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Evolution of locomotion in slug caterpillars (Lepidoptera: Zygaenoidea: Limacodid group)

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Abstract. Larval locomotion of species in the limacodid-group families Limacodidae, Dalceridae, Megalopygidae, Aididae, and Somabrachyidae is described in phylogenetic context. Function of structures involved in locomotion reported include thoracic legs, abdominal prolegs or suckers, and spinnerets. Additional segments with prolegs or suckers in the limacodid-group families increase their ventral surface contact with the substrate. The limacodid + dalcerid clade has the most fluid waves of locomotion because of a highly flexible ventrum, tactile lateral setae and size reduction of prolegs and thoracic legs. On flat surfaces aidids have a similar locomotion to limacodids due to short prolegs and smooth lateral and subventral warts, which contact the substrate, whereas in megalopygids the motion of each proleg segment is more apparent because contact of the substrate is primarily with membranous pads on their prolegs. Ventral adhesion in the limacodid + dalcerid clade is increased by the spinneret both in laying down wet silk and in cleaning debris off the ventrum. Evolution of locomotion and its adaptive significance in the limacodid group are discussed.

Key Words. Limacodid group, larval locomotion, prolegs, crochets, suckers, spinneret, silk, smooth hostplants

INTRODUCTION

External feeding larvae in the moth family Limacodidae are often referred to as "slug caterpillars" because their sticky ventrum and locomotion are superficially similar to those of slugs. Dyar (1899:69) referred to the wave-like motion of their ventral abdominal segments during locomotion as "the creeping disk." Hinton (1955:516) noted that when limacodids crawl, "a liquid is secreted over the cuticle... if not sticky... may function... by increasing the efficiency of the suckers or by surface tension binding the abdomen to the leaf surface." Epstein (1996) found semifluid silk to be a source of this liquid.

Limacodidae is part of a monophyletic assemblage that includes Megalopygidae, Dalceridae, Aididae, and Somabrachyidae that is referred to as the limacodid group. A summary of relationships of the limacodid group, based on cladistic analysis found in Epstein (1996) is as follows: megalopygid subfamilies Trosiinae and Megalopyginae form a clade at the base of the limacodid group, and Aididae, often considered a subfamily of Mega-

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lopygidae, is a family and sister group to the Limacodidae + Dalceridae. Somabrachyidae are thought to be a sister group of Megalopygidae, Aididae or to the remaining families in the limacodid group.

Larvae of each family in the limacodid group have prolegs on the second and seventh abdominal segments (A2 and A7), unique in Lepidoptera families with external feeding caterpillars. Megalopygidae are the only family in the group with species that possess well developed membranous pads on proleg segments A2–7. Dalcerids and limacodids have ventral abdominal suckers that are considered to be derived from proleg bases on A2–7, and from warts on A1 and A8 (Epstein 1996).

In this study I present observations on the locomotion found in all limacodid-group families. This is followed by discussion of phylogenetic trends in locomotion in these families as they relate to plants and defense.

MATERIALS AND METHODS

Locomotion was observed with larvae of a variety of instars crawling at all angles on clear glass or plastic, and on wires or stems. Larvae were filmed using a 16 mm movie camera with a macro lens or videotaped, either directly or through a microscope, using an 8 mm camcorder. For larvae crawling on glass, locomotion of the ventrum was recorded from below by using an inverted phase-contrast microscope. Species observed are included in Table 1.

LOCOMOTION

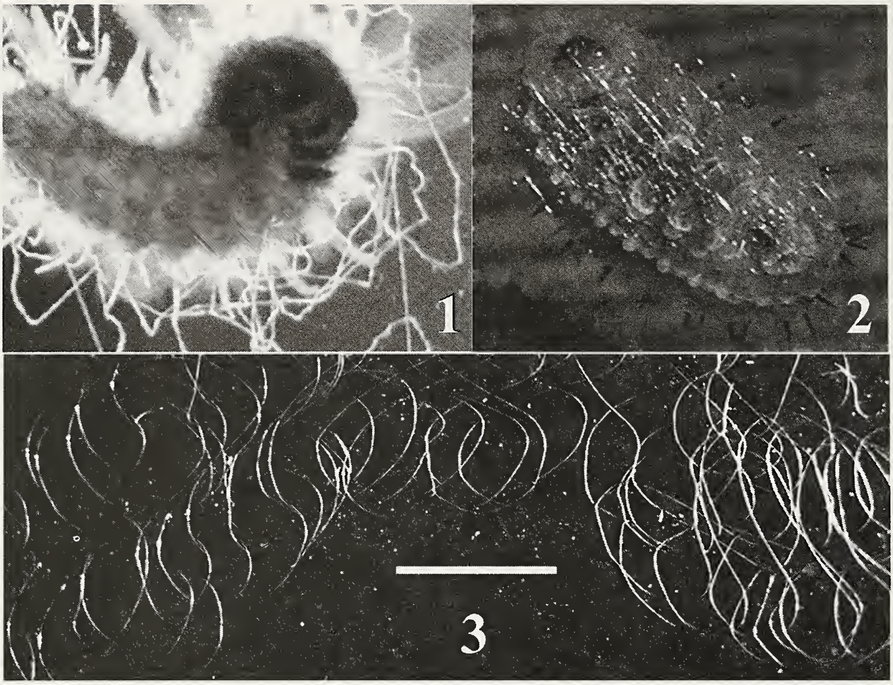
Caterpillars crawl by serial muscle contractions surrounding a fluid skeleton (Casey 1991). Forward motion begins as the anal prolegs, or claspers (A10), are lifted and planted, and continues sequentially with each segment by contraction of dorsal longitudinal muscles of the segment to the anterior; this lifts several trailing segments while dorsoventral muscles retract the prolegs. The prolegs are then set down, beyond their original position, by a contraction of the ventral longitudinal muscle of its segment (Hughes & Mill 1974). Whether in motion or at rest, the amount of ventral surface contact with the substrate of free-feeding caterpillars can be viewed as a

Table 1. Larvae of species in the limacodid group on which observations of locomotion are based in this study.

Limacodidae:	*Phobetron pithecium* (Abbott & Smith), *Isochaetes beutenmuelleri* (Hy. Edwards), *Tortricidea pallida* (H.-S.), *Semyra coarctata* complex, *Prolimacodes badia* (Huebner), *Isa textula* (H.-S.), *Acharia stimulea* (Clemens), *Parasa indetermina* (Bdv.), *Euclea delphinii* (Bdv.)
Dalceridae:	*Dalcerides ingenita* (Hy. Edwards)
Megalopygidae:	*Megalopyge* sp. from Belize, *Megalopyge crispata* (Packard), *M. basalis* (Walker), *Norape cretata* (Grote)
Aididae:	*Aidos amanda* (Stoll)
Somabrachyidae:	*Psycharium* sp.

Table 2. Morphological characters of the limacodid group and Zygaenidae that relate to locomotion (from Epstein 1996).

Family	Spinnerets	Thoracic legs	Ventral abdominal segments(A1–9): prolegs, crochets or suckers	Anal prolegs (A10): with crochets	Texture of ventral surface, thorax to anal proleg	Lateral surface, setae
Zygaenidae	tubular/normal	easily visible	prolegs on A3–6 with crochets	crochets present	shagreened	lateral and subventral verrucae
Somabrachyidae	"	"	prolegs on A2–7, crochets on A3–6	"	shagreened	"
Megalopygidae	"	"	prolegs on A2–7, crochets on A3–6, or A2–7	"	shagreened except on membranous proleg pads	"
Aididae	tubular with amorphous apex	"	prolegs on A2–7, crochets on A3–6	"	shagreened	lateral warts with tactile setae, subventral warts
Dalceridae	brushlike, broad at apex (all instars)	small	suckers A1–8, crochets absent until mid instars	crochets absent	smooth and flexible	lateral setae tactile, near and above spiracle
Limacodidae	brushlike, often broad at apex (often narrowing after first instars)	small to minute	suckers A1–8, crochets usually absent	crochets usually absent	"	lateral setae tactile, below spiracle



Figs. 1–3. Use of silk in larvae of Somabrachyidae, Aididae, and Megalopygidae. 1) Haphazard laying down of silk of a first instar *Psycharium* sp. (Somabrachyidae), viewed from beneath through glass; 2) Middle instar *Aidos amanda* clinging to glass, viewed from above through glass (photo courtesy of Max and Eileen Price); 3) Figure-8 silk on glass from *Megalopyge* sp. (photo by Kjell Sandved) (scale is in mm).

continuum. Limacodids and dalcerids are at one extreme, with most of the ventrum minus the A10 segment in contact, while the condition commonly found in geometrids, with only thoracic legs and A6 and A10 prolegs in contact, is at the other extreme. Other free-feeding caterpillars fall in between by having a maximum of five prolegs in contact.

Caterpillar locomotion involves a complex of structures, behaviors, and positions in relation to the contact surface. Morphological characters relating to locomotion in each of the limacodid-group families is given in Table 2. These include external aspects of the spinneret, thoracic legs, abdominal prolegs or suckers, anal prolegs, the texture of the ventral surface, and lateral structures.

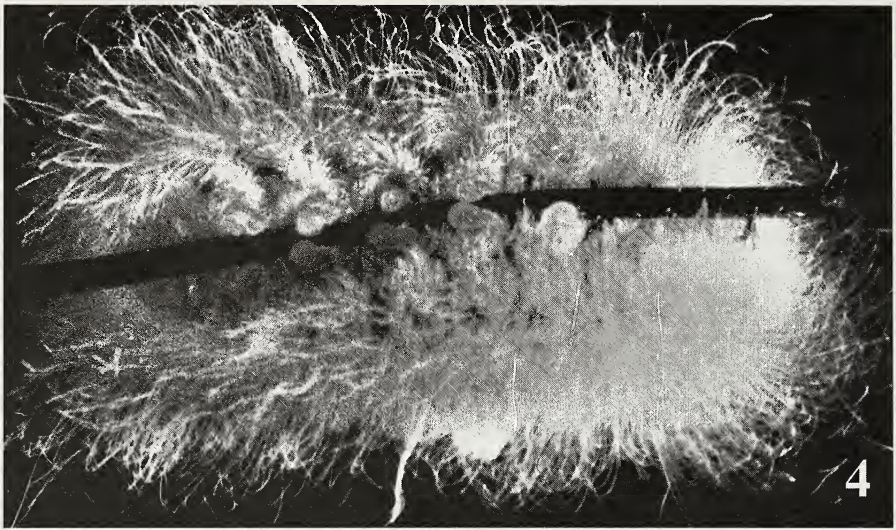
The descriptions of locomotion in the limacodid-group families are ordered from plesiomorphic to derived taxa based on the phylogeny from Epstein (1996). Somabrachyidae, of uncertain relationship to the other families, is placed after the Megalopygidae. The descriptions include information from these categories: 1) locomotion on narrow surfaces; 2) locomotion on flat surfaces; 3) use of silk and the spinneret; 4) feeding and resting positions. For the families for which I have the most information, Limacodidae and Megalopygidae, I will use these categories as subheadings.

