, 11 (73%) of the 15 species were polyphagous, three were intermediate, and only one was restricted in its diet. He suggested from these data that a polyphagous diet may predispose a species to cannibalism (or that a restricted diet may somehow inhibit a species from expressing this behavior), although firm conclusions are again not possible without a phylogeny for the group.

Experimental studies of cannibalism by other noctuid species have found cannibalism rates to increase with a decline in food quality. Al-Zubaidi & Capinera (1983) found a negative correlation between percent cannibalism and foliar nitrogen content of host plants (sugarbeet) that had been treated with different amounts of fertilizer. Similarly, Raffa (1987) showed that larvae of the fall armyworm, *Spodoptera frugiperda* J. E. Smith, were more likely to be cannibalistic when reared on a less preferred host, red kidney bean seedlings, than on their preferred diet of corn seedlings, and that this higher degree of cannibalism helped them to compensate digestively for feeding on the less suitable host. Joyner & Gould (1985) demonstrated nutritional benefits to cannibalism by *Heliothis zea* Boddie under low moisture conditions.

Although much is known about factors governing insect feeding (e.g., Gelperin 1971, Bernays & Chapman 1974, Bernays 1988, 1989, Bernays & Graham 1989, Simpson & Bernays 1983, Simpson et al. 1988), little of this work has focused on cannibalistic feeding behaviors. Dethier (1939) found that larvae of *Estigmene acrea* Drury and *Isia isabella* J. E. Smith (Arctiidae) were stimulated to cannibalize conspecifics whose tissues were exposed by having been crushed or cut open. Heinig (1989) showed that the emptiness of the gut, as well as deficiencies in water, ions, and amino acids, played a role in eliciting cannibalism in the noctuid species *Agrotis segetum* Denis & Schiff. and *Mamestra brassicae* (L.). In particular, he found that levels of trehalose in the haemolymph were particularly important in predicting cannibalistic behavior in *M. brassicae*. Other factors, such as larval density (Breden & Chippendale 1989), time of fasting (Abdel-Salam & El-Lakwah 1973), age and larval size (Semlitsch & West 1988, Dial & Adler 1990), genetic predispositions (Richter 1990) and even parasitism (Dindo & Cesari 1985) can influence rates of cannibalism.

Several studies of cannibalism have investigated the potential difficulties of being restricted to carnivorous diets. Dethier (1939) concluded that both *Estigmene acrea* and *Isea isabella* could meet all their dietary requirements by cannibalism. Tripathi & Singh (1990) found that development of *Heliothis armigera* (Hubner) was possible only when larvae were given conspecific prey, and not when they were given larvae of different species as prey. Bernays and Cornelius (1989) found that generalist caterpillar prey were more palatable than specialists to

the generalist predator, *Iridomyrmex humilis* Mayr. In related research, Stanley-Samuels et al. (1990) investigated the nutritional challenges posed by diets that consist entirely of ant larvae and pupae, with particular interest in the acquisition of polyunsaturated fatty acids that are usually only available from eating plants. They found that the fatty acid composition of fly parasites that feed entirely on ants closely matched those of their ant prey.

Most physiological studies of cannibalism have focused on the possible nutritional benefits to be gained from this behavior in terms of growth and development. Bogner and Eisner (1991, 1992) added an interesting twist to this approach when they demonstrated that larvae of the arctiid moth, *Utetheisa ornatrix* L., are more likely to cannibalize eggs and pupae that are rich in pyrrolizidine alkaloids (PA) than those that are free of PAs. The PAs themselves are powerful phagostimulants for the larvae of this species. The moths sequester PAs for protection against predation, and they usually acquire these substances from their host plants. It is reasonable to postulate that procurement of additional defensive secondary compounds such as PAs may represent a more general, hitherto unappreciated selective mechanism favoring cannibalism in chemically protected species. This would depend, however, on the nature of defense in these species. It might be unlikely to play a strong role, for example, among species that advertise their unpalatability through aposematic displays, since the relative number of distasteful models is crucial in maintaining effective defense in these species.

II. CARNIVORY IN THE LYCAENIDAE

A possible preadaptation for the evolution of carnivory in the Lycaenidae is the close association that the caterpillars of many species have with ants (Cottrell 1984, Pierce 1987, Fiedler 1991, DeVries 1991a). These associations can be mutualistic or parasitic, and range from loose interactions in which caterpillars are not tended but not attacked by ants, to those in which the caterpillars are occasionally tended by ants (often by many species), to yet others in which caterpillars are obligately dependent upon a single species of host ant for food or defense. Typically, the caterpillars of mutualistic species produce nutritious secretions of sugars and amino acids for ants in exchange for protection against insect predators (e.g., Pierce & Eastal 1986, Pierce et al. 1987, DeVries 1988, 1991, Fiedler & Maschwitz 1988, 1989a). In order to produce these secretions, caterpillars must feed on high quality food sources. For example, in the case of the ant-associated lycaenid, *Jalmenus evagoras* Don., larvae feeding on nitrogen-enriched plants were more attractive to attendant ants and had greater survivorship in the

field than larvae on nitrogen-poor controls, and females preferred to lay eggs on the higher quality plants (Baylis & Pierce 1991). Phytophagous lycaenid larvae of many species have a predilection for nitrogen-rich parts of plants such as flowers and terminal foliage, and also frequently exhibit cannibalistic behavior (Mattson 1980).

A variety of larval glands are involved in maintaining lycaenid/ant associations, and these have been reviewed in some detail (Cottrell 1984, Malicky 1969, Downey & Allyn 1973, 1979, Kitching & Luke 1985, Tautz & Fiedler 1994). Three of these glands appear to be of central importance, and have been systematically examined in many species. These are: (1) the pore cupola organs (PCOs), single-celled epidermal glands found in the epidermis, and thought to secrete substances that appease and attract ants; (2) the dorsal nectary organ (DNO), a large secretory organ located on the seventh abdominal segment, which, upon solicitation, secretes a sweet and nutritious reward for ants; and (3) the tentacular organs (TOs), eversible, finger-like projections that flank the DNO on the eighth abdominal segment and appear to secrete volatile substances. The exact function of the TOs is still not entirely clear, although they tend to be everted under conditions of danger or alarm when a larva would be most likely to signal to its attendant ants (Axen & Leimar 1993, Axen pers. comm.). All lycaenid larvae that have been examined possess PCOs; many species have a DNO; others have TOs; and others have both a DNO and TOs.

Of the approximately 1,000 species of lycaenids for which full life histories have been described (review in Fiedler 1991), about 80 have been directly observed to feed on homopterans, honeydew, ants or ant regurgitations, or inferred to feed on ants or ant regurgitations because they spend the entire larval period inside ant nests without other apparent food sources (Tables 2 & 3). Because of incomplete information, this number represents only a fraction of the total number that are predatory (including, for example, all of the Miletinae) but whose life histories are as yet unknown. In some genera, such as *Maculinea*, all members of the genus feed on plants in the early instars, and then on ant and/or ant regurgitations in later instars, and all the ones that have been studied are species-specific with respect to ants hosts (Thomas et al. 1989). In others, such as *Arhopala* or *Spindasis*, only one or two species in an otherwise herbivorous genus feed on ants, ant regurgitations and/or honeydew (K. Dunn pers. comm., Fukuda et al. 1984).

Lycaenids other than Miletinae. Predation in lycaenid taxa other than Miletinae consists largely of myrmecophagous species whose larvae eat ants or ant regurgitations (Table 2). Only a few records exist of non-miletines that feed on Homoptera. However, these records are from species in tribes in two different subfamilies, and each is likely to

represent an independent evolution of homopterophagy. Within the subfamily Lycaeninae, larvae of *Shirozua jonasi* Janson (Theclini) feed on aphids in addition to regurgitations from attendant ants, *Camponotus japonicus* Mayr (Fukuda et al. 1984, but see Yamaguchi 1988), and larvae of *Chilades lajus* Cr. (Polyommataini) have been observed to eat aphids (Agarwala & Saha 1984). In the subfamily Riodininae, *Setabis lagus* Butler is known to consume scale insects (DeVries et al. 1992).

Of the species that feed on ants, the habit of feeding on ant regurgitations either instead of, or in addition to, feeding on the ant brood itself also appears in disparate groups. Species of *Spindasis* (Aphnaeini), *Shirozua* (Theclini), and *Niphanda*, *Maculinea* and possibly *Anthene* (Polyommataini) feed by trophallaxis, as does *Audre aurina* Hewitson among the Riodininae (Table 2). *Acrodipsas* (Theclini) in Australia appears to be an exclusively myrmecophagous genus, whereas species in both *Lepidopchrysops* in Africa and *Maculinea* in the Palearctic (Polyommataini) are phyto-predatory in the sense that they begin life on specific host plant taxa, but spend their later instar(s) as predators in ant nests. *Lepidochrysops* has over 100 species, but details of the life histories of only a handful of these have been described (Cottrell 1984, Table 2). All are thought to parasitize species of *Camponotus* ants in the third and fourth instars (Cripps 1947, Clark & Dickson 1971, Henning 1983).

