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Cover illustration: Cover photo of *Callophrys irus* adult and larva by Michael W. Nelson with permission from the Massachusetts Natural Heritage & Endangered Species Program. Adult photographed in wild on 29 May 2003 in Myles Standish State Forest, Plymouth, MA. Larva photographed in lab on 17 July 2005; collected on 16 June 2005 in Myles Standish State Forest, Plymouth, MA.

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LARVAL FEEDING BEHAVIOR AND ANT ASSOCIATION IN FROSTED ELFIN, *Callophrys irus* (LYCAENIDAE)

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ABSTRACT. *Callophrys irus* is a rare and declining lycaenid found in the eastern U.S., inhabiting xeric and open habitats maintained by disturbance. Populations are localized and monophagous. We document a previously undescribed larval feeding behavior in both field and lab reared larvae in which late instar larvae girdled the main stem of the host plant. Girdled stems provide a unique feeding sign that was useful in detecting the presence of larvae in the field. We also observed frequent association of field larvae with several species of ants and provide a list of ant species. We suggest two hypotheses on the potential benefits of stem-girdling to *C. irus* larvae: 1) Stem girdling provides phloem sap as a larval food source and increases the leaf nutrient concentration, increasing larval growth rates and providing high quality honeydew for attending ants; 2) Stem girdling reduces stem toxicity by inhibiting transport of toxins from roots to the stem.

Additional key words: *Baptisia tinctoria*, girdle, feeding sign, Massachusetts, phytochemical defense

The frosted elfin, *Callophrys irus* (Godart, 1824) (Lycaenidae), is an oligophagous butterfly that is reliant on disturbance-dependent habitats (Scott 1986, Schweitzer 1992, Opler 1998). During the past century, the eastern North American range of *C. irus* extended from Ontario to Florida, and west to Texas and Wisconsin (Opler *et al.* 1995, Layberry 1998). The species is univoltine and non-migratory, and although it has a broad geographic distribution, it typically occurs in small, localized populations. *C. irus* appears to be in decline, as indicated by its extirpation in Canada and two US states, and its listing as endangered, threatened or of special concern in 11 of the 27 U.S. states in which it is still found (Packer 1998, NatureServe 2006). Many *C. irus* populations have disappeared or declined in the past 50 years, and remaining populations are limited to xeric sand barrens and savanna habitat with an open vegetation structure, often maintained by anthropogenic activities in the absence of other disturbance (Wagner *et al.* 2003).

A taxonomic account of the immature stages of *C. irus* is beyond the scope of this paper, however, it should be noted that much of the early literature failed to recognize this species as distinct from *Callophrys henrici* (Grote & Robinson, 1867) (Lycaenidae). Many of the early accounts of the immature stages and larval host plants of *C. irus* actually refer to *C. henrici*. For example, Cook (1906) attributes original description of the larva and pupa of *C. irus* to Boisduval & Le Conte (1829-[1837]), however these descriptions (from John Abbot's notes) and figures (by Abbot) are actually of *C. henrici* (Calhoun 2004). Descriptions of the second, third, and fourth-instar larva, pupa, larval hosts, and feeding habits of *C. irus* in Scudder (1888-1889) are from W. H. Edwards' notes on *C. henrici* (Cook 1906), and the larva and pupa figured in Scudder (1888-1889) are reproduced from Abbot's drawings of *C. henrici* in Boisduval & Le Conte (1829-[1837]) (Calhoun 2004). Recently, color photographs of the larva and pupa of *C. irus* have been published by Allen (1997), Allen *et al.*

(2005), and Minno (2005).

The larval host plants of *C. irus* are all legumes (Fabaceae), with most populations feeding on either wild indigo *Baptisia tinctoria* (L.) or wild lupine *Lupinus perennis* (L.), but not both (Schweitzer 1992, Wagner *et al.* 2003). *Baptisia australis* (L.) and *Crotalaria sagittalis* (L.) have also been reported as occasional hosts (Scott 1986). Geographic patterns of host use and concordant morphological differences among populations have led to the suggestion that populations of *C. irus* feeding on *L. perennis* may not be conspecific with those feeding on *B. tinctoria* (Schweitzer 1992). Cook (1906) provided the first detailed life history observations of *C. irus*, from a population feeding on *L. perennis* in the Pine Bush east of Albany, New York. However, little has been published on the life history of *C. irus* populations feeding on *B. tinctoria*.

A unique and reliable feeding sign can be useful in detecting the presence of a larva on a host plant and may be used as a surrogate for direct observations of larvae during research on rare Lepidoptera (Swengel 1995, Smith *et al.* 2002, Albanese *et al.* in preparation). A feeding sign is especially useful when it is persistent and consistent in form and location. In this paper we provide observations on larval feeding behavior of *C. irus* on *B. tinctoria*, including documentation of an unusual feeding sign that is present throughout most of the year and can be used to determine the presence of the species.

Associations between lycaenids and ants (Formicidae) are not unusual, with approximately 75% of the species known to associate with ants. These associations range from loose facultative to obligate (Pierce *et al.* 2002). The costs and benefits of interacting with ants vary among lycaenid species (Fiedler & Saam 1992, Wagner 1993, Cushman *et al.* 1994). With regard to the benefits of ant attendance, two hypotheses have been proposed: appeasement and protection (Pierce *et al.* 2002). Larvae may appease potentially aggressive ant species with food rewards. Ants may also protect larvae from predators and parasitoids because larval secretions are a valuable food resource (Atsatt 1981, Pierce & Mead 1981, Pierce *et al.* 1987, Peterson 1993). Providing food rewards to ants can negatively affect both larval development and adult reproductive success (Robbins 1991, Fiedler & Hölldobler 1992, Wagner 1993, Wagner & Kurina 1997), and the selection of legumes or other protein-rich host plants by ant-attended lycaenids may serve to offset this increased nutritional cost (Pierce *et al.* 1985, Fiedler 1996). Such complex interactions between host plants, larvae, and ants are of immense importance and

interest in the study of lycaenid ecology and evolution, and the documentation of ant association is an important step in furthering the conservation of rare lycaenid species (Pierce *et al.* 2002). In this paper we report the association of *C. irus* larvae with several ant species.

METHODS AND RESULTS

We conducted field and laboratory studies from 2002 through 2005 as part of a larger research project designed to assess the multi-scale habitat requirements of *C. irus*. The fieldwork was conducted at four sites in southeastern Massachusetts, U.S.: 1) Crane Wildlife Management Area (WMA), Barnstable County; 2) Gavins Pond Municipal Water Authority (MWA) property, Norfolk County; 3) Myles Standish State Forest (SF), Plymouth County; and 4) Noquochoke WMA, Bristol County. All of these areas are on the coastal plain and are characterized by xeric, sandy soil and relatively flat topography.

In results reported below, we use the terms early-, mid- and late-instar to describe larvae when the exact instar was not determined. Relative to the four larval instars of *C. irus*, early-instar = first or second instar, mid-instar = second or third instar, and late-instar = third or fourth instar. Results of statistical analyses are presented as the mean \pm SE.

Larval behavior: Field observations. Late-instar *C. irus* larvae produced "feeding rings" on host plants at all study sites. Larvae produce rings by consuming the epidermis near the base of the main stem of the *B. tinctoria* plant (Fig. 1). Feeding continued around the circumference of the stem until the outer tissue (epidermis and cortex) was completely consumed, exposing the inner vascular tissue in a complete ring, effectively "girdling" the main stem of the host plant (Fig. 2). Although a single stem typically had only one complete feeding ring, in some cases two or more rings were present. Only late-instar larvae were observed feeding in this manner. Host plants developed scar tissue in the area of the feeding ring, causing it to persist throughout the growing season. For 15 of the 198 late-instar larvae found between 2003 and 2005, we did not inspect the host plant stems for feeding rings. Of the 183 remaining host plants, feeding rings were present in 172 cases (94%). It is possible that the 11 larvae found on plants without feeding rings were encountered prior to commencement of stem-feeding, and that we have underestimated the number of larvae that produced feeding rings prior to pupation.

At Gavins Pond, from 13 to 18 June 2005, 20 larvae not used in other parts of the study were found in the second instar, and their host plants were flagged to allow



FIG. 1. Late-instar *Callophrys irus* larva beginning to feed on the epidermis of a *Baptisia tinctoria* stem.

periodic field observation of feeding behavior. The lengths of all 20 larvae were < 4 mm (3.4 ± 0.2) at the commencement of observations. During each observation, we relocated each larva and examined the host plant for evidence of feeding. Early-instar larvae skeletonized young leaves on the apical shoots of the host plants. Middle- and late-instar larvae fed on entire leaves, frequently initiating feeding on the younger foliage near the tips of branches and sequentially consuming leaves while descending a branch. Larvae often defoliated an entire branch top before ascending a new apical shoot. We monitored 13 of the 20 larvae until the final instar; by this time all 13 had produced a feeding ring. The body length of final-instar larvae was 14.9 ± 0.7 mm ($n = 13$), and the development time from commencement of observations to the final instar was 25.2 ± 0.6 days (range = 21–30 days).

Larval behavior: Captive rearing observations.

At Myles Standish SF, on 25 May 2002, we observed an adult female *C. irus* oviposit on the new apical growth of a *B. tinctoria* plant. The plant was dug up and potted for rearing in a screen cage, and kept outdoors in a shaded location. The egg hatched on 30 May (5 days after oviposition), the larva exiting through a small hole, leaving the remainder of the egg shell intact. The first-instar larva fed preferentially on new apical growth, skeletonizing the surface of the leaves. In the second instar the larva began to feed at the edges of leaves. During the third instar the larva and potted host plant were brought indoors for more frequent observation. In the third and fourth instars the larva consumed entire leaves, and feeding was concentrated on a particular branch of the plant, leaving it defoliated (as noted in observations of late-instar larvae in the field). The fourth-instar larva produced a feeding ring near the base of the main stem of the host plant. In this stage the



Fig. 2. In the foreground, a late-instar *Callophrys irus* larva rests on a *Baptisia tinctoria* stem. This larva previously consumed the epidermis and cortex layers of the stem to produce a characteristic "feeding ring." In the background, another late-instar larva feeds on different stem.

larva spent most of its time at the base of the main stem, either resting or feeding on the stem, although it would periodically ascend to the top of the plant to consume leaves, later returning to its position at the base of the main stem. On 1 July the larva escaped through the open top of the cage and was not located for several days. When found it was beneath a wicker basket about 1 m from the potted plant, and had spun a small amount of silk around itself in preparation for pupation. The larva was transferred to a plastic vial where it pupated on 6 July (total larval period = 36 days).

On 4, 10, and 19 July 2003, we collected three larvae from *B. tinctoria* at Myles Standish SF. These larvae were reared on separate potted *B. tinctoria* plants, each enclosed in a large acrylic tube covered at the top with fine-mesh netting and kept outdoors in a shaded location. In the fourth instar, all three larvae produced feeding rings near the base of the main stem of the potted host plants, with one larva producing two separate rings. Like the larva reared in 2002, all three fourth-instar larvae would rest and feed at the base of the main stem, periodically ascending to the top of the plant to consume leaves. After 13, 8, and 4 days in captivity, respectively, each of the larvae ceased feeding and moved about the inside of their enclosure for 1–2 days before burrowing into the dry *Sphagnum* moss provided as a substitute for leaf litter. Several weeks later, it was observed that all three larvae had pupated at the surface of the soil, beneath 5–7 cm of dry *Sphagnum*. Each was resting on a thin pad of silk, dorsal side down, with surrounding pieces of moss held together with a few strands of silk, forming a loose chamber around the pupa.

In 2005 we collected five adult female *C. irus* from

the Gavins Pond site, brought them to the laboratory, and placed them in an enclosure with branches of *B. tinctoria* and 15 hours of natural and supplemental light per day. Within 48 hours, we observed > 25 ovipositions on *B. tinctoria*, and left the eggs undisturbed. We detected the first larvae within leaves of the apical shoots eight days following oviposition. After 2–5 additional days of development, we removed the larvae from the oviposition enclosure, and transferred each to a separate 480-ml, covered plastic cup. Larvae were provided with fresh *B. tinctoria* leaves and a 4–6 cm section of stem daily. Eighteen of the larvae were successfully reared to pupation. First and second larval instars skeletonized young developing leaves. Second through fourth instars consumed entire leaves. None of the larvae consumed the epidermis of a *B. tinctoria* stem until the fourth instar, at which time 17 of the 18 larvae produced a feeding ring. Stem-feeding damage of laboratory-reared larvae was typically less extensive than that observed in the field. Body length of the fourth-instar, lab-reared larvae was 12.8 ± 1.0 mm. Larval development time from initial detection of a first instar to pupation was 33 ± 0.3 days (range = 30–36 days). The larvae attached themselves with several strands of silk at the bottom of the cup, on the side of the cup, or to a piece of *B. tinctoria* before pupation.

Ant associations. Of the 198 late-instar *C. irus* larvae found at the four field sites between 2003 and 2005, 55 (28%) were observed interacting with ants (Table 1). We collected 13 ants from the dorsal surface of 13 different *C. irus* larvae at two of the sites between 1 and 15 July 2005. Specimens were preserved in 70% ethyl alcohol, identified to species and deposited at the University of Connecticut Insect Collection. The 13 specimens consisted of five ant species, of which only one, *Tapinoma sessile* (Say, 1836), was collected at both sites (Table 1). Due to small sample size, we likely underestimated the number of ant species associating with *C. irus* larvae across sites.

We observed ants interacting with *C. irus* larvae in the field for several minutes and interpreted and

categorized the interactions according to the descriptions in Pierce *et al.* (2002). We classified all but one ant association as loose facultative and mutualistic, though it is unknown whether the ants defended the larvae from predators or parasitoids. The single non-mutualistic association observed was predatory, and consisted of 10–20 ants (species undetermined) overwhelming and killing a single *C. irus* larva.

We typically observed ants on the dorsal surface of late-instar larvae with their heads proximal to the larva's posterior end in the area of the seventh abdominal segment and dorsal nectary organ (Fig. 3). We never observed ants associating with early-instar larvae. Ant-tended larvae were often located on the main stem of a host plant, feeding on the epidermal and cortex tissues, or resting. Ants frequently circled the dorsal surface of a larva, intermittently stopping to tap the larva with their antennae or mouthparts. Ants often approached the larva's head and then returned to the area of the seventh abdominal segment, presumably to receive a secretion from the dorsal nectary organ. One to several ants often tended a single larva for several minutes. In one case we observed a single ant (*Formica dolosa* Buren, 1944) tending a larva for over two hours, but such long-term observations were seldom performed for logistical reasons.

DISCUSSION

The outer tissue of the stem of *B. tinctoria* is presumably more difficult to consume and digest, and lower in nutrients than newly-flushed apical leaves. Therefore it seems likely that the nearly universal behavior of stem-feeding among late-instar *C. irus* larvae serves a purpose other than directly deriving nutrition from stem tissue. We hypothesize two possible benefits to larvae following stem girdling of *B. tinctoria*: 1) increased access to water and carbohydrates; and 2) improved feeding conditions due to deactivation of an induced phytochemical defense.

Access to water and carbohydrates. The "honeydew" secreted by the dorsal nectary organ of lycaenid larvae provides ants with water containing a

Table 1. Listed ant species were observed associating with late-instar *Callophrys irus* larvae on *Baptisia tinctoria* at two study sites in 2005. Ant specimens were collected from the dorsal surface of *C. irus* larvae and preserved for later identification. Total number of late-instar larvae found from 2003 to 2005, and the number of larvae associated with ants at each of four study sites, is given in the last row of the table.

Species of ant (Formicidae)	Crane WMA	Gavins Pond MWA	Myles Standish SF	Noquochoke WMA
<i>Crematogaster lineolata</i> (Say, 1836)		X		
<i>Formica dolosa</i> (Buren, 1944)				X
<i>Lasius neoniger</i> (Emery, 1893)		X		
<i>Tapinoma sessile</i> (Say, 1836)		X		X
<i>Tetramorium caespitum</i> (L., 1758)				X
Total larvae (total ant-associated larvae)	47 (7)	109 (26)	11 (1)	31 (21)



Fig. 3. *Formica dolosa* in a typical position on the dorsal surface of a late-instar *Callophrys irus* larva. The ant's head is positioned proximal to the larva's dorsal nectary organ. The larva is at the base of a *Baptisia tinctoria* stem.

relatively high concentration of carbohydrates and amino acids (Pierce *et al.* 2002). Growing caterpillars also need carbohydrates, amino acids, and other nutrients, and water obtained from food is often at a premium (Slansky 1993). This is especially true for larvae of *C. irus*, because their habitat is typically very dry and warm during the latter half of larval development. It therefore seems likely that *C. irus* larvae girdle the stem of their host plant in order to tap phloem sap, thereby obtaining additional water and nutrients. Although phloem sap could be obtained by simply chewing a hole in the stem, complete girdling of a vascular plant stops phloematic flow back to the roots, resulting in accumulation of carbohydrates (soluble sugar and starch) in the portion of the plant above the girdle (Noel 1970).

Therefore, stem-girdling of *B. tinctoria* by *C. irus* probably provides both phloem sap and leaf tissue with greater concentrations of carbohydrates. The larva obtains these carbohydrates (and water) by consuming phloem sap at the girdle, and by periodically ascending the plant to consume leaves. Water, amino acid, and protein content of the leaves remains the same because water and nitrogen transport from the roots through the xylem is unaffected by girdling (Noel 1970). Although herbivore growth is usually limited by dietary nitrogen (Mattson 1980), *B. tinctoria* is a nitrogen-fixing legume and its leaves presumably have a relatively high nitrogen concentration (especially the young, growing leaves preferred by *C. irus*). Therefore larvae may be more limited by access to carbohydrates. Larval consumption of excess water and carbohydrates may allow production of honeydew without adversely affecting their own growth and metabolism by compensating for the loss of these resources. The greater availability of water and

carbohydrates may also enable larvae to produce honeydew in greater quantity or of higher quality (greater carbohydrate concentration), thereby attracting a larger "standing guard" of ants to protect them from predators and parasitoids (Pierce *et al.* 2002).

Deactivating phytochemical defense. Plants have a diversity of chemical defenses (Arnason *et al.* 2004), and the mechanism of these defenses may be either direct, such as toxicity to an herbivore, or indirect, such as release of volatile chemicals that attract parasitoids (Turlings & Wäckers 2004). Furthermore, phytochemical defenses may be either constitutive (always expressed in the plant), or induced (expressed following an herbivore attack). While many induced defenses are synthesized locally in the tissue damaged by an herbivore, some involve a long-distance signal-transduction pathway that triggers transport of a defensive compound from another part of the plant (Karban & Baldwin 1997). One such example is the induction of nicotine defense in tobacco (*Nicotiana* spp.). When the leaves of a tobacco plant are damaged, a chemical signal is sent from the leaves, via the phloem, to the roots of the plant where nicotine is synthesized. This signal results in a dramatic increase in the amount of nicotine exported from the roots, through the xylem, back to the leaves. Karban & Baldwin (1997) note that an herbivore could "short-circuit" such a defense by girdling the plant, thereby blocking the phloem-borne signal from leaves to roots. We suggest that *C. irus* larvae may girdle *B. tinctoria* stems to deactivate a phytochemical defense induced by leaf consumption. Since only late-instar larvae girdle the host plant, induction of such a defense may require more extensive tissue damage than produced by early-instar larvae. It is also possible that the fresh leaf tissue fed upon by early-instar larvae is low in defensive compounds, and if a plant is not girdled by the time larvae are in final instars, the plant will have synthesized and accumulated a sufficient concentration of defensive compounds to be detrimental to larvae.

These two hypotheses are not mutually exclusive. For example, it is possible that stem-girdling by *C. irus* larvae reduces attack rate by parasitoids via three separate yet simultaneous mechanisms: 1) reduction in larval development time due to increased consumption of nutrients; 2) increased protection from ants due to a greater quantity and quality of honeydew produced; and 3) deactivation of an induced indirect defense of the host plant.

We recommend that further research be conducted on the adaptive significance of host plant stem-girdling by *C. irus* larvae. Nutritional analysis of *B. tinctoria* tissues pre- and post-girdling, and investigation of how

this behavior affects the production, transport, and storage of both nutrients and defensive chemicals in *B. tinctoria* plants would be informative. Further experiments would be needed to link host plant physiology with larval development and survivorship. To further understand the role and importance of ant association in *C. irus*, we recommend more widespread documentation of associated ant species and more detailed observations of larval interactions with ants.

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DAILY HABITAT SHIFTS BY THE NEOTROPICAL BUTTERFLY *MANATARIA MACULATA*
(NYMPHALIDAE: SATYRINAE) IS DRIVEN BY PREDATION

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ABSTRACT: The nymphalid butterfly *Manataria maculata* in the Monteverde cloud forest in Costa Rica moves daily between communal day roosts on the ground and individual night roosts in the trees. We studied these movements through an experimental setup where we exposed dead butterflies on the ground and in trees to natural predation for 24 h periods. *M. maculata* glued to the ground were never taken by predators during the day but often by rodents (*Peromyscus* sp.) at night. Butterflies glued to branches and leaves of trees were taken day and night, but most often by birds during the day. We conclude that the daily habitat shifts of *M. maculata* may be driven by differential predation pressure, so that the ground is unsafe by night (rodents) and the trees by day (birds).

Key words: Costa Rica, Monteverde, migration, tropical rain forest

Manataria maculata (Hopffer), a large brown forest nymph (forewing length 40–45 mm; Nymphalidae: Satyrinae) of the neotropics, is known for its peculiar behavior, including a predominantly crepuscular activity period and strange movement patterns (DeVries 1987, Stevenson & Haber 1996, 2000). It is also unusual because it is the only known true butterfly (Superfamily Papilionoidea) with functional ultrasonic hearing, strongly suggesting that flying individuals are subject to predation pressure from echolocating bats at night (Rydell *et al.* 2003).

In Costa Rica *M. maculata* reproduces in deciduous forests on the Pacific lowland during the April–May wet season, when the larvae feed on bamboo. In July–August the recently emerged and virgin butterflies migrate eastwards upslope to the cloud forest at Monteverde and other evergreen forests east of the continental divide, a distance of 100 km or more. The butterflies stay in this area and remain in reproductive diapause for 9–10 months until the following wet season, when they return west to the lowlands to mate and breed. Hence the adults live for almost a year before they reproduce. Adult butterflies feed on rotting fruit and tree sap during the day, just like most other satyrines, but during the reproductive diapause in the highlands feeding occurs only sporadically and is seldom observed (Murillo and Nishida 2003, Stevenson and Haber 1996, 2000).