Megalopygidae. 1) *Narrow surfaces*: Larvae use thoracic legs and all prolegs, including the anal pair, to grasp (Fig. 4). 2) *Flat surfaces* (Fig. 5): Membranous pads (Fig. 6) are the primary contact of the prolegs on A2–7 (as indicated through glass); a pair of tactile, subventral setae positioned at the anterior margin of each pad touches the substrate. Lateral and subventral verrucae have little contact with the substrate except in certain instances (e.g., *Mesoscia pusilla*). The anterior, non-crochet portion of the anal prolegs contacts substrate at the beginning of a wave of locomotion, while at least two adjoining proleg pairs are retracted (and compressed) from the substrate as the wave progresses. 3) *Silk*: Early instars spin silk on horizontal surfaces in a linear or haphazard manner (as in Somabrachyidae, Fig. 1), and can dangle from silk, while later instars issue silk on the substrate in a figure-8 (Fig. 3), especially when they are at an angle of ≥ 45 degrees. 4) *Feeding and resting*: Larvae cling to silk they deposit on the substrate with their thoracic legs and crochets.

Discussion: Packard (1893) noted that the prolegs on A2 and A7 in *Megalopyge* (*Lagoa*) *crispata* functioned like the others, even though they lacked the crochets. Dyar (1899) observed that the membranous pads (=disks) of *Megalopyge opercularis* were in exclusive contact with a smooth glass surface during locomotion. Some species of megalopygids have sucker-like pads below subventral verrucae in addition to the membranous pads on the prolegs (e.g., *Mesoscia pusilla*; Fig. 6). These presumably contact the substrate much the same way as the proleg pads. The size of the membranous pads relative to the prolegs varies between species, and on A2 and A7 depending on whether crochets are present or absent (Epstein 1996).

Somabrachyidae (*Psycharium* sp., first and second instars, only). These larvae prefer to crawl on narrow surfaces such as found on its hostplants (Restionaceae and *Pinus*, H. Geertsema pers. comm.). When viewed from underneath on a glass surface the prolegs sometimes clasped together, as if to grip a narrow substrate, rather than push directly on it. Silk is deposited in the same, haphazard way as in early instar megalopygids (Fig. 1).

Aididae. Movement on flat surfaces of proleg segments has a fluid wave-like appearance similar to limacodid and dalcerid species, because they closely contact the substrate with short, broad prolegs and smooth lateral and subventral warts below the spiracles (Fig. 2). Most megalopygids, in contrast, have only the membranous pads contact flat surfaces, whereas the proleg base and crochets and the spiny and plumose setae on lateral and subventral verrucae have less contact with flat surfaces. The major difference between locomotion found in *Aidos amanda* and in limacodid and dalcerid species relates to the presence of a flexible ventral cuticle found in the latter two families. Larvae of *A. amanda* are difficult to dislodge at rest because they have a large number of crochets hooked onto silk (Fig. 2) (Epstein 1996); they issue silk while crawling onto a leaf or on smooth



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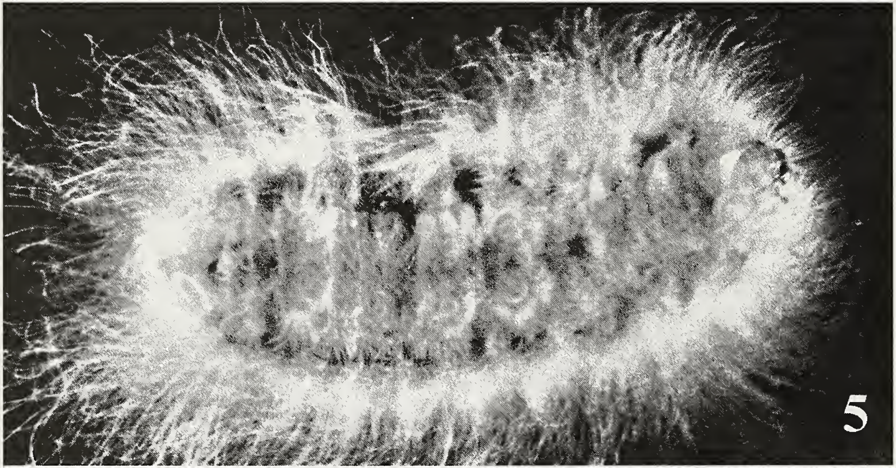

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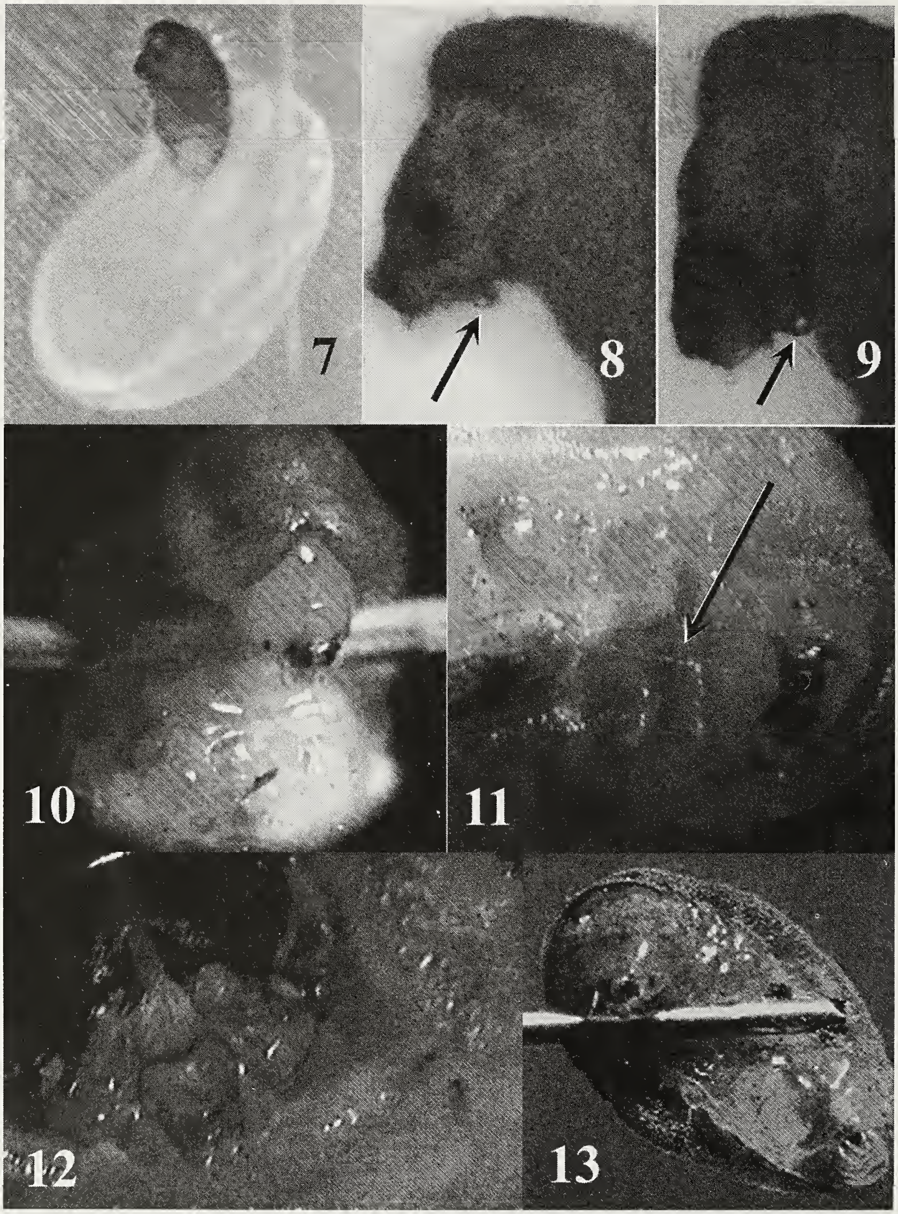
Figs. 4–6. Locomotion and ventral surface of larval Megalopygidae. 4–5: Late instar *Megalopyge basalis* (head on right end) (from 16 mm film by Kjell Sandved). 4) Clasping a wire with prolegs and thoracic legs; 5) Viewed through a horizontal piece of plexiglass; 6) Scanning electron micrograph of abdominal prolegs and subventral pads on A2 (top) to A3 of *Mesoscia pusilla* (scale bar = 0.5 mm).

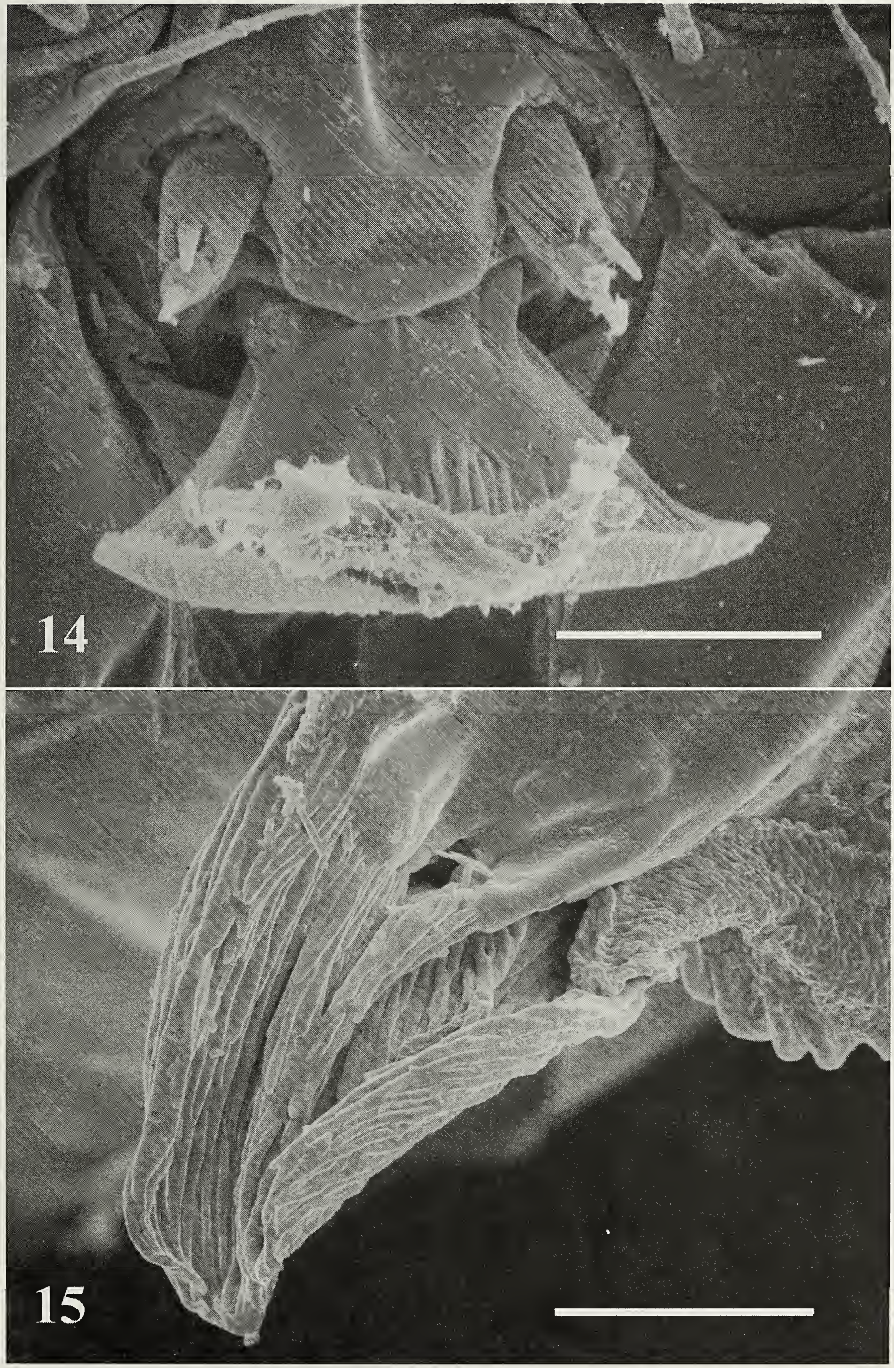
surfaces, as in species of megalopygids and caterpillars in other families (Epstein 1995).