Myrmecophagy in the genus *Maculinea*. The biology of the large blue, *Maculinea arion* Schiff. has long been of interest to lepidopterists (e.g., Frohawk 1906, 1916, Chapman 1916a, 1916b), but advances in our understanding of the ecology of the species of this genus have only come in the past ten years. Jeremy Thomas, Graham Elmes and their colleagues have been systematically identifying factors that influence the development, survival and reproductive success of different species of *Maculinea*, and have used these variables, measured in the field, to construct models that predict their population dynamics (Thomas 1981, 1984, Thomas et al. 1989, 1991, 1993, Thomas & Elmes 1993, Thomas & Wardlaw 1990, 1992, Elmes & Thomas 1985, 1992, Elmes & Wardlaw 1982, 1983, Elmes et al. 1991a, 1991b, 1994, Hochberg et al. 1992, 1994, DeVries et al. 1993).

All five species of European *Maculinea* (*arion*, *teleius* Bergs., *nau-sithous* Bergs., *alcon* Schiff. and *rebeli* Hirschke) are univoltine, and lay their eggs on flower heads of one or two plant species (Elmes & Thomas 1987), which are the hosts for the developing larvae until they reach the third instar, two or three weeks after hatching. At this point, they undergo a dramatic life history change—the final instar occurs in the nests of host ants, where larvae obtain more than 90% of their

ultimate biomass by feeding on the ant brood, trophic eggs, prey, or regurgitations from their host ants. The exact nature of the food consumed varies depending upon the species involved (Elmes et al. 1991a, 1991b, Thomas & Wardlaw 1992).

Species of *Maculinea* live in highly restricted populations which are particularly sensitive to environmental perturbations, and the extinction of British populations of *Maculinea arion* has served as a model invertebrate system for conservation biologists (Thomas 1983). Key variables that have been shown to affect mortality in ant nests include: the species of ant adopting the caterpillars (Thomas et al. 1989); the condition of the host ant colony, such as its size, and whether or not it contains a queen (Elmes & Wardlaw 1982, 1983, Thomas & Wardlaw 1990); as well as the presence or absence of specialized parasites (Thomas & Elmes 1993).

By examining no less than 994 host ant nests, Thomas et al. (1989) firmly established that, although larvae of different *Maculinea* species will readily be adopted into the nests of a number of different species of *Myrmica* ants, each species of *Maculinea* survives well only in the nests of one particular ant partner (Table 2). This discovery was important from both an ecological and conservation point of view because it demonstrated how remarkably narrow the ecological niche is for species of *Maculinea*—not only do the larvae of each species require appropriate host plants to begin their development, but they also require the appropriate host ant species in order to survive. Habitats that appear to be suitable because they contain host plants and colonies of *Myrmica* are not necessarily acceptable unless they contain the correct species of *Myrmica*.

The life histories of two species of *Maculinea* found in Japan, *M. teleius* and *M. arionides* Staud., are not as well studied as their European counterparts. However, one distinctive facet of the biology of these species is that, in addition to parasitizing colonies of the ant *Myrmica ruginodis* Nylander, as in Europe, both *M. teleius* and *M. arionides* in Japan enter and survive successfully in nests of the ant *Aphaenogaster japonica* Forel (Fukuda et al. 1984, Yamaguchi 1988).

Given the high degree of host specificity involved in survival, it is surprising that females of each species of *Maculinea* do not generally appear to use ants as cues in laying eggs. Although some phytophagous species of Lycaenidae lay eggs in response to the presence of associated ant taxa (e.g., Atsatt 1981b, Pierce & Elgar 1985, Jordano et al. 1992), females of several species of *Maculinea*, including *M. arion* and *M. teleius*, do not respond to the presence of appropriate *Myrmica* colonies (Thomas 1977, 1984a, Elmes & Thomas 1987, van der Heijden et al. 1995). However, the density of females of *Maculinea nausithous* is

correlated with the nest density of its host ant, *Myrmica rubra* L., as is its number of ovipositions. Thus, *M. nausithous* has behavioral mechanisms, perhaps including low vagility and fidelity to a particular habitat, that insure appropriate ant association by ovipositing females (van der Heijden et al. 1995).

Maculinea species have at least two strategies for parasitizing ant colonies. Most of the species, including *Maculinea arion*, are predators that feed directly on the ant brood. They forage in an adaptive manner, selecting the largest larvae and prepupae first, and sparing the eggs and younger brood that are still developing and will presumably provide more profitable food later on (Thomas & Wardlaw 1992). In contrast, two species, *Maculinea rebeli* and *M. alcon*, do not eat the ants themselves, but feed instead on regurgitations obtained through trophallaxis with their host ants (Elmes & Thomas 1987, Elmes et al. 1991). Thomas and Wardlaw (1992) proposed that feeding on regurgitations represents an evolutionarily derived condition within the genus, with simple predation representing the ancestral state.

Predation in the Miletinae. All the known members of the lycaenid subfamily Miletinae are aphytophagous, and the diversity of different feeding strategies is greatest in this group (Corbet & Pendlebury 1978, Cottrell 1984, Maschwitz et al. 1988). Much of our knowledge of the ecology of the Miletinae comes from recent work on South East Asian taxa, particularly *Logania* and the species-rich genera *Miletus* and *Allotinus*, by Ulrich Maschwitz, Konrad Fiedler and their colleagues (Maschwitz et al. 1985a, 1985b, Maschwitz et al. 1988, Fiedler 1992, 1993, Fiedler & Maschwitz 1989, see also Kitching 1987, Banno 1990). We now have life history data for about 30% of the approximately 120 species of miletines (Table 3). Unlike other lycaenid subfamilies, whose predatory members feed primarily on ants, most of the miletines are specialized to feed on homopterans. Homoptera commonly taken by miletine larvae include coccids, jassids, psyllids, membracids and aphids, particularly those in the closely related aphid families Hormaphididae and Pemphigidae (Table 2).

Maschwitz et al. (1988) proposed that feeding on Auchenorrhyncha is a derived condition with respect to preying on the Sternorrhyncha. They suggested that species such as *Logania malayica* Distant represent the ancestral pattern, feeding primarily on ant-attended aphids, whereas species of *Miletus* and *Allotinus* show greater feeding specializations. They identified three derived strategies among the latter taxa: (1) feeding on a broad spectrum of homopteran prey, and possibly using ants as cues in finding these homopterans (e.g., *Miletus biggsii*); (2) feeding on ants or ant regurgitations as a form of kleptoparasitism (e.g., *Allotinus apries*); and (3) feeding on members of the suborder Auchenor-

rhyncha in addition to or as an alternative to Stennorrhyncha (e.g., *Allotinus subviolaceus* C. & R. Felder).

III. THE EVOLUTION OF CARNIVORY

Although several patterns emerge from the distribution of carnivory in the Lepidoptera and from the limited information we have on the life histories of carnivorous species, we can make few strong inferences about the evolution of predatory behavior. While considerable advances have been made in recent years in reconstructing the phylogeny of Lepidoptera, particularly basal groups, we are handicapped in any such analysis by our lack of reliable phylogenies in many cases, and this discussion must accordingly start with both a caveat and an exhortation: (1) that the following conclusions are inevitably tentative; and (2) that generating phylogenies for these groups should be a high priority. Not only will phylogenetic analysis confirm or reject evolutionary-transition hypotheses such as those of Thomas and Wardlaw (1989) on the shift from myrmecophagy to kleptoparasitic trophallaxis, or of Maschwitz et al. (1988) on the shifts in prey niche of species of *Miletus* and *Allotinus*, but it also will throw light on a number of other evolutionary and ecological issues. For example, I noted earlier the apparent phylogenetic clustering of taxa that are carnivores, scavengers, and/or lichen feeders. In physiological terms, this is not surprising, because these lifestyles probably make similar demands on, for example, aspects of foraging and digestion. Phylogenetic information, however, will determine whether there is any consistent polarity to shifts between them. Does scavenging and/or fungivory or lichen feeding give rise to predation? Is scavenging typically an intermediate lifestyle between phytophagy and predation? Is predatory behavior more likely to evolve in taxa prone to cannibalism and the kind of incidental predation exhibited by many scavengers?