In Monteverde *M. maculata* are inactive most of the time. The main exceptions are at dusk and dawn when the butterflies move between communal day roosts on

the ground and individual night roosts in the tree canopies (Stevenson and Haber 1996, 2000). Day roosts are typically located in protected and shady places on or near the ground such as behind roots and in crevices and hollows in trees, places to which the coloration of the butterflies is well matched. At dusk the butterflies usually leave the day roosts as cohesive groups, which may contain from a few to *ca.* 30 individuals, occasionally 50. The butterflies then disperse among the canopies of surrounding trees and form individual night roosts on leaves and branches. They return to the communal day roost on or near the ground at dawn, usually one by one (Rydell *et al.* 2003).

In general daily movements between day- and night roosts are unusual among butterflies, but at least in Monteverde the movements are regular and apparently consistent among all individuals of *M. maculata* (Stevenson and Haber 2000). It seems hard to explain these habitat shifts by anything related to mating or feeding, because the butterflies are reproductively inactive and feed only occasionally during this period. Instead, we hypothesized that the movement is a response to differential predation pressure at different times of the day, so that the day roosts become unsafe during the night and vice versa. This implies, of course, that diurnal and nocturnal predators on roosting butterflies hunt in different places and that there is no place that is safe both day and night.

We tested the differential predation hypothesis in a field experiment. We displayed dead *M. maculata* in groups on the ground, thus simulating a communal day

roost, for 24 hours, and recorded predation frequencies during the day and night. We followed the same procedure for night roosts, where dead butterflies were glued individually to branches and leaves of trees. According to our hypothesis, we predicted that butterflies in day roosts (on the ground) should be predated predominantly at night and butterflies at night roosts (among the foliage) should be predated predominantly during the day. Possible predators could be, for example, small mammals and insectivorous birds, respectively, but also spiders, ants and other invertebrates.

MATERIALS AND METHODS

The study was made at Estación Biológica de Monteverde in Costa Rica, 15–20 November 2001 and 19–25 September 2005. The study area mostly consists of mature cloud forest and is located at 1550–1600 m above sea level.

The experiments were made at three sites within 1 km of Estación Biológica; site A, used in 2001, and sites B and C, used in 2005. On each site 5–8 dead butterflies were glued to the ground in a cohesive group, forming a day roost in a shady spot beneath a tree root or in a small rock crevice. Another 5–9 butterflies were spaced out >0.5 m above the ground among branches and leaves of surrounding trees, forming a night roost. All roosts were in places where *M. maculata* had been seen roosting naturally. The roosts were examined for removed or destroyed butterflies before dusk (about

1700 h) and after dawn (about 0700 h). Occasional observations were made in between. Removed or destroyed butterflies were replaced at dusk and dawn whenever fresh specimens were available. The same procedure was repeated for 3–5 consecutive days at each site. Butterflies for the experiments were collected as needed from day roosts in the vicinity of the station. Before the experiments they were killed by quickly squeezing the thorax.

In both years we set a live mousetrap overnight (one or two days per roost) within part of the day roosts in order to catch and identify the presumed predator. The trap was baited with dead *M. maculata*. Caught rodents were released at the site of capture after identification.

RESULTS

During both study periods the trade winds blew strongly from the east and brought frequent and sometimes heavy rain and mist. In 2005 rains were particularly heavy and persistent and often accompanied by strong winds. In fact it rained most of the time during the 2005 experiment and for the last two days it rained continuously. It was our impression that the activity of birds and insects was much lower during the 2005 experimental period compared to 2001, when the weather was more normal and much drier.

Our data from day roosts on the ground were clear and supported our hypothesis. We observed no predation by day but substantial predation at night. The butterflies (5–8 individuals) disappeared over night in

Table 1. Predation at communal day roosts where groups (5–8 individuals) of dead butterflies were glued to the ground in crevices and behind tree roots and left for one day (24 h). Predation was scored if the butterflies were obviously affected or had disappeared at the end of the observation period.

Site	Day no.	Daytime		Nighttime		Sign. (χ^2)
		% predated	N	% predated	N	
Site A 2001	1	0	8	100	8	p<0.001
	2	0	7	100	7	p<0.001
	3	0	5	100	6	p<0.01
Site B 2005	1	0	5	0	5	ns
	2	0	5	0	5	ns
	3	0	5	100	7	p<0.001
	4	0	5	100	5	p<0.01
	5	0	5	100	6	p<0.01
Site C 2005	1	0	5	0	5	ns
	2	0	6	0	5	ns
	3	0	5	100	7	p<0.001
	4	0	7	100	7	p<0.001
	5	–	–	100	7	–
Predation (% of days)		0	N=12	69.2	N=13	

Table 2. Predation at individual night roosts, where dead butterflies were glued to branches and leaves of trees and left for one day (24 h). Predation was scored if butterflies were obviously affected or had disappeared at the end of the observation period.

	Day no.	Daytime		Nighttime		Sign. (χ^2)
		% predated	N	% predated	N	
Site A 2001	1	88	8	0	5	p<0.01
	2	60	5	20	5	ns
	3	40	5	0	7	ns
	4	80	5	–	–	
Site B 2005	1	0	6	0	5	ns
	2	33	6	0	6	ns
	3	0	7	0	7	ns
	4	33	6	43	7	ns
	5	60	5	60	5	ns
Site C 2005	1	33	6	0	6	ns
	2	0	9	0	8	ns
	3	25	8	38	8	ns
	4	57	7	71	7	ns
	5	–	–	12	8	–
Predation (% of days)		83.3	N=12	50.0	N=12	

eight out of twelve cases, so predation either affected all or none of the individual butterflies in a roost. The result was consistent across the two years and three sites (Table 1). We typically found *M. maculata* wings piled up in a spot near the roost, suggesting that the same predator had eaten them all (Table 3). We caught one *Peromyscus* sp. (*P. mexicanus* or *P. nudipes* – the two are hard to distinguish) in the trap set at the roost both at site A (2001) and site B (2005).

Predation at night roosts in the trees was qualitatively and quantitatively different from that at the day roosts, partly because the butterflies were spread out. The results were less clear with respect to our hypothesis. At night roosts predation only affected some individuals at a time, occurring both by day and by night, but it was slightly more frequent and affected more individuals on average during the day (Table 2). This difference was consistent and significant at site A (2001) but not at sites B and C (2005). The only predators actually observed eating butterflies in a night roost were a wasp and a wolf spider. However, most attacked butterflies showed beak marks on the remaining wings, suggesting that insectivorous birds were in fact the most frequent predators (Table 3).

DISCUSSION

Communal roosts on the ground appeared relatively safe during the day, as expected, but very unsafe during the night, when they were heavily exploited by

Peromyscus. Hence, nocturnal predation by rodents seems to explain why *M. maculata* leaves the ground at dusk.

The 2001 results from the night roosts suggest that diurnal predation by birds could explain why *M. maculata* leave the trees at dawn and return to the ground. The 2005 results are difficult to evaluate, because the predation pressure did not differ significantly between the day and the night. We suspect that the unusually wet weather in 2005 resulted in depressed foraging activity of insectivorous birds in daytime, so that the diurnal predation pressure on the experimental butterflies became lower than normal. Furthermore, we cannot exclude the possibility that some of the specimens that disappeared from the night roosts in 2005 actually were washed away by the rain. Regardless of the details, the ground was clearly safer than the trees in daytime, and the trees appeared safer than the ground at night. Hence, our results are not inconsistent with the hypothesis that the switching between day- and night roosts of *M. maculata* facilitates the avoidance of nocturnal and diurnal predators, respectively.

The diurnal defense of *M. maculata* is not only a matter of location of the communal roosts on the ground and the cryptic coloration of the butterflies, but also of the behavior and cohesiveness of the roosting group. In daylight roosting butterflies are very alert to visual and tactile stimuli. They are easily flushed when

Table 3. Details of the observations presented in Tables 1 and 2. Nocturnal predation at communal day roosts (a) and diurnal (b) and nocturnal (c) predation at individual night roosts. Diurnal predation at communal day roosts was zero and is not included in the table.

a) Nocturnal predation at communal day roosts (butterflies in groups on the ground).		
Site	Day no.	Observation
A	1	All 8 disappeared, wings left in pile
	2	All 7 disappeared, wings left in pile
	3	All 6 disappeared, wings left in pile; <i>Peromyscus</i> caught at roost
B	1	No predation
	2	No predation
	3	All 7 disappeared, wings left in pile
	4	All 5 disappeared, wings left in pile
	5	All 6 disappeared, wings left in pile; <i>Peromyscus</i> caught at roost
C	1	No predation
	2	No predation
	3	All 7 disappeared, wings left in pile
	4	All 7 disappeared, wings left in pile
	5	All 7 disappeared, wings left in pile
b) Diurnal predation at individual night roosts (butterflies spaced out in trees)		
Site	Day no.	Observation
A	1	7 of 8 bodies removed, wings found with beak marks
	2	3 of 5 bodies removed, wings found with beak marks
	3	2 of 5 bodies removed
	4	4 of 5 bodies removed, wings found with beak marks
B	1	No predation
	2	1 disappeared; 1 seen eaten by wasp; 4 left intact
	3	No predation
	4	1 disappeared; 1 body removed, wings left behind; 4 left intact
	5	3 of 5 bodies removed, wings left behind
C	1	2 of 6 individuals with beak marks
	2	No predation
	3	1 disappeared; 1 body removed, wings with beak marks; 6 left intact
	4	1 disappeared; 3 bodies removed, wings with beak marks; 3 left intact
c) Nocturnal predation at individual night roosts (butterflies spaced out in trees)		
Site	Day no.	Observation
A	1	No predation
	2	1 of 5 with body eaten
	3	No predation
B	1	No predation
	2	No predation
	3	No predation
	4	3 of 7 disappeared
	5	2 disappeared; 1 with body eaten; 2 left intact
C	1	No predation
	2	No predation
	3	2 disappeared; 1 with body eaten; 5 left intact
	4	3 disappeared; 2 with body eaten; 2 left intact
	5	1 of 8 disappeared

disturbed and usually leave the roost as a cohesive group. This means that a predator attack on a real day roost of *M. maculata* would probably be less disastrous than our experiment with dead butterflies suggests. The predator would most likely be able to catch one butterfly at most before the others disappear, not all as in our experiment.

The results of this study suggest that *M. maculata* uses different defensive strategies at different parts of the day. Its defensive behavior is also dependent on the kind of stimuli. For example, *M. maculata* resting in daytime do not react at all when exposed to ultrasound, stimuli to which flying individuals at night are very sensitive and react evasively (Rydell *et al* 2003). Thus the predatory defense strategy of *M. maculata* is complex and the defensive behavior is strongly dependent on the prevailing situation.

It has been suggested that wintering monarch butterflies, *Danaus plexippus* (L.) in Mexico minimize predation by rodents by roosting in trees rather than on the ground (Brower *et al.* 1985). Our results give substantial support to this idea. In contrast to *M. maculata*, which is cryptically colored, *D. plexippus* has warning coloration and possesses a strong chemical defense functional against birds (Rothschild 1985). Presumably lacking such protection against birds, *M. maculata* apparently cannot spend the day in the trees but has to pay the energetic cost of daily movements and vigilance in the day roost.

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INTRASPECIFIC BODY SIZE VARIATION IN MACROLEPIDOPTERA AS RELATED TO ALTITUDE OF CAPTURE SITE AND SEASONAL GENERATION

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Abstract. As a proxy for body size, forewing lengths of individual geometrids and noctuids were measured with respect to altitude of capture site in five species in North Carolina and one in Costa Rica. Number of specimens ranged 48–373 per species, number of capture sites 2–15 per species, and site altitudes ranged 2–2209 m. Forewing length in all six species increased significantly with increasing altitude at rates of $\approx 0.3\text{--}1.1$ mm/500 m. These relations held where investigated for both first and second annual generations and for both sexes even though second-generation individuals were smaller-bodied. Thus examples of Geometridae and Noctuidae are added to a list mainly of micromoths previously known to exhibit positive size–altitude relations. Some adaptive and nonadaptive body-size hypotheses are discussed as possible explanatory factors, but thus far no explanation is fully satisfactory. In contrast to measurement results in these six macromoths, other moths known to be widely dispersive appeared to display flat size–altitude relations, and published butterfly size–altitude data varied irregularly. Degree of dispersiveness is hypothesized as a condition to the manifestation of size–altitude phenomena in lepidopterans. Many more minimally dispersive moths will likely be found to increase in body size with increasing altitude.

Additional key words: *Chytolita morbidalis*, *Eubaphe mendica*, *Glena cribrataria*, *Hypagyrtis unipunctata*, *Iridopsis pandrosus*, *Trichodezia albovittata*.

Using new and refined data, we examine here intraspecific body size relative to altitude of capture site in individuals of six species of multivoltine and univoltine Geometridae and Noctuidae, five Nearctic and one Neotropical. All six increased in body size with increasing altitude of capture site. Up to now, few moth species beyond examples of Nearctic and Neotropical Tortricidae were known to increase in body size with increasing altitude of capture site (Miller 1974, 1991a, b; 1993, Miller and Nayak 1998, and evidence in Brown 2003). Although not documented statistically, other moths known to be widely dispersive appeared to display flat relations between size and altitude of capture site. In butterflies, which also tend to be dispersive, and sometimes migratory, published body size–altitude relations are inconsistent, some decreasing, increasing, or switching erratically (Hovanitz 1942, Burns 1964, 1985; Guppy 1986, Hawkins and DeVries 1996, and others). The sum of findings in the present study leads us to hypothesize that degree of dispersiveness conditions the manifestation of lepidopteran size as related to altitude of capture site. In the six macromoths studied, we also examined where possible how different seasonal generations within the same year, gender, and to a lesser extent latitude, affected wing length. We discuss some adaptive and nonadaptive factors that might contribute to lepidopteran size–altitude phenomena.

MATERIALS AND METHODS

In Lepidoptera, forewing length serves as a surrogate for body weight, which changes approximately as the square or cube of forewing length (Miller 1977, 1997; Wasserman and Mitter 1978, Loder *et al.* 1998). The six study species here are taxonomically unambiguous, not widely dispersive, and with gender usually recognizable from secondary sexual characters. All were sufficiently common to yield ≥ 17 individuals per site per generation. Examination of museum holdings showed that even moderate numbers of individuals from a single site were rarely available, except at the American Museum of Natural History for *Hypagyrtis unipunctata* (Haworth), as detailed later. We trapped adults using standard 15-w ultraviolet fluorescent light traps (Hall *et al.* 1999). They were killed with potassium cyanide and promptly frozen. In the laboratory, they were spread, oven-dried, after which forewings were measured from the costal base to the outer edge of the fringe at the apex to an accuracy of 0.1 mm using a Wild binocular stereomicroscope (MS 52958) equipped with an ocular micrometer. In pristine specimens it was necessary to estimate length of the wing base beneath the tegula, and in worn specimens, to estimate fringe length. The right wing was measured unless damaged. Locations and altitudes sampled in North Carolina—the main area of study—were the coastal counties of Carteret and Craven (alt. 2–27 m), Hanging Rock State Park in

Stokes Co. (alt. 274–457 m), New River and Mt. Jefferson State Parks in Alleghany and Ashe Counties (alt. 792–1402 m), Grandfather and Moore Mountains in Avery Co. (alt. 1219–1676 m) and Great Smoky Mountain National Park and nearby areas in Swain and Haywood counties (alt. 640–1478 m). Distances between these sites ranged up to ≈600 km, but most were less distant from one another. Costa Rican adults were collected at the Monteverde Biological Station in Puntarenas (alt. 1526 m) and at the Quetzal Education and Research Center in San Jose (alt. 2209 m). *Hypagyrtis unipunctata* beyond North Carolina were used only in the analyses involving latitude, which included sites in New Jersey (lat. 40° 01' N, alt. 22 m, and lat. 40° 51' N, alt. 55 m), New York (lat. 41° 13' N, alt. 93 m), Maine (lat. 45° 36' N, alt. 67 m), and Ontario (lat. 49° 07' N, alt. 344 m). Altitudes for U. S. sites were obtained at <http://www.topozone.com>; for Canadian sites (Ontario), they were estimated from nearby points of known altitude as given at <http://GeoNames2.NRC.gc.ca>; and for Costa Rica they were furnished by the Instituto Nacional de Biodiversidad, San Jose. Statistics were generated using SYSTAT software (SYSTAT 1992). Tests of differences between intraspecific size–altitude regressions for different seasonal generations and genders were based on the General Linear Model, with a categorical variable for generation, a continuous variable for altitude, and an interaction term between the two. The interaction term enabled testing differences in slope value; the categorical variable enabled testing differences in slope elevation.

RESULTS

***Hypagyrtis unipunctata* (Haworth)** (Geometridae: Ennominae). This species is multivoltine in North America (Wagner *et al.* 2001). We used males only, as females were rarely light-trapped. In both the first and second generations, forewing length increased with increasing altitude ≈0.4 mm/500 m (Fig. 1). Generation slope values did not differ significantly ($P = 0.39$), but generation slope elevations did ($P < 0.001$), statistically confirming the nearly uniform ≈20% smaller forewing length of the second generation. The second-generation regression is truncated (Fig. 1) because we omitted late-season (August and September) individuals due to uncertainty about the generation to which they belonged; however, casual observations suggested no further change in size after the second generation. (Incidentally, the very similar *H. piniata* Packard has been reported from North Carolina, but the records likely pertain to misidentified large, first-generation *H.*

unipunctata males.)

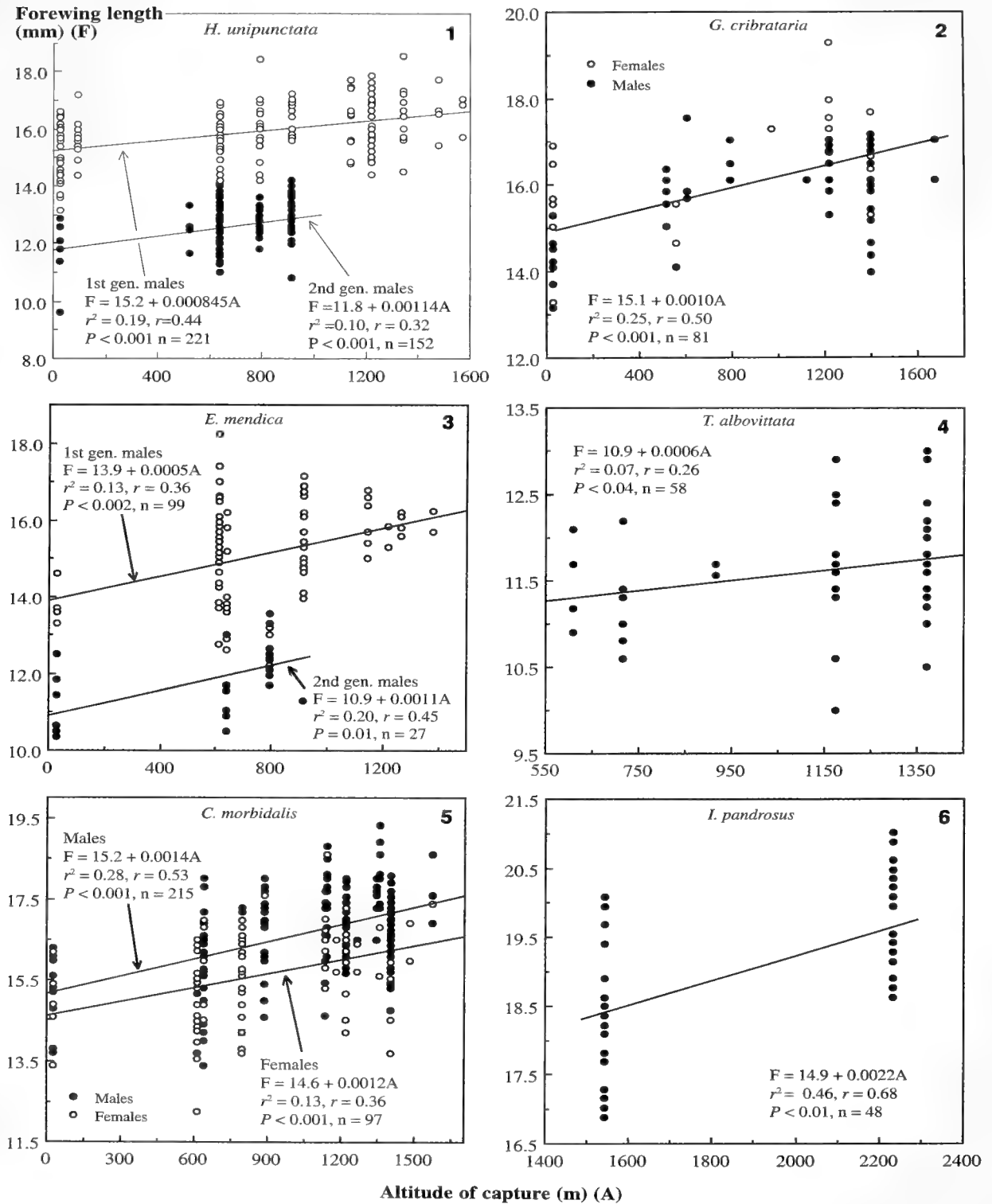
When regressed on latitude (L) alone in the North Carolina-to-Canada sample, forewing length (F) decreased significantly with increasing latitude, that is, wing length decreased northward, indicating a negative correlation with latitude ($r = -0.13$, $n = 331$, $P < 0.02$). However, in multiple regression that also included altitude (A) and the interaction [A X L], a different picture emerged, with forewing length increasing with increasing altitude ($P < 0.001$) as in the North Carolina-only sample (Fig. 1), reversing from decreasing to increasing with increasing latitude ($P < 0.004$), and decreasing with increasing interaction [A X L] ($P < 0.001$) ($F = 0.012 A + 0.06 L - 0.0003 [L \times A] + 13.2$). Thus, effects of altitude and latitude modified each other, and together acted negatively on forewing length. This effect, if not spurious, is a new finding for moths. It needs confirmation and should be examined further in other moths.

***Glena cribrataria* (Guenée)** (Geometridae: Ennomiinae). This species is multivoltine in North Carolina (Wagner *et al.* 2001). Males and females of the first generation are plotted separately (Fig. 2), but their regressions did not differ significantly in slope value or slope elevation (P 's ≥ 0.31). Forewing length increased with altitude ≈0.5 mm/500 m. Too few individuals of the second generation were available for analysis.

***Eubaphe mendica* (Walker)** (Geometridae: Larentiinae). Males of both the first and second generations showed positive relations between forewing length and altitude (Fig. 3). Generation slope values did not differ significantly ($P = 0.37$), but generation slope elevations did ($P < 0.001$), statistically confirming the nearly uniform ≈20% smaller forewing length of the second generation. The second-generation regression is truncated (Fig. 3) because we omitted late-season individuals, being uncertain to which generation they belonged. Forewing length increased with altitude ≈0.75 mm/500 m.