Limacodidae. 1) *narrow surfaces*: Larvae ventrally grasp leaf edges, stems, or narrow vines along the midline (Figs. 11, 19), or from anterior to posterior (Fig. 10); anal prolegs do not grasp. Sticky silk can also help proximal abdominal segments stick together while wrapping around a stem. Reduced thoracic legs have tactile function, while the pretarsal claw assists in grasping a leaf or petiole or in clutching silk applied to the posterior ventrum. 2) *flat surfaces*: The locomotory surface, which consists of a highly flexible cuticle with fungiform tactile setae, moves in fluid waves that expand laterally along the leading edge, progressively retracting from the substrate (Figs. 16, 17). Tactile lateral setae, located between the margins of the ventral surface and the spiracles, contact the substrate during locomotion. Waves can move in oblique angles when the larva shifts its head and thorax to either side. Larvae readily reverse motion either in straight or oblique waves. The vestigial anal prolegs, spinulose with less elastic cuticle, are raised off the substrate during locomotion. This assists in expelling frass while in motion or while feeding. 3) *silk*: Semifluid silk, or a fluid along with the silk, is laid down in figure-8 fashion by the spinneret on substrates during or prior to locomotion. The fluid can spread from the thoracic region to the 9th abdominal segment and aids in the adhesion of the suckers. The silk is also applied directly to the anterior ventrum by rearing up the head or to the entire ventrum on narrow surfaces when clasping from anterior to posterior. The apparently sticky silk strands on the ventrum help the suckers grip to flat or narrow substrates (Fig. 10). Unlike megalopygids, aidids and numerous other lepidopterans, the larvae often do not leave discrete strands of silk behind until the onset of cocoon construction. 4) *feeding and resting*: Larvae have heads retracted beneath the prothorax while the ventrum is laterally expanded and is suckered down to the substrate (assisted by surface film) (Fig. 18). When the ventral surface gets dirty, larvae will raise their anterior off the substrate and brush the thorax and first few abdominal segments with their spinneret from side to side.

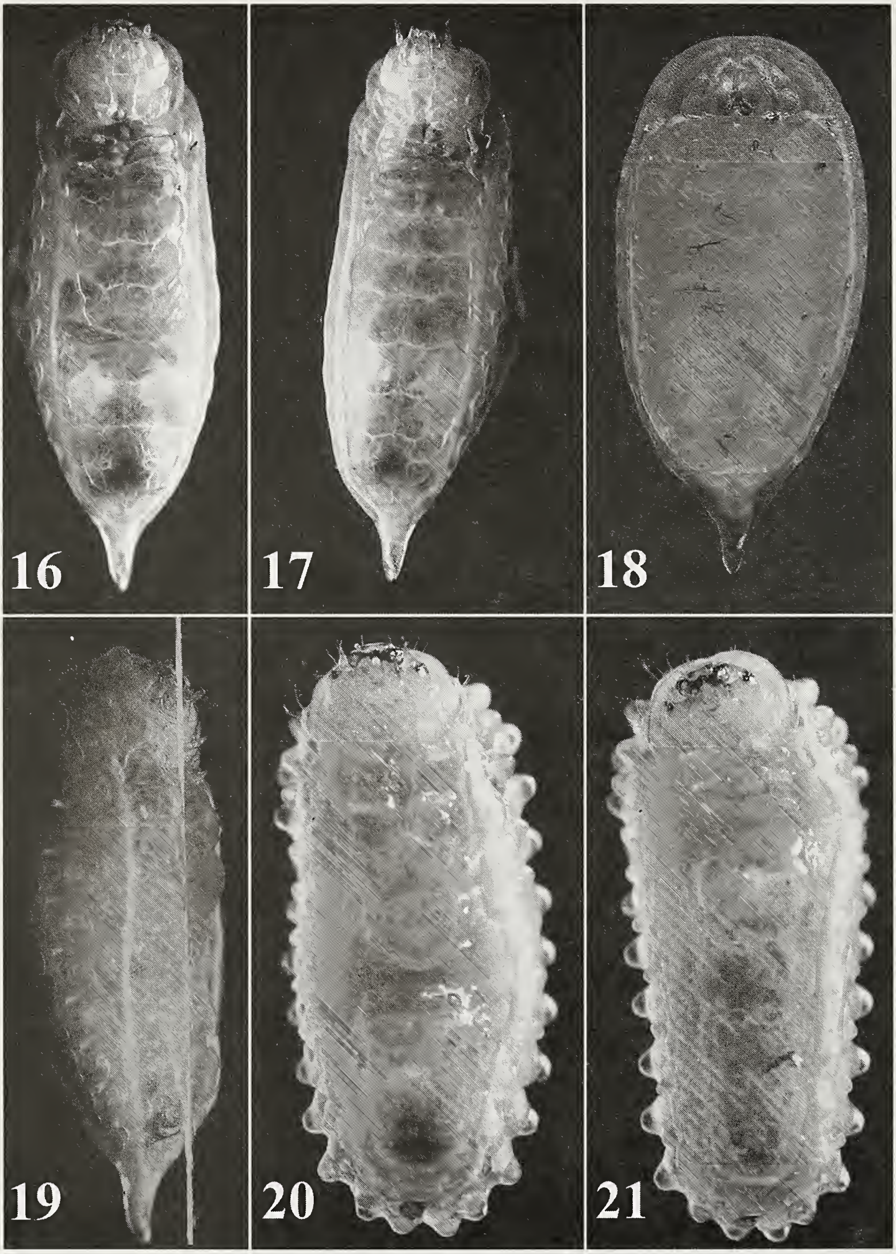
Discussion: The tight adhesion of the ventrum to the substrate, during locomotion or at rest, requires only small amounts of the liquid silk to provide surface tension. Use of scanning electron microscopy revealed no pores for fluid secretion on the ventral and lateral surfaces (Epstein 1996), as suggested by Holloway (1986). The presence of a liquid silk droplet was observed in *Prolimacodes badia* during egg eclosion (Figs. 7–9), although not during this stage in other species (e.g., *Isa textula, Tortricidia pallida*). The



Figs. 7–13. Use of semifluid silk in larval Limacodidae (from 8 mm video). 7) Egg eclosion of *Prolimacodes badia*; 8, 9) Detail of silk droplet on end of spinneret during egg eclosion of *P. badia* (arrows point to droplet); 10) Late instar larva of *Tortricidia pallida* clasping stem from anterior to posterior while applying silk to posteroventral segments; 11) Silk strand of *T. pallida* at the end of a twig (arrow points to silk strand) (note medial clasping of ventral surface on the left); 12) Detail of spinneret and ventral thorax of late instar *P. badia* (viewed through clear plastic from above); 13) Late instar *T. pallida* obliquely grasping stem while applying fluid silk to it.



Figs. 14–15. Spinnerets of first and last instar Limacodidae in related genera *Prolimacodes* and *Semyra* (scale bar length in parentheses). 14) First instar *Prolimacodes badia* with silk debris on distal margin (50 μm); 15) Last instar *Semyra coarctata* complex (27 μm).



Figs. 16–21. Locomotion in larval Limacodidae and Dalceridae (viewed from above through glass). 16–19: *Semyra coarctata* complex (photos by Chip Clark). 16) Near middle of locomotion sequence; 17) At the end of a locomotion sequence; 18) Larva at rest with ventrum laterally expanded and head retracted; 19) Lateroventral view of larva medially clasping the edge of the glass. 20, 21: *Dalcerides ingenita* (photos by Laurie Minor-Penland). 20) Near middle of locomotion sequence; 21) At the end of a locomotion sequence.

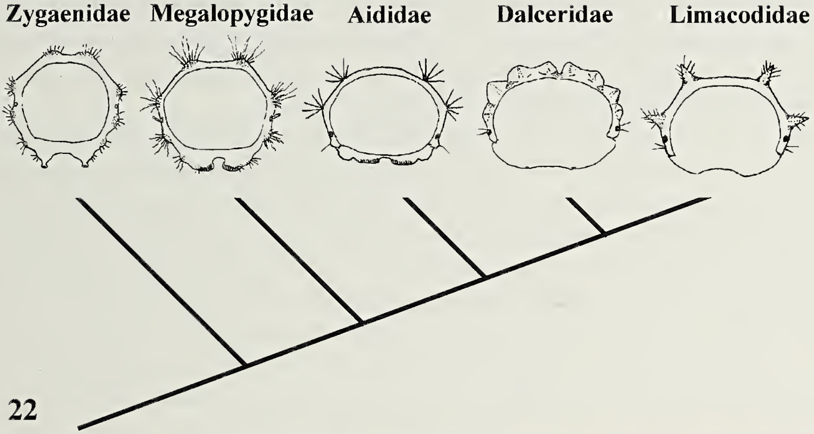


Fig. 22. Evolution of the ventral surface in the limacodid-group families viewed in cross section of proleg segment (after Epstein 1996).

spinneret, whether broad at the apex in early instars (Fig. 14) or narrow in late instars (Figs. 12, 15), functions similarly in both the use of the silk and in cleaning the ventral surface. Although the prolegs are highly reduced, their gripping of narrow substrates appears to be aided by a dense pad of ventral muscles revealed by dissection.

Dalceridae. Locomotion (Stehr & McFarland 1985; Figs. 20, 21) and spinneret function in dalcerid larvae are similar to those found in limacodids. Tactile lateral setae used to touch the substrate during locomotion are shifted dorsad, above or near the spiracles, compared to those in limacodids. This probably is due to the relative closeness of spiracles to the locomotory surface. Semifluid silk was observed in *Dalcerides ingenita,* though not at egg eclosion. Reports of a "shiny path" trailing behind dalcerid larvae (Genty et al. 1978) may have been from broad ribbons of silk laid on the substrate or the result of cleaning with the spinnerets. Fluid debris has been observed following "brushing" on the anteroventral abdominal segments. Small crochets, present only in mid- to late instars (Stehr & McFarland 1985, Epstein 1996), appear not to have any function on smooth leaf surfaces. However, they may be used by the prepupa when crawling inside the diffuse cocoon.