Predatory feeding strategies appear to have evolved repeatedly within the Lepidoptera. This we can surmise even without a full phylogeny. As discussed earlier, given that the Micropterigidae are likely to be the sister group to the rest of the Lepidoptera, and that these moths feed on detritus or plants, it is reasonable to conclude that predation is an evolutionarily derived state with respect to either detritus feeding or phytophagy in the Lepidoptera (Common 1990, Nielsen & Common 1992). Moreover, we see carnivory in groups that are so disparate taxonomically that parsimony would argue the trait to be homoplastic. Indeed, once we have reliable phylogenetic information, it is likely that the number of instances of the independent evolution of carnivory will be found to be greater rather than less than current estimates—in other words, existing carnivorous taxa that are regarded as monophyletic may

well be found to be polyphyletic. After all, the convergent (or parallel) acquisition of carnivory in a number of related taxa might result in the concomitant acquisition of a set of lifestyle-associated traits which might well mislead the systematist into classifying them as constituting a monophyletic group.

The multiple origins of carnivory within the order suggest that (1) in teleological terms, carnivory is a relatively "desirable" life history trait, and (2) the physiological, behavioral and ecological hurdles that must be cleared in the course of the transition from herbivore to carnivore are easily overcome (indeed, most studies of lepidopteran feeding behavior are concerned with the hurdles faced by phytophagy, rather than the other way around.) Nevertheless, despite its desirability and the apparent ease with which carnivory can be acquired, lepidopteran predators are comparatively rare. This pattern is reflected generally throughout the insects (Mitter et al. 1988), although from the numbers of species involved, it is especially dramatic in the Lepidoptera. Weigmann et al. (1993) noted that carnivorous parasitism appears to have originated more than 60 times among insects, but in the 19 sister-group comparisons that they were able to perform with reliable phylogenies, they found no evidence that these insects with their highly specialized feeding habits diversify more rapidly than their more generalist relatives, including predators, saprophages and herbivores. If anything, their results indicate an opposite trend, and they suggested that one explanation for the great evolutionary success of phytophagous relative to carnivorous insect parasites is simply the trophic pyramid, with its differences in the quantity and availability of resources at each level.

Predatory behavior in the Lepidoptera seems to lack evolutionary staying power, suggesting that it is in some way evolutionarily unstable. This argument is analogous to the conundrum regarding the mysterious evolutionary disadvantage of asexuality—although it arises in evolution regularly, most instances are apparently recent, inasmuch as the taxonomic distribution of asexuality seldom creeps beyond the generic level. The same, broadly speaking, is true for predatory behavior in the Lepidoptera. There are numerous genera in which one or a few species are carnivorous while the others remain phytophagous. Given the assumption that carnivory is the derived state, we conclude that carnivory in these cases has arisen recently, after the origin of the genus.

There are a few notable exceptions to this pattern. The Epipyropidae and Cyclotornidae are small families which, perhaps significantly, both share the trait of parasitizing auchenorrhynchine Homoptera such as Fulgoroidea during some portion of their lifetimes. The Miletinae is a well-developed group, considered widely to have originated early on in the evolution of the Lycaenidae (Eliot 1973, Scott & Wright 1990),

all of whose members are carnivorous, and whose phylogenetic depth goes well beyond the genus level. More detailed analysis, both phylogenetic and ecological, of the miletines and related taxa will help to determine why they have apparently succeeded where others have failed. Our analysis here, however, indicates a number of possible causes for the general failure of this evolutionary experiment.

It is for good evolutionary reasons that *Maculinea arion* has become the symbol of conservation in the United Kingdom. Because of the complexity (and specificity) of their life cycles, species of *Maculinea* are extremely sensitive to environmental perturbations. These perturbations are currently especially traumatic and rapid because they are human-caused; but, from an evolutionary viewpoint, life history "brittleness" in terms of overspecialization could also be costly in the long run. For example, *M. arion* is at best a rather inefficient predator. Whereas a single *Myrmica* nest of some 350 workers can accommodate only one carnivorous *Maculinea arion* larva, a similar sized nest can accommodate as many as six larva of the "cuckoo" species, *Maculinea rebeli*, which feeds on ant regurgitations (Thomas & Wardlaw 1992). Thomas & Wardlaw (1992) propose that feeding on regurgitations represents an evolutionarily derived condition within the genus, with simple predation representing the ancestral state. This hypothesis requires phylogenetic verification but, if we assume it to be correct, argues strongly that predation is evolutionarily unstable—so unstable in fact that it can readily be displaced by an alternative, ecologically complex lifestyle.

Maculinea illustrates well the problems of being a lepidopteran predator. Like other phytophages, Lepidoptera are entrenched not only in feeding on plants, but also in living on them (Southwood 1973). The evolutionary acquisition of carnivory, while representing a substantial diet shift, is rarely accompanied by a concomitant shift in habitat away from a plant-based existence. In essence, it often seems to involve the *addition* of a trophic level rather than the *replacement* of one. The simple case of this is *Maculinea*, where herbivory is retained in the early instars prior to the switch over to carnivory, but other predatory species, strictly carnivores, are also jointly plant- and prey-dependent. This is because of the nature of lepidopteran carnivory: with the single exception of the sit-and-wait geometrids in the genus *Eupithecia*, lepidopteran predators are sluggish browsers that are severely restricted in their ability to seek prey. This results in two strategies: (1) ant deception whereby the caterpillar induces its own import into an ant nest; and (2) oviposition on a plant populated by the prey species (usually Homoptera). Except for a few cases where caterpillars are myrmecophagous throughout their life cycles (e.g., *Liphyra brassolis*), both

TABLE 1. Moths that eat other insects as their primary food source. Moth species are grouped by family, following Common 1990, Nielsen & Common 1991, and Scoble 1992. Under feeding type: PRF = facultative predator, PRO = obligate predator, PA = parasite and/or parasitoid. Under food: homopteran taxa in Sternorrhyncha begin with S (Sal = Aleyrodoidea, Sap = Aphidoidea, Sc = Coccoidea, Sp = Psylloidea); homopteran taxa in Auchenorrhyncha begin with A (Acl = Cicadelloidea, Aci = Cicadoidea, Af = Fulgoroidea); F = ants (Formicidae).

Taxon	Type	Food	Notes	References
Tineoidea				
Tineidae				
<i>Atticonviva</i> sp.	PRO	F?	may consume ant brood	Busck 1935, Hinton 1951
<i>Ereunetis miniuscula</i>	PRO	Sc	<i>Icerya purchasi</i> and other scales	Leonard 1932
<i>Hypophrictis dolichoderella</i>	PRO	F	mature larvae form cases, eat brood of <i>Dolichoderus bituberculatus</i> and <i>Plagiolepis longipes</i>	Roepke 1925, Robinson et al. 1994
<i>Hypophrictis</i> (23 spp.)	PRO	F?	eat ant brood?	Robinson et al. 1994
<i>Monopsis hemicitra</i>	PRF	other	mantid egg masses	Fletcher 1920
<i>Myrmecozela ochraceella</i>	PRF	F?	may eat ant brood in <i>Formica</i> nests, scavengers in nests	Hinton 1951
<i>Pringleophaga marioni</i>	PRO	other	earthworms in captivity	French & Smith 1983, Scoble 1992
<i>Tineola biselliella</i>	PRF	other	animal fibers, occasionally mites, conspecifics	Webster 1912, Illingworth 1917
Psychidae				
<i>Ardiosteres moretonella</i>	PRF	F?	scavenger in ant nests	Hinton 1951, Common 1990
<i>A. dryophracta</i>	PRF	F?	collected from "small tree ant nest"	Dodd in Common 1990
<i>Iphierga macarista</i>	PRF	F?	scavenger in <i>Iridomyrmex purpureus</i> nests	Hinton 1951, Common 1990
<i>Cryptothelea</i> (<i>Platoeceticus</i>) <i>gloverii</i>	PRF	Sc	<i>Pseudoaonidia duplex</i>	Plank & Cressman 1934, Clausen 1940
Gelechioidea				
Oecophoridae				
<i>Stathmopoda arachnophthora</i>	PRO	other	spider eggs	Clausen 1940
<i>S. basipleetra</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>)	Imms & Chatterjee 1915, Beeson 1941, Hinton 1981
<i>S. callichrysa</i>	PRO	Sc	galls, mealybugs	Tillyard 1929, Hinton 1981, Common 1990
<i>S. coccophanes</i>	PRO	Sc	mealybugs	Tillyard 1929, Hinton 1981
<i>S. contioma</i>	PRO	Sc	coccids	Hinton 1981
<i>S. cypris</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>lacca</i>	Fletcher 1933
<i>S. melanochra</i>	PRO	Sc	<i>Ceroplastes</i> , <i>Coccus bacca-</i> <i>tum</i> , <i>Eriococcus cori-</i> <i>aceus</i> , <i>Icerya purchasi</i>	Hinton 1981, Common 1990, Fletcher 1933
<i>S. oesteeitis</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>decorella</i>	Gowdy 1917
<i>S. ovigera</i>	PRO	Sc	coccids	Fletcher 1920, Hinton 1981
<i>S. theoris</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>), coccids	Imms & Chatterjee 1915, Clausen 1940, Hinton 1981
<i>Oedematopoda cypris</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>lacca</i>	Imms & Chatterjee 1915, Fletcher 1933, Hinton 1981
<i>O. pyromyia</i>	PRO	Sap	<i>Oregma</i> spp.	Fletcher 1933
<i>O. semirubra</i>	PRO	Sap	<i>Ceratovacuna japonica</i>	S. Aoki, pers. comm.