***Trichodezia albovittata* (Guenée)** (Geometridae: Larentiinae). This univoltine species is both a day- and night-flyer, and thus may be somewhat dispersive. The sample of pooled males and females increased in forewing length with increasing altitude (Fig. 4); the rate of increase, ≈0.3 mm/500 m, was the smallest of the study.

***Chytolita morbidalis* (Guenée)** (Noctuidae: Herminiinae). The sexes of this univoltine species are readily distinguished by antennal characters. Males and females both showed a positive relation between forewing length and altitude (Fig. 5). Their respective slope values did not differ significantly ($P = 0.44$), but their respective slope elevations did ($P < 0.001$),



FIGS. 1-6. Relations of forewing length (F) to altitude of capture site (A) in investigated species of Geometridae and Noctuidae. 1, *Hypagyrtis unipunctata* (1st gen. males, open circles; 2nd gen. males closed circles). 2, *Glena cribrataria*. 3, *Eubaphe mendica* (1st gen. males, open circles; 2nd gen. males, closed circles). 4, *Trichodezia albovittata*. 5, *Chytolita morbidalis*. 6, *Iridopsis pandrosus*. Figs. 1-5 depict North Carolina individuals, Fig. 6, Costa Rican individuals.

statistically confirming that female forewing lengths are $\approx 5\%$ less than in males. Forewing length increased with altitude ≈ 0.75 mm/500 m.

***Iridopsis pandrosus* (Schaus)** (Geometridae: Ennominae). Male forewing lengths in this Costa Rican species also increased with increasing altitude (Fig. 6). The rate of increase, ≈ 1.1 mm/500m, was the largest of the study. The species identity is based on similarity of maculation with the type specimen in the U. S. National Museum, the genitalia of which had not been dissected and examined at the time of this study. However, males from both altitudes had indistinguishable genitalia. Distance between the two capture sites was 130 km. Despite the limit of material to just two sites, we believe a linear (rather than curvilinear) relation is appropriate and valid here because of the large slope value and evidence of linear relations among the other geometrids (Figs. 1–4).

Other taxa and counterexamples. Many other North Carolina macromoths were seen during this study, but not in sufficient numbers for statistical analysis. Examples of Saturniidae, Notodontidae, and less dispersive Noctuidae seemed to show wing lengths positively correlated with altitude. However, wing lengths of *Paonias excaecata* (J. E. Smith) (Sphingidae), which were followed over a large altitudinal range, did not appear to increase with increasing altitude. Many sphingids, like many butterflies, are strong flyers and disperse widely so that their capture sites may not represent sites of development. The same is true of widely dispersive noctuids such as *Helicoverpa zea* (Boddie), *Pseudaletia unipuncta* (Haworth), and species of *Leucania*, *Anticarsia*, *Spodoptera*, and *Catocala*, which also seemed to show flat relations between wing length and altitude.

DISCUSSION

In all six macromoths measured, statistically significant positive relations emerged between individual forewing lengths, hence body size, and altitudes of capture sites, as previously observed mainly in the micromoth family Tortricidae (Miller 1974, 1991a, b; 1993, Miller and Nayak 1998, and evidence in Brown 2003). More examples will likely be found among other minimally dispersive moths. In North Carolina and Costa Rica, increases in size are usually apparent to the eye as one proceeds to higher altitudes provided individuals of the same generation are observed.

Also, where examined, individuals of the second generation were smaller-bodied than those of the first generation, yet still increased in size with increasing

altitude. Individuals of the first generation often are larger-bodied than those of subsequent generations, as noted for geometrids by Rindge (1968, 1974, 1978, 1979, and others) and for noctuids (*Chytolita petralis* Grote) by Forbes (1954). Wagner *et al.* (2001) reported that larvae produced by first-generation *Hypagyrtis unipunctata* are smaller than last-generation larvae that become the next year's first generation, thus confirming the above adult size results in the larval stage.

In Costa Rica, it was difficult to find suitable species free of taxonomic complexities that spanned wide ranges in altitude. Because of narrow altitude distribution and greater species diversity there, fewer intraspecific individuals were collected. Moreover, on genitalic dissection, individuals from different altitudes sometimes proved to be different species despite similarities in maculation. Thus, moths that show either unusually large size increases with increasing altitude or none at all may signal taxonomic problems.

Brehm and Fiedler (2004) found geometrid wing lengths negatively correlated with altitude in the Andes, which is contrary to our findings, but their investigative approach was interspecific and thus fundamentally different from our intraspecific individual approach. Size correlations of grouped taxa with altitude can obscure inherent intraspecific responses.

No satisfactory explanation for positive size–altitude relations in moths is yet available. Some studies of single species have focused on abiotic factors, namely temperature, based on findings that lepidopterans grow to maximal size at temperatures somewhat lower than they normally experience (Atkinson 1994, Partridge and French 1996, Atkinson and Sibly 1997, Miller 2005).

Biotic factors may also be involved. Foliar nitrogen content within the same plant species, and among different plant species, also increases with increasing altitude (Körner 1989, Erelli *et al.* 1998), and lepidopterans feeding on high-nitrogen foliage grow commensurably larger (Mattson 1980, Mattson and Scriber 1987). Further, body weight in a saturniid moth was positively correlated with quantity of food consumed during the larval stage, as well as with higher altitudes and cooler temperatures (Miller and Nayak 1998). A notable positive correlation between female size and fecundity in moths insures that increased size will increase fecundity and other fitness factors (Dey *et al.* 2004, Miller 2005). The role of such factors in size–altitude relations needs investigation.

Body-size variation in butterflies. In an extensive study, Hawkins and DeVries (1996) examined butterfly size as related to altitude of capture site in Costa Rica. Their method of analyzing forewing length using the median altitude at which each species occurred is not

strictly equivalent to our intraspecific approach. Their results proved group-specific: for instance, only species of Pieridae exhibited a negative size relation with altitude among four families including Papilionidae, Nymphalidae and Riodinidae. Species of the latter three families showed some evidence of positive size relation with altitude, but these relations were irregular and not always statistically significant or linear. As stated earlier, butterflies, particularly males, tend to be dispersive so that their capture sites may not accurately represent sites of development.

Using less extensive data, Opler and Krizek (1984) reported positive and negative generational size differences within the same season for some North American butterflies. However, when dispersive tropical species and species that winter as adults were removed, the remaining butterflies increased in size after the first generation. This result is consistent with our observations of butterflies in North Carolina (unpublished). Opler and Krizek (1984) also noted that butterfly populations in Florida are often larger-bodied than those farther north, and Burns (1985) found that *Wallengrenia egeremet* (Scudder) and *W. otho* (J. E. Smith) (Hesperiidae) increased in size from north to south, revealing a negative correlation of size with latitude, except for a decrease in size of *W. egeremet* associated with its shift from uni- to bivoltinism. McQuillan and Ek (1996) also noted that body size of an Australian butterfly is larger in warmer areas. In North Carolina, many butterfly species appear larger-bodied in warmer areas (unpublished). Wagner and Hansen (1980) documented a southward size decrease in a pierid butterfly in the Great Lakes region, representing a positive correlation of size with latitude. In direct contrast, Scholtens and Wagner (1997) in the same region documented the opposite trend in a saturniid moth, representing a negative correlation. Available data suggests that butterflies and moths respond differently to the physical factors discussed in this paper.

Other factors that might influence differences between moth and butterfly size variability. A physiological and behavioral difference between moths and butterflies occurs in their preparation for flight (Bartholomew and Heinrich 1973), which can be framed in the context of altitude. All fly at temperatures above ambient (Srygley and Chai 1990, Rydell and Lancaster 2000, Utrio 1995), but butterflies usually increase body temperature by solar basking while moths do so by muscular activity. In moths encountering cool flight temperatures, increased wing length might facilitate raising body temperature by increased resistance to wing flapping. Further, larger butterfly wings can accumulate solar radiation faster than smaller

ones (Berwaerts *et al.* 2001). Individual high-altitude butterflies tend to be darkly pigmented, which speeds their accumulation of solar heat compared with low-altitude lightly pigmented conspecifics (Watt 1968, Kingsolver 1985, Guppy 1986).

Behavioral or life history modifications might artificially influence size–altitude relations, as possibly in day- and night-flyers represented in this study by *T. albovittata*. This species, which acts partly like a butterfly and may be somewhat dispersive, showed the least increase in wing length with increasing altitude. Also, where different microhabitats lead to second or third seasonal generations during the same season, or to a shift from uni- to multivoltinism, different generations may be on the wing at the same time. For instance, larvae feeding on the north slope of a mountain might be univoltine while those feeding just over the crest on the south slope might be multivoltine so that trapping nearby could include individuals of both.

In conclusion, intraspecific variability in body size has numerous ramifications, ambiguities, as well as inconsistencies in study methods. Yet it offers many possibilities for experimentation both in the field and in the laboratory to account for the evidence that body size increases with increasing altitude of development, and also to illuminate whether the underlying forces are adaptive, nonadaptive, or some combination of the two.

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ARGYRIINI (LEPIDOPTERA: CRAMBIDAE) OF MISSISSIPPI AND ALABAMA WITH A
REDESCRIPTION OF *ARGYRIA RUFISIGNELLA* (ZELLER)

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Abstract: The tribe Argyriini (Lepidoptera: Crambidae) is represented in Alabama and Mississippi by seven species of *Argyria* and *Urola*, all of which are associated with grasslands and other open habitats. *Argyria rufisignella* is a rarely collected species previously reported from Texas, Florida, and North Carolina. A series of this species recently was collected at Bibb County Glades Preserve, Alabama, a floristically unique habitat. The imago, wing venation, and genitalia of *A. rufisignella* are illustrated for the first time, and new distributional records are reported. Diagnoses, distribution maps, and photographs are provided as well for the other Argyriini that occur in Alabama and Mississippi.

Additional key words: *Urola*, distribution, grasslands, Bibb County Glades Preserve.

Argyria Hübner and related genera in the Argyriini (Crambidae: Crambinae) are considered to be restricted to the New World (Landry 1995). *Argyria* includes 38 species, of which seven occur in America north of Mexico, primarily in the eastern states and provinces (Klots 1983, Landry 1995, Landry 2003, Munroe 1995). The only other species of Argyriini in America north of Mexico is *Urola nivalis* (Drury).

Argyria species in America north of Mexico have been divided into three groups (Munroe 1995): one including *A. lacteella* (F.), one including *A. nummulalis* Hübner, *A. subaenescens* (Walker), and *A. rufisignella* (Zeller), and one including *A. auratella* (Clemens), *A. critica* Forbes, and *A. tripsacas* (Dyar), the latter three formerly assigned to *Vaxi* (Klots 1983). Hosts and immature stages are unknown for all species of *Argyria*, although most other Crambinae feed on grasses (Poaceae) (Landry 1995).

Argyria species and *U. nivalis* have short labial palpi, forewings dominated by a satiny-white color, and females with segment VIII dorsally shortened and bearing short anterior apophyses. *Argyria* species differ from *U. nivalis* in having male genitalia with a long, narrow uncus, rather than short and rounded, and a vinculum without an arm projecting posteriorly. The female ductus bursae is long and unsclerotized in *Argyria* species, and short and heavily sclerotized in *U. nivalis*.

Argyria rufisignella was described by Zeller (1872) as a species of *Catharylla* Zeller based on a male specimen collected by Jacob Boll in Texas (Landry, 1993). Dyar (1913) described *Argyria rileyella*, a junior synonym of *A. rufisignella*, from a male specimen, which was collected by C. V. Riley at an unknown locality and deposited at the U.S. National Museum of Natural

History (USNM). Only two other specimens of *A. rufisignella* are in the USNM, both collected at Southern Pines, North Carolina. Kimball (1965) listed a single record of *A. rufisignella* (as *A. rileyella*) from Myrtle Grove, Florida, but this specimen could not be located in the Florida State Collection of Arthropods (FSCA). Ed Knudson (personal communication) has collected a few specimens in Texas at Jeff Davis Co., Davis Mts. State Park, and Tyler Co., Big Thicket Nature Preserve, and Bernard Landry (personal communication) has a few specimens in his collection from Wisconsin at Burnett Co., Minnesota at Orrock, Sherburne CO., and Ontario, Canada at Grand Bend, but these were not examined.

A series of nine specimens of *A. rufisignella* was collected with blacklights recently in the Bibb County Glades, a Nature Conservancy Preserve in western Alabama (Fig. 1). The uniqueness of these glades, which are formed on Ketona Dolomite, has been documented in a treatment of the vascular flora that includes descriptions of eight new endemic taxa, one species, *Solanum pumilum* Dunal (Solanaceae), previously thought to be extinct, and more than 60 plant taxa of conservation concern (Allison and Stevens 2001).

The purpose of this contribution is to provide new distributional records for *A. rufisignella* in Alabama and other localities, to describe the male and female genitalia of this rarely collected species, and to provide distributional records for other species of Argyriini in Mississippi and Alabama.

MATERIALS AND METHODS

Descriptions of female and male genitalia of *Argyria rufisignella* are based on material in the Mississippi Entomological Museum (MEM) at Mississippi State

University. Distribution records are based on material in the American Museum of Natural History (AMNH), Cornell University Insect Collection (CUIC), FSCA, MEM, USNM, and the private collections of Edward Knudson and Bernard Landry. Dissections of male and female genitalia and preparation of wing venation slides follow Landry (1995) with some modifications. Euparal was used as the mounting medium and Safranin and Chlorazol Black were used for staining genitalia. Genitalia and wings were illustrated and measured using a Leica MZ 12.5 stereomicroscope, a drawing tube, and a micrometer. Specimens were photographed and forewing lengths (FWL) were measured with the use of a Media Cybernetics Evolution MP digital camera (5 mega pixels) mounted on a Leica MZ 12.5 stereomicroscope with use of Image Pro Plus auto formatting software. Terminology for wing venation and genitalia structures follows Munroe and Solis (1998).

RESULTS

Seven species of Argyriini (Figs. 2-10) have been collected in Mississippi and Alabama (Fig. 11-14). Several of these species are associated with unique habitats including *A. nummulalis* and *A. auratella* from remnants of Black Belt Prairie and coastal savannas in Mississippi, *A. tripsacas* from coastal dunes in Alabama, and *A. rufisignella* from dolomite glades in Alabama. Other species have been collected primarily in fields and other open habitats where grasses and herbs dominate. *Argyria nummulalis* varies greatly in the color of the hindwing, ranging from almost white to various shades of brown (Figs. 4-6), in contrast to species of *Argyria* having little variation. A redescription of *A. rufisignella* and its distribution follows.

Redescription of *Argyria rufisignella* (Zeller)

Figs. 10, 12, 15-19

Adult (Fig. 10) *Head*: Head and appendages dark yellow except frons, base of proboscis, and base of labial palpus yellowish white.

Thorax: Silvery white with dark yellow longitudinal stripe medially.

Forewing: Length 6.0-6.72 mm (mean 6.38 mm) in female ($n = 7$), 4.80-5.12 mm (mean 4.96 mm) in male ($n = 2$). Silvery white with costal margin from base to near apex light brown; two brown spots, one in middle of costal margin and one in middle of dorsal margin, usually connected by weak yellow line; similar yellow line present between R_2 and R_3 on costa, extending weakly to M_1 , sometimes extending to dorsal margin and forming spot; submarginal scales forming wide



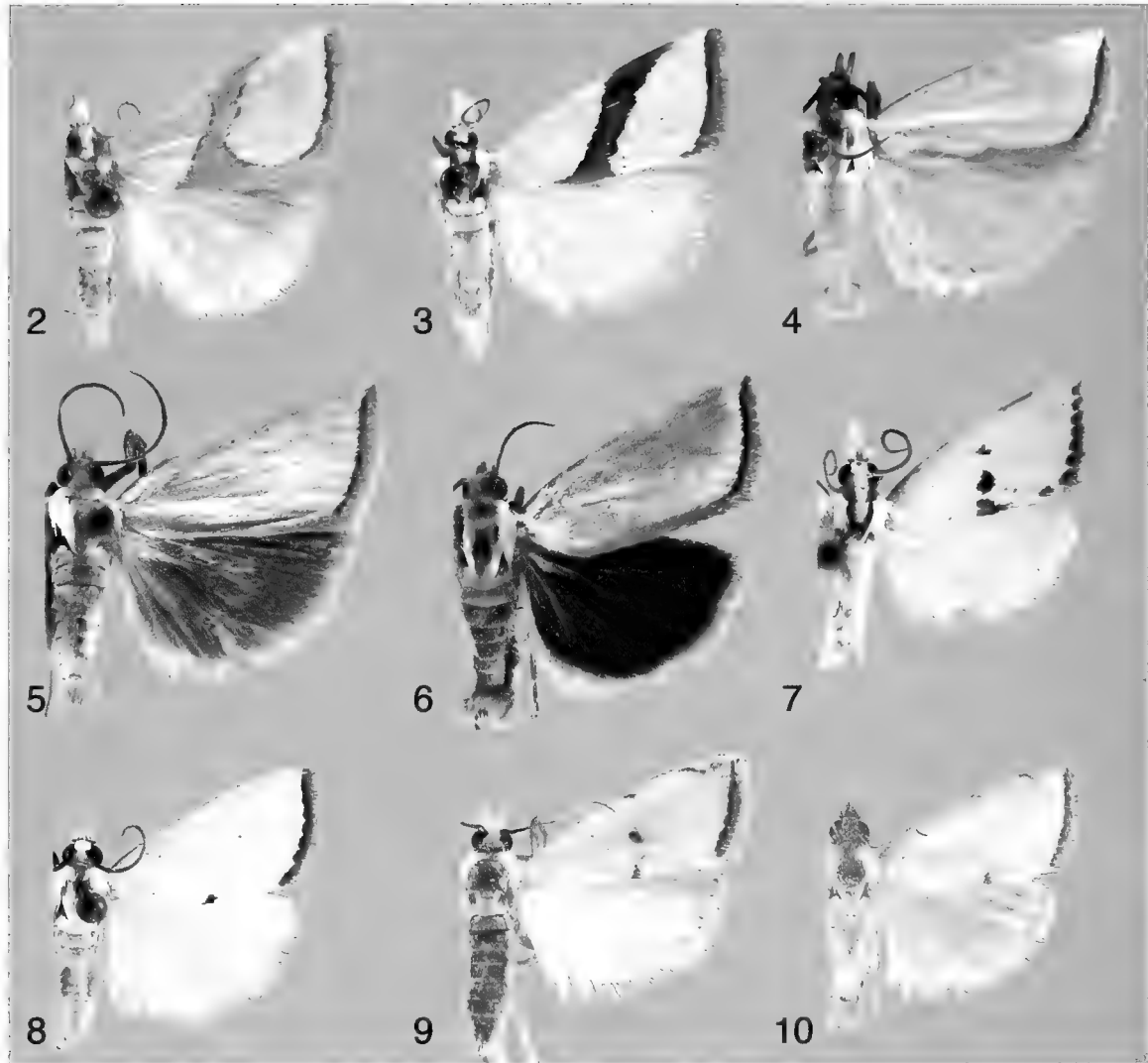
FIG. 1. Dolomite outcrops and vegetation at the Bibb County Glades Nature Conservancy Preserve.

yellow band from apex to tornus, bordered basally by line of dark brown scales; marginal scales short, brown. Venation (Fig. 15) with R_3 and R_4 stalked to near costa; M_2 and M_3 with bases approximate; discal cell closed apically.

Hindwing: White. Venation (Fig. 16) with Sc and R_1 stalked to near costa; female frenulum with three spines.

Male genitalia (Figs. 17, 18): Intersegmental membrane with large hair pencil arising near base of tegumen, extending to more than one half the height of tegumen. Uncus relatively long, narrow, with down-curved apex, opposing similarly shaped gnathos. Valvae with basicostal arm, flattened, widened basally, and with macrotrichiae and small setae; mediocostal lobe subquadrate, basal half sclerotized, apical half membranous and supporting hair pencil consisting of five hairs dorsally, cucullus covered with long setae directed apically and striate dorsally; sacculus forming medial ridge. Vinculum broad and convex; pseudosaccus absent. Aedeagus with patch of basally directed spinules on dorsoapical surface; vessica without cornuti.

Female genitalia (Fig. 19): Segment VII with sternum and tergum smooth, evenly scaled, posterior half of tergum with scales and setae intermixed. Tergum VIII lacking scales and setae, expanded ventrolaterally, forming acute medioposterior angle and rounded medioanterior lobes projecting over ostium. Papillae anales with ventral one-fourth curved ventroposteriorly, posterior margin not cleft, with ventral surface moderately rugose, marginal setae long; apophyses posteriores long. Apophyses anteriores 0.23X length of apophyses posteriores. Ostium bursae forming invaginated and expanded antrum beneath sternum VII, posteriorly bordered by two concave, slightly sclerotized depressions. Ductus bursae



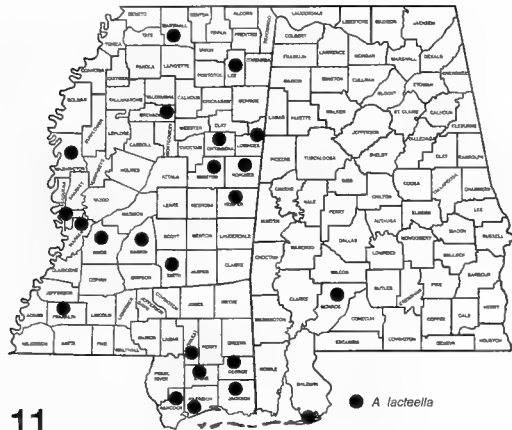
FIGS. 2-10. Species of *Argyria* and *Urola* in southeastern United States. (2) *A. auratella* (FWL 7.40 mm), (3) *A. critica* (FWL 11.43 mm), (4) *A. nummulalis* (FWL 11.17 mm), (5) *A. nummulalis* (FWL 12.69 mm), (6) *A. nummulalis* (FWL 12.07 mm), (7) *A. tripsacas* (FWL 6.28 mm), (8) *U. nivalis* (FWL 10.00 mm), (9) *A. lacteella* (FWL 5.47 mm), and (10) *A. rufisignella* (FWL 9.56 mm).

moderately long, membranous, with ductus seminalis originating near middle. Corpus bursae membranous.