EVOLUTION OF LOCOMOTION IN THE LIMACODID GROUP

The most noticeable trend when viewing locomotion of the limacodid group in phylogenetic sequence is the increased proportion of the ventral surface in direct contact with the substrate (Fig. 22). In megalopygids, at the base of the limacodid group, this is suggested by the shortness of prolegs relative to presumed zygaenid ancestors and the addition of prolegs on A2 and A7. Moving from megalopygids to aidids, contact increases as a result of the reduction of lateral and subventral verrucae to smooth warts. In the limacodid + dalcerid clade, further contact results from reduction of the prolegs on A2–7 to suckers, formation of suckers on A1 and A8, and the flexibility to the ventral cuticle (Epstein 1996). The relatively large thoracic legs and grasping of narrow surfaces in Somabrachyidae, in addition to other plesiomorphies (Epstein 1996), suggest that this family may be a primitive lineage of the limacodid group.

The increased contact of the larval ventral surface suggests a specialization toward smoother host plants. Features of megalopygids that are effective in clinging to smooth surfaces include the membranous pads on the prolegs, and presumably, in some species, pads on subventral verrucae. The presence of smooth subventral and lateral warts in aidids, which contact the substrate during locomotion (versus setose verrucae), are also indicative of this type of host plant specialization. Absences of crochets on A2 and A7 proleg segments in many megalopygids and in aidids, apparently independent losses (Epstein 1996), are also suggestive of this trend. The smooth and flexible ventrum in the limacodid + dalcerid clade, in conjunction with the spinneret and silk, assists in sticking to smooth host plant surfaces (see further discussion below).

Species in the limacodid group are often polyphagous, with the ability to switch host plants even in later instars (Dyar 1905, 1909, Epstein 1995). Perhaps predator selection influenced evolution in this direction, since a combination of slow growth (found throughout the group) and increased foraging time in seeking a specific host plant could lead to heavy losses of larval populations from parasitoids and predators. Switching to other host plant species with similar smooth-leaf textures and suitable chemical makeups would theoretically decrease foraging time.

Caterpillar adaptations to predators have been thought to relate to defenses, such as group feeding in spiny caterpillars or crypsis, with locomotion not playing a role (Casey 1991). The majority of caterpillars of the limacodid group employ these defenses against predators and parasitoids. However, in limacodids and dalcerids especially, ventral adhesion to the hostplant and locomotion are so closely linked that locomotion can indeed be considered an adaptive strategy to avoid predation. Species in the two families show a marked specialization for cryptic behavior in their ability to crawl beneath smooth plant surfaces. This is further enhanced by having less visible mouthparts at leaf edges due to retractile feeding beneath the thorax, as in other members of the limacodid group (Epstein 1996). These larvae may also be less easily detected by parasitoids from their less apparent silk trails, perhaps gaining in survival from cryptic silk-use what they lose in not having the ability to dangle on silk to reach new host plants.

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Territoriality by the dawn's early light: the Neotropical owl butterfly *Caligo idomenaeus* (Nymphalidae: Brassolinae)

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Abstract. Males of the Neotropical owl butterfly *Caligo idomenaeus* defend unusual dawn territories along dirt roads in the Linhares Forest Reserve, Espírito Santo, Brazil. The territories are notable for their wide spacing and the brief period in which owners are present. During mid-winter insects arrived on the territories shortly after 0550 h, as the last bright stars disappeared from the sky, and remained approximately 15 min before flying back into the forest. Dawn perching seemed unaffected by substrate temperatures as low as 12.5° C. Perches were about 100 m apart and resident butterflies returned to and seemingly repelled invaders from their territories on consecutive mornings. Territories contained no material resources. The brief dawn occupancy may be related to the activity period of receptive females and to predator risk in these large, palatable insects.

Key Words. Brassolinae, Brazil, *Caligo*, crepuscular, mating behavior, territoriality

INTRODUCTION

Male defense of encounter sites is a common mate-locating tactic in butterflies (Baker 1983, Rutowski 1991). Mating territories have been recorded for many taxa and geographic regions, but are especially well documented for temperate zone species, especially papilionids (Lederhouse, 1982), lycaenids (Douwes 1975, Alcock 1983a, Alcock & O'Neill 1986) and the nymphalid subfamilies Nymphalinae (Baker 1972, Bitzer & Shaw 1980, 1983, Alcock 1983b, Alcock & Gwynne 1988, Rosenberg & Enquist 1991) and Satyrinae (Davies 1978, Knapton 1985, Wickman 1985). The few tropical studies to date have reported territorial behavior in typical tropical taxa (Riodininae, Alcock 1988; Heliconiinae, Benson et al. 1989) as well as in taxa already studied in temperate areas (Papilionidae, Pinheiro 1990; Nymphalinae, Rutowski 1991b, 1992, Lederhouse et al. 1992).

Independent of region, territorial behavior, like flight activity in general (Srygley & Chai 1990), is characteristic of sunny habitats with mild thermal environments (Alcock 1983b, Wickman 1985a, Alcock & O'Neill 1986). This rule is not universal, and several species of *Vanessa* defend near sundown (Alcock & Gwynne 1988, Brown & Alcock 1991). The exclusively Neotropi-

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cal Brassolinae may provide other exceptions. In Panama, *Caligo memnon* Felder engages in territorial-like mating behavior at dusk, and *Opsiphanes cassina* Felder (Brassolinae) behaves similarly (Srygley 1994). In the state of Espírito Santo in southeastern Brazil *Caligo illioneus* Cramer and *Catoblepia amphirrhoe* Hübner perch along roadsides at dusk (W.W. Benson, pers. obs.), whereas *Caligo idomenaeus rhoetus* Staudinger does this shortly before dawn, even during cool winter weather. In the winter of 1992 we studied *C. idomenaeus* with the intent of clarifying the significance of dawn perching behavior in this insect and gain insights into the possible influence of light and temperature.

METHODS

The study was carried out from 27.VII to 6.VIII.1992 (no observations were made on 4.VIII) along an east-west stretch of 4 m wide dirt road passing through mature subtropical moist forest in the Linhares Forest Reserve (Reserva Florestal de Linhares) at Linhares, Espírito Santo, Brazil (19° 10′ S, 40° 00′ W). Mean winter temperatures at the reserve are near 20° C, with extremes for the months of July and August (mid-winter) approximately 10° and 30° C (Companhia Vale do Rio Doce, unpub. data).

The study area was selected based on the confirmed presence of *Caligo idomenaeus.* A 450 m long area was marked off in 50 m segments to aid mapping of butterfly perches and behavioral events. We conducted observations daily from about 0545 to 0620 h (early dawn to shortly after sunrise). The owl butterflies were very difficult to see in the dim light at the beginning of their activity period, especially where trees arched over the road, and we were only able to follow insects at this time by spacing ourselves along the road and calling to each other as butterflies passed. When possible, butterflies were netted and marked by cutting distinguishing notches along wing margins. The owl butterflies are large and robust and apparently not impaired by this procedure. Some uncaptured individuals could be individually recognized by distinctive wing damage. Road-surface temperature was measured daily at the beginning of butterfly activity using a mercury thermometer. On one morning during the *Caligo idomenaeus* activity period we measured incident light at road level near the perch site at the widest and least obstructed part of the road using a digital luximeter with 1 lux sensitivity (Extech Instruments). Civil twilight period and sunrise were obtained from the computer program Earthsun 4.5 (© W. Scott Thoman, Dryden, NY, 1995).

RESULTS

The only large owl butterfly observed at dawn was *Caligo idomenaeus.* We observed three of the four individually recognizable insects on more than one day. Two individuals marked on perches at dawn were males, and others observed in the study area were inferred to be males by their behavior. Other *Caligo* captured during twilight hours while perched along reserve roadways have always proved to be males of *C. illioneus* and *C. idomenaeus* (W.W. Benson, pers. obs.).

On most mornings we observed 3–5 *Caligo* perching in the area and as many as four non-residents making "fly-throughs." Perching *Caligo* were punctual, with the first individual arriving between 0550 and 0556 h($\bar{x}$ = 0552.7 h, s.d. = 2.3 min , n = 7; six observations on marked individual #3) and the last *Caligo* departing around the time of sunrise between 0609 and 0612 h ($\bar{x}$ = 0610.1 h, s.d. = 0.9 min, n = 8; seven observations on individual #3). Between 27.VII and 2.VIII, when the bulk of the observations were made, civil twilight began between 0547 and 0545 h and the sun rose between 0609 and 0607 h. Brighter stars remained visible until about 0550 h, and the planet Venus could be seen until 0553 h.

Butterflies occasionally arrived in the area and patrolled back and forth as much as 3 min before perching. The time span over which one or more individuals were present in the area on a given morning varied between 13 and 20 min ($\bar{x}$ = 16.7 min, s.d. = 2.5 min, n = 6). The time of arrival and departure did not seem to be strongly influenced by cloud conditions (clear to cloudy) or temperature (12.5–18.0° C), and even with a soil temperature of 12.5° C, four butterflies were active. On 2.VIII under an almost cloudless sky, the light intensity increased approximately exponentially from about 2 lux at 0551 h when the first *Caligo* arrived to 180 lux when the last one departed at 0610 h.

When arriving in the area, an owl butterfly often patrolled back and forth several (maximum of nine) times along 10–50 m of road before landing. The flight was swift and erratic about 1–2 m above the ground. After arrival, butterflies perched near the center of the patrolled area on the ground in the roadway or on low (< 1 m high) roadside vegetation. Although most arriving (and departing) butterflies that we followed left (or entered) the forest within 25 m of the perch, one was observed to fly approximately 240 m before entering the forest.

Interactions occurred when flying butterflies met or a presumed male was chased when it flew over a perched resident. Interacting owl butterflies flew in tight circles about each other in level or ascending flight approximately 1–2 m (up to 5 m) above the ground while batting their wings together. Most interactions terminated after a few 10s of seconds. In six of the seven observed encounters involving marked resident males, the original male returned to its perch after the intruder had left. In the remaining case observed near the end of the territorial period neither butterfly returned. On two occasions, two *C. idomenaeus* were observed to perch 10–20 m apart, apparently without seeing one another.

During nine days of observations we identified five sites preferred by *Caligo idomenaeus* for perching: 10 m (used on 2 d), 100/120 m (3 d), 160 m (7 d), 220/280 m (3 d), and 380 m (9 d) from the west boundary of the study area. The three marked males that returned to the area showed perch fidelity on successive days. On five consecutive days (27–31.VII) male #1 landed at the 160 m perch (and once at the 10 m perch as it was leaving the area). Unmarked individual(s) occupied this perch on the two days following the disappearance of #1. Male #2, seen in the area 27–28.VII, occupied perches at 100 and 120 m, from which it was expelled by male #1. Male #3 perched in the road at 380 m on seven consecutive days (28.VII–3.VIII) and subsequently on 5– 6.VIII. Males #1 and #3 usually rested in the road near fallen, dead *Cecropia* leaves. Otherwise, there was no indication that the butterflies selected perching sites with respect to specific habitat features.