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>O. venusta</i>	PRO	Sc	<i>Kerria (Laccifer) lacca</i>	Fletcher 1920, Hinton 1981
<i>Cynarmostis vectigalis</i>	PRO	Sc	<i>Eulecanium</i>	Silvestri 1943, Hinton 1981
Coleophoridae				
<i>Batrachedra arenosella</i>	PRO	Sc	<i>Poliaspis</i> , scale insects	Hudson 1928, Hinton 1981, Common 1990, Scoble 1992
<i>B. myrmecophila</i>	PRO	F	ant brood (<i>Polyrachis dives</i>)	Hinton 1951
<i>B. silvatica</i>	PRO	Sc	<i>Pseudococcus</i>	Fletcher 1921, Hudson 1928, Hinton 1981
<i>Eustaintonia phragmatella</i>	PRO	Sc	<i>Alcerda</i>	Silvestri 1943, Hinton 1981
Blastobasidae				
<i>Blastobasis coccivorella</i>	PRO	Sc	<i>Kermes</i>	Walsingham 1907, Glover 1933, Comstock in Clausen 1940, Hinton 1981
<i>B. lecaniella</i>	PRO	Sc	<i>Lecanium</i> , <i>Ceroplastes floridensis</i> , <i>Saissetia nigra</i> , <i>S. oleae</i> , <i>S. coffeae</i> (hemisphaerica)	Busck 1913, Bodkin 1917, Balduf 1939
<i>B. thelymorpha</i>	PRO	Sc	<i>Lac</i>	Stebbing 1910, Clausen 1940, Hinton 1981
<i>B. transcripta</i>	PRO	Sc	<i>Ripersia</i>	Fletcher 1920, Glover 1933, Clausen 1940
<i>Holocera iceryaella</i>	PRO	Sc	<i>Lecanium persicae</i> , <i>Icerya purchasi</i> , <i>Saissetia oleae</i> , <i>Parthenolecanium (Eulecanium) persicae</i> , <i>Pseudococcus bakeri</i>	Dietz 1910, Essig 1916, Basinger 1928, Clausen 1940, Hinton 1981
<i>H. phenacocci</i>	PRO	Sc	<i>Coccus (Phenacoccus) colmani</i>	Braun 1927, Hinton 1981
<i>H. pulvereae</i>	PRO	Sc	<i>Kerria (Laccifer) lacca</i>	Misra & Gupta 1934, Glover 1933, Clausen 1940, Hinton 1981
<i>Zenodochium coccivorella</i>	PAo	Sc	<i>Kermes</i>	Glover 1933, Clausen 1940
Momphidae				
<i>Coccidiphlia gerasimovi</i>	PRO	Sc	<i>Sphaerolecanium (Eulecanium) prunastri</i>	Danilevskii 1950, Hinton 1981
<i>C. ledereriella</i>	PRO	Sc	<i>Trabutina</i> , <i>Pseudococcus</i>	Danilevskii 1950, Hinton 1981
<i>Lacciferophaga yunnanana</i>	PRO	Sc	scales	Zagulyaev & Din-si 1959, Hinton 1981
Cosmopterigidae				
<i>Euclementia bassettella</i>	PRO	Sc	<i>Kermes galliformis</i> , <i>Kermes</i> spp.	Hollinger & Parks 1919, Clausen 1940
<i>Limnoecia peranodes</i>	PRO	Sc	<i>Saissetia</i> spp.	Fletcher 1920
<i>Pyroderces bicincta</i>	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981
<i>P. falcatella</i>	PRO	Sc	<i>Kerria (Laccifer) lacca</i> , <i>K. (L.) lobata</i> , <i>K. (L.) albiziae</i> , <i>Ceroplastes (Lakshadia) communis</i> , <i>Dactylopius</i>	Norris 1931, Fletcher 1920, 1933, Glover 1937, Beeson 1941, Hinton 1981
<i>P. gymnocentra</i>	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981
<i>P. holoterma</i>	PRO	Sc	scales	Glover 1937, Beeson 1941, Hinton 1981

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>P. philogeorgia</i>	PRF	Sc	<i>Pseudococcus perniciosus</i> , <i>Coccus</i>	Meyrick 1933, Glover 1937, Beeson 1941, Hinton 1981
<i>P. rileyi</i>	PRO	S	<i>Icerya purchasi</i> , <i>Pulvinaria</i> <i>psidii</i>	Berger 1917, Hinton 1981
Gelechiidae				
<i>Brachmia</i> spp.	PRF	other	spider eggs, insect prey in spider webs	Meyrick 1912, Scoble 1992
Tortricioidea				
Tortricidae				
<i>Tortrix callopista</i>	PRO	Sc	<i>Strictococcus sjostedti</i>	Lamborn 1914, Clausen 1940, Hinton 1981
<i>T. podana</i>	PRO	other	<i>Eriophyes ribis</i> (gall-mite)	Mumford 1931
<i>Russograptis</i> spp.	PRO	Sc	coccids	Scoble 1992
<i>Pammene isocampta</i>	PRO	Sc	<i>Lecanium</i>	Ayyar 1929, Hinton 1981
<i>Cnephasia</i> spp.	PRO	Sc	<i>Pseudococcus</i>	Edwards et al. 1934, Hinton 1981
<i>Coccothera spissana</i>	PA	Sc	<i>Waxiella egbara</i> (<i>Cero-</i> <i>plastes egbarium</i>)	Bevis 1923, Clausen 1940
Zygaenoidea				
Epipyropidae				
<i>Agamopsycha thren-</i> <i>odes</i>	PA	Af	<i>Perkinsiella saccharicida</i> and related species	Perkins 1905, Kato 1940, Common 1990
<i>Epteurybrachys eury-</i> <i>brachidis</i>	PA	Af	<i>Eurybrachys tomentosa</i> , <i>E.</i> <i>spinosa</i>	Fletcher 1920, Krishnamurti 1933, Clausen 1940
<i>Epimesophantia dila-</i> <i>bolai</i>	PA	Af	<i>Mesophantia kangonica</i>	Fletcher 1939, Krishnamurti 1933, Krampl & Dlabola 1983
<i>E. schawerdae</i>	PA	Af	<i>Mesophantia kangonica</i>	Fletcher 1939, Krishnamurti 1933, Krampl & Dlabola 1983
<i>Epipomponia nawai</i>	PA	Af, Aci	<i>Tanna japonensis</i> , <i>Oncot-</i> <i>ympana maculaticollis</i> , <i>Meimuna opalifera</i> , <i>Ma-</i> <i>crosemia kareisana</i> , <i>Grap-</i> <i>tosaltria nigrofascata</i> , <i>Ri-</i> <i>cania japonica</i>	Nawa 1903, Kirkaldy 1903, Dyar 1904, Balduf 1938, Kato 1940, Ohgushi 1953
<i>E. multipunctata</i> group	PA	Af	<i>Laternaria lucifera</i>	Jordan 1928, Krampl & Dlabola 1983
<i>E. elongata</i>	PA	Af	<i>Laternaria lucifera</i>	Jordan 1928, Krampl & Dlabola 1983
<i>Eptricania hagomoro</i>	PA	Af	<i>Ricania japonica</i> , <i>Euricania</i> <i>ocellus</i> , <i>Dictyophara pa-</i> <i>truellis</i> , <i>Oliarus subnubi-</i> <i>lus</i>	Kato 1940
<i>E. melanoleuca</i>	PA	Af	<i>Pyrilla</i> sp.	Fletcher 1939
<i>Fulgoraecia barber-</i> <i>iana</i>	PA	Af	<i>Metacalfa pruinosa</i> , <i>Hys-</i> <i>teropterus aurorum</i> , <i>Theonia bullata</i> , <i>T. ellip-</i> <i>tica</i> , <i>Acalonia conica</i>	Kato 1940, Wilson & Mc- Pherson 1979
<i>F. bowringi</i>	PA	Af	<i>Laternaria candelaria</i> (waxy secretions)	Bowring 1876, Westwood 1876, Kato 1940
<i>F. cerolestes</i>	PA	Af	<i>Metaphaena cruenta</i> , <i>M.</i> <i>militaris</i>	Tams 1947
<i>F. epitryraea</i>	PA	Af	<i>Ityraea nigrocincta patricia</i>	Sheven 1974
<i>F. (Epipyrops) fuligi-</i> <i>nosa</i>	PA	Acl	<i>Idiocerus niveosparus</i> , <i>I.</i> <i>atkinsoni</i> , <i>I. clypealis</i> (waxy secretions)	Subramaniam 1922, Clausen 1940
<i>F. (E.) fulvipunctata</i>	PA	Af	<i>Rhinortha guttata</i>	Bell-Marley 1913
<i>F. (E.) poliographa</i>	PA	Af	<i>Eurybrachys tomentosa</i>	Ayyar 1929