Diagnosis: Forewing veins R_3 and R_4 are partly fused in *A. rufisignella*, *A. critica*, *A. auratella*, and *U. nivalis*, whereas they are completely fused in *A. nummulalis* and separate in other species. Vein R_5 is separate from R_{3+4} in *A. rufisignella* and *U. nivalis*, but it is fused with the basal portion of R_{3+4} in *A. critica* and *A. auratella*. The male genitalia of *Argyria rufisignella* differ from other species of *Argyria* and *Urola nivalis* as follows: 1) the uncus has a pointed and straight apex, whereas the apex is rounded or bent in the other species; 2) the valva has a distinctive form in *A. rufisignella*, differing from, other species. In particular, the mediocostal lobe of the valvae is rectangular in *A.*

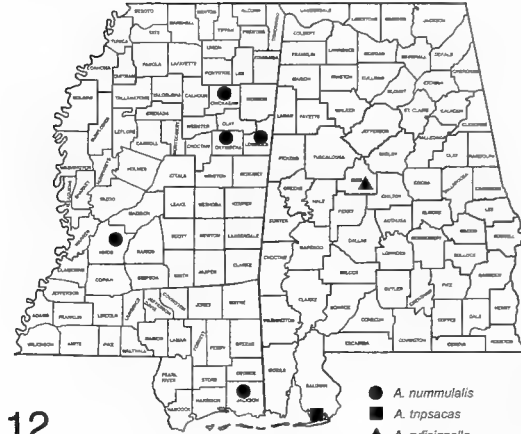
rufisignella, whereas it is rounded or absent in other species. The female genitalia differ as follows: 1) the papillae anales have long marginal setae, whereas marginal setae are short or absent in other species; 2) tergum VIII is expanded ventrolaterally, forming an acute medioposterior angle and rounded medioanterior lobes that project over the ostium, whereas the tergum is not expanded in other species; 3) the ductus bursae is membranous in *Argyria* species and sclerotized in *U. nivalis*, and is relatively short compared to length of sternum VII in *A. rufisignella* and relatively long in other species.

Material examined and distribution: Alabama: Bibb Co., Bibb Co. Glades Preserve, 33°03'26"N 87°02'02"W, 4 June 2003, R.L. Brown, S.M. Lee, J.A.



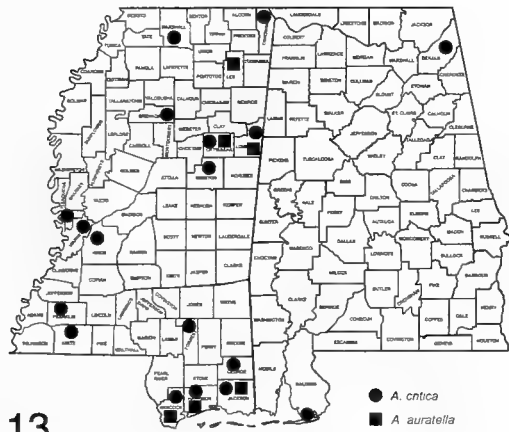
11

● *A. lacteella*



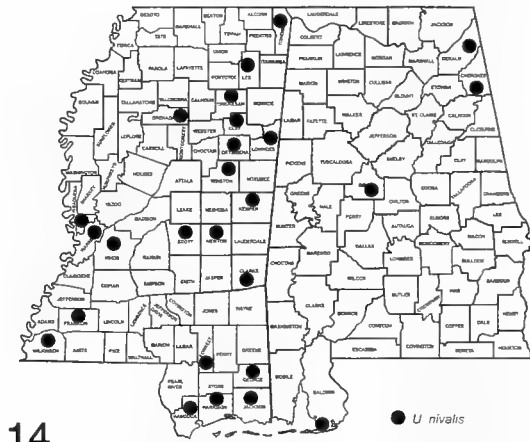
12

● *A. nummulalis*
 ■ *A. tripsacis*
 ▲ *A. rufisignella*



13

● *A. critica*
 ■ *A. auratella*



14

● *U. nivalis*

FIGS. 11-14. Distribution maps of *Argyrja* species and *Urola nivalis* in Mississippi and Alabama. (11) *A. lacteella*, (12) *A. nummulalis*, *A. tripsacis*, and *A. rufisignella*, (13) *A. critica* and *A. auratella*, and (14) *U. nivalis*.

Key to species of *Argyriini* in southeastern United States

- 1. Forewing with oblique brown or yellow band 2
- 1'. Forewing without oblique band 3

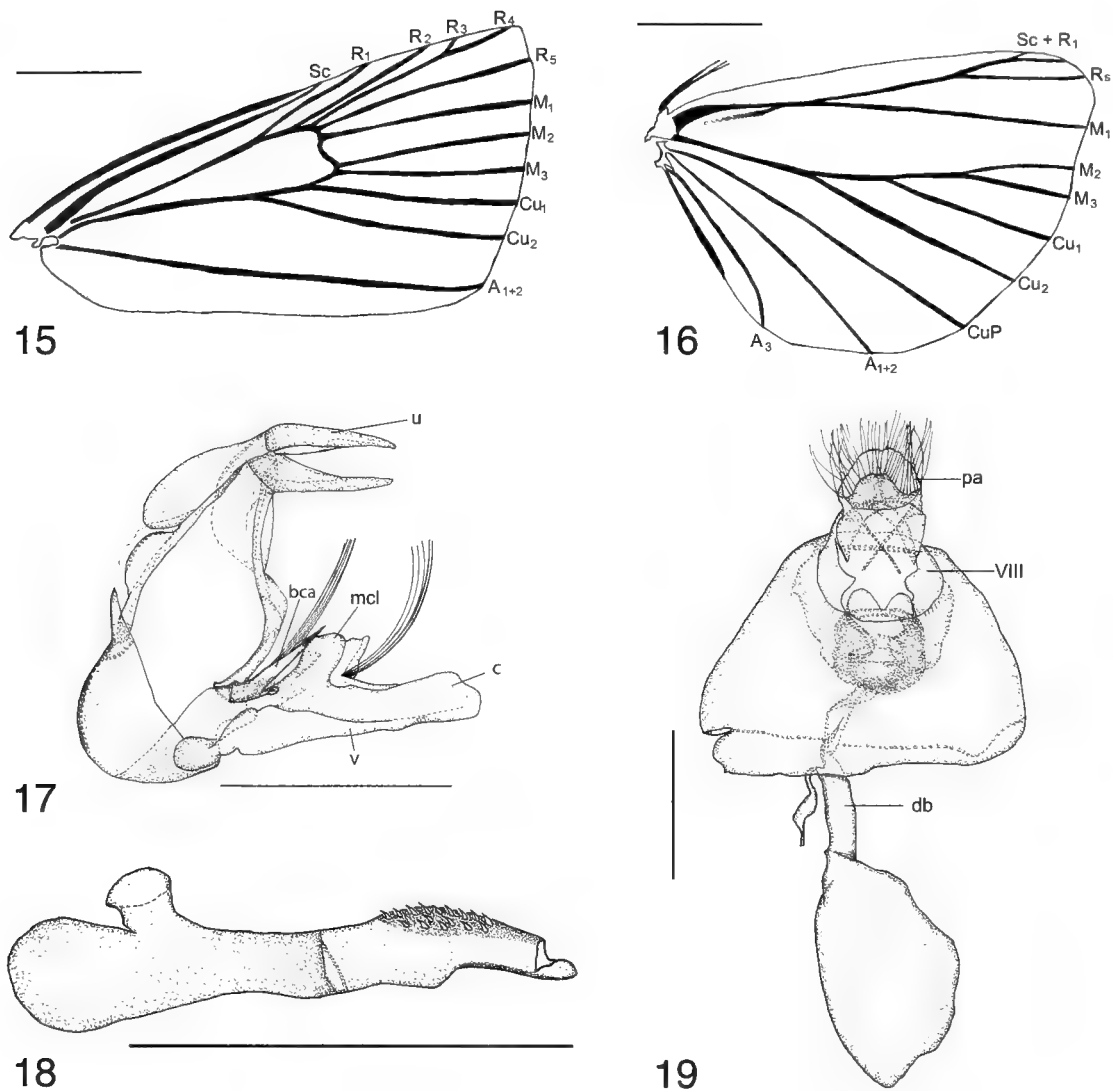
- 2. Forewing with oblique band light yellow, widened on dorsum *A. auratella* (Fig. 2)
- 2'. Forewing with oblique band yellowish brown to dark yellow, not widened on dorsum *A. critica* (Fig. 3)

- 3. Forewing dorsum and fringe margined with yellow, dorsum without dark spot *A. nummulalis* (Fig. 4-6)
- 3'. Forewing dorsum without yellow margin, fringe with or without yellow margin, dorsum with dark spot near middle 4

- 4. Thorax with two, dark yellow, longitudinal stripes *A. tripsacis* (Fig. 7)
- 4'. Thorax with one, light yellow, longitudinal stripe 5

- 5. Forewing without dark spots on costa, fringe brown *U. nivalis* (Fig. 8)
- 5'. Forewing with two or more dark spots on costa, fringe yellow or brown 6

- 6. Forewing discal cell with dark spot, fringe brown *A. lacteella* (Fig. 9)
- 6'. Forewing discal cell without dark spot, fringe yellow *A. rufisignella* (Fig. 10)



FIGS. 15-19. *Argyria rufisignella*. Scale bar = 1mm. (15) forewing (female), (16) hindwing (female), (17) Male genitalia, (18) Aedeagus, (19) Female genitalia. (bca) basicostal arm, (c) cucullus, (db) ductus bursae, (mcl) mediocostal lobe, (pa) papillae anales, (u) uncus, (v) valva, (VIII) tergum VIII.

MacGown (2 ♂, 7 ♀; MEM). Florida: Okaloosa Co., Shalimar, 20 Aug. 1964 (1, sex not recorded), Ocean City, 7 June 1963 (1, sex not recorded), H.O. Hilton (FSCA). Georgia: [county unknown] Spring Ck., 18-21 May 1916, J.C. Bradley, (1 ♀, genitalia slide A.B. Klots 24 Oct. 1965 #2; CUIC). North Carolina: Moore Co., Southern Pines, Aug. 24-30 (1 ♂, genitalia slide CH 28 Apr 32 #17, 1 ♀, genitalia slide CH 28 Apr. 32 #22; USNM).

ACKNOWLEDGMENTS

We thank David Grimaldi (AMNH), James Liebherr (CUIC), John Heppner (FSCA), and Alma Solis (USNM) for assistance in examining specimens of *Argyria* and Ed Knudson for supplying Texas records. Alma Solis provided a photograph of the holotype of *Argyria rufisignella* for confirmation of its identity. Joe MacGown provided a photograph of Bibb Co. Glades and guidance in preparing and formatting drawings, maps and photographs. Research was supported by the Mississippi Agricultural and Forestry Experiment Station and the William H. Cross Expedition Fund, MSU Development Foundation.

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A NEW SPECIES OF *PELOCHRISTA* LEDERER FROM EASTERN NORTH AMERICA (TORTRICIDAE)

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ABSTRACT. *Pelochrista milleri*, new species, is described from eastern North America. This moth seems to have no particularly close congeners and in some respects appears to be affiliated with certain species of *Eucosma*. Illustrations of the adult and genitalia are included.

Additional key words: Nearctic, Olethreutinae, Eucosmini, *fiskeana*, *pulveratana*

Faunal surveys in Ohio and Kentucky during the past two decades generated numerous records of a previously unnamed olethreutine moth described below as *Pelochrista milleri*, new species. Additional specimens found in institutional and private collections suggest that the range of this insect includes northeastern United States, the eastern half of southern Canada, and much of the Midwest. The purpose of this note is to make a name available for this species for inclusion in a regional guide to the Olethreutinae currently in preparation.

The olethreutine genera *Pelochrista* Lederer and *Eucosma* Hübner together account for nearly 180 named species in the Nearctic region, the vast majority of which are currently assigned to *Eucosma*. The distinction between the two taxa, however, is not particularly well defined, and it isn't difficult to find instances, *milleri* for one, in which the choice of genus seems somewhat arbitrary. Current practice places species with an especially stout spiniform seta at the anal angle of the cucullus in *Pelochrista*, and I have followed that precedent in this case. Nevertheless, on the basis of forewing color and maculation *milleri* could easily be confused with *E. fiskeana* Kearfott, and the female sterigma has the distinctive structure found in members of the *E. pulveratana* (Walsingham) group. Revisionary work that addresses the considerable variety found in these groups and includes an assessment of the female genitalic characters is clearly needed. Until then generic assignments must often be tentative.

To my knowledge there are no published images of the adult of *E. fiskeana*, so I've included one for comparison. The drawing in Miller (1987) of the sterigma of *E. consobrinana* Heinrich is typical of the members of the *E. pulveratana* group. Illustrations of the male genitalia of these two species can be found in Heinrich (1923).

MATERIALS AND METHODS

I examined 57 adult specimens (8 ♂, 49 ♀) and 21

associated genitalia slides from the following collections: Canadian National Collection (CNC), Dennis Profant (DP), George J. Balogh (GJB), Illinois Natural History Survey (INHS), Loran D. Gibson (LDG), United States Museum of Natural History (USNM) and Donald J. Wright (DJW). Forewing length (FWL) refers to the distance from base to apex, including fringe. Aspect ratio (AR) is defined as FWL divided by medial forewing width, the latter measurement taken perpendicular to the dorsal margin. The letter n signifies the number of measurements supporting a particular statistic. Forewing pattern terminology follows Brown & Powell (1991) as modified by Baixeras (2002).

SYSTEMATICS

Pelochrista milleri, new species

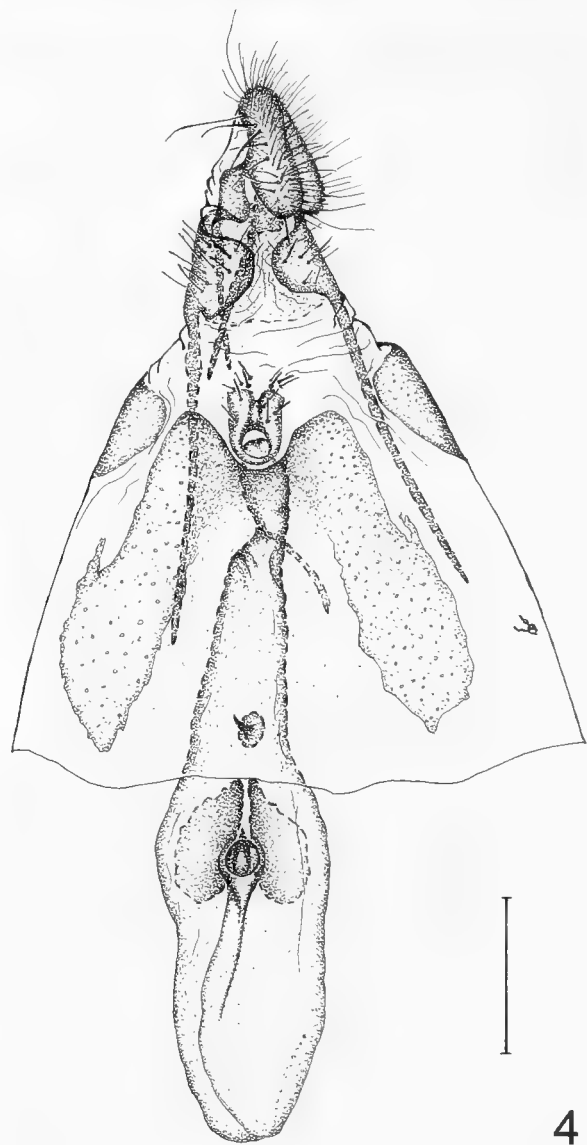
(Figs. 1, 3, 4, 5)

Diagnosis. This is the only grayish-brown *Pelochrista* in eastern North America with both a fasciate forewing pattern and a circularly shaped cucullus. *Eucosma fiskeana* Kearfott (Fig. 2) is similar in forewing color and maculation but has quite different male genitalia (Heinrich (1923): Fig. 152). Members of the *Eucosma pulveratana* group are similar to *milleri* in the structure of the sterigma, in the pattern of sclerotization of sternum VII, and in having variably shaped sclerotized patches on the surface of the corpus bursae, but they are easily distinguished from *milleri* by both forewing pattern (see, e.g., the photograph of *consobrinana* in Miller (1987)) and by the shape of the male valva (Heinrich (1923): Figs 238, 242, 243).

Description. *Head:* Lower frons pale tan; scales of upper frons and vertex gray-brown with pale apices and bases; labial palpus with brown to tan lateral surface and ventral edge, creamy white to tan medial surface and dorsal edge, third segment brown, often with pale tan apex; antenna grayish brown. *Thorax:* Dorsal surface concolorous with head, ventral surface white to pale tan; legs brown to pale tan with dark tarsal annulations. *Forewing* (Fig. 1): ♂ FWL 5.5–7.2 mm (mean = 6.5, n = 6), AR = 2.56, ♀ FWL 6.5–9.6 mm (mean = 7.9, n = 32), AR = 2.53; basal one half of costa mildly convex, distal one half nearly straight, terminal margin straight and perpendicular to costa, tornal angle gently rounded. Dorsal surface grayish-brown with dark brown markings as follows: basal and subbasal fasciae confluent, outer



FIGS. 1-2. 1, *P. milleri*, ♂ holotype, Adams Co., Ohio. 2, *E. fiskeana*, ♂ Adams Co., Ohio.



FIGS. 3-4. *P. milleri* genitalia. 3, ♂ slide DJW 384. 4, ♀ slide DJW 569. Scale bars = 0.5 mm.

margin of resulting basal patch sharply defined from dorsum to discal cell and barely distinguishable from there to costa, median fascia extending from mid costa to dorsum, usually interrupted anterior to cubital vein, resulting in triangular mark on pretornal portion of dorsum, a narrow band along anterior and distal margins of ocellus, and a small apical spot, all edged to varying degrees with white scaling; ocellus with brown central field crossed longitudinally by 2 or 3 black dashes and bordered basally and distally by transverse silvery-gray bars; costa usually with 5 paired, white strigulae and associated silvery-gray stria; fringe scales gray brown with lighter apices. *Hindwing*: uniformly gray brown, fringe a shade lighter. *Male genitalia* (Fig. 3): uncus very weakly divided medially into two dorsally setose lobes; socii long, finger like, and moderately setose; gnathos a narrow band; aedeagus long and narrow, vesica with one deciduous cornutus; valva with costal margin mildly concave, invagination of ventral margin moderate; cucullus with apical margin circular, ventral angle produced into semitriangular projection supporting one stout spine, and medial surface densely setose. *Female genitalia* (Fig. 4): papillae anales facing laterally and moderately setose; sterigma with anterior margin rounded and ringlike, lamella postvaginalis well developed, with shallow central trough and medially indented posterior margin; sternum VII strongly sclerotized along posterior and lateral margins, posterior margin invaginated to two thirds length of sterigma; ductus bursae short, constricted anterior to ostium; corpus bursae long and narrow, a large signum at mid bursa on ventral surface, flanked by two sclerotized patches on opposite dorsolateral surfaces, a smaller thorn-like signum on dorsal surface posterior to dorsolateral sclerotization.

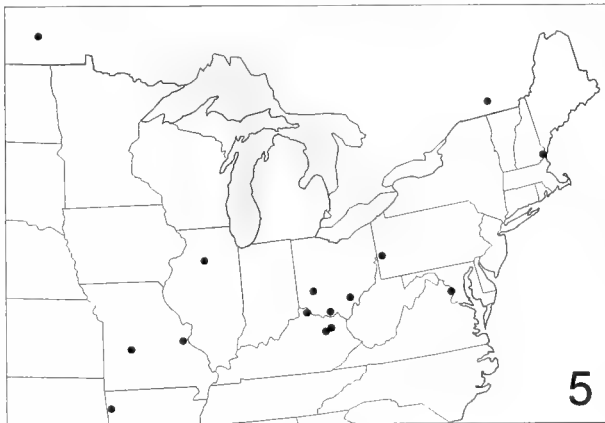


FIG. 5. Distribution records for *milleri*.

Holotype. ♂, Ohio, Adams Co., 1 mi. S. E. of Lynx, 25 July 1997, D. J. Wright, genitalia slide DJW 384, deposited in USNM. Type locality at 38°47'37"N, 83°24'19"W.

Paratypes. ILLINOIS: Putnam Co., M. O. Glenn, 7 August 1966 (1 ♂, genitalia slide DJW 452). KENTUCKY: Bath Co., Cave Run Rec. Area, Rt. 129 & Zilpo Rd., L. D. Gibson, 17 August 1990 (1 ♀); Campbell Co., A. J. Jolly Co. Pk., 23 July 1991, L. D. Gibson (1 ♀; genitalia slide LDG 154); Laurel Co., DBNF, Powerline Cut W. side Marsh Branch Rd., L. D. Gibson, (1 ♀); Rowan Co., 3.3 mi. S. of 519 on Co. Rd. 1274, D. J. Wright, 26 August 1994 (5 ♀; genitalia slides DJW 812, 821); W. side Rt. 1274, 3.3 mi W. Rt. 519, L. D. Gibson, 26 August 1994 (5 ♀); Rt. 1274, 2 mi. W. of Rt. 519, L. D. Gibson, 16 July 1994 (1 ♀). MANITOBA: Aweme, N. Criddle, 11 July 1925 (1 ♀; genitalia slide JFL1609). MISSOURI: Jefferson Co., Victoria Glade, 2.5 mi. SE Hillsboro, G. J. Balogh, 8 August 1982 (1 ♀). OHIO: Adams Co., 1 mi. SE of Lynx, D. J. Wright, 2 July 2003 (1 ♀), 5 July 1996 (1 ♀), 12 July 1998 (1 ♂, 5 ♀; ♀ genitalia slides DJW 563, 569), 25 July 1997 (6 ♀; genitalia slide DJW 820), 25 July 1998 (2 ♀, genitalia slide DJW 813), 1 August 1997 (1 ♀), 3 August 2000 (1 ♀), 12 August 1998 (1 ♀);

Athens Co., Hocking College, D. Profant, 29 July 2005 (1 ♀); Greene Co., Wright-Patterson AFB, Huffman Prairie, Site G-3, E. H. Metzler, 28 August 1992 (3 ♂; genitalia slides LDG 146, 156). QUEBEC: St-Liboire, em. 18 June 2002 (1 ♂; genitalia slide JFL 1608). Paratype depositories: CNC, DP, GJB, INHS, LDG, USNM, and DJW.

Etymology. This species is named in honor of William E. Miller. His generosity with advice and encouragement over the years is greatly appreciated by the author.

Distribution and biology. Figure 5 illustrates the geographic range of *milleri* based on specimens I examined. Adult flight occurs between early July and the end of August. The male from Quebec was reared from a larva found boring in roots of *Helianthus tuberosus* L.