DISCUSSION

Patrolling behavior, interactions between individuals and spacing in male *Caligo idomenaeus* are almost certainly related to territorial defense. Individuals returned daily to specific perches spaced about 100 m apart. These residents seemed to patrol road segments around their perches and interact by expelling intruders. Although we saw neither courtship nor mating, defense of mating territories is common in butterflies (see Introduction), and other *Caligo* mate during crepuscular encounters (Srygley 1994). Although only three individually recognizible butterflies were monitored, we believe that our observations on these are representative of the study population. On the other hand, our unsuccessful attempts to capture unmarked individuals may have frightened some butterflies from the area and diminished perch occupation.

Territorial *Caligo idomenaeus* patrol corridors up to 50 m long around their perches. In contrast, territorial *Heliconius* patrol corridors about 15 m long (Benson et al. 1989), and similar territory sizes seem to exist in tropical *Heraclides* and *Battus* (Pinheiro 1990). *C. idomenaeus* is large for a butterfly (wing length 80 mm), and for this reason territory size may be less constrained than in smaller species. The wide spacing between perches may be advantageous in reducing mate competition between neighbors. Although *C. idomenaeus* occurs spottily along roadsides in the Linhares Forest Reserve, males do not seem to lek around conspicuous landmarks as has sometimes been reported for other butterflies (DeVries 1980, Lederhouse 1982, Alcock 1983a, Knapton 1985, Alcock & Gwynne 1987) and population distribution may be more related to habitat favorability than classical lek formation.

Low temperature can prevent butterfly flight, and the ability of *C. idomenaeus* to maintain full activity before sunrise with substrate temperatures below 13° C is probably aided by its large size and *Caligo*'s ability to increase body temperature by shivering (Srygley, 1994). Our study site is subtropical with cool winters, and it is interesting to note that *C. idomenaeus* was active at temperatures ($\overline{x} = 16.2°$ C, s.d. = 1.9° C, n = 8) uniformly lower than Srygley's (1994) estimate of 19–20° C for the lower critical temperature for flight in Panamanian *C. eurilochus.*

Two possibly unique characteristics of territoriality in *Caligo idomenaeus* and other brassolids (see Introduction; Srygley 1994) are its occurrence during twilight hours and the extreme brevity of the territorial bouts. Because owl butterflies are palatable (Chai 1986) and presumably especially profitable prey items due to their large body mass and high visibility when in movement, birds may select strongly against late-flying *C. idomenaeus* and thereby constrain activity to situations where their visiblity to predators is hampered. Restricted activity of receptive females could have the same cause, and same effect on mating conventions.

Published studies suggest that tropical forest butterflies usually spend less time in territorial defense than butterflies of other environments. Excluding desert butterflies such as *Chlosyne californica* (Wright) (Alcock 1983b) and *Strymon melinus* Hübner (Alcock & O'Neill 1986) whose activity is apparently limited by high midday temperatures, and species of the cosmopolitan genus *Vanessa* that defend territories just before sundown (Bitzer & Shaw 1980, 1983, Alcock & Gwynne 1988; Brown & Alcock 1991), 64% of the 14 temperate-zone butterflies for which data are available typically defend territories 3–6 h daily (Powell 1968, Baker 1972, Douwes 1975, Davies 1978, Wickman & Wicklund 1983, Alcock 1983a, Bitzer & Shaw 1983, Rutowski & Gilchrist 1988) and an additional 29% defend 6 h or more (see Lederhouse 1982, Wickman 1985b, Knapton 1985, Rosenberg & Enquist 1991). Similarly long shifts of territorial defense have been reported for *Hypolimnas* and *Junonia* in tropical savanna (Rutowski 1991b, 1992). Excluding the desert species and *Vanessa* mentioned above, *Polygonia comma* Harris is to our knowledge the only temperate butterfly reported to be territorially active for three or fewer hours a day (Bitzer & Shaw 1983).

The seven tropical forest butterflies for which data have been published defend territories over relatively shorter time spans, five for 3 h or less daily and the two remaining for up to 6 h. Besides the 0.25 h period reported here for *C. idomenaeus*, the heliconiines *Heliconius sara* (Fabr.), *H. leucadia* (Bates) and *Eueides tales* (Cramer) defend for 1–2.5 h daily in Brazil, and *E. aliphera* (Godart) is territorial for about 5 h daily in Costa Rica (Benson et al. 1989). Alcock (1988) reports that the Costa Rican forest hesperiids *Celaenorrhinus approximatus* William & Bell and *Astraptes galesus cassius* Evans defend for about 2 and 3 h respectively, whereas males of the riodine *Mesosemia a. asa* Hewitson spend about 4 h per day on territories. Although each species is no doubt adapted to a unique set of ecological conditions, we believe the general phenomenon of shorter defense shifts in tropical forest butteflies may be related to fine-tuning in mate search resulting from the greater temporal structuring of this environment. However, because of the small number and limited taxonomic distribution of species studied to date, and the general lack of information on temporal variation in the costs and benefits of territorial defense, our purpose here is more to draw attention to the phenomenon than to provide explanations.

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A review of the genus *Panara* Doubleday, 1847 (Riodinidae) in southeast Brazil, with a description of two new subspecies

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Abstract. The species of the riodinid genus *Panara* Doubleday, 1847 in southern Brazil are reviewed and corrections are made in the nomenclature of the the extra-Amazonian species. Two new subspecies, *Panara soana bacana* and *Panara soana ruschii* are described. The characteristics of the genus *Panara* are reviewed, and two taxa are removed: *Pterographium elegans* (Schaus), new combination; and *Phaenochitonia brevilinea* (Schaus), new combination, new synonomy. Separate keys are presented for adult males and females, as well as comments on the range, adult behavior, and habitats.

Key Words. Neotropical South America, *Panara*

INTRODUCTION

The genus *Panara* consists of five species, four of which are confined to extra-Amazonian Brazil and one distributed throughout the Amazon and Orinoco drainage. All species have black ground color with a diagonal yellow band from the costa to the distal margin, and some of the southern Brazilian phenotypes also have an orange band on the hindwing from the apex to the inner margin, a characteristic which varies within species. This has led to much confusion in the literature (e.g., D'Abrera 1994), such as the mixing of the species and subspecies as well as the inclusion in the genus of unrelated riodinid taxa with orange forewing bands. The lack of a basis for the proper identification of these species has hindered potential research in the biodiversity of southern Brazil.

The purpose of this review is to 1) present biological and morphological information on each species of extra-Amazonian *Panara*, 2) provide a key to both males and females which will help in their rapid determination, 3) correct the nomenclature of the extra-Amazonian species of *Panara*, and 4) review the characteristics of the genus *Panara* with the removal of those taxa which do not belong there.

MATERIALS AND METHODS

During the study I examined numerous museum collections in addition to my own (CJC), which includes material on loan by Dr. Keith Brown: the Museu Nacional, Rio de Janeiro (MN); the Universidade Federal de Paraná (UFP); the Smithsonian Institution, Washington, DC (NMNH), the Museum National d'Histoire Naturelle in Paris (MNHN); the Senckenburg Museum, Frankfurt (SM);

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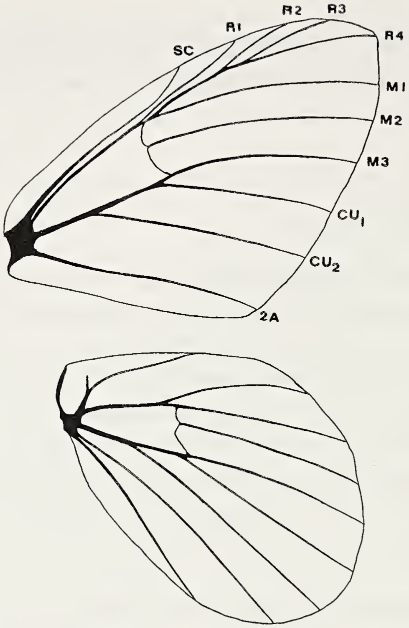


Fig. 1. Venation of *Panara*

the Humboldt Museum, Berlin (MNK); and the Natural History Museum (London) (BMNH). I examined 334 specimens and made 52 genitalia preparations. Measurements were made with an ocular micrometer and calipers. References to wing cells and veins follow the Comstock-Needham system in Miller (1969) and the genitalia terminology follows Klots (1970). In addition, my field trips over a 25-year period provided data on habitats and adult habits of *Panara.*

The Genus *Panara* Doubleday

Harvey (1987) followed Stichel (1910) in placing *Panara* in the Ancyluris section of the tribe Riodinini. This tribe is characterized by a deeply indented notch in the posterior margin of the tegumen of the male genitalia. A true saccus is also absent, the vinculum being ribbon-like ventrally, and not fused to the valvae.

Within the tribe Riodinini, *Panara* is related to *Lyropteryx* Westwood, [1851], *Necryia* Westwood, [1851], *Cyrenia* Westwood, [1851], *Ancyluris* Hubner, [1819], *Nirodia* Westwood, [1851], *Rhetus* Swainson, [1829], *Chorinea* Gray, 1832, *Nahida* Kirby, 1871, and *Ithomeis* Bates, 1862, all of which have 1) a normal strap-like pedicel in the male genitalia, 2) forewing vein R2 originating beyond the end of the cell, stalked with R3 and R4, and 3) the ostium bursa located in the middle of the ventral surface of the abdomen, not displaced to the right as in the Riodina section of the tribe.

Panara may be separated from related genera by 1) the black ground color of the wings and the transverse orange band on the forewing, 2) the male genitalia which are broad and triangular shaped laterally, 3) the wing venation. At the end of the forewing cell, M2–M3 forms a junction with M3 and

CU1, whereas in related genera this junction is considerably more basad of the cell (Fig. 1).

The genitalia of the southern Brazilian *Panara* species show considerable individual variation which makes classification on this basis tenuous. The most constant character in the male genitalia is the height of the valvae relative to the transtilla. However, I found an individual of *Panara iarbas* with the left valva higher and the right valva lower.

Synonyms and New Combinations

The last revisor of the genus *Panara* was Stichel (1930) who defined six species and five subspecies, as follows:

P. phereclus (Linné, 1758)
    a) *barsacus* Westwood, [1851]
    b) *elegans* Schaus, 1920
    c) *episatnius* Prittwitz, 1865
        =*sicora* Hewitson, 1865
        =*arctifascia* Butler, 1874
    d) *lemniscata* Thieme, 1907
        =*comes* Stichel, 1909
P. aureizona Butler, 1874
        =*ornata* Stichel, 1909
P. thisbe (Fabricius, 1782)
        =*iarbus* (Drury, 1782)
        =*perditus* (Fabricius, 1783)
        =*ovifera* Seitz, 1913
    a) *eclypsis* Seitz, 1913
    b) *soana* Hewitson, 1875
P. brevilinea Schaus, 1920
P. thymele Stichel, 1909
P. trabalis Stichel, 1916

As constituted by Stichel, the genus *Panara* is polyphyletic. Three taxa have been included erroneousely in the genus: "*Panara*" *elegans* Schaus, 1920, "*Panara*" *brevilinea* Schaus, 1928, and "*Panara*" *sicora* Hewitson, 1875. The removal of *P. brevilinea* was facilitated by its being a junior synonym of an existing taxon. *P. sicora* was removed to the genus *Pterographium* Stichel, 1910 by Hall and Willmott (1996).