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>Heteropsyche aenea</i>	PA	Af	<i>Platybrachys</i> spp., <i>Scolyopopa australis</i>	Rothschild 1906, Common 1990
<i>H. doddi</i>	PA	Af	<i>Dictyophora praeferrata</i> , <i>Olonia</i> , Flatidae	Rothschild 1906, Clausen 1940
<i>H. dyscrita</i>	PA	Af	Fulgoridae	Perkins 1905
<i>H. melanochroma</i>	PA	Af	<i>Scolyopopa australis</i>	Perkins 1905, Common 1990
<i>H. micromorpha</i>	PA	Af	<i>Platybrachys</i> spp., <i>Scolyopopa australis</i>	Rothschild 1906, Common 1990
<i>H. poecilochroma</i>	PA	Af	Fulgoridae	Perkins 1905
<i>H. stenomorpha</i>	PA	Af	<i>Platybrachys</i> spp., <i>Scolyopopa australis</i>	Rothschild 1906, Common 1990
<i>Paleopsyche melanias</i>	PA	Acl	Cicadellidae	Kato 1940
Cyclotornidae				
<i>Cyclotorna egena</i>	PA	Sp, F	Psyllidae for first instar, then ants	Dodd 1912, Common 1990
<i>C. monocentra</i>	PA	Acl, F	<i>Iridomyrmex purpureus</i>	Dodd 1912, Clausen 1940, Common 1990
<i>Cyclotorna</i> spp.	PA	Sc, F, Acl	<i>Eriococcus coriaceus</i> , <i>Iridomyrmex purpureus</i> , Eurytomelidae, ants	Common 1990
Pyraloidea				
Pyralidae				
<i>Chalcoela pegasalis</i>	PRF	other	larvae of vespid wasp, <i>Polistes annularis</i>	Ballou in Balduf 1939
<i>Creobota cocco-phthora</i>	PRO	Sc	<i>Eriococcus coriaceus</i>	Common 1990, Scoble 1992
<i>Cryptoblabes gnidella</i>	PRF	Sal	<i>Aleurocanthus</i> spp. (also a plant feeder)	Clausen 1940
<i>C. proleucella</i>	PRO	Sc	<i>Coccus viridis</i>	Rutherford in Balduf 1939
<i>Dicymolomia julianalis</i>	PRF	other	eggs of <i>Thyridopteryx ephemeraeformis</i> , heads of <i>Typha</i>	Gahan 1909, Balduf 1938, Clausen 1940
<i>Dipha (Conobathra) aphidovora</i> (= <i>Thiallela</i> sp.)	PRO	Sap	<i>Ceratovacuna japonica</i> , <i>Pseudoregma bambucicola</i> , <i>P. alexanderi</i>	Lopez 1930, Takano 1941, Arakaki & Yoshiyasu 1988
<i>Ephestia cautella</i>	PRO	Sc	<i>Coccus</i> , <i>Tachardia lacca</i> , <i>Eublemma</i> , <i>Holococera</i> spp.	Keuchenius 1915, Balduf 1939, but see Hinton 1981
<i>Euzophera cocci-phaga</i>	PA	Sc	<i>Aspidoproctus xyliae</i>	Jordan 1926, Ayyar 1929, Clausen 1940
<i>Laetilia coccidivora</i>	PRO	Sc	<i>Icerya purchasi</i> , <i>Dactylopius</i> spp., <i>Trionymus</i> , <i>Pseudococcus</i> spp., <i>Eriococcus</i> , <i>Coccus hesperidum</i> , <i>Lecanium nigrofuscium</i> , <i>Toumeyella liriodendri</i> , <i>Pulvinaria innumerabilis</i> , <i>P. psidii</i> , <i>Kermes</i> spp., Lepidoptera	Ayyar 1929, Berger 1917, Chaffin 1921, Comstock 1924, Douglas 1888, Felt 1933, Howard 1895, Parks 1919, van der Merwe 1921, Simanton 1916
<i>L. obscura</i>	PRO	Sc	<i>Saissetia hemisphaerica</i>	Blahutiak & Alayo Soto 1982
<i>Macrotheca unipunctata</i>	PRO	Sc	scales	Forbes 1923, Hinton 1981
<i>Myelois grossipunctella</i>	PRF	Sc	<i>Icerya</i> sp.	Ragonot 1893, Hinton 1981
<i>Niphopyralis aurivillii</i>	PRO	F	ant eggs and larvae (<i>Polyrachis bicolor</i>)	Kemner 1923, Robinson et al. 1994
<i>N. chionestis</i>	PRF	F?	scavenger in ant nests (<i>Oecophylla smaragdina</i>)	Common 1990

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>N. myrmecophila</i>	PRO	F	ant brood (<i>Oecophylla smaragdina</i>)	Roepke 1916, Robinson et al. 1994
<i>Niphopyralis</i> (28 spp.)	PRO	F?	may all be myrmecophages	Robinson et al. 1994
<i>Pachypodistes goeldii</i>	PRF	F?	may eat brood of <i>Dolichoderus gibbosanalis</i> , eats nest carton	Hagmann 1907, Hinton 1951
<i>Phycita dentilinella</i>	PA	Sc, other	scales, other insects, <i>Parasalepida</i> (larvae and pupae), <i>Cricula trifenesetrata</i>	Ayyar 1929, Clausen 1940
<i>Stenachroia myrmecophila</i>	PRO	F?	may consume brood of <i>Crematogaster</i>	Turner 1912, Hinton 1951
<i>Sthenobaea</i> (<i>Stenauge</i>) <i>parasitus</i>	PA	other	<i>Automeris</i> and <i>Dirphia</i> (Saturniidae)	Jordan 1926, Clausen 1940, Scoble 1992
<i>Titanoceros thermoptera</i>	PRO	other	eggs of <i>Ochrogaster lunifer</i> (Thaumetopoeidae)	Common 1990
<i>Tirathaba parasitica</i>	PRF	other	dead insects, hepialid larvae	Common 1990, Scoble 1992
<i>Vitula bodkini</i>	PRO	Sc	<i>Saissetia oleae</i> , <i>S. nigra</i> , <i>S. coffeae</i> (<i>hemisphaerica</i>), <i>Ceroplastes floridensis</i>	Bodkin 1917
<i>V. saissetiae</i>	PRO	Sc	<i>Saissetia</i> sp.	Simanton 1916, Dyar 1929, Clausen 1940, Hinton 1981
<i>V. toboga</i>	PRO	Sc	<i>Saissetia oleae</i> , <i>S. nigra</i> , <i>S. coffeae</i> (<i>hemisphaerica</i>), <i>Ceroplastes floridensis</i>	Bodkin 1917
Geometroidea				
Geometridae				
<i>Biston zonarius</i>	PRF	other	larvae of ichneumonid parasitoids that emerged from conspecifics	Sorhagen 1899
<i>Eupithecia craterias</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. niphorias</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. oblongata</i>	PRO	Sap	aphids	Hawkins 1942
<i>E. orichloris</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. prasinombra</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. rhodopyra</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. scoriodes</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>E. staurophragma</i>	PRO	other	small insects, spiders	Montgomery 1982
<i>Eupithecia</i> (8 spp.)	PRO	other	small insects, spiders	Montgomery 1982
Noctuoidea				
Noctuidae				
<i>Aglossa dimidiata</i>	PRF	other	stored eggs of <i>Bombyx mori</i>	Nishikawa in Balduf 1939
<i>Calymnia tapezema</i>	PRF	other	forms rolled leaf hiding place and emerges to attack other insects	Sorhagen 1919, Gauckler 1911, Balduf 1939
<i>Calyptra eustrigata</i>	PA	other	blood of ungulates (adults have piercing mouthparts)	Common 1990
<i>Catoblemma dubia</i>	PRO	Sc	<i>Coccus hesperidum</i> , <i>Eriococcus coriaceus</i> , <i>Parthenolecanium</i> , <i>Saissetia oleae</i> , <i>Ceroplastes rubens</i>	Blumberg 1935, Flanders 1932, Common 1990
<i>C. mesotaenia</i>	PRO	Sc	<i>Eriococcus coriaceus</i>	Common 1990
<i>C. sumbavensis</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>aurantica</i>	Jacobson 1913, Clausen 1940, Hinton 1981
<i>Coccidophaga</i> (<i>Erastria</i>) <i>scitula</i>	PRO	Sc	black olive scale and others	Rouzaud 1893, Balduf 1931
<i>Eublemma amabilis</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>lacca</i> , <i>K. (L.) javanus</i>	Rouzaud 1893, Misra 1924, Balachowsky 1928, Misra et al. 1930, Mahdihassen 1934, Glover & Negi 1935, Miller 1933