Remarks. In my experience, males are much less likely to be attracted to ultraviolet light than females (only 8 of the 57 specimens examined were males). Males are also smaller than females, the difference in average FWL being 1.4 mm.

This species has occasionally been confused with *Eucosma wandana* Kearfott. In the USNM there are two rather old female specimens of *milleri* that have previously been determined as *wandana*. One, which was cited in Gibson and Miller (1993), bears a red label with the inscription "Type No. 8243 U.S.N.M", but it has no pin label indicating a specific name. This specimen cannot be a syntype of *wandana*, which was described from a single male. The intent of the label is unknown.

ACKNOWLEDGMENTS

Thanks to J. W. Brown, J.-F. Landry and K. R. Methven for the loan of specimens under their care and to Paul Knoop for providing access to his property in Adams Co., Ohio, the type locality for *milleri*.

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A NEW SPECIES OF *EUXOA* (NOCTUIDAE) FROM WASHINGTON STATE

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ABSTRACT. *Euxoa emma* Crabo & Crabo, allied to *Euxoa annulipes* (Smith), is described from North Central Washington. It is the second member of the *annulipes* group of the subgenus *Euxoa*. Adults and genitalia of both species are illustrated.

Additional key words: Columbia Basin, endemic

An undescribed species of the genus *Euxoa* was discovered in 2004 from north central Washington state. It is superficially similar to *Euxoa annulipes* (Smith) and the two species are closely related based on similarity of the genitalia.

MATERIALS AND METHODS

Male and female genitalia dissections were performed using the methods of Lafontaine (1987).

Euxoa emma Crabo & Crabo, new species

(Figures 1, 3a-b, 4a)

Diagnosis. The male genitalia of the new species (Fig. 3a) differ from those of *annulipes* (Fig 3b) in several respects. The valves of *emma* are wider than those of *annulipes*. In *emma* the mean ratio of length to mesial width is 4.12 (range 3.96-4.35) compared to 4.70 (range 4.42-4.95) for *annulipes*. The sacculus of *emma* is shorter, the harpes are longer, and the saccular extensions tend to be shorter than those of *annulipes*.

The mean ratio of the lengths of either harpe to the ipsilateral sacculus length is 0.78 for *emma* (range 0.75-0.82) compared to 0.66 for *annulipes* (range 0.63-0.71).

In the female (Fig. 4a), the anterior apophyses of *emma* tend to be shorter than those of *annulipes* (Fig. 4b), although this difference is not consistent. Females are best identified by superficial appearance and association with the males.

The two species are superficially similar but there are several subtle differences. The forewing of *E. emma* is warmer cream colored and less gray than that of *annulipes*. It is also smoother appearing than that of *annulipes* due to the presence of fewer black scales. The forewing lines are more distinct in *E. emma* than in *annulipes*.

The two species can also be separated by locality. *Emma* occurs in northern Washington whereas *annulipes* is found south of east central Oregon.

Description. Head, thorax, and abdomen nearly concolorous, light grayish tan, a darker spot on the dorsum of abdominal segment VIII; frons with thin transverse black line dorsal to frontal tubercle; palpi with first and second segments covered with mixture of black



FIG. 1. Adult of *E. emma*. Holotype ♂. Washington, Ferry County



FIG. 2. Adult of *E. annulipes*. ♂. Oregon, Malheur County, Namorf.

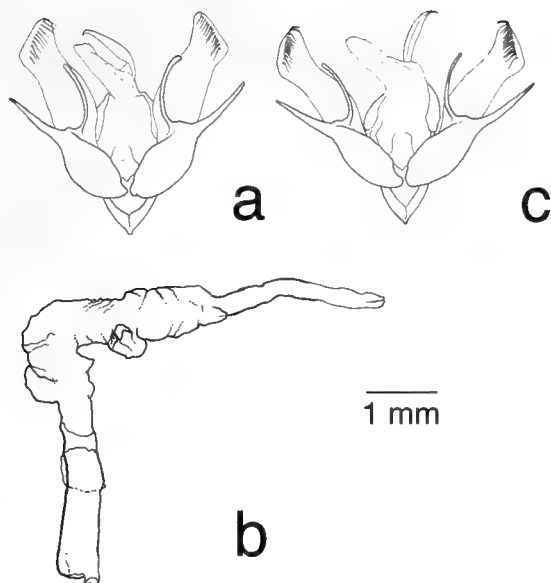


FIG. 3. Male genitalia. a) *E. emma* genital capsule b) *E. emma* aedeagus with everted vesica c) *E. annulipes* genital capsule

and grayish white scales, the third segment grayish white. Male antennae biserrate and bifasciculate; female filiform and ciliate ventrally; dorsal antenna of both sexes with two-toned light gray, dark gray to black tipped scales; scape grayish white. Legs proximal to tarsus grayish white to gray; tarsal segments black proximally and white distally, producing a striped appearance.

Forewing length: mean 14 mm, range 13-15 mm. Forewing with mixture of grayish white and light tan to reddish tan and occasional black and grey scales, appearing smooth light gray tan, a few specimens with warm red-brown suffusion, posterior margin and areas distal to postmedian line with variable darker gray suffusion (more in females), subterminal space darker gray than remainder of forewing, greatest on veins and darkest at costa, fringe ground color with two very faint gray lines. Basal, antemedian, median, and postmedian lines black, prominent at costa; basal line incomplete; antemedian line double with weak proximal component, toothed inwardly on veins, sometimes interrupted; median line most prominent, with convex contour below reniform spot; postmedian line double with weak distal component, prominently scalloped, toothed outwardly on veins; subterminal line faint, pale, evident mostly due to dark gray shading in adjacent spaces; terminal line a series of dark gray chevrons on veins. Claviform spot absent; orbicular spot pale gray white, barely traceable, evident mostly due to pale filling; reniform spot pale gray white, filled with pale gray and pale gray white scales. Hindwing ground color light gray white, terminal third, veins and discal spot darker gray, median line absent, fringe whitish.

Male genitalia (Fig 3a-b). Valves symmetrical, 4.12X as long as wide, wide mesially with convex dorsal margin, cucullus foot shaped with corona of 12-16 stout setae; sacculus 0.45X as long as valve and 2.1X as long as wide, oval, with convex dorsal margin; saccular extensions cylindrical, asymmetrical, projecting slightly dorsad, the right 0.33X and the left 0.31X as long as the valves; harpes C-shaped, symmetrical, 0.78X as long as sacculus. Uncus relatively short, expanded mesially, with thin hooked apex. Juxta shield shaped. Aedeagus 4X as long as wide; vesica 1.9X length of aedeagus, bent 90° dorsad subbasally, bearing single subbasal, median, and very small apical diverticula.

Female genitalia (Fig 4a). Ovipositor lobes triangular, stout, 1X as long as wide, medial margins with a short sclerotized flange, lateral surfaces covered with short thin setae and base with skirt of innumerable long hairlike setae which cover the lobes. Abdominal

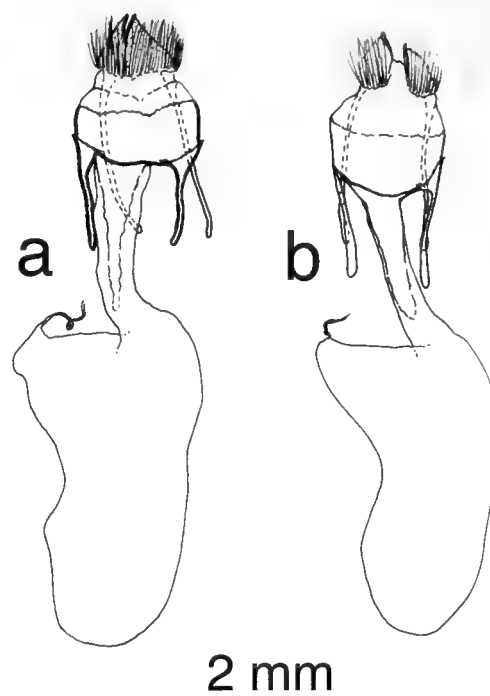


FIG. 4. Female genitalia. a) *E. emma* b) *E. annulipes*.

segment VIII short, 1X as long as ovipositor lobes; anterior apophyses 1.3X as long as abdominal segment VIII and posterior apophysis 3X as long as segment VIII. Ductus bursae 3X as long as wide and 3X as long as abdominal segment VIII, with dorsal and ventral sclerotized bands extending anteriorly from sclerotized ostium bursae. Bursa copulatrix unisaccate, 1.8X longer than the ductus bursae and 1.5X as long as wide, attached to ductus bursae at right posterior end and ductus seminalis at left posterior end.

Type Material. *Holotype*: ♂: WASHINGTON: Ferry Co., Lake Roosevelt S. Jim Mt, 47.900° N, 118.495° W, 24 June 2004, 2175', EK and LG Crabo, deposited in the Canadian National Collection (CNC), Ottawa, Ontario, Canada. *Paratypes*: 31 ♂, 10 ♀. Same data as holotype (21 ♂, 5 ♀); same locality and collectors as holotype, 6 July 2005 (10 ♂, 5 ♀). The paratypes are deposited in the CNC and the personal collection of Lars Crabo. Additional paratypes will be distributed to Washington State University, Pullman, Washington and the United States National Museum, Washington D. C.

Distribution and Biology. *E. emma* is known only from the type locality in Washington. It is a south facing slope near the Columbia River (Lake Roosevelt) with rocky outcrops. The rocks at this location are metamorphic (Stoffel et al 1991), not basalt which covers most of central Washington. The vegetation is sparse ponderosa pine (*Pinus ponderosa* Dougl. (Pinaceae)) forest with antelope brush (*Purshia tridentata* (Pursh) (Rosaceae)) understory.

The type series was collected at light in late June.

The early stages of *E. emma* are unknown.

Etymology. *Euxoa emma* is named in honor of Emma Crabo, the authors' youngest family member and an eager camper and moth collector. Emma helped to collect the type series and was directly responsible for

selecting the collecting site. Without her, this species might never have been discovered.

DISCUSSION

Euxoa is a very large genus of drably colored medium sized moths. Most species occur in dry temperate habitats, often open forests or steppe. Over three hundred species occur world wide, with over 175 in North America (Lafontaine 1987). Nearly one hundred of these occur in the Pacific Northwest. The North American *Euxoa* were revised by Lafontaine (1987), who defined subgenera and species groups.

E. emma is the second member of the *annulipes* species group in the subgenus *Euxoa*. This group is defined by characters of the male genitalia, specifically the hook shaped uncus, oval sacculus, and pincer-like harpe and saccular extension (Lafontaine 1987). The distributions of these two species are disjunct. *E. emma* occurs several hundred miles north of the range of *annulipes*. The latter is found in the intermountain West north to the Burnt River in east-central Oregon.

E. emma is endemic to Washington as it is known only from the type locality. The Columbia Basin region has several other endemic noctuid taxa, including

Copablepharon mutans Crabo & Lafontaine, *C. columbia* Crabo & Lafontaine, *C. spiritum spiritum* Crabo & Fauske, *C. viridisparva hopfingeri* Franclemont, and *Oncocnemis parvacana* Troubridge & Crabo. These are restricted to sand habitats, particularly dunes. *E. emma* is the only endemic species not restricted to sand and might therefore be more widely distributed. It should be sought at other locations in northern Washington and southern British Columbia, particularly in rocky habitats along the Columbia River.

ACKNOWLEDGMENTS

We are indebted to Dr. J. Donald Lafontaine who first identified *E. emma* as a new species and kindly encouraged us to name it.

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THE INFLUENCE OF FOREST FRAGMENTATION ON THE LOCATION OF OVERWINTERING MONARCH BUTTERFLIES IN CENTRAL MEXICO

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AND

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ABSTRACT. The endangered status of the overwintering phenomenon of monarch butterflies (*Danaus plexippus* L., Lepidoptera, Nymphalidae, Danainae) that migrate from eastern North America to Mexico has resulted from anthropogenic degradation of the forests where the butterflies spend the winter. During their five month overwintering period, the monarchs need to remain inactive and clustered in semi-closed or intact forests to reduce mortalities caused by freezing, lipid depletion and predation. We analyzed forest and landscape metrics to determine the forest characteristics preferred by monarchs when colonizing their overwintering sites.

Forest metrics at two different spatial scales were derived from a forest cover map generated from multi-spectral IKONOS satellite imagery. Landscape metrics of forest areas occupied by monarch colonies during the 2002–2003 overwintering season were significantly different than randomly selected non-colony areas. Colony sites had greater forest cover (> 60%), though even these forest patches were fragmented and thinned. Immediate colony areas (100 m radial from colony center) exhibited greater forest coverage in more closely spaced patches than did extended colony areas (1 km radial from colony center). Forest degradation was more evident in the extended colony landscapes than the immediate colony areas. Though forests in many of the immediate colony areas appeared to have been thinned and selectively logged, most have a semi-closed canopy.

Conservation efforts should focus on protecting the forest canopy. Continued forest degradation is likely to increase mortality for the eastern North American population of monarch butterflies, and may cause extinction both of its migration and the spectacular overwintering phenomenon in Mexico.

Additional key words: butterfly site selection, forest quality, habitat degradation, FRAGSTATS, IKONOS satellite imagery, landscape metrics

The destination of the fall migration of North American monarch butterflies that breed east of the Rocky Mountains was discovered in January 1975 by cooperators of Urquhart and Urquhart (1976, 1978). We now know that up to a billion butterflies migrate southward out of their nearly one million square mile breeding range (Brower, 1999a) and form overwintering colonies on approximately twelve separate densely forested mountain massifs in Central Mexico (Brower *et al.*, 2002; Slayback *et al.*, 2007). Recent data indicate that the colonies are astoundingly dense, with up to 50 million butterflies per hectare (Brower *et al.*, 2004). The overwintering period lasts from November through March and is a unique biological phenomenon (Brower and Malcolm, 1991). Butterflies en route to the overwintering grounds can be up to four generations removed from their migrating ancestors, and frequently return to the same areas of trees as did their predecessors (Brower, 1986). The individual monarchs that survive the overwintering season return to the Gulf

Coast states in early to mid-March when their larval food source, milkweed, is again available (Malcolm, 1993).

All known overwintering sites in Mexico occur in the states of Michoacán and Mexico, within an area of approximately 10,000 km² (Brower *et al.*, 2002; Bojórquez-Tapia *et al.*, 2003). This area, part of which is shown in Fig. 1, is in the central part of the Neo-Transvolcanic belt that crosses Mexico just south of the Tropic of Cancer (Brower, 1995). Monarchs colonize in dense, protective, semi-closed oyamel fir forests (*Abies religiosa* H.B.K., Pinaceae) in order to conserve energy and avoid freezing and desiccation during the winter months (Masters *et al.*, 1988; Weiss *et al.*, 1991; Alonso-Mejia *et al.*, 1997). Presumably, after the last glacial retreat, these oyamel forests retreated to the higher peaks in this area (Slayback *et al.*, 2007) and are now restricted to elevations ranging from 2700 m to 3400 m and occur within the summer cloud belt (Brower, 1995). The oyamel forest micro-climate protects the butterflies from severe warm and freezing weather, and also from wind and desiccation. The cool temperature that is moderated by the high altitude forest canopy limits butterfly activity, thereby conserving their lipid reserves. The extreme concentration of the monarchs in so few small areas during the overwintering season makes the entire Eastern North American population vulnerable to minor perturbations to the forest system (Brower, 1977; Brower and Malcolm, 1991; Malcolm, 1993).

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Over the last few decades prior to 1986, forest degradation increased in and near critical monarch colony sites, primarily from logging for domestic or commercial use and clearance for cattle grazing or agriculture (Snook, 1993). Neither a 1986 presidential decree nor the 2000 Monarch Butterfly Biosphere Reserve (MBBR) (Fig. 1) has protected the colony sites from ascendant illegal logging. Destruction of the forest continued after the 1986 decree due to ignorance and deliberate exploitation (Malcolm and Zalucki, 1993b; Brower *et al.*, 2002). The current extent and increasing rate of forest degradation and fragmentation within and around the core overwintering sites is of great concern (Brower *et al.*, 2002; Ramírez *et al.*, 2003; Honey-Roses and Galindo, 2004; Anon., 2006). These destructive practices not only remove sections of the habitat by clear-cutting, but they also degrade the forest through thinning and selective logging. Reductions in tree canopy cover alter the forest micro-climate, increase both exposure and access by predators, and ultimately lead to a severe increase in butterfly mortality, especially during strong winter storms (Calvert *et al.*, 1983; Fink *et al.*, 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Bebi *et al.*, 2001; Brower *et al.*, 2004). Monarchs are also sensitive to small perturbations that allow more sunlight to penetrate their overwintering environment. This can warm the butterflies and cause more rapid burning of their lipid reserves, which can become critically low during the overwintering season (Alonso-Mejia *et al.*, 1997). The loss and fragmentation of the forest has impacted many of the traditional colony sites, some of which have moved, while several others have disappeared altogether (L. Brower *et al.*, unpublished data). Continued reductions in forest cover may soon negatively affect the entire overwintering North American monarch populations, both east and west of the Rocky Mountains (Calvert *et al.*, 1983; Brower and Malcolm, 1991; Snook, 1993; Brower *et al.*, 2002; Brower and Pyle, 2004).

As deforestation throughout the world continues to increase at alarming rates (Wilson, 2002), research into the ecological impacts caused by forest fragmentation on specific species has also increased. There are two primary components to fragmentation, total reduction of specific habitat types, and the reduction of habitat into small isolated patches (Meffe *et al.*, 1997). Even slight perturbations to the quality of the habitat caused by initial fragmentation can affect the availability of resources for sensitive species using or living within the habitat area (Hargis *et al.*, 1999; Ramírez *et al.*, 2003; Ramírez *et al.*, 2005).

Early habitat fragmentation studies concentrated on remnant habitat patches (Diamond, 1975; Verboom and

Van Apeldoorn, 1990), while more recent studies have focused on the configuration of habitat patches (Hargis *et al.*, 1999). Many fragmentation studies are consistent in stating that no single metric can be used to describe the response of a species to alterations in forest configuration (Haines-Young and Chopping, 1996; Gustafson, 1998; Hargis *et al.*, 1999). The specific metrics, or combination of metrics, used to answer a particular research question need to be determined separately for each independent study. For example, Luoto *et al.* (2002) used a number of landscape metrics derived from satellite imagery, including habitat composition and largest patch size. They discovered that spatial variation of habitat (which was not originally considered a critical factor) is the dominant factor in determining the distribution of Clouded Apollo butterflies (*Parnassius mnemosyne* (Linnaeus), Papilionidae) in southwestern Finland.

Forest fragmentation can have a critical impact on the survival of the monarch butterflies (Calvert and Brower, 1981; Calvert *et al.*, 1982; Weiss *et al.*, 1991; Brower, 1999b; Ramírez *et al.*, 2003). However, limited research has been conducted on the detailed forest requirements of colonizing monarchs at the landscape scale and, therefore, the full extent to which forest degradation affects the overwintering monarchs remains unknown.

We addressed two general research questions in this paper: (1) What are the forest fragmentation characteristics of monarch colony overwintering sites and how do they differ relative to non-colony sites? (2) How do characteristics of forests utilized by monarch colonies vary at two different spatial scales, one that is an immediate (100 m) and one that is an extended (1 km) radial area, as measured from the center of the colony?

The answers to these questions can help explain the relationship between forest degradation caused by human practices, i.e. clearcutting and thinning, and monarch colony locations. Answering these questions will also lead to a better understanding of the monarch's overwintering biology, which in turn should lead to more effective conservation efforts to prevent the loss of the monarch's migration and overwintering behavior that clearly has become a severely endangered biological phenomenon (Brower and Malcolm, 1991; Honey-Roses and Galindo, 2004).

METHODS

The study area. The general study area is the Monarch Butterfly Biosphere Reserve (MBBR) as decreed by Mexican President Ernest Zedillo (2002) and is located in central Mexico in the states of

Michoacán and Mexico. Our primary study area was delineated by the extent of coverage of specific IKONOS satellite imagery (Fig. 1).

Colony and non-colony location data. A number of trained field personnel from the MBBR and Universidad Nacional Autónoma de México (UNAM)

recorded the locations of monarch colonies (L. Brower, unpublished data) between 31 December 2002 and 8 January 2003. The team first conversed with local people to locate possible colonies and then traversed on foot through the forest to determine whether colonies were actually present. Colony locations were recorded

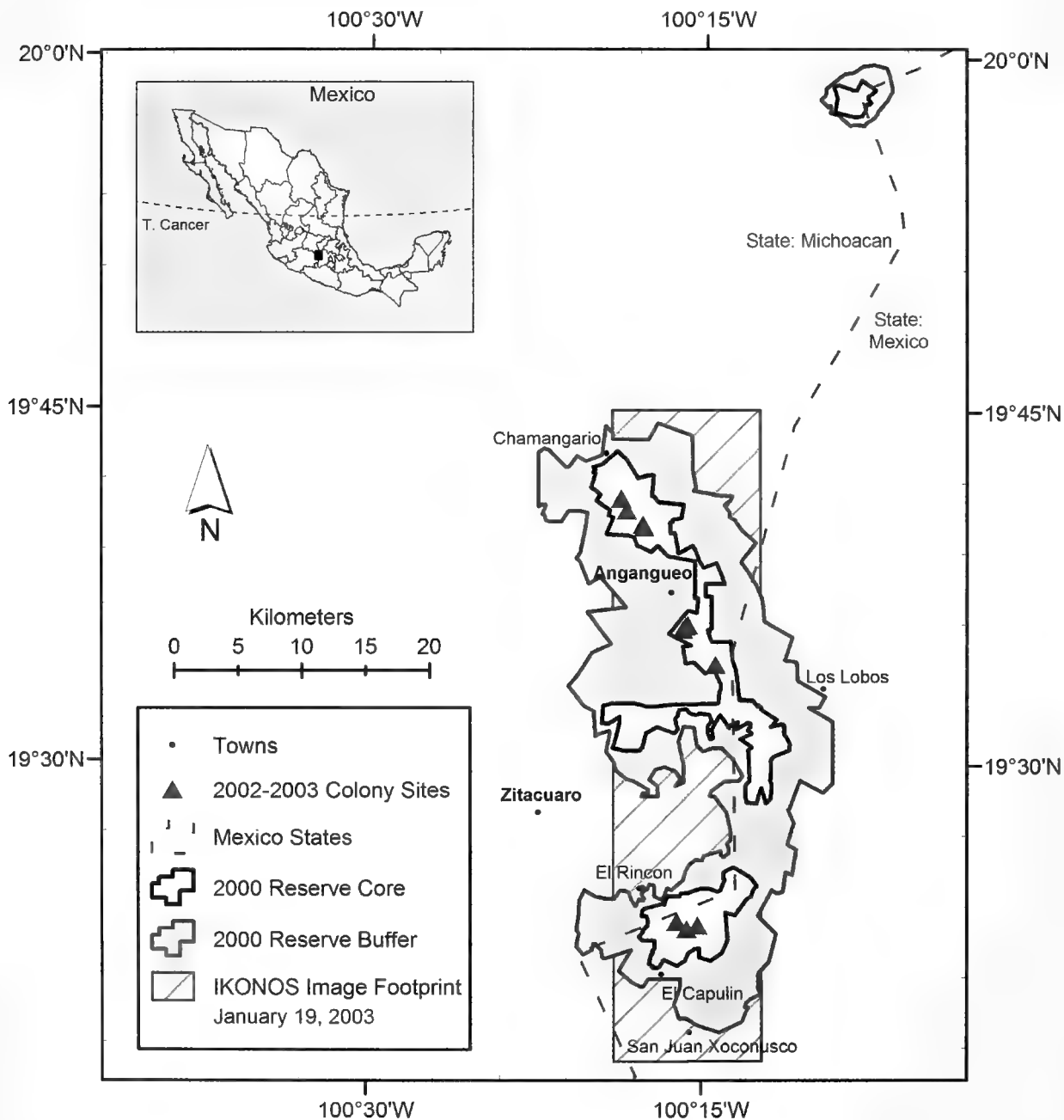


Figure 1. Location of the Monarch Butterfly Biosphere Reserve zones showing 11 overwintering sites located during the 2002–2003 season (the third black triangle from the top represents two sites and the fourth three).

using a Garmin Global Positioning System (GPS) with an estimated 5–15 m horizontal positional error. The error is a function of the instruments positional accuracy (Garmin, 2003) and a reduced signal caused by dense canopy cover.