Phaenochitonia brevilinea (Schaus, 1920), **new combination, new synonomy**. My examination of the type of *P. brevilinea* at the NMNH suggests that it is a synonym of *Phaenochitonia iasis* Godman, 1903, the type of which is in the BMNH.

Pterographium elegans Schaus, **new combination**. Harvey (1987) discovered that *Panara elegans* has the androconia on the anterior margins of the abdominal sclerites, characteristic of the tribe Symmachiini. However, he did not assign this species to a genus. My examination of *P. elegans* suggests that it is near to *Pterographium* based on the presence of erectile scent hairs in cell CU2–2A of the dorsal hindwing, the principal character for this genus

(Zikan 1949). Therefore, I provisionally place it in *Pterographium* until the limits of the genera of the tribe Symmachiini can be better defined. The remaining group of species is monophyletic, sharing the characteristics described for the genus *Panara* above.

With the changes proposed in this review, the following synonymic list summarizes the classification of *Panara*:

P. phereclus (Linné, 1758)
    ssp. *barsacus* Westwood, [1851]
    ssp. *lemniscata* Thieme, 1907
    =*comes* Stichel, 1909
P. iarbas (Drury, 1782), **replacement name**
    =*thisbe* (Fabricius, 1782), preocc. (*thysbe* Linné, 1764)
    =*perditus* (Fabricius, 1793)
    ssp. *episatnius* Prittwitz, 1865
    =*arctifascia* Butler, 1874
    =*eclypsis* Seitz, 1913, **new synonymy**
    ssp. *thymele* Stichel, 1909, **new status**
P. aureizona Butler, 1874
    =*ornata* Stichel, 1909
P. soana Hewitson, 1875, **reinstated status**
    =*trabalis* Stichel, 1916, **new synonymy**
    =*dilata* Lathy, 1932, **new combination**, **new synonymy**
    ssp. *bacana*, **new subspecies**
    ssp. *ruschii*, **new subspecies**
P. ovifera Seitz, 1913, **new status**

Ecology and Behavior

Habitat. The genus *Panara* is distributed in tropical South America to the east of the Andes. One species, *Panara phereclus* (Linn.) ranges from the Guianas throughout the Amazon and Orinoco drainages to Peru and Bolivia at elevations less than 200 m (Fig. 37), a region characterized by Tropical Moist Forest habitats (Tosi 1983, Holdridge 1947). The other species are concentrated in northeastern (Pernambuco) to southeastern Brazil (Paraná, Santa Catarina), reaching the central Planalto (Goiás). In southern Brazil, the species distributions are correlated with climatic zones. *Panara soana* and its subspecies inhabit the Subtropical Wet Forest and Warm Temperate Moist Forest zones, north through subtropical lower montane moist forest in the Serra da Mantiqueira, and the montane formations of the Subtropical Moist Forest habitat which reach their northern limit at Santa Teresa, Espirito Santo (Tosi 1983). This distribution more or less parallels that of the Paraná pine tree *Araucaria*. *Panara iarbas* and its subspecies inhabit the lower elevations of Subtropical Moist Forest in Rio de Janeiro State north to Pernambuco, then west along gallery forests penetrating the Planalto Central to central Goiás, and south to western Paraná. The two other species have limited distribution: *Panara ovifera* inhabits the cloud forests of the Serra do Mar above 1300 m and *Panara aureizona* the coastal

Subtropical Moist Forest areas of Santa Catarina and Paraná, and occasionally to 900 m.

All species inhabit secondary as well as primary forest habitats. I have never observed them flying outside the forest, except when visiting nectar sources.

Seasonality. Those species inhabiting lowland areas fly all year round, whereas *P. soana* flies from September to May, and *P. ovifera* February and March.

Biology. Early stage biology of the genus is unknown.

Adult Nectar Sources. I have observed *Panara* feeding during the morning on flowers, especially *Eupatorium*, and on one occasion on bird droppings in the forest.

Wing Pattern and Predation. All *Panara* species are black with a yellow-orange band on the forewing, a pattern shared by many other riodinids (*Melanis, Pterographium, Stichelia, Riodina*) and day flying moths (Pericopinae). It is not known whether *Panara* is distasteful, however males rest on the dorsal surfaces of leaves with wings spread advertising of their color pattern. I have never observed attacks by birds, nor have I captured specimens with beak marks, which suggests that vertebrate predation is minimal.

Mating Behavior. All *Panara* use perching as mate locating behavior. Localities for perching are small clearings in the forest, such as along roads and trails. Forested hilltops are frequented, but so are clearings in the same area which suggests that the forest opening is more important than the physical summit. From 1100–1500 h males rest on the edge of the dorsal surface of sunlit leaves with wings outspread and antennae apart (Fig. 4) awaiting females. When disturbed, they fly with a rapid, gliding flight, returning shortly to their original perching site. When not perching, they rest on the ventral leaf surfaces with a wingtip protruding beyond the edge. Females are rarer, but are encountered at nectar sources or in the forest.

Key to the Males of *Panara* in Southeast Brazil

la. Ventral surface of both wings with dull dark purple scaling at apex of forewing and base of hindwing 2
lb. Ventral surface with strong, iridescent light blue scaling at apex of forewing and base of hindwing 4
2a. Male hindwing band present .... *P. iarbas*
2b. Male hindwing band absent .... *P. aureizona*
3a. Male forewing band reduced to an elongated, oval spot; hindwing band wide and rounded towards costa, tapering to inner margin .... *P. ovifera*
3b. Male forewing and hindwing bands narrow (1.5 mm) elongated; hindwing band straight .... *P. soana*

Key to the Females of *Panara* in Southeast Brazil

la. Veins on both wings outlined with lighter scaling. .... *P. soana*
lb. Veins not outlined with lighter scaling 2
2a. Band on forewing reaches distal margin 3

2b. Band on forewing does not reach distal margin .... *P. ovifera*
3a. Forewing band wide (>3 mm) .... *P. aureizona*
3b. Forewing band narrow (<3 mm) .... *P. iarbas*

SPECIES ACCOUNTS

Panara iarbas (Drury, 1782) (*Papilio*), **replacement name**
=*Papilio thisbe* (Fabricius, 1782), preocc. (*Papilio thysbe* Linné, 1764)
= *Hesperia perditus* Fabricius, 1793

Nomenclature. *Panara iarbus* (Drury 1782): *Papilio thisbe* was described by Fabricius as having yellow bands on both fore- and hindwings, and as coming from "Brazil." However, Fabricius' name is a primary homonym of *Papilio thysbe* Linné, which refers to a South African lycaenid butterfly currently in the genus *Poecilmitis* Butler, 1899. Drury (1782) essentially repeated Fabricius' description in describing *Papilio iarbas,* which becomes the next available replacement name for *P. thisbe.* No type of either taxa has been located; however, as no strong ventral surface blue reflections are mentioned in either description, the name probably refers to the coastal populations of *P. iarbus* from central-southeast Brazil, the males of which consistently have yellow bands on both the fore- and hindwings.

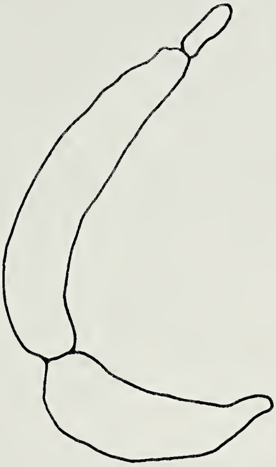
Hesperia perditus Fabricius, 1793: This taxon, described from "French Guiana" is identical to *P. iarbas.* However, information supplied by C. Brevignon, a resident collector (pers. comm.), suggests that this taxon is not found there. Scudder (1875) designated *P. iarbus* as the type species of the genus *Panara* Doubleday, 1847.

In view of the inadequacy of the original descriptions, the species is redescribed as follows:

Male. Medium sized (forewing length average 20 mm), robust riodinid butterfly with black appendages and a yellow lateral line on the abdomen. Palpae (Fig. 2) and male foreleg (Fig. 3) as illustrated. Vein R1 on the forewing rises before the discal cell with R2 following it (Fig. 1). Wings black with an orange-yellow 2–3 mm wide transverse band on the forewing between the costa to less than 1 mm from the distal margin, and with a second transverse band of variable width (0.3–3 mm) on hindwing between 0.5 mm from the apex and the inner margin. Ventral wing surface with same transverse bands as on dorsal surface, ground color black with a faint purple reflection, stronger at the forewing apex. Fringe black.

Female. Fore- and hindwing more rounded than male; forewing transverse band width variable (1–3 mm), reaching from costa to distal margin, curving to anal angle; hindwing band dorsal surface when present extends from costa to inner margin, convex to base and is duplicated on the ventral surface; when absent dorsally, is reflected by a band of lighter scaling on the ventral surface.

Genitalia. Male genitalia (Fig. 29) with pedicel a strap-like band connecting aedeagus to base of valvae; tergum deeply indented caudad; vinculum ribbon-like ventrally, not fused to valvae; valvae sickle-shaped, serrated



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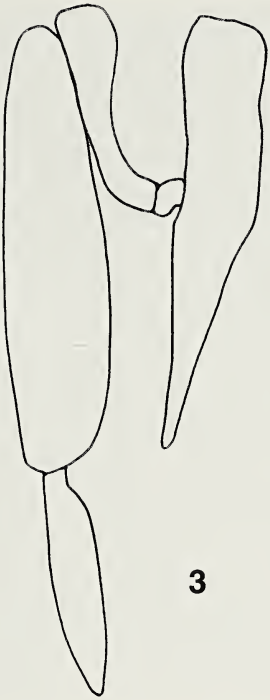

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Fig. 2. *Panara* male palpus
Fig. 3. *Panara* male foreleg

caudad; tips of valvae reaching to transtilla; transtilla with two small projections caudad; saccus reduced.

Female genitalia (Fig. 33) with blade-like papillae anales fused dorsad; ostium bursae squared, sclerotized; corpus bursae without signa.

Geographical Distribution. *Panara iarbas* ranges from Rio de Janeiro State north to Pernambuco, then west across the Planalto to Goiás, from sea level to 1000 m, then south through western São Paulo State to western Paraná.

Geographical Variation. I recognize three distinct populations, represented by the nominate subspecies, *P. iarbas episatnius,* and *P. iarbus thymele.*

Panara iarbas iarbas (Drury, 1782) (*Papilio*), **replacement name**

Identification. The nominate subspecies has wide hindwing bands on both sexes. The male can be separated easily from *Panara soana* by the lack of strong blue reflections on the ventral surface at the apex and base of the wings.