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>E. coccophaga</i>	PRO	Sc	<i>Coccus</i> spp., <i>Saissetia oleae</i> , esp. eggs	Douglas 1988, Balachowsky 1928, Clausen 1940, Froggatt 1922, Vosler 1919
<i>E. communimacula</i>	PRO	Sc	<i>Parthenolacanium</i> (<i>Lecanium</i>) <i>persicae</i> , <i>Sphaerolacanium</i> (<i>L.</i>) <i>prunastri</i>	Hampson 1910, Hinton 1981
<i>E. costimacula</i>	PRO	Sc	<i>Ferrisia virgata</i> , <i>Pseudococcus perniciosus</i> , <i>Coccus viridis</i> , <i>Strictococcus diversiseta</i> , <i>S. dimorphus</i>	Hampson 1910, Fiedler 1950, Hinton 1981, Ritchie 1926, Ritchie 1929, Gowdy 1915, Gowdy 1917
<i>E. deserta</i>	PRO	Sc	<i>Margarodes</i> spp.	Balachowsky 1929
<i>E. dubia</i>	PRO	Sc	scales	Froggatt 1910, Hinton 1981
<i>E. gayneri</i>	PRO	Sc	<i>Phenacoccus hirsutus</i>	Hall in Ayyar 1929, Hinton 1981
<i>E. ochrochroa</i>	PRO	Sc	<i>Stictococcus sjostedti</i>	Lamborn 1914, Hinton 1981
<i>E. pulvinariae</i>	PRO	Sc	scales	Hampson 1910, Hinton 1981
<i>E. roseonivea</i>	PRO	Sc	<i>Kerria</i> (<i>Laccifer</i>) <i>javanus</i>	Miller in Balduf 1939
<i>E. rubra</i>	PRO	Sc	<i>Coccus optimum</i> , <i>C. africanus</i>	Rouzaud 1893, Jacobson 1913, Balachowsky 1928, Clausen 1940
<i>E. rufiplaga</i>	PRO	Sc	scales	Ayyar 1929, Hinton 1981
<i>E. scitula</i>	PRO	Sc, Sal	<i>Parthenolecanium</i> (<i>Aspidiotus</i>) <i>orientalis</i> , <i>Saissetia oleae</i> , <i>Inglisia conchiformis</i> , <i>Megapulvinaria</i> (<i>Pulvinaria</i>) <i>maxima</i> , <i>M. (P.) psidii</i> , <i>Kerria</i> (<i>Laccifer</i>) <i>lacca</i> , <i>Anomalococcus indicus</i> , <i>Saessetia coffeae</i> (<i>hemisphaerica</i>), <i>Bodenmeimera rachelii</i> , <i>Pseudococcus lilacinus</i> , <i>Ceroplastes rusci</i> , <i>C. actiniformis</i> , <i>C. lecanium</i> , <i>C. ceriferus</i> , <i>C. rubens</i> , <i>Ceroplastes</i> (<i>Lakshaida</i>) <i>communis</i> , <i>Coccus</i> (<i>Lecanium</i>) <i>cajani</i> , <i>Aleurodes africanus</i>	Misra 1924, Ayyar 1929, Panis 1974, Hinton 1981, Glover 1933, Wiedez 1932, Gowdy 1917, Farquharson 1921, Bodenheimer 1924, Rousaud 1893, Douglas 1888, Mahdihassan 1925
<i>E. trifasciata</i>	PRO	Sc	<i>Phenacoccus hirsutus</i>	Fletcher 1919
<i>E. versicolora</i>	PRO	Sc	coccids	Jacobson 1913, Clausen 1940
<i>E. virginalis</i>	PRO	Sc	<i>Margarodes</i> spp.	Balachowsky 1928
<i>E. vinctincta</i>	PRO	Sc	scales, <i>Lecanium</i> spp.	Ayyar 1929, Hinton 1981
<i>Cosmia trapezina</i>	PRF	other	other Lepidoptera	Crawley 1983
<i>Cosmia</i> spp.	PRF	other	other Lepidoptera	Forbes 1954, Hinton 1981, Scoble 1992
<i>Energia</i> spp.	PRF	other	other Lepidoptera	Forbes 1954, Schweitzer 1979
<i>Erastria venustula</i>	PRO	Sc	scales	Wolff & Krause 1922, Hinton 1981
<i>Eupsilia transversa</i>	PRF	other	other Lepidoptera	Stokoe & Stovin 1948, South 1948, Schweitzer 1979
<i>Heliothis dispacaeus</i>	PRF	other	<i>Pteris rapae</i> pupae	Huguenin 1914
<i>Lithophane querquera</i>	PRF	other	<i>Tenebrio</i> (in lab)	Schweitzer 1979
<i>L. bethunei</i>	PRF	other	<i>Malacosoma</i> pupae	Sanders & Dustan 1919, Schweitzer 1979
<i>Nola innocua</i>	PRF	Sap	kleptoparasite of gall aphids, <i>Nipponaphis distylicola</i> , <i>Monzenta globuli</i>	Ito & Hattori 1982, 1983

TABLE 1. Continued.

Taxon	Type	Food	Notes	References
<i>N. sorghiella</i>	PRF	other	<i>Chrysops</i> sp. eggs (tabanid fly)	Johnson & Hays 1973, Hinton 1981
<i>Ozopteryx basalis</i>	PRO	Sc	<i>Coccus</i> spp.	Hargreaves 1928
<i>Selepta leucogonia</i>	PRO	Sc	wine palm scale	Farquharson 1921, Hinton 1981
<i>Senta maritima</i>	PRF	other	eats conspecifics and braconid parasitoids emerging from conspecifics	Rangnow 1909

these strategies are plant-dependent because they entail either early-instar phytophagy, or oviposition and subsequent habitation on the host plant of the prey insect. Thus, the life cycles of predatory Lepidoptera are typically more complex in terms of the number of factors contributing to them than those of phytophagous Lepidoptera. Such complexity, as is apparently the case for *Maculinea*, can result in enhanced sensitivity to environmental perturbation because there is simply more that can go wrong. Perhaps such life cycle complexity is, over evolutionary time, correlated with a relatively high extinction rate (discussed below).

A second possible reason for the lack of evolutionary persistence of carnivory in the Lepidoptera may be related to phylogenetic constraints (*sensu* Gould & Lewontin 1979). The lepidopteran larva is a well designed plant-eating machine that apparently has been modified by evolution only to a minor extent in the course of the acquisition of predatory habits. The result is a somewhat limited predator. We see this in the range of prey choice of predatory Lepidoptera. They consume sedentary, poorly defended insects, and this has resulted in their specialization on the sternorrhynchine Homoptera such as aphids and coccids. In keeping with this view of historical constraint, it is not surprising that the only ambush predators that have evolved among the Lepidoptera, the *Eupithecia* of Hawaii, are "inchworm" geometrids, whose particular morphology enables them to rear up on their hind claspers and strike at passing prey. Species of Epipyropidae and Cyclotornidae whose first instar larvae parasitize auchenorrhynchine Homoptera also have unusual, hypermetamorphic larvae—the first instars have a tapered body plan, and can stand up on their claspers and wave their heads about in a leech-like fashion when seeking a new host. These then molt into a more customary, slug-like morphology in later instars.

Myrmecophagy, especially in the lycaenids, also may be largely an heirloom from the phytophagous past, in which lycaenids evolved the ability to interact with ants, usually in a mutualistic way. Once the wherewithal, such as specialized exocrine glands for ant appeasement

TABLE 2. Feeding specializations in the Lycaenidae, not including Miletinae. HO = Homoptera, AR = ant regurgitations, AB = ant brood; X = direct observation, V = inferred. In the Polyommatainae, an additional 32 species of *Lepidochrysops* are thought to feed on ant brood (see e.g., Clark & Dickson 1971).