To account for a broader range of forest conditions (Pereira and Itami, 1991), in addition to data from the 11 observed colony locations, we generated 33 random sample points, referred to as ‘available’ or likely non-colony points for the MBBR area. These non-colony locations may have been utilized by monarchs during the study period, but extensive aerial and field surveys during four subsequent overwintering seasons (Slayback *et al.*, 2007; and Slayback and Brower, in press) indicated that no colonies were located at these sites.

Fine spatial resolution satellite data. IKONOS imagery has been used in many studies to map and classify land cover categories (Franklin *et al.*, 2001; Song and Woodcock, 2002; Asner and Warner, 2003; Roberts *et al.*, 2003; Thenkabail *et al.*, 2004). The high spatial resolution (1 m) of the IKONOS panchromatic data enables individual plant canopies to be detected (Asner and Warner, 2003). IKONOS multi-spectral image data, with a nominal ground sampling distance of 4 m also has a very high spatial resolution by satellite image standards (Cablak and Minor, 2003), and provides information that can be utilized to separate subtle differences within cover types, such as tree cover, urban areas, or riparian zones (Goetz *et al.*, 2003).

We acquired IKONOS panchromatic and multi-spectral imagery (11-bit radiometric quantization) of the Central Mexico study area for 13 January 2003, coinciding with the winter dry season for which the colony data were recorded. We ortho-rectified the IKONOS imagery to the UTM WGS84 coordinate system, using a digital elevation model based on a 12 m grid. The ortho-rectification procedure accounted for the extreme relief displacement in the study area and transformed the image so that it was planimetrically correct and therefore aligned to the monarch colony site locations. A scene-specific IKONOS rational polynomial coefficients (RPC) model was used in the ortho-rectification procedure to define the interior and exterior geometry of the sensor (Dial *et al.*, 2003). The root mean square error of the ortho-rectification was approximately 2 pixels (or 8 m), based on 124 independent checkpoints.

We visually interpreted digital color imagery (2 m spatial resolution) produced by scanning color aerial photographs captured by Armando Peralta of UNAM in 2003, and IKONOS panchromatic imagery (1 m spatial resolution) captured by Space Imaging, Inc. in 2003, to

identify canopy reference data points (randomly generated) as either open or closed forest. Sample data (1200 points) were randomly generated to achieve approximately one point per 50 hectares. Congalton (1991) suggested that at least 250 reference pixels are required to determine the mean accuracy to within + 5% (assuming an overall accuracy of 85%). Thus, we used three-quarters of the canopy reference data (900 points) to train the image classification processes, and the remaining one-quarter (300 points) to validate the output classification image.

We produced a map of forest and non-forest pixels using an expert classifier approach with inputs from supervised and unsupervised classification procedures, as well as by selecting class-boundary thresholds for spectral and spatial transform images (Stow *et al.*, 2003). The fine 4 m spatial resolution of the IKONOS multi-spectral imagery enabled tree canopy cover and occasionally individual trees to be identified. To effectively distinguish tree canopy from shadow or agricultural vegetation, the expert classifier incorporated both IKONOS spectral band and image transform data, such as the normalized differential vegetation index (Read and Lam, 2002; Staus *et al.*, 2002; Goetz *et al.*, 2003; Chen *et al.*, 2004), tasseled cap indices (Horne, 2003), and texture enhancement (Franklin *et al.*, 2000; Franklin and Wulder, 2002). We integrated these image-based products into the ERDAS Knowledge Engineer software tool to produce a digital map consisting of forest and non-forest cover classes. We generalized this two-category map through the elimination of single pixels of a given class, so that forest fragmentation parameters could be extracted more effectively and efficiently. The accuracy of the classification was determined from 300 randomly generated points visually interpreted as forest or non-forest from the IKONOS panchromatic image and the aerial photographs. While image classification procedures were used to extract forest canopy patches, the canopy/non-canopy classification process and resultant map are referred to as forest and non-forest areas in this study, the more common terminology used in forest fragmentation studies.

Fragmentation analysis. To quantify the pattern of forest cover, we used FRAGSTATS version 3.3 (McGarigal *et al.*, 2002) to create 250 landscape metrics, such as patch size, edge length, and patch density, from the forest and non-forest map. For those unfamiliar with the FRAGSTATS procedure and landscape metrics terminology, see Anon. (2007). The landscape metrics were calculated at the IKONOS pixel resolution (4 m) and extracted at two different scales, immediate colony (circle with 100 m radius) and extended colony (circle

with 1000 m radius) centered on the 11 monarch colony and 33 random non-colony sites (Fig. 2). The radial distance used to generate the immediate colony landscapes was determined from the average radial size of colonies (100 m) and the estimated penetration range of edge effects, such as changes to microclimate and predation rate (Chen and Franklin, 1990; Staus *et al.*, 2002). The radial distance for the extended colony landscapes was based on the estimated active range of monarchs within the overwintering area. Research shows that most colonies are located within 1 km of a water source to and from which monarchs regularly fly (Calvert *et al.*, 1983; Masters *et al.*, 1988; Calvert and Lawton, 1993; Alonso-Mejia *et al.*, 1998; Brower *et al.*, unpublished data).

FRAGSTATS metrics were generated from the classified image representing forest cover (Fig. 3) at

both the class-level (forest only) and landscape-level. Class-level metrics refer to the relationship between forest and non-forest pixels, while landscape-level metrics refer to the composition or configuration of forest and non-forest land within a specified area. Similar to the methods of Imbernon and Branthomme (2001), several steps were followed to select appropriate metrics. We generated a correlation matrix for all the landscape pattern metrics and removed redundant metrics where correlation values were greater than 0.8. Descriptive and inferential statistics were used to compare landscape pattern metrics for colony and non-colony ('available') sites. Based on interpretation of statistical boxplots, metrics with similar distributions for colony and non-colony forest areas were removed from further analysis, i.e., were deemed to have no explanatory power for colonization requirements. We

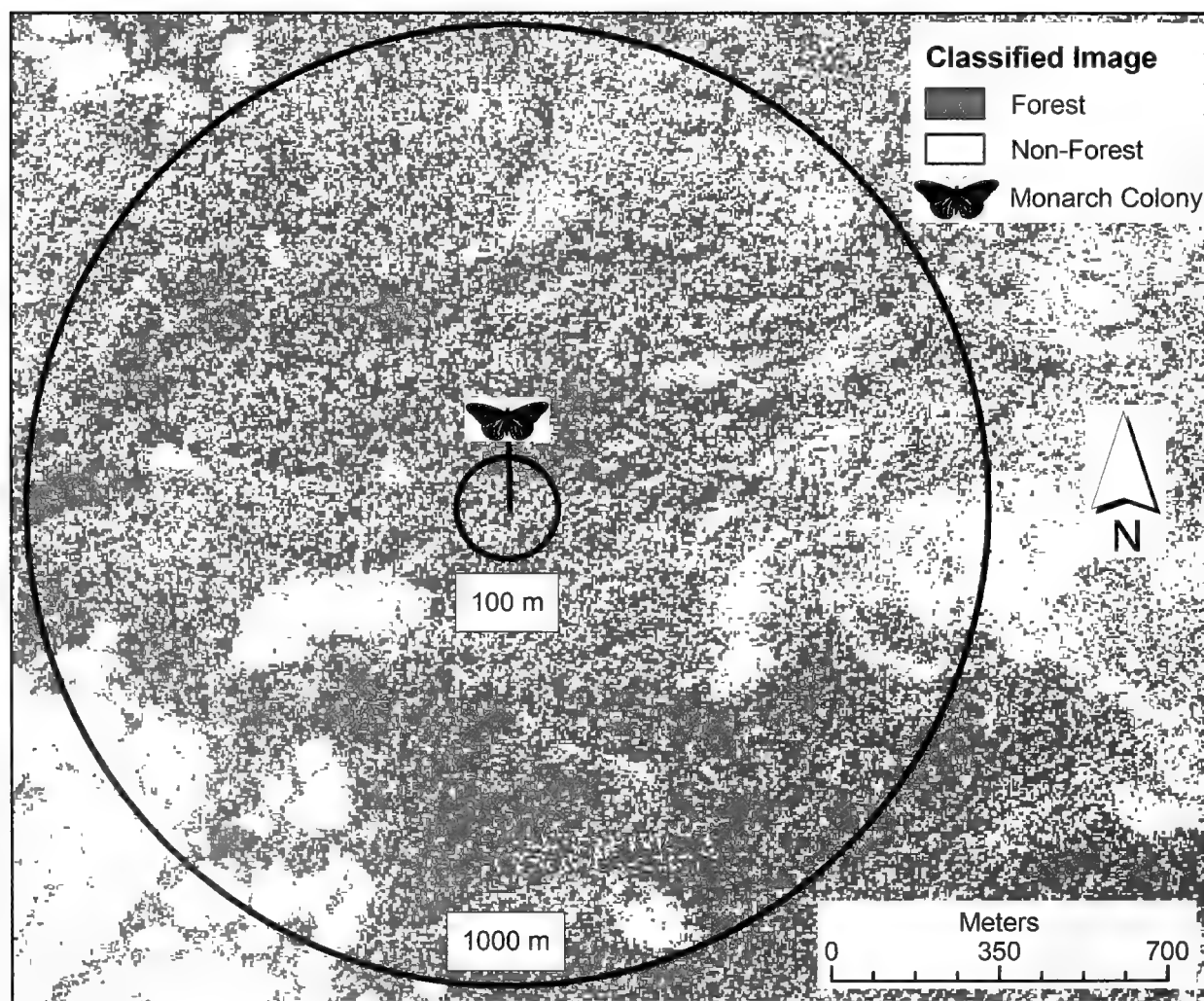


Figure 2. Concentric radial landscapes extend from the monarch colony centroid.

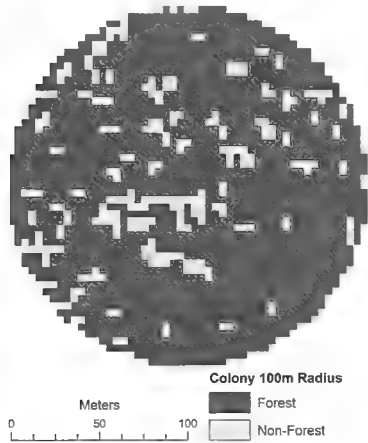


Figure 3. An example of colony areas at the immediate colony scale (100 m radius).

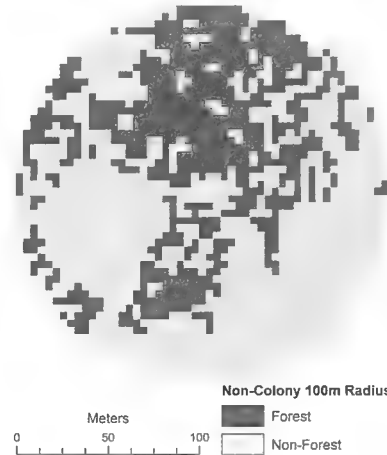


Figure 4. An example of non-colony areas at the immediate colony scale (100 m radius)

used the small sample Student's *t*-tests and one-sided unequal variance Welch's tests to compare the mean values of the colony and non-colony landscapes for the remaining metrics. Metrics showing no significant difference ($p > 0.05$) between the landscapes were removed. The final set of selected metrics indicated specific monarch colony habitat characteristics, and differentiated between colony and non-colony sites. The complete set of metrics used to quantify landscape pattern, structure and composition at both the single-class (forest) and multiple-class (forest and non-forest,

indicating landscape heterogeneity) are listed in Table 1 (for a detailed explanation of FRAGSTATS metrics, see Williams, 2005, Appendix D). Abbreviations for landscape metrics listed in Table 1 are provided within parentheses throughout the Results section.

We also used Student's *t*-tests to assess differences in landscape metrics for the immediate and extended colony areas. This was done to explore whether or not differences were evident in the spatial characteristics of forests required by the monarchs to colonize (immediate colony) and to fly to water sources

Table 1. Selected FRAGSTATS fragmentation metrics, (modified from McGarigal and Marks, 1994, p. 24).

Patch density and size metrics		Core area metrics	
PD	Patch Density (#/100 ha)	TCA	Total Core Area (ha)
PLAND	Percentage of Landscape (%)	CORE	Core Area
AREA	Patch Area Distribution	CAI	Core Area Index Distribution
		NDCA	Number of Disjunct Core Areas (#)
		DCAD	Disjunct Core Area Density (#/100 ha)
Edge metrics		Isolation and proximity metrics	
ED	Edge Density (m/ha)	ENN	Euclidean Nearest Neighbor Distance Distribution
Shape metrics		Contagion metrics	
LSI	Landscape Shape Index	AI	Aggregation Index (%)
GYRATE	Radius of Gyration Distribution	PLADJ	Percentage of Like Adjacencies (%)
SHAPE	Shape Index Distribution	Diversity metrics	
FRAC	Fractal Dimension Index Distribution	PRD	Patch Richness Density (#/100 ha)
CIRCLE	Related Circumscribing Circle Distribution		
CONTIG	Contiguity Index Distribution		
Connectivity metrics			
COHESION	Patch Cohesion Index		

(extended colony) during the 2002–2003 overwintering season.

The comparison of colony to non-colony areas was conducted in order to determine (1) whether specific forest characteristics affect where monarch colonies are located, or (2) whether colony locations are determined independently of forest characteristics, i.e. forest characteristics in colony and non-colony areas are not significantly different. The comparison of immediate and extended colony areas characterized the whole environment in which the monarchs reside and interact whilst overwintering, rather than just their colony site. This may indicate that for an area to be suitable for monarchs to colonize, the forest composition and configuration at both the immediate and extended scales must match the monarchs' forest requirements.

RESULTS

Classification accuracy. Overall classification accuracy values for the forest/non-forest map derived from IKONOS multi-spectral data were 92.3% and 88.6%, with kappa values of 0.847 and 0.766, when compared against reference data generated from visual interpretation of IKONOS panchromatic imagery and aerial photography, respectively. The kappa statistic incorporates omission and commission errors and corrects for chance agreement between reference and classified data (Jensen 1996, Lillesand and Kiefer 2000).

The average overall classification accuracy estimated with the two reference sets was 90.4% and the average kappa value was 0.806. For the forest category, user's (commission) accuracy values were 92.3% and 87.3%, and producer's (omission) accuracy values were 92.9% and 92.9%, based on IKONOS panchromatic imagery and aerial photography, respectively. For the non-forest category, user's (commission) accuracy values were 92.4% and 90.3%, and producer's (omission) accuracy values were 91.8% and 83.2%, based on IKONOS panchromatic imagery and aerial photography, respectively. All of these measures suggest that the forest cover map is a highly accurate representation of forest cover in 2003 and a reliable source for quantitatively assessing forest fragmentation.

Influence of forest fragmentation on colony locations. Examples of the more discriminatory landscape metrics, their distributions, and significance levels in relation to variations in colony and non-colony sites at the 100 m radial scale are shown in Table 2. Significance levels for all other metrics are listed in the text. At this scale, colony sites contained more forest (PLAND) in fewer patches (PD) than the non-colony sites. In addition the forest patches of the colony sites were more complex (FRAC 0.0332, TCA), elongated

(GYRATE 0.0374), and irregular in shape (SHAPE 0.0417). However, they were also less contiguous (CONTIG 0.0396) and aggregated (LSI, AI) than the non-colony sites. The aggregation index (AI) (approximately 73%) indicated that colony sites contained closely spaced patches, but in general, colony sites were less aggregated than non-colony sites. This may be due, in part, to aggregated non-forest patches at the non-colony sites. Despite high edge densities (ED) within colony sites, the high percentage of forest in combination with the close proximity of forest patches (AI) appears to provide habitat conditions suitable for monarch colonies (e.g., good canopy cover and protection). In some cases the negative effects of edge (or high edge density, ED), such as high predation, may be reduced or counter-acted by positive edge effects, such as slight increases in insolation, when patches are located in close proximity (Weiss *et al.*, 1991).

Examples of the more discriminatory landscape metrics at the 1 km radial scale are shown in Table 3. Colony landscapes contained smaller forest patches (AREA, ED 0.0042), which were more complex (FRAC), elongated (GYRATE), irregular in shape (SHAPE 0.0009), contained less core area (CORE 0.0005), and were higher in density (PD 0.0499), than the non-colony sites. The forest canopy in the extended colony landscape was more highly fragmented than the non-colony sites, there were fewer core areas (CORE 0.0005) and as a result, much of the forest area contained a high proportion of 'edge'. The forest patches in the colony landscapes were less contiguous (CONTIG), connected (COHESION 0.0418), and circular (CIRCLE 0.0111) than the non-colony landscapes, but were also less isolated (ENN). Low patch connectivity (COHESION) may indicate that when monarchs fly through the landscape they use both the forest and non-forest patches (Masters *et al.*, 1988). Shape complexity (SHAPE, GYRATE, FRAC 0.006) and associated edge density (PD) were higher for colony landscapes, but the patches were less isolated (ENN). However, there is no significant difference in the percentage of forest cover (PLAND 0.1717) between the colony and non-colony landscapes.

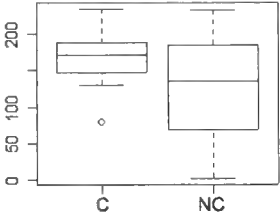
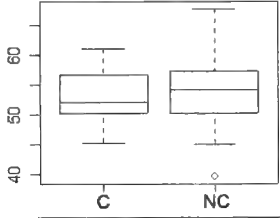
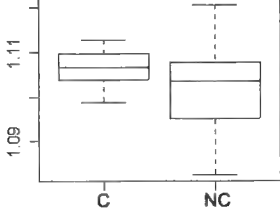
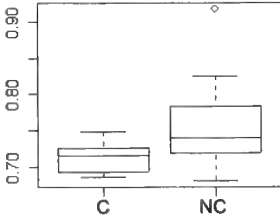
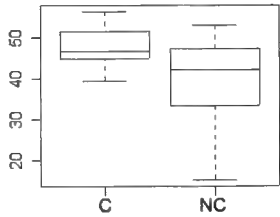
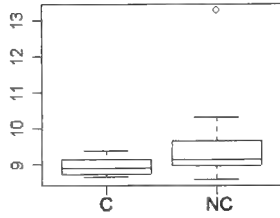
The top priority for monarchs seems to be the colonization of immediate sites that contain the greatest total forest cover even though many of these forest areas are fragmented and appear to be thinned.

Comparison of fragmentation at site and landscape scales. The monarchs seem to have different forest composition and configuration requirements for areas in which they colonize, than the more extensive areas in which they interact and move.

Table 2. Selected fragmentation metrics used to compare colony and non-colony sites at the 100 m radial scale.

Landscape Metrics	T-test (2-tail)	Boxplot	Ecological interpretation of colony landscapes
Class Level (Forest Patches)			
Edge Density (ED)	0.0385		greater edge density
Patch Density (PD)	0.0413		fewer patches
Percentage of Landscape (Forest) (PLAND)	0.0455		greater forest cover
Landscape Level (Forest and Non-Forest patches, indicating landscape heterogeneity)			
Landscape Shape Index (LSI)	0.0242		less aggregated
Total Core Area (TCA)	0.0376		less core area
Aggregation Index (AI)	0.0374		less patch aggregation
<p>C = Colony site, NC = Non-colony site T-test significance difference < 0.05</p>			

Table 3. Selected fragmentation metrics used to compare colony and non-colony sites at the 1 km radial scale.

Landscape Metrics	T-test (2-tail)	Boxplot	Ecological interpretation of colony landscapes
Class Level (Forest Patches)			
Patch Area Distribution (AM)	0.0311		Landscape: Smaller patches
Radius of Gyration Distribution (AM)	0.0083		Patch: Less elongated and compact
Fractal Dimension Index Distribution (MN)	0.0007		Landscape: More complex and convoluted
Landscape Level (Forest and Non-Forest patches, indicating landscape heterogeneity)			
Contiguity Index Distribution (AM)	0.0006		Landscape: Less contiguous
Shape Index Distribution (AM)	0.0007		Patch: More irregular and complex
Euclidean Nearest Neighbor Distance Distribution (MN)	0.0068		Patch: Less isolation

Distribution metrics measure the aggregate properties of the patches: FRAGSTATS computes the following: (1) mean (MN), (2) area-weighted mean (AM), (3) median (MD), (4) range (RA), (5) standard deviation (SD), and (6) coefficient of variation (CV).

T-test significance difference < 0.05.

The metrics used for this analysis are summarized in Table 4.

In general, the immediate colony sites contained a greater percentage of forest cover (PLAND), had greater edge densities (ED), had more elongated

(GYRATE), complex (FRAC), irregular (SHAPE), and less compact (CIRCLE) forest patches than the 1 km colony landscapes. However, they also had larger core areas (CORE) and were less isolated (ENN) than the extended colony landscapes. The immediate colony sites

Table 4. Comparison of landscape metrics between immediate and extended colony landscape scales.