Geographic Distribution. The distribution of *P. iarbas iarbas* is disjunct, from the Serra da Carioca and Serra do Mar in western Rio de Janeiro State to southeastern Minas Gerais, and again in the Zona da Mata from northern coastal Espirito Santo State north to Pernambuco.

Brazil. Rio de Janeiro: Rio de Janeiro, 0–600 m, 25♂, 2♀, MN; 5♂, 1♀, NMNH; 4♂, 6♀, UFP; Novo Friburgo, 2♂, 1♀, NHML; Jacarepaguá, 3♂,

Fig. 4. *P. iarbus* perching, Barra de São João, R.J. Brazil

UFP; Angra dos Reis, 8♂, 1♀, MN; Paineiras, R.J., 3♂, 1♀, MN. Minas Gerais: Passa Quatro, MG, 1♀, NHML. Bahia: "Bahia," 1♀, SM; Itamaraju, 1♂, MN; Ilheus, 2♂, MN; Pernambuco: 10 km E. João Pessoa, 7♂, 2♀; São Lourenço, 1♂, NMNH; Tiuma, PE, 1♀, CJC.

Ecology and Behavior. In coastal Brazil, *P. iarbas iarbas* inhabits primary and disturbed humid subtropical forest. Males perch in the late morning to early afternoon in light gaps and other small clearings and on hilltops, resting on dorsal leaf surfaces with their wings outspread and head and body raised at a 30° angle from the leaf surface (Fig. 4). Females are encountered less frequently, flying near the ground in the forests. It is local and uncommon.

P. iarbas episatnius Prittwitz, 1865, **new combination** (Figs. 8–10)
= ***P.artifascia*** Butler, 1874
= ***P. eclypsis*** Seitz, 1913, **new synonymy**

Nomenclature. *Panara episatnius* Prittwitz,1865: Prittwitz described *Panara episatnius* from a female from Rio de Janeiro, currently in the Natural History Museum, London. Stichel (1930) subsequently designated *P. episatnius* a subspecies of *phereclus* based on the absence of the hindwing band. This was in error, as *P. phereclus* is limited to the Amazonian drainage.

Panara arctifascia Butler, 1874: Butler described this taxon from a female


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Fig. 5. *P. iarbas iarbas*, male dorsal surface
Fig. 6. *P. iarbas iarbas,* male ventral surface
Fig. 7. *P. iarbas iarbas,* female dorsal surface
Fig. 8. *P. iarbas episatnius*, male dorsal surface
Fig. 9. *P. iarbas episatnius,* male ventral surface
Fig. 10. *P. iarbas episatnius,* female dorsal surface

from Espirito Santo presently in the Natural History Museum, London, which is identical to *P. episatnius.* The two were synonymized by Stichel (1930).

Panara eclypsis Seitz, 1913: Seitz based his description of *Panara eclypsis* on a male from Espirito Santo, designating it as a form of *Panara thisbe,* which was subsequently raised to a subspecies by Stichel (1926). *P. eclypsis* is in fact the male of *P. episatnius,* thus becoming a junior synonym of that taxon. The locality of the type of *P. eclypsis* is unknown; however the butterfly is distinct enough as to make the designation of a neotype unnecessary.

Identification. The males *P. i. episatnius* differ from the nominate subspecies in the reduced width of the band on the dorsal hindwing to 0.5 mm and ventrally to 1 mm. Females differ in the absence of the hindwing band. *P. i. episatnius* intergrades to the east of Rio de Janeiro State with *P. i. iarbus,* some individuals showing characteristics of both phenotypes. The male genitalia of material from central Espirito Santo have long points on the valvae, whereas those from eastern Rio de Janeiro State are identical to nominate *P. i. iarbas.*

Geographic Distribution. *P. i. episatnius* is found throughout Espirito Santo and adjoining eastern Minas Gerais State below 800 m. This suggests that

P. i. episatnius is an isolated population of *P. i. iarbas* which has recently come into secondary contact.

Brazil. Minas Gerais: Parque Estadual de Rio Doce, 2♂, 2♀, CJC; Espirito Santo: Linhares, 1♂, CJC: B. Guapemirim, 1♂, MN; Boitacazes, 1♂, MN; "Espiritu Santo," 3♂, MN; Colatina, 6♀, MN; Conceição da Barra, 1♂, 1♀, UFP; Linhares, 1♀, UFP; Baixu Guandu, ES, 2♂,UFP.

Intergrades to *P. iarbas iarbas*: Rio de Janeiro: km 27, Rio-Teresopolis, 1♂, CJC; Barra de São João, 2♂, CJC; Fazenda União, 4♂, CJC.

Ecology and Behavior. These are the same as the nominate subspecies.

P. iarbas thymele Stichel, 1909, **new status** (Figs. 11–13)

Nomenclature. *Panara thymele* was described from a male from Casa Blanca, São Paulo, currently in the Museum für Naturkunde, Humboldt Universitat, Berlin. *P. i. iarbas* intergrades in central Bahia with *P. i. thymele*, suggesting that they are conspecific.

Identification. The male can be distinguished by the slight S-shaped forewing band and both males and females by the hindwing band concave to the margin. Specimens from Bahia have thinner bands than those from Goiás.

Geographic Distribution. *P. i. thymele* is found from western Bahia south to western Paraná, then across the Planalto Central to Goiás State.

Brazil. Federal District: Sobradinho, 3♂, CJC; Parque da Gama, DF, 2♂, 1♀, UFP; Agua Limpa, DP, 3♂, UFP. Goiás: Goiás Velho, 2♂, 1♀, CJC; 1♀, UFP Bahia: km 997, Rio-Bahia, 1♀, CJC; "Bahia," 9♂, 1♀, BMNH; Campo Formosa, Juazeiro, 1♂, UFP. Paraná: Guarapuava, 1000 m, 1♂, UFP.

Ecology and Behavior. On the Planalto, the subspecies inhabits the gallery forests along streams and cabeceira (headwater) woods where it flies during the early afternoon hours, frequenting the edges of clearings where the males perch on the dorsal leaf surfaces with wings open.

Panara aureizona Butler, 1874 (Figs. 14–16)

=*P. aureizona f. ornata* Stichel, 1909

Nomenclature. Butler described *P. aureizona* from a female from "Minas Gerais," currently in the Natural History Museum (London). It is sympatric at Joinville, Santa Catarina with *P. soana* and allopatric with *P. i. thymele* to the west. The genitalia are intermediate between *P. iarbas* and *P. soana*.

Geographical Variation. *P. aureizona* is very rare in collections, so its distribution and variation are not well known. An occasional male has a spot of orange where the band should be on the hindwing.

Identification. Males may be separated by the 3.5 mm wide band from the costa to the outer margin, and the females by the 4 mm wide forewing band which extends basad and distad along the costa, and is curved towards the anal angle on the distal margin. Both sexes lack the hindwing band, but on the VHW is a faint transverse line of lighter scaling in the normal position of orange band. In the male genitalia (Fig. 30), the valvae do not reach the transtilla; the ostium bursae in the female genitalia (Fig. 34) has V-shaped sides.


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Fig. 11. *P. iarbas thymele,* male dorsal surface
Fig. 12. *P. iarbas thymele,* male ventral surface
Fig. 13. *P. iarbas thymele,* female dorsal surface
Fig. 14. *P. aureizona,* male dorsal surface
Fig. 15. *P. aureizona,* male ventral surface
Fig. 16. *P. aureizona,* female dorsal surface
Fig. 17. *P. soana soana,* male dorsal surface
Fig. 18. *P. soana soana,* male ventral surface
Fig. 19. *P. soana soana,* female dorsal surface

Geographic Distribution. *P. aureizona* ranges from coastal Santa Catarina and Paraná north and west to eastern Minas Gerais(?). As no other records have been found between Paraná and Minas Gerais, the locality of Butler's type is suspect.

Brazil. Santa Catarina: Itaiopolis, 900 m, 1♂, SM; Garcia, 60 m, 3♂, SM; Blumenau, 50 m, 3♂, SM; Macaranduba, 130 m, 1♂, SM; Joinville, 3♂, UFP; 10♂, 10♀, NM; 1♂, 1♀, CJC; Jaragua, 200 m, 1♂, UFP. Paraná: Marumbi, 500 m, 1♂, UFP; 5♂, 4♀, no locality, BMNH.

Ecology and Behavior. *P. aureizona* inhabits disturbed tropical forest from sea level to about 900 m. The males are found hilltopping at Joinville, Santa Catarina (H.W. Miers, pers. comm.). The females are encountered more often beside roads and in the forest.

Panara soana Hewitson, 1875

Identification. *Panara soana* males may be separated from other *Panara* by the blue sheen at the apex of the forewing, at the base and along the margin of the hindwing combined with a straight, narrow, band on the fore- and hindwings; and the females by a dusting of lighter scaling along the veins.

Geographical Variation. I recognize three distinct geographical populations of *P. soana,* two of which are new. All three are allopatric with no known intergrades, which future investigations may show to be separate species.

Panara soana soana Hewitson, 1875, **reinstated status** (Figs. 17–19)

= ***P. trabalis*** Stichel, 1916, **new synonymy**
= ***P. dilata*** Lathy, 1932, **new combination, new synonymy**

Nomenclature. *Panara soana* Hewitson, 1875: *P. soana* was described by Hewitson from a male labeled "Brazil." Comparison of the type with material from Santa Catarina, Paraná, and São Paulo suggests that the specimen originated from this region. Stichel (1909) designated *P. soana* as a subspecies of *P. thisbe* (*iarbas*). Examination of these two taxa suggests that this was in error, as they maintain consistent morphological differences, even when sympatric (Santa Teresa, ES; Novo Friburgo, Rio de Janeiro). The type of *P. soana soana* is in the Natural History Museum (London).

Panara trabalis Stichel, 1916. *Panara trabalis* was described as a species by Stichel from a female from Santa Catarina, Brazil, located in the Natural History Museum, London. The type represents the female of *P. soana soana,* the white scaling along the veins and no band on the hindwing being typical of southern Brazilian populations.

Panara dilata Lathy, 1932. *P. dilata* was described by Lathy from a female from Ponto Grosso, Paraná, and who assigned it to the genus *Lymnas,* Blanchard (currently *Melanis* Hubner). The type in the Natural History Museum (London) is the female of *P. soana.*

Identification. The male of the nominate subspecies is distinguished by strong light blue reflections on the ventral forewing at the apex and ventral hindwing at the base and around the margin, when viewed at an angle. The female lacks the band on the hindwing and has light scaling along the veins of both wings.

The valvae in the male genitalia (Fig. 31) extend above the transtilla, and the ostium bursae in the female genitalia (Fig. 35) has V-shaped sides.

Geographical Variation. The nominate subspecies *Panara soana soana* (Figs. 12–13) ranges from northern Rio Grande do Sul State north along the Serra do Mar to São Paulo State.