Taxon	HO	AR	AB	References
Lycaeninae				
Aphaeini				
<i>Aphnaeus adamsti</i>		x		Callaghan 1993
<i>Argyrocupha malagrida</i>			v	Clark & Dickson 1971, Henning & Henning 1989
<i>Axtocerses harpax</i>		x		Jackson 1947, Larsen 1983, Ackery & Rajan 1990
<i>A. (Chloroselas) umbrosa</i>		x		Jackson 1937, Larsen 1991
<i>Cigarittis (Apharittis) acamas</i>		x	x	Larsen & Pittaway 1982
<i>Oxychaeta dicksoni</i>			x	Clark & Dickson 1971
<i>Spindasis nyassae</i>		x		Hinton 1951, Sevastopulo 1975
<i>S. takanonis</i>		x	x	Iwase 1955, Yamaguchi 1988
<i>Trimenia argyropлага</i>			v	Clark & Dickson 1971
<i>T. wallengrenii</i>			v	Clark & Dickson 1971
Theclini				
<i>Acrodipsas cuprea</i>			x	Common & Waterhouse 1981
<i>A. illidgei</i>			x	Samson 1989
<i>A. myrmecophila</i>			x	Common & Waterhouse 1981
<i>Arhopala wildei</i>			x	Dunn, pers. comm.
<i>Shirozua jonasi</i>	x			Shirozu 1961, Fukuda et al. 1984, Yamaguchi 1988
Polyommataini				
<i>Anthene levis</i>		v		Jackson 1937, Hinton 1951
<i>Athsanota ornata</i>			x	Kielland 1990
<i>Chilades lajus</i>	x			Bell 1915, Agarwala & Saha 1984
<i>Lepidochrysops ignota</i>			x	Henning 1983
<i>L. longifalces</i>			x	Cottrell 1984
<i>L. methymna</i>			x	Cottrell 1965
<i>L. niobe</i>			x	Henning & Henning 1989
<i>L. oreas</i>			x	Claassens & Dickson 1980
<i>L. patricia</i>			x	Clark & Dickson 1971
<i>L. pephredo</i>			x	Pennington et al. 1978
<i>L. phasma</i>			x	Farquharson 1922, Chapman 1922
<i>L. robertsoni</i>			x	Claasens & Dickson 1980
<i>L. trimeni</i>			x	Clark & Dickson 1971
<i>L. variabilis</i>			x	Cottrell 1965
<i>L. victoriae</i>			x	Cripps 1947
<i>Maculineaalcon</i>		x	x	Thomas et al. 1989
<i>M. arion</i>			x	Chapman 1916a, 1916b, Thomas et al. 1989
<i>M. arionides</i>			x	Fukuda et al. 1984
<i>M. nausithous</i>			x	Thomas et al. 1989
<i>M. rebeli</i>		x	x	Thomas et al. 1989
<i>M. teleius</i>			x	Thomas et al. 1989, Fukuda et al. 1984
<i>Niphanda fusca</i>		x		Fukuda et al. 1984, Hama et al. 1989
<i>Oboronia punctatus</i>			x	Lamborn 1914
Riodininae				
<i>Setabis lagus</i>	x			DeVries et al. 1992
<i>Audre aurina</i>		x		DeVries pers. comm.

TABLE 3. Feeding specializations in the Miletinae. HD = honeydew, HO = Homoptera, AR = ant regurgitations, AB = ant brood; X = direct observation, V = inferred.

Taxon	HD	HO	AR	AB	References
Miletinae					
Miletini					
Spalgiti					
<i>Feniseca tarquinius</i>		x			Riley 1886, Edwards 1886, Scott 1986
<i>Spalgis epius</i>		x			Aitken 1894, Green 1902, Misra 1920, Cottrell 1984
<i>S. lemolea</i>		x			Lamborn 1914, Cottrell 1984
<i>S. substrigata</i>		x			Smith 1914
<i>Taraka hamada</i>	x	x			Banno 1990
Miletiti					
<i>Allotinus apries</i>		x		v	Maschwitz et al. 1988
<i>A. davidis</i>		x			Maschwitz et al. 1985
<i>A. major</i>		x			Kitching 1987
<i>A. substrigosus</i>		x			Maschwitz et al. 1988
<i>A. subviolaceus</i>		x			Maschwitz et al. 1988
<i>A. unicolor</i>	x	x			Maschwitz et al. 1985
<i>Logania hamptoni</i>	v	v	v		Parsons 1991
<i>L. malayica</i>	x	x	x		Maschwitz et al. 1988, Fiedler 1993
<i>L. marmorata</i>	x	x	v		Fiedler 1993
<i>Megalopalpus zymna</i>		x			Lamborn 1914, Cottrell 1984
<i>M. biggsii</i>		x			Maschwitz et al. 1988
<i>M. boisduvali</i>		x			Roepke 1918, Cottrell 1984
<i>Miletus chinensis</i>		x			Kershaw 1905, Cottrell 1984
<i>M. nymphis</i>		x			Maschwitz et al. 1988
<i>M. symethus</i>		x		v	Roepke 1918, Eliot 1980
Lachnocnemiti					
<i>Lachnocnema bibulus</i>	x	x	x		Cripps & Jackson 1940, van Someren 1974, Cottrell 1984
<i>L. brimo</i>		x			Ackery 1990
<i>L. durbani</i>		x			Ackery & Rajan 1990, Larsen 1991
<i>Thestor basutus</i>				v	Clark & Dickson 1971
<i>T. brachycerus</i>				v	Clark & Dickson 1971
<i>T. dicksoni</i>				v	Clark & Dickson 1971
<i>T. dukei</i>				v	Clark & Dickson 1971
<i>T. holmesi</i>				v	Clark & Dickson 1971
<i>T. protumnus</i>				v	Clark & Dickson 1971, Migdoll 1988
<i>T. rileyi</i>		x		v	Clark & Dickson 1971
<i>T. yildizae</i> (as <i>obscurus</i>)				v	Claassens & Dickson 1980, Henning & Henning 1989
Liphyrini					
<i>Aslauga atrophifurca</i>		x			Cottrell 1984, Villet 1986
<i>A. lamborni</i>		x			Lamborn 1914, van Someren 1974, Cottrell 1984
<i>A. latifurca</i>		x			Jackson 1937, Cottrell 1981, Ackery & Rajan 1990
<i>A. orientalis</i>		x			Cottrell 1981
<i>A. purpurascens</i>		x			Boulard 1968, Cottrell 1981
<i>A. vininga</i>		x			Lamborn 1914, Cottrell 1984, Ackery & Rajan 1990
<i>Euliphyra leucyania</i>			x		Kielland 1990, Dejean 1991
<i>E. mirifica</i>			x		Hinton 1951, Dejean 1991
<i>Liphyra brassolis</i>				x	Dodd 1902, Johnson & Valentine 1986, Cottrell 1987
<i>L. grandis</i>				x	Parsons 1991

and communication, had evolved, however, evolutionary opportunities for exploiting ants as prey became available. Myrmecophagy (and exploitation through trophallaxis) is likely therefore to be a derived trait in the otherwise myrmecophilic lycaenids, although this claim requires rigorous phylogenetic corroboration.

It also is possible that phylogenetic constraints operate in this system at levels other than the actual acquisition of predatory habits. It is notable that a large proportion of the miletine lycaenids prey on aphids of the closely related families Hormaphididae and Pemphigidae, whereas the Aphididae, for example, are seldom consumed by this group. Is this failure to exploit the entire range of potential aphid prey the product of a phylogenetic constraint in which the biology of the entire predatory miletine lineage became locked into the exploitation of the Hormaphidine/Pemphigidine group? Such a hypothesis would be refuted if it were found that Hormaphidine/Pemphigine feeding had arisen independently in separate miletine groups, suggesting that they are particularly amenable to such exploitation while other groups of aphids are not. For example, it may be somehow easier for carnivorous miletines to feed on woolly aphids than on other kinds of aphids, in which case the constraint would be functional, rather than phylogenetic. Alternatively, the Hormaphididae and Pemphigidae may happen to feed on the same host plants as those favored by phytophagous miletine-ancestors.

A discussion of "phylogenetic constraint" addresses a familiar topic in evolutionary biology: the assumption that specialized life history strategies represent more highly derived conditions than generalist interactions (Futuyma & Moreno 1988, Thompson 1994). Having once accumulated adaptations necessary to exploit a particular resource or survive in a special habitat, reversion to more general resource or habitat use is increasingly difficult. For example, specializations may include modifications such as the loss of eyes, or chewing mouthparts, making reversals unlikely.