Landscape Metrics		T-test (2-tail)	Ecological Interpretation of Landscapes (immediate colony > or < extended colony)
<u>Class-Level Metrics (Forest Patches)</u>			
PLAND	Percentage Land Cover (Forest)	0.002	> percentage forest cover
ED	Edge Density	0.004	> edge density
GYRATE	Radius of Gyration Distribution (MN)	0.011	> elongation and compaction
SHAPE	Shape Index Distribution (MN)	0.000	> irregularity and complexity
FRAC	Fractal Dimension Index Distribution (MN)	0.011	> complexity and convolution
FRAC	Fractal Dimension Index Distribution (SD)	0.000	> heterogeneity in patch fractal dimensions
CIRCLE	Related Circumscribing Circle Distribution (MN)	0.017	< circularity and compaction
CORE	Core Area Index Distribution (MN)	0.036	> patch core area
ENN	Euclidean Nearest Neighbor Distance Distribution (MN)	0.019	< patch isolation
COHESION	Patch Cohesion Index	0.020	< connectivity and greater division
<u>Landscape-Level (Forest and Non-Forest patches, indicating landscape heterogeneity)</u>			
PD	Patch Density	0.006	> patch density
AREA	Patch Area Distribution (MN)	0.042	< patch size
GYRATE	Radius of Gyration Distribution (MN)	0.004	> elongation and compaction
GYRATE	Radius of Gyration Distribution (SD)	0.002	> uniformity in gyration
SHAPE	Shape Index Distribution (MN)	0.014	> irregularity and complexity
CORE	Core Area Index Distribution (MN)	0.009	> patch core area
CORE	Core Area Index Distribution (SD)	0.000	> heterogeneity in patch core area
COHESION	Patch Cohesion Index	0.000	< connectivity and greater division

Distribution metrics measure the aggregate properties of the patches: FRAGSTATS computes the following: (1) mean (MN), (2) area-weighted mean (AM), (3) median (MD), (4) range (RA), (5) standard deviation (SD), and (6) coefficient of variation (CV).

T-test significance difference < 0.05

also had less space between patches, which suggests that the extended colony landscapes were more open, possibly due to greater forest degradation. In general, the immediate colony sites contained forest patches that were greater in density and more complex, irregular and small in shape than the extended landscapes, suggesting that the immediate landscapes may have been more fragmented than the extended landscapes. Some landscape metrics (ED, PD and COHESION) suggest that the immediate colony landscapes were patchier than the extended sites. However, when combined with their greater total forest cover (PLAND), many of the immediate colony landscapes may actually be considered less fragmented. This suggests that forest patch composition should be assessed along with forest patch configuration to properly characterize forest fragmentation.

In addition to the significantly greater percentage of forest cover in immediate colony areas, the range of forest cover was different for the two spatial scales selected for fragmentation analysis (Table 5). The majority of the immediate colony sites had between 60% and 75% forest cover, while the majority of the extended colony landscapes had between 54% and 66% forest coverage. The 2002–2003 colony extended landscapes were more frequently associated with moderate forest cover than the immediate colony landscapes, suggesting that the monarchs utilized areas of forest in the extended landscapes that were somewhat fragmented or semi-open.

DISCUSSION

Reliability of the fragmentation analysis. The reliability of the fragmentation analysis was dependent on the accuracy of image georeferencing and classification procedures for the forest and non-forest pixels. This was challenging in a few areas, particularly for northwest facing slopes. However, the high average overall accuracy of 90.44% and a kappa value of 0.8064 for the image classification suggest that the satellite image-driven map of forest cover was suitable for

fragmentation analysis.

Colony and non-colony forest characteristics. Certain forest configuration and composition characteristics of the colony sites and surrounding landscapes were significantly different than those of the randomly generated non-colony ('available') sites and landscapes. In general, the analysis suggests that the monarchs colonize areas containing at least 60% forest cover, with trees frequently arranged in closely packed, small irregular patches. However, as most of the MBBR has been subjected to some level of forest degradation and ongoing forest incursions (Snook, 1993; Brower *et al.*, 2002; Ramírez *et al.*, 2003; Honey-Roses and Galindo, 2004; Ramírez *et al.*, 2005), many of the current overwintering sites may contain sub-optimum colonizing conditions and may have only represented the best forests available.

Forest characteristics of immediate and extended colony areas. The immediate and extended colony areas had significantly different forest configuration characteristics. Monarchs appear to have colonized the immediate sites that had the maximum amount of forest cover, provided that the location also had suitable environmental conditions such as close proximity to water (< 1 km), cool moist micro-climate, south-west facing slopes and an approximate elevation of 3000m (Bojórquez-Tapia *et al.*, 2003). This is possibly because greater forest cover in the immediate colony sites enables larger numbers of monarchs to be supported on branches or trunks, and the higher the density of monarchs in the clusters, the greater protection afforded against weather and predators.

Differences in forest pattern or fragmentation between the two spatial scales of analysis may be related to actual differences in forest disturbances, deforestation practices, and/or total forest cover. The selective logging of larger trees may have occurred within the densely forested colony sites (Brower *et al.*, 2002; Honey-Roses and Galindo, 2004), resulting in fragmented and closely spaced forest patches, as quantified by the landscape metrics (ED, COHESION

Table 5. Frequency distribution of forest cover (PLAND) for colony sites.

Colony Cover (%)	Cover Type	Minimum	1st Quartile	Mean	Median	3rd Quartile	Maximum
100 m radius	Forest	42.05	59.88	67.53	67.66	74.36	90.28
	Non-Forest	9.72	25.64	32.47	32.34	40.12	57.95
1 km radius	Forest	48.27	53.69	59.72	58.83	65.94	74.74
	Non-Forest	20.21	34.06	39.36	41.17	46.31	51.73

and PLAND) (Calvert *et al.*, 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Bebi *et al.*, 2001).

The most noteworthy statistical difference between the immediate and extended colony areas was the forest composition metric PLAND (percentage of forest cover). Forest cover was both greater within the immediate colony sites and more uniform (ENN) than in the extended colony landscapes. This suggests that the monarchs tended to colonize areas where forest canopy protection immediately surrounding their colony was the greatest and where evenly spaced forest patches in the extended landscape (used occasionally by the overwintering monarchs to fly out to find water or food) provided some forest protection to the immediate colony area (Calvert *et al.*, 1979; Masters *et al.*, 1988; Weiss *et al.*, 1991). Many of these immediate colony areas were fragmented and had been thinned (Honey-Roses and Galindo, 2004).

Colony forest fragmentation caused by forest degradation. The fragmentation of the forest caused by anthropogenic forest degradation or natural forest disturbances (e.g., fire or tree fall) could not be distinguished. However, the monarch colony fragmentation analysis was used to indicate or infer the impact that various disturbance and forest degradation practices may have had on the location of monarch colonies at two different scales.

The immediate colony sites contained a high percentage of forest (PLAND) in many closely spaced forest patches (AI, PD). If forest degradation had occurred in these sites, it was most likely to have been the result of forest thinning and selective logging practices (Honey-Roses and Galindo, 2004). In general, the extended colony landscapes were subject to more forest disturbance, degradation and deforestation than the immediate colony areas. Tree clearance practices seem to have been more common in the extended colony landscapes (Brower *et al.*, 2002; Honey-Roses and Galindo, 2004), as indicated by the simple forest patch shapes (GYRATE, FRAC, SHAPE, CIRCLE) and lower total percentage of forest cover (PLAND) than the 100 m landscapes. In addition, the high patch density (PD) and low isolation (ENN) of forest patches in the 1 km landscapes indicate that forest degradation caused by forest thinning or selective logging had also taken place in the remaining or remnant forest patches.

In general, deforestation seems to be more detrimental than forest thinning for the overwintering monarchs, if it occurs close to persistent colony sites, because it increases the impact of edge effects on the monarch colonies (Calvert and Brower 1981; Calvert *et al.*, 1981, 1982). However, forest thinning can also have a negative effect on the monarch colonies, as it

decreases the protection afforded by the forest canopy. Though the monarchs may continue to colonize a site that has been subject to some forest thinning, this thinning may have adverse effects on the monarch colony population, such as reduced survival (Anderson and Brower, 1996). These effects have not been adequately studied and documented.

Despite widespread forest degradation, the MBBR is still able to provide some suitable habitat for monarchs to colonize. However, further forest degradation activity within the MBBR could negatively impact the colonizing monarchs (Alonso-Mejía *et al.*, 1993). Though logging is legally restricted in the MBBR buffer and supposedly prohibited in the MBBR core zones, extensive illegal logging and clear cutting activities continue. The effects that these activities have on the overwintering monarch colonies and population may not be fully understood, but clearly, the loss of forest or increased fragmentation of existing forest within the MBBR will produce a steady decrease in areas suitable for monarchs to colonize (Calvert and Brower, 1981; Brower, 1996, 1999b; Brower, 1999a; Ramírez *et al.*, 2003). The findings of this study provide a better understanding of the relationship of forest fragmentation and the locations used by monarchs to colonize throughout the overwintering season.

CONCLUSIONS.

The use of high resolution IKONOS imagery with 4 m spatial resolution allowed a unique, spatially-detailed assessment of forest fragmentation in this study and has enabled the habitat for overwintering monarch butterflies to be characterized in terms of forest patches and gaps within the forest canopy. As a result, the forest composition and configuration metrics were produced at a fine spatial scale, comparable to the scale at which the monarchs use and interact with the forest canopy. Forest characteristics govern forest micro-climate, the maintenance of which is critical to the winter survival of the monarchs. The more predictive landscape metrics may well be surrogates for micro-climate conditions, though this could not be verified in our study.

The research literature indicates that high levels of forest degradation in or near habitat traditionally used for colonization will result in fewer monarchs surviving the overwintering season (Calvert *et al.*, 1983; Fink *et al.*, 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Brower *et al.* 2004). This study increases the understanding of forest conditions required by monarchs to colonize and, as a result, may allow further insight into the parameters of forest degradation (such as opening of the canopy) that may have the greatest negative impact on overwintering monarch colonies.

Results from this study show that the monarchs colonize areas having specific composition and configuration of forest patches, as well as specific environmental conditions (Bojórquez-Tapia *et al.*, 2003). Both the immediate site and extended colony landscape scales should be considered when determining the effects of forest configuration and composition on the location of monarch colonies. The butterflies seem to require a combination of semi-closed protective forests to colonize and semi-open extended colony landscape to enable them to fly to water sources. Forest degradation is seen to have a mainly negative effect with respect to a forest area's suitability as a colony site, with low forest cover rather than forest patchiness appearing most detrimental to colonizing monarchs. This is because large openings in the forest canopy lead to increased exposure, freezing and monarch mortality, especially during storms (Anderson and Brower, 1996; Brower, 1996; Brower *et al.*, 2004). Information from this study also suggests that continued forest degradation in the MBBR will have a negative affect on overwintering monarchs as their colony locations change as the dry season progresses and also from year to year.

Several important research tasks need to be undertaken on overwintering monarchs. A coordinated method of ground searching and aerial reconnaissance (Slayback *et al.*, 2007) can provide a more complete colony location dataset, as well as a definite record of areas without colonies. These data will provide a better non-colony dataset than the randomly generated points used in this study. A multi-temporal image-based analysis of forest fragmentation for both colony and non-colony areas should also be undertaken. This could determine the total amount and spatial distribution of changes in forest cover that are occurring throughout the MBBR relative to the forests chosen by monarchs to colonize. The forest conditions required by the monarchs may or may not remain the same as winter progresses and the colonies move downhill closer to water sources. Colony location data that are based on tracking each colony throughout the overwintering season would provide a more in depth understanding of the monarchs forest requirements for their immediate colony landscape throughout the winter.

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THE IDENTITY OF *PAPILIO DAUNUS* CRAMER (HESPERIIDAE):
A RE-EXAMINATION WITH NEW EVIDENCE

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ABSTRACT. The identity of *Papilio daunus* Cramer, 1777, has long been disputed. Some authors have treated it as a senior subjective synonym of *Papilio bathyllus* J. E. Smith, 1797 (now recognized as *Thorybes bathyllus*). To determine the validity of this association, the original description and accompanying illustration are evaluated. The more detailed original drawing of *P. daunus* is examined for the first time. Evidence indicates that *P. daunus* resembles not only *T. bathyllus* but also *Thorybes confusus* Bell, 1923. Because the identity of *P. daunus* is uncertain, the priority replacement of *P. bathyllus* is unsupported. Moreover, the suppression of *Papilio daunus* Cramer is undesirable as it could force the priority replacement of *Papilio multicaudata* W. F. Kirby by the primary homonym *Papilio daunus* Boisduval.

Additional key words: *Cabares potrillo*, description, drawing, *Lintneria*, *Papilio bathyllus*, *Thorybes confusus*

One of the most controversial of all butterfly taxa is *Papilio daunus* Cramer. It was described in 1777 by the Dutch naturalist Pieter Cramer (1721–1776) in his monumental work (completed by Casper Stoll) entitled *De Uitlandische Kapellen Voorkomende in de Drie Waereld-deelen Asia, Africa en America* [The Foreign Butterflies Occurring in the Three Parts of the World Asia, Africa and America], which was published between 1775 and 1782. With a type locality of “Surinamen” (Suriname), the identity of *P. daunus* has long been a topic of disagreement among lepidopterists. The holotype of *P. daunus* is believed to be lost or unrecognizable. All opinions about the identity of the species have been based solely on a brief written description and an engraved illustration of the type specimen. Most authors have simply reiterated earlier opinions without further scrutiny. Naive interpretations of Cramer’s questionable taxa have complicated efforts to identify them (de Jong 1982).

Although recent authors have generally ignored *P. daunus* or considered it to be of dubious identity, Mielke (2005) listed it as a senior synonym of *Papilio bathyllus* J. E. Smith, 1797. This usage, most popular during the first half of the twentieth century, threatens the name *bathyllus* for a widespread North American species. The continuing debate over the identity of *P. daunus* demands a more thorough review of the existing evidence. It must be determined if the original description and figure are sufficient to threaten the name of *P. bathyllus* as proposed by Mielke (2005) and others. As part of this study, the original drawing for Cramer’s illustration is critically examined for the first

time to better evaluate the taxonomic status of *P. daunus*.

METHODS

The original Dutch and French descriptions of *Papilio daunus* in Cramer (1777) were translated into English and the accompanying illustration was closely examined. The original drawing of *P. daunus* was located and a digital photograph was obtained. The description and drawing of *P. daunus* were compared with numerous specimens of HesperIIDae in my private collection and that of the McGuire Center for Lepidoptera and Biodiversity (Florida Museum of Natural History, Gainesville, Florida).

RESULTS

Historical background. Some authors have overlooked the purported type locality of Suriname (Surinam) in South America and considered *Papilio daunus* Cramer to represent the North American hesperiid commonly recognized as *Thorybes bathyllus* (J. E. Smith). This notion began with Latreille ([1824]), who observed that the illustration of *Papilio bathyllus* in Smith & Abbot (1797) was similar to that of Cramer’s *P. daunus*. The name *daunus* was subsequently used on occasion to identify the North American insect (e.g. Kirby 1879). Monographs on HesperIIDae by Dyar (1905), Mabille & Boulet ([1919]), and Lindsey (1921) further encouraged this usage, which was supported by the checklists of Barnes & McDunnough (1917) and Barnes & Benjamin (1926). Evans (1952) continued this trend, but most lepidopterists by this time preferred to follow McDunnough (1938), who identified the species as *Thorybes bathyllus* in his widely popular checklist of North American Lepidoptera. This usage was later reinforced by dos Passos (1964). Nonetheless, a few authors continued to associate *daunus* with *bathyllus*. In his list of the HesperIIDae of Suriname, de

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Jong (1983) included *Thorybes daunus* and added that Suriname is apparently the “wrong locality for this strictly North American species.” In their catalog of Mexican Hesperidae, Llorente-Bousquets et al. (1990) also listed the species as *T. daunus*. Most recently, Mielke (2005) used this name in his exhaustive catalog of American Hesperidae.

Several authors have openly questioned this synonymy, arguing that Cramer's published figure of *P. daunus* is indeterminate and that the species was attributed to Suriname, where *T. bathyllus* does not occur. Skinner & Williams (1923) remarked, “from the Cramer figure it is doubtfully possible to identify the species, which may be an unidentified Surinam insect.” Lindsey et al. (1931) agreed, stating, “the *daunus* of Cramer for this species [*bathyllus*], as adopted by several writers, is not adequately supported by Cramer's figures.” Although Evans (1952) initially promoted the use of the name *daunus*, he later questioned its identity (dos Passos 1960). Miller & Brown (1981) proposed that *P. daunus* “could as easily fit one of several Neotropical skippers.” Several authors, including Lindsey et al. (1931), Holland (1931), Bell (1938), and dos Passos (1964), recognized the interpretation of *daunus* = *bathyllus* as published elsewhere, but refused to accept this synonymy based directly on Cramer's description. As such, they listed the name *daunus* as a junior synonym of *bathyllus*. This treatment led the online Integrated Taxonomic Information System to incorrectly consider Cramer's *daunus* as an “invalid junior synonym” of *bathyllus* (ITIS 2006).

It should be mentioned that *T. bathyllus* is not the only species that has been associated with *P. daunus*, albeit in a somewhat convoluted fashion. Butler (1877) designated *P. daunus* as the type species of a genus that Edwards (1877a) published at Butler's urging, calling it *Lintneria*. Edwards soon realized that this name was preoccupied by a genus of sphingid moths that Butler had previously described. Butler suggested the replacement name of *Systasea*, which Edwards (1877b) dutifully proposed. It was assumed by Lindsey (1921) and Hemming (1967) that Butler's *daunus* was the same species as *T. bathyllus*. As a result, several checklists have placed *Lintneria* Butler, 1877, within the synonymy of the genus *Thorybes*. However, Butler's specimen of *daunus* was purportedly from “St. Domingo” (Santo Domingo, Dominican Republic) where *T. bathyllus* is not found. Butler also placed his *daunus* into a group of skippers that included *Systasea zampa* (W. H. Edwards), a Neotropical species with scalloped hindwings. He did not associate it with any species of *Thorybes*. Edwards (1877a) noted that Butler had sent him a “pen drawing of *Daunus*, its antennae,

palpi, etc.” In light of this, Edwards did not include *daunus* within the synonymy of *bathyllus*. Moreover, Edwards noted that Butler's *daunus* possessed “angulated” hindwings. This evidence suggests that Butler's *daunus* was more likely *Cabares potrillo* (Lucas), a *Thorybes* look-alike that is widespread throughout much of the Greater Antilles and bears forewing spots similar to Cramer's *P. daunus*. The hindwings of *C. potrillo* are not rounded as in *P. daunus*, but slightly lobed, agreeing with Edwards' definition of “angulated.” This discrepancy probably prompted Butler (1877) to complain that “Cramer's figure of *daunus* gives a false idea of the form of the species.” Butler may have overlooked the obscure 1857 description of *Thanaos potrillo* Lucas or considered it to be a junior synonym of Cramer's *P. daunus*. Butler stated that his specimen of *daunus* was in the British Museum. Although a recent search of The Natural History Museum, London, failed to locate any existing specimens of *C. potrillo* or *T. bathyllus* from “St. Domingo,” it is unlikely that any other species was involved. The genus *Lintneria* Butler, 1877 (a homonym of *Lintneria* Butler, 1876), arguably belongs within the synonymy of *Cabares*, not *Thorybes*.

During the search for Butler's specimen of “*daunus*,” an old hand-written label was found pinned with a series of *T. bathyllus* in The Natural History Museum, London. It reads “Synonymy: *Lintneria* Edw. 1877 *daunus* Cram., *Cocceius* G&S 1900 *pylades* Scud.” This label was obviously prepared after 1900 and indicates that a subsequent researcher interpreted *Lintneria* to be synonymous with *Thorybes*. The label also lists the type species of the given genera: *P. daunus* for *Lintneria* and *Eudamus pylades* Scudder for *Cocceius* Godman & Salvin, 1894 (not 1900). The author of this label probably followed the treatment of Lindsey (1921) and may have further encouraged Hemming (1967) to connect Butler's *daunus* with *T. bathyllus*, despite evidence to the contrary.

The dispute over the identity of *P. daunus* parallels that of another controversial Cramerian name, *Papilio coras* (type locality “Surinamen”). Early on, *P. coras* was associated with the North American species now recognized as *Wallengrenia otho* (J. E. Smith). Following several publications dating back to Kirby (1879), Evans (1955) considered *P. coras* to be a senior synonym of the North American species *Polites peckius* (W. Kirby). dos Passos (1964) popularized this treatment, which was hesitantly continued by Miller & Brown (1981, 1983). Disagreement over the identity of Cramer's figure has led to a gradual migration back to the name of *P. peckius* (e.g. Stanford 1980, Ferris 1989, Miller 1992, Opler & Warren 2002). However, Mielke

(2004, 2005) continued to give priority to *coras*, declaring, “It is impossible to associate *Papilio coras* to any neotropical species.” Just as contentious is *Papilio hyllus* Cramer, which has been associated with North American and Old World butterflies (Butler 1899, Brown & Field 1970, Koçak 1983, Opler & Warren 2002). The identity of *Papilio ladon* Cramer was also disputed until it was established to represent the North American species now recognized as *Celastrina ladon* (Butler 1885, Elwes 1900, Clench & Miller 1980). As noted by Clench & Miller (1980), such nomenclatural disagreements resurface every few decades until they are adequately resolved.

The published figure. *Papilio daunus* was illustrated life-sized as figure F on Plate 126 of Cramer (1777) (Figs. 1, 3). The broad wings suggest that the specimen was a female. It superficially resembles *T. bathyllus*, but as Lindsey et al. (1931) observed, “Cramer’s figure is a very poor likeness of any species of the genus.” Based on the published figure of *P. daunus*, de Jong (1983) and Mielke (2005) rejected potential Neotropical species.

Cramer’s *P. daunus* exhibits the same number of forewing spots as *T. bathyllus*, but their shapes are indistinct and vary from one copy of the book to another. This variability is an inherent problem associated with hand-colored engraved reproductions. Engravers usually overlooked subtle characters, while colorists often obscured critical pattern elements. Clench & Miller (1980) compared actual specimens with several figures on Cramer’s published plate 270, noting inconsistencies in wing shape and coloration. Butler (1899) had earlier noted the “unequal merit” in the quality of the plates. Original drawings can therefore be more valuable in assessing problematic taxa (Calhoun 2003, 2004, 2006). The original drawing of *P. daunus* must be consulted to ensure that the resemblance of the published figure to any given species is not a result of the reproduction process. The identity of *Papilio ladon* was also reinforced by an examination of its original drawing (postscript footnote in Clench & Miller 1980).