However, generalizations about the evolutionary trajectory of specialization remain problematic. A phylogeny of the Papilionidae shows a generalist strategy, polyphagy in *Papilio glaucus* L., evolving from specialist ancestors (Miller 1987). The phylogeny of yucca moths and their related genera shows transitions in both directions (Thompson 1994). Futuyma & Moreno (1988:222) conclude: "Far more phylogenetic analysis is required than has been done, to document patterns of evolution of generalized and specialized habits" In the same vein, Thompson (1994:64) advocates: "The ideal analysis for understanding whether extreme specialization is generally a phylogenetically derived condition would be to take a group of fairly large monophyletic lineages

and determine the proportion of times that specialization is the evolutionarily derived condition within each lineage." Further research on the evolution of predatory Lepidoptera, and particularly the phylogeny of groups such as the Lycaenidae, provide an ideal opportunity to do just that.

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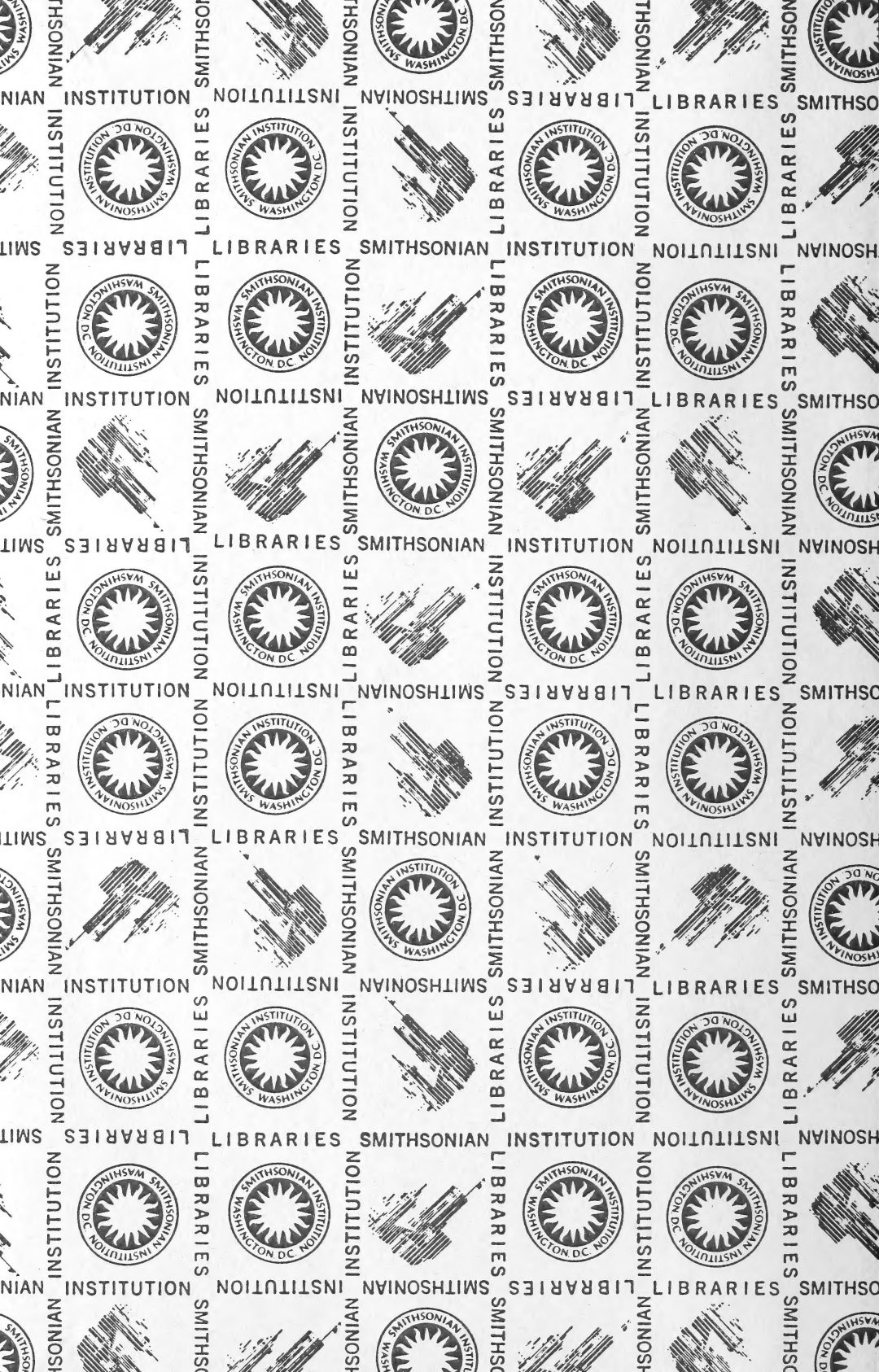
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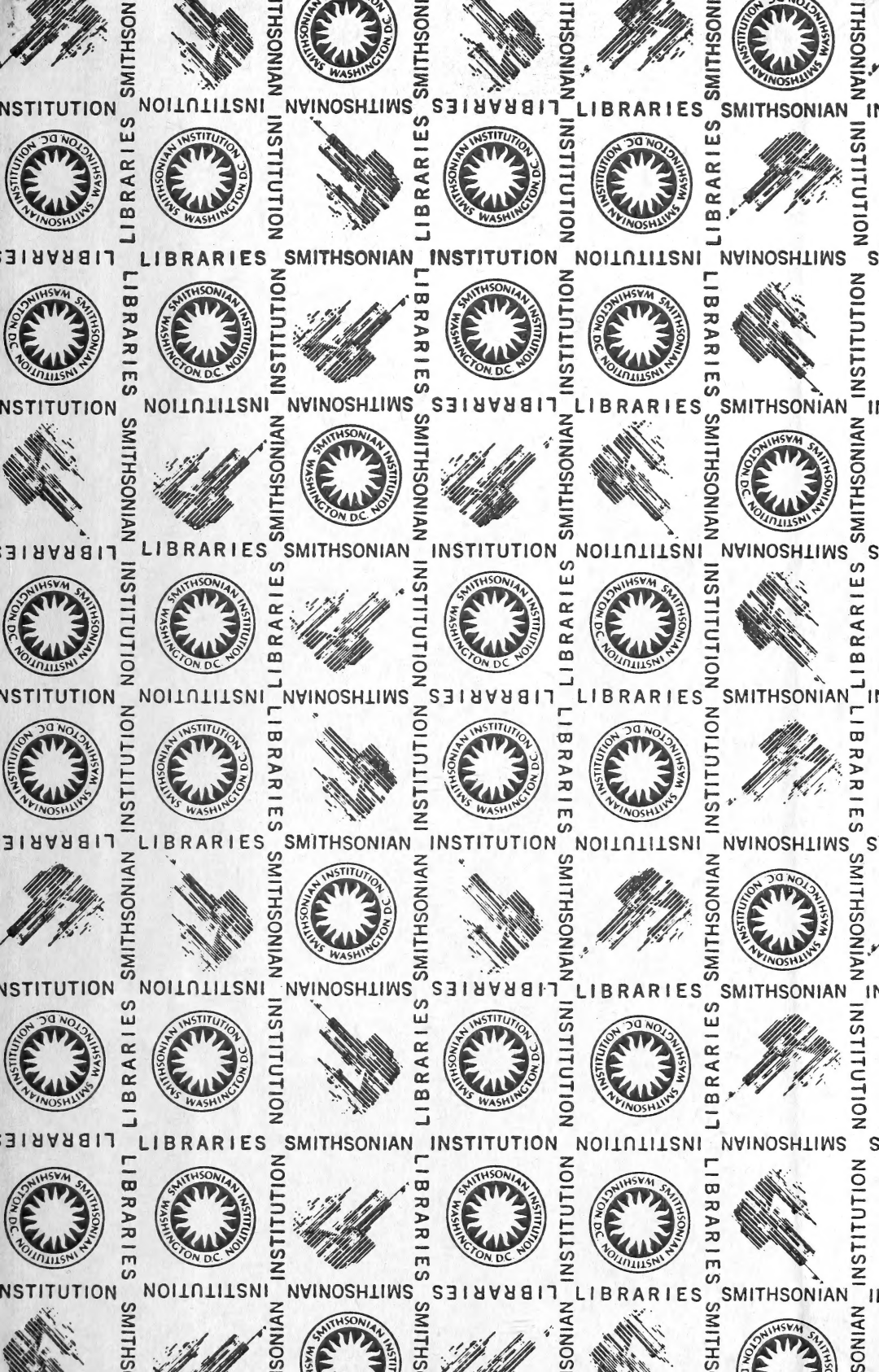
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