The original figure. The production of the plates for *Uitlandische Kapellen* has historically been misunderstood, with some authors believing that Cramer himself created the illustrations (e.g. Clench & Miller 1980). The original drawings for Cramer’s plates were completed ca. 1770 by the Dutch artist Gerrit Warenaar Lambertz (1747–1803). According to the preface in Cramer (1775), Lambertz was commissioned to provide illustrations of the specimens of Lepidoptera in Cramer’s collection, as well as those in the collections of other Dutch naturalists. Originally intended for his

own amusement, Cramer later decided to publish the resulting artwork. Through a series of owners, the watercolors were acquired in 1913 by The Natural History Museum, London, where they are now deposited in the Entomology Library (Gilbert 2000, Harvey 2005). The arrangement and compositions of the drawings differ from the engraved reproductions (Figs. 1, 2). To assist in locating specific drawings, the Entomology Library also preserves an unpublished cross-reference that was prepared by a suspected early owner (Labouchere [179?]). The original drawings are generally more accurate and detailed than the engraved plates. Chainey (2005) noted that the originals more closely resemble surviving type specimens than do the published versions. Earlier researchers, including W. H. Evans of the British Museum (Natural History), were apparently unaware that the original drawings were preserved in London. Clench & Miller (1980) referred to them as “pattern plates.” Because of variation in the published figures, assessments of Cramerian taxa should be restricted to the original drawings.

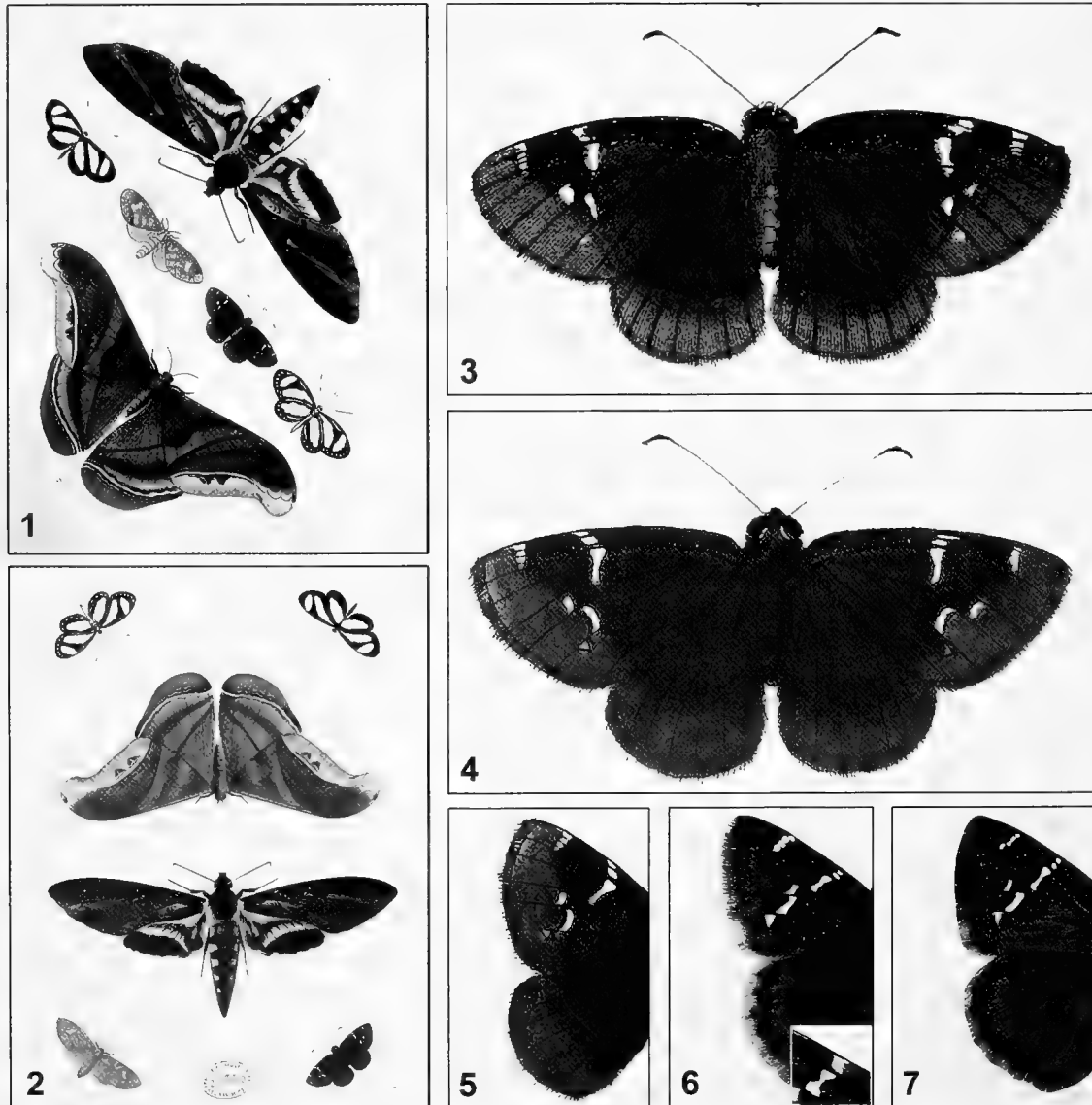
The original drawing of *P. daunus* is labeled in faded ink as “E” on Lambertz’s drawing no. 91 (Figs. 2, 4). The wing shape is more refined and the forewing spots are clearly delineated. The wing fringes are dark and the brown ground color fades less sharply towards the outer wing margins than in the published figure. The forewing possesses ten pale spots. There is a large, vaguely hourglass-shaped discal spot. Two costal spots are placed adjacent to the discal spot, at an oblique angle. A postmedian spot in cell Cu_1 is linear, slightly crescent-shaped, and separated from an adjacent spot in cell M_3 . A submarginal spot in cell Cu_2 is small and triangular. There is a row of four subapical spots that subtly curves towards the outer margin (most obvious on the right forewing). Surrounding each eye is white coloring, which is completely lacking in the published version. The wing veins are too generalized for consideration.

Females of *Thorybes bathyllus* are extremely variable, but can resemble *P. daunus* (Figs. 5, 6). The ground color is often paler toward the outer wing margins and there are ten forewing spots. The discal spot is typically large and hourglass-shaped. Adjacent to the discal spot are two costal spots, which can be obliquely placed similar to those of *P. daunus* (Fig. 6 inset). This is contrary to Forbes (1960), who argued that *T. bathyllus* does not have oblique costal spots. The size and shape of the postmedian spot in cell Cu_1 varies from rectangular to somewhat crescent-shaped. The submarginal spot in cell Cu_2 is triangular. The four subapical spots in *T. bathyllus* are usually arranged in a

straight or slightly curved row. The eyes are surrounded by white scales.

Despite this resemblance to *T. bathyllus*, another species is even more similar to *P. daunus*. *Thorybes confusus* Bell was not described until 1923, thus it was unknown to earlier authors who identified specimens as *T. bathyllus*. *Thorybes confusus* is less common, but occurs over a wide range with *T. bathyllus*, primarily in the southeastern United States from Virginia southward. Females of these species are very similar

and often difficult to distinguish. The subapical spots tend to be somewhat smaller with an outward disjunction in the lowermost spot (Fig. 7). The lowermost spot on the right forewing of *P. daunus* also appears to be slightly offset (Fig. 4). Compared to *T. bathyllus*, a greater percentage of *T. confusus* possess postmedian spots in the same configuration as *P. daunus*. The spot in cell Cu_1 is generally narrower and frequently crescent-shaped in *T. confusus*, while it is usually more squared or hourglass-shaped in *T.*



Figs. 1-5. *Papilio daunus* and *Thorybes* species. 1, Plate 126 from Cramer (1777) (*P. daunus*: center row, second from bottom). 2, drawing no. 91 by G. W. Lambert (*P. daunus*: bottom right). 3, engraved figure of *P. daunus*. 4, original figure of *P. daunus*. 5, rotated ("mounted") view of the original figure of *P. daunus*. 6, female *T. bathyllus* (Pendleton Co., West Virginia; MGCL). Inset shows obliquely placed costal spots on another female (Alachua Co., Florida; MGCL). 7, female *T. confusus* (Moore Co., North Carolina; MGCL). ©The Natural History Museum, London.

bathyllus. A significant feature that has been unrecognized in prior diagnoses of *T. confusis* is the proximity of the spots in cells M_3 and Cu_1 . These spots are almost always coupled, or nearly so, in *T. bathyllus* (Fig. 6). The inner edge of the spot in cell M_3 is usually aligned with the outer edge of the spot in cell Cu_1 . These spots are distinctly separated in *T. confusis*, which is more consistent with *P. daunus* (Figs. 4, 5, 7). Though variable, the wing fringes also tend to be darker in *T. confusis* than in *T. bathyllus*.

Plate 171 in Seitz ([1907]–1924) includes dorsal and ventral figures of female specimens, identified as “*daunus*,” with spot patterns not unlike the original drawing of *P. daunus*. These figures accompanied the treatment of *Thorybes daunus* (= *bathyllus*) by Draudt (1921–1924). Based on these illustrations, Lindsey et al. (1931) and Bell (1938) credited Draudt for this synonymy (“Draudt, not Cramer”). However, the separated postmedian spots and markedly offset subapical spots suggest that the dorsal figure portrays *T. confusis*, while the elongated spots of the ventral figure are more evocative of a well-marked *Thorybes pylades* (Scudder). A similar discrepancy was discovered on Plate 22 of *Papilio bathyllus* in Smith & Abbot (1797). An examination of the original drawing revealed that the females are consistent with *T. confusis* (Calhoun 2006).

Of course, there are other pyrgine skippers that share the general forewing pattern of *P. daunus*. These include *C. potrillo* and *T. pylades*, as well as species of *Cogia* and *Codatractus*. These species, however, do not as closely resemble the drawing of *P. daunus*. Also similar is *Thorybes mexicana* (Herrich-Schäffer). Evans (1952) proposed that *T. confusis* was a subspecies of *T. mexicana* and this synonymy was recently reiterated by Mielke (2004, 2005). *Thorybes mexicana* is a less likely candidate for *P. daunus*, as it is more diminutive, usually lacks forewing costal spots, and occurs in the mountains of the western United States and Mexico. These regions remained unexplored in the 1770s.

Source of the figured holotype. As with many other species in his book, Cramer stated that *P. daunus* occurred in Suriname. Shortly after Suriname became a Dutch colony in the late seventeenth century, naturalists began acquiring insect specimens from the region. One of the first to study the insects of Suriname was Maria Sibylla Merian (1647–1717). She departed the Netherlands in 1699 and spent two years in Suriname (Wettengl 1998, Todd 2007), later publishing an illustrated book about some of the insects she had encountered (Merian 1705). Later in the eighteenth century, Cramer and other Dutch naturalists obtained numerous insect specimens from Suriname, which was then known as Dutch Guiana. Due to the large amount

of insect material pouring into Europe at that time, the origins of many specimens became forgotten and confused. Loose standards for labeling specimens also resulted in erroneous localities. In addition, naturalists sometimes associated specimens with more exotic locales to promote their rarity and value. North American butterflies that Cramer erroneously attributed to Suriname include those that he described as *Papilio clarus* and *Papilio cocyta* (now *Epargyreus clarus* and *Phyciodes cocyta*). The figured specimen that accompanied Cramer’s description of *Papilio ladon* (now *Celastrina ladon*) was attributed to South Africa, resulting in much disagreement over its identity. Other North American butterflies that were given erroneous localities are *Papilio palamedes* (Drury) (New York) and *Polygonia interrogationis* (Fabricius) (Jamaica). A number of additional North American butterflies, principally species of Papilionidae, were attributed to Jamaica. Butler (1899) complained about the “utter unreliability of many of Cramer’s localities.” It is obvious that the reference to Suriname in the description of *P. daunus* cannot be trusted.

The illustrated holotype of *P. daunus* purportedly came from the collection of the Dutch physician and naturalist Pieter Boddaert (1730–1795/96). Boddaert, a subscriber to Cramer’s opus, lectured on natural history and published several works on zoology (Burkhardt 1989). In 1772, he began to publish a Dutch abridgement of Linnaeus’ *Systema Naturae*, but did not complete the project (Cassin 1864). Boddaert provided several specimens to Cramer, but later criticized the quality of the plates in *Uitlandische Kapellen*. Casper Stoll, who completed the work after Cramer’s untimely death, condemned Boddaert for his negative appraisal of the book (Cramer 1779–1780). Boddaert described numerous species, particularly birds and mammals, from the collections of another Dutch naturalist, Johannes Albertus Schlosser (?–1769) (Hoefler 1853, Larousse 1867). During the 1780s, Boddaert described many New World birds, including the North American brown-headed cowbird (*Molothrus ater*) (Fringillidae). It is possible that he acquired the specimen of *P. daunus* from Schlosser’s extensive collections after Schlosser’s death in 1769. Dutch naturalists obtained specimens from many sources, such as Dru Drury of London, who possessed a large number of North American insects (Chainey 2005). Cramer himself attributed species of Lepidoptera to New York, Virginia, Maryland, and “Carolina.” Drury (1770–1782) listed these same locations as the sources of many of his own insect specimens. The provenance of the *P. daunus* specimen, via Boddaert, does not restrict its origin to Suriname.

Original description. The brief written description of *P. daunus* has virtually been ignored by subsequent researchers. It was given in Dutch and French on page 44 of Cramer (1777). The Dutch description reads “De witte vlakken en stippen op de vleugelen van deze eenkleurige Dikkop-Kapel (Pap. Pleb. Urbicol.) zyn eenigzints doorschynend. Op den binnengrond ziet men een donker paarschen weerschyn” [The white patches and spots on the wings of this unicolorous skipper (Pap. Pleb. Urbicol.) are somewhat hyaline. There is a dark purple irradiation on the ground color]. The French version differs slightly; “Les taches blanches & les points blancs des ailes de ce Plebeien noble (Pap. Pleb. Urbicol.) dont les deux surfaces ont la même couleur, sont un peu transparentes. On voit sur le fond brun un chatoyant violet pale” [The white spots & the white points of the wings of this noble Plebeien (Pap. Pleb. Urbicol.), of which the two surfaces have the same color, are a little transparent. One sees on the brown bottom a shimmering pale violet]. The abbreviation of “Pap. Pleb. Urbicol.” refers to the Linnaean classification system, where *Papilio* is the genus, *Plebijus* is a group of smaller species that includes the skippers, and *Urbicolae* is a subgroup of species that possess white or transparent spots.

The original description could define a number of New World hesperiids with hyaline spots. However, a significant detail is the mention of a radiant purple or violet in the ground color. Under the proper lighting, the dorsal wings of *T. bathyllus* and *T. confusis* display a distinct purplish luster. This was observed by Scudder (1889), who described *T. bathyllus* as “very dark rich brown, usually with an olivaceo-purplish tinge.” The French version of the original description of *P. daunus* seems to restrict the violet coloring to the ventral surfaces of the wings. Again, the undersides of both *T. bathyllus* and *T. confusis* have a gleaming reddish-purple overtone, which is most obvious on the hindwings of fresh specimens. Dyar (1905) noted that the underside of *T. bathyllus* is “brown, with violet reflections.” This coloration is visible in a photograph of *T. bathyllus* in Glassberg (1999, Plate 49, fig. 3).

DISCUSSION

Unlike physical specimens, illustrations are affected by the proficiency of the artist. Slight adjustments by the artist can alter our perceptions of the intended species. As a result, extreme caution must be exercised when attempting to identify species portrayed in drawings or engravings, particularly when other evidence is lacking and the figured specimens are of questionable origin. Published reproductions are the most troublesome, as they are also influenced by the skills of engravers and colorists. Hasty identifications

and neotype designations that are based only on engraved illustrations can result in critical misinterpretations (Calhoun 2003).

The limited evidence indicates that *Papilio daunus* Cramer is most likely a North American species of *Thorybes*. The holotype was probably collected prior to 1770 along the Atlantic coast between the colonial American ports of New York and Savannah, Georgia. Although *P. daunus* has repeatedly been associated with *T. bathyllus*, the drawing of the holotype is more reminiscent of *T. confusis*. Nonetheless, the identity of *P. daunus* cannot be confidently determined.

As shown by the detailed synopsis in Mielke (2005), prevailing usage has strongly favored *Papilio bathyllus* for over two centuries. *Thorybes confusis* has been applied without dispute to the same species for over 80 years. Neither name should be upset by a priority replacement involving *Papilio daunus* Cramer, including the designation of a neotype to objectively identify this taxon. The evidence is insufficient to ensure that such a neotype would be consistent with the missing holotype. Furthermore, it could be undesirable to pursue the suppression of *Papilio daunus* Cramer, as it is a primary homonym of *Papilio daunus* Boisduval, 1836 (Papilionidae). This action would force a priority replacement of *Papilio multicaudata* W. F. Kirby, 1884, by *Papilio daunus* Boisduval. To preserve nomenclatural stability, *Papilio daunus* Cramer is best considered a *nomen dubium*.

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DISCOVERY OF A LARVAL HOST PLANT FOR *OLETHREUTES MONETIFERANA* (RILEY)
(TORTRICIDAE) IN NORTHERN KENTUCKY

Additional key words: *Aesculus flava*, *Aesculus glabra*, *Macrocentrus*, Hymenoptera, Braconidae

On 8 April 1997, the second author located larvae of a species of *Olethreutes* feeding on rolled leaves of Yellow Buckeye (*Aesculus flava* Ait. = *A. octandra* Marshall, Hippocastanaceae) along Pools Creek Road in Highland Heights, Campbell County, Kentucky. Three larvae were collected and placed in plastic bags with leaves of the host plant. Two pupated among leaves on 15 April 1997. Two females emerged on 29 April 1997. The third individual was infested with small, parasitic wasps. The two imagoes were identified by the first author as *O. monetiferana* (Riley), a species for which no host information has been reported.

Another search of the same area, conducted on 2 April 1998, produced two additional late instar larvae on leaves of small (one to two meters tall) understory trees of *A. flava*. These larvae were dull, olivaceous green with shining black heads, unlike congeneric *Aesculus* feeders *O. ochrosuffusana* (Heinrich), *O. sciotana* (Heinrich), and *O. appalachiana* (Braun) whose larvae are all bright, kelly green with shining black heads. They were very well developed compared to larvae of *O. ochrosuffusana* and *O. sciotana* at that same location which were still in very early instars. Collected larvae were placed in plastic, zip-lock bags and fed leaves of *A. flava*. A male *O. monetiferana* emerged on 18 April 1998, a female (figure 1) emerged on 20 April 1998.

On the same date, after finding larvae in Campbell County, another search was conducted at a location along Middle Creek in Boone County, Kentucky. This site was selected because adults of *O. monetiferana* had been captured there in early June 1984 and late May 1988. Three more of the olivaceous green larvae were



Figure 1: *Olethreutes monetiferana* (Riley), Campbell County, Kentucky

collected on tied leaves of Ohio Buckeye (*Aesculus glabra* Willd.). One of these was stored in alcohol for future study. The other two were reared as before but were heavily parasitized by small wasps in genus *Macrocentrus* (Hymenoptera: Braconidae).

We thank Dr. Michael Sharkey of University of Kentucky for identification of braconid wasps. We thank Todd Gilligan for the photograph in figure one.

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A BIBLIOGRAPHY OF THE WORKS OF ANNETTE F. BRAUN

Additional key words: microlepidoptera, bibliography

Annette Frances Braun (1884–1978) was one of the most accomplished microlepidopterists of the 20th century. During her life she described at least 335 species (Solis, 1990) and published numerous scientific papers, including four major monographs. While she has been the subject of three biographies (Stein, 1988; Solis, 1990; Platt, 2002), we are unaware of a complete bibliography of her published works. The following is what we believe to be a complete list of her 73

publications, all as sole author, beginning in 1908 with her descriptions of new species of *Lithocolletis* and ending in 1972 with her monograph on North American Tischeriidae. This list was compiled over several years, starting with a manual search of the Zoological Record, and with additional records being incorporated as they were discovered. It has been checked against numerous partial bibliographies, informal lists, and reprint collections. Page and volume numbers have been

verified with the original publications. It is hoped that this list will become a useful reference for current and future microlepidopterists.

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Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. *Adv. Genet.* 10:165–216.

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CONTENTS

LARVAL FEEDING BEHAVIOR AND ANT ASSOCIATION IN FROSTED ELFEN, CALLOPHRYS IRUS (LYCAENIDAE) Gene Albanese, Michael W. Nelson, Peter D. Vickery and Paul R. Sievert ----- 61
DAILY HABITAT SHIFTS BY THE NEOTROPICAL BUTTERFLY MANATARIA MACULATA (NYMPHALIDAE: SATYRINAE) IS DRIVEN BY PREDATION. Henrik Hedelin and Jens Rydell ----- 67
INTRASPECIFIC BODY SIZE VARIATION IN MACROLEPIDOPTERA AS RELATED TO ALTITUDE OF CAPTURE SITE AND SEASONAL GENERATION J. Bolling Sullivan and William E. Miller----- 72
ARGYRIINI (LEPIDOPTERA: CRAMBIDAE) OF MISSISSIPPI AND ALABAMA WITH A REDESCRIPTION OF ARGYRIA RUFISIGNELLA (ZELLER) Edda L. Martinez and Richard L. Brown----- 78
A NEW SPECIES OF PELOCHRISTA LEDERER FROM EASTERN NORTH AMERICA (TORTRICIDAE) Donald J. Wright ----- 84
A NEW SPECIES OF EUXOA (NOCTUIDAE) FROM WASHINGTON STATE Anders Crabo and Lars Crabo ----- 87
THE INFLUENCE OF FOREST FRAGMENTATION ON THE LOCATION OF OVERWINTERING MONARCH BUTTERFLIES IN CENTRAL MEXICO. Jennifer J. Williams, Douglas A. Stow, and Lincoln P. Brower ----- 90
THE IDENTITY OF PAPILIO DAUNUS CRAMER (HESPERIIDAE): A RE-EXAMINATION WITH NEW EVIDENCE John V. Calhoun----- 105
GENERAL NOTES
DISCOVERY OF A LARVAL HOST PLANT FOR OLETHREUTES MONETIFERANA (RILEY) (TORTRICIDAE) IN NORTHERN KENTUCKY Loran D. Gibson and John A. Merkle----- 113
A BIBLIOGRAPHY OF THE WORKS OF ANNETTE F. BRAUN Todd M. Gilligan, Steven Passoa and Terry Harrison----- 113