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Fig. 20. *P. soana bacana*, male dorsal surface
Fig. 21. *P. soana bacana*, male ventral surface
Fig. 22. *P. soana bacana*, female dorsal surface
Fig. 23. *P. soana ruschii*, male dorsal surface
Fig. 24. *P. soana ruschii*, male ventral surface
Fig. 25. *P. soana ruschii*, female dorsal surface
Fig. 26. *P. ovifera*, male dorsal surface
Fig. 27. *P. ovifera*, male ventral surface
Fig. 28. *P. ovifera*, female dorsal surface

Brazil. Minas Gerais: Virginia, 900 m, 1♂, MN; Parque Nacional Itatiaia, 900 m, 1♂, MN; 1♂, 1♀, UFP; Itajuba, 4♂; São Paulo: "São Paulo," 1♀, MN; 1♂, UFP; 2♂, NHML; Amparo, 1♀, MN; Cantareira, 1♂, 1♀, MN, 1♀, UFP, 4♀, SM; Sa. Japi, 1♀, CJC. Paraná: Ponta Grossa, 4♂, 4♀, UFP; Rio Vermelho, 2♂, CJC; Curitiba, 1♂, CJC; 7♂, 5♀, UFP; São Luiz, Puruna, 2♂, UFP; Vossoroca, 3♂, UFP; Santa Catarina: Joinville, 2♂, CJC; Campo Alegre, 7♂, NMNH; São Bento do Sul, 2♂, 1♀, CJC: São Luis de Paraná, 2♂, 1♀, CJC; Blumenau, 3♂, SM; Massaranduba, 1♂, SM.








Fig. 29. *P. iarbas iarbas,* male genitalia
Fig. 30. *P. aureizona,* male genitalia
Fig. 31. *P. soana,* male genitalia
Fig. 32. *P. ovifera,* male genitalia
Fig. 33. *P. iarbas iarbas,* female genitalia
Fig. 34. *P. aureizona,* female genitalia
Fig. 35. *P. soana,* female genitalia
Fig. 36. *P. ovifera,* female genitalia

Ecology and Behavior. *P. soana soana* inhabits montane subtropical forest above 600 m. Males perch on the forest edges during the early afternoon, resting on dorsal leaf surfaces with wings spread. At some localities they are common.

Panara soana bacana Callaghan, **new subspecies** (Figs. 20–22)

Description. Male differs from the nominate subspecies in having a wider band on the dorsal hindwing and a reduction of the blue iridescence at the apex and base of hindwing. Caraça specimens have less blue than those to the southeast. Female differs in a marked reduction in the white scaling along the veins and the presence of a yellow transverse band on the hindwing

Fig. 37. Distribution of the species of *Panara*. ■ *P. phereclus* ● *P. iarbas* ▲ *P. auerizona*, □ *P. soana*, △ *P. ovifera*

from the inner margin near the anal angle narrowing to the costa, where it turns slightly basad.

Holotype Male. With label "BRAZIL, Minas Gerais, Caraça, 2500 m, 26-iv-1975, C. Callaghan," a genitalia label #424 and a red holotype label. The holotype is deposited in the Museu Nacional, Rio de Janeiro, Brazil.

Paratypes. Passa Quatro, MG, 1♂, MN; Caraça, MG, 1500 m, 3♂, 3♀, CJC; 15♂, 8♀, NHML; Barbacena, 1200 m, MG, 4♂, 2♀, CJC; Poço de Caldas, 600 m, 9♂, 1♀, MN; Caxambu, MG, 5♂, MN; Novo Friburgo, R.J., 3♀, NHML.

Etymology. "Bacana" means "nice" in Portuguese.

Ecology and Behavior. *Panara soana bacana* inhabits subtropical humid forest patches in the Serra de Mantiquera and Serra do Mar at 600–1800 m

Fig. 38. Distribution of *Panara* in southeast Brazil. ● *P. iarbas iarbas,* ◗ *P. iarbas thymele,* ○ *P. iarbas episatnius,* ▲ *P. aureizona,* □ *P. soana,* ■ *P. soana bacana,* ▼ *P. soana ruschii,* Δ *P. ovifera*

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from southeastern Minas Gerais to the Serra de Caraça. It is sympatric with *P. iarbas* in Novo Friburgo, 900 m, Rio de Janeiro.

Panara soana ruschii Callaghan, **new subspecies** (Figs. 23–25)

Description. Male differs from the nominate subspecies in having a longer, more pointed forewing; forewing band narrower, tapering from costa to 2 mm from distal margin above anal angle; ventral surface blue reflections at forewing apex and base of hindwing stronger and more extensive, that on apex of forewing extending along distal margin to 3 mm above anal angle. Female with very light white dusting along veins, band on forewing 4 mm wide at costa, tapering to a rounded point 1 mm from distal margin above anal angle, hindwing without transverse band. Genitalia as in nominate subspecies.

Holotype Male. With label "BRAZIL E. Santo Santa Teresa 800 m, 5-iv-1973 C. Callaghan," a genitalia label #420, and a red holotype label.

Paratypes. Santa Teresa, Espirito Santo, 900 m 2♂, 2♀, CJC. The holotype and a female paratype are deposited in the Museu Nacional, Rio de Janeiro.

Etymology. This taxon is named in memory of the famous Brazilian conservationist, Augusto Ruschi, who I got to know during my visits to Santa Teresa where he lived.

Ecology and Behavior. The subspecies is currently known only from the type locality where the males frequent hilltops in the early afternoon, perching on dorsal leaf surfaces with wings spread.

Panara ovifera Seitz, 1913, **new status** (Figs. 26–28)

Nomenclature. *Panara ovifera* was described by Seitz (1913) from a male from Petrópolis, Rio de Janeiro as a form of *P. thisbe.* The phenotype is representative of a unique isolated *Panara* population. The truncated bands, extensive blue sheen on the ventral surface, high mountain habitat and absence of intergrades separate it from *P. iarbas. Panara ovifera* is allopatric with *P. soana.* There are no clines and it is consistently distinct morphologically. The type is in the Natural History Museum (London).

Identification. The males of *P. ovifera* can be separated by the triangular orange spot tapering below the cell on the forewing, and the wide, short band on the hindwing. The ventral wing surface has the same pattern of shiny blue scaling at the apex of the forewing and the base and margin of the hindwing as *P. soana soana,* but more extensive. In the male genitalia (Fig. 32), the tips of valvae extend beyond transtilla and the female ostium bursae (Fig. 36) has V-shaped sides, and a wide sinus vaginalis.

Ecology and Behavior. *Panara ovifera* is restricted to the pygmy chusquea cloud forests above 1300 m in the Serra do Mar, Rio de Janeiro State. The males rest on the upper leaf surfaces with wings outspread beside roads and other openings in the forest between 1100–1500 h. It is rare.

Material examined. Petrópolis, Estrada Imperial, 1300 m, 3♂, 3♀, CJC; Petropolis, RJ, 1♂, MN.

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Lepidoptera of different grassland types across the Morava floodplain

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Abstract. The occurrence of the diurnal and readily disturbed Lepidoptera species were studied during the 1992–1994 flight seasons on different types of grassland resulting from management practice: mowing, cattle grazing, and application of liquid manure. Observations were made across the southern part of the Morava River alluvia on 9 study sites. The transect method was used with 111 lepidopterous species in 15 families recorded. Five of these species are vulnerable and two species endangered. *Zerynthia polyxena, Iphiclides podalirius, Colias chrysotheme, Melanargia galathea, Minois dryas, Erynnis tages, Agriphila inquinatella, Loxostege sticticalis, Zygaena loti, Zygaena angelicae, Scopula virgulata, S. immutata, Idaea* spp., and *Euclidia glyphica* were associated with relatively well preserved xerothermic grassland habitats (no cutting history). *Heteropterus morpheus, Colias hyale, Lycaena dispar,* and *Maculinea teleius* associated with semi-annually cut and regularly flooded extensive wet meadows. *Psammotis pulveralis, Elophila nymphaeata, Coenonympha glycerion, Lycaena tityrus,* and *Phlogophora meticulosa* were found in bog habitat. The Lepidoptera community from the non-mown undisturbed areas with *Crataegus* sp. (forest-steppe vegetation) showed the highest diversity (H′ = 2.944) and relatively high evenness (e = 0.760). The community from cut wet meadow that is heavily fertilized with liquid manure has both the lowest diversity (H′ = 1.036) and evenness (e = 0.383).

INTRODUCTION

The Morava River forms the border between the Slovak Republic and Austria and partly between the Slovak and Czech Republics. The total length of the river is 353 km. In Slovakia the Morava River flows across the Borska Nizina lowland which forms part of the Pannonian region (Kulfan & Kulfan 1992). The lower reach of the Morava floods annually, usually in spring and often in summer after rainstorms. The territory where the field study was done, on the border near Austria, is relatively well preserved because it was inaccessible before 1990 (see map, Fig. 1). The study region is now part of the protected landscape territory Zahorie, where 1000 ha of inundation meadows are covered with the subcontinental plant association *Cnidion dubii* (Ruzickova, 1994). J. Kulfan (1989, 1990a, b) studied the lowland butterfly communities of Borska Nizina on irregularly cut meadows near the village of Rohoznik.

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Fig. 1. Map of the lower Morava River showing approximate location of the sites used in this study.

The only data on the grassland Lepidoptera of the lower Morava River alluvia deal with the distribution of heliophilous species across Borska Nizina where these species were evaluated by trophic relations to host plants and from a conservation perspective (Kulfan & Kalivoda 1994).

The purpose of this paper is to compare the Lepidoptera communities across different grassland management regimes that vary according to cutting intensity, cattle grazing, and the application of liquid manure.

METHODS AND STUDY AREAS

Our investigations were carried out on the lower Morava River near a border between Slovakia and Austria during the flight seasons of 1992–1994 on sunny days at about 2 week intervals. Day flying and easily disturbed (roused) Lepidoptera were caught by net following the transect method of Erhardt (1985). The length of each transect was 200 m with 414 samples taken.

Nine sites were sampled:

Site 1: Alluvial meadow near Marchegg village cut twice and partly flooded during the annual cycle (*Carici praecoci-Alopecuretum pratensis* association, Spanikova 1975, subassociation *typicum* Bal.-Tul. 1963, with occurrence of *Iris sibirica*).

Site 2: Partly cut narrow area near Marchegg village along the field path, between *Prunus* and *Crataegus* shrub grove and the Morava river (*Carici praecoci-Alopecuretum pratensis,* subassociation with *Filipendula vulgaris* Bal.-Tul. 1974 with occurrence of *Aristolochia clematitis*).

Site 3: Alluvial meadow near Marchegg village cut twice annually and flooded regularly in spring and summer following heavy rains (*Carici praecoci-Alopecuretum pratensis,* subassociation *typicum* with occurrence of *Lychnis flos-cuculi, Iris sibirica, Iris pseudacorus, Clematis integrifolia*).

Site 4: Non-mown narrow area near the Devinske Jazero railway station between the path and the *Phragmites australis* stand (*Carici praecoci-Alopecuretum pratensis,* subassociation *typicum* with occurrence of *Aster lanceolatus* and *Clematis integrifolia*).

Site 5: Alluvial meadow near the Devinske Jazero railway station, usually partly mown twice annually with spring flooding, edged with *Phragmites australis* growth (*Lathyrus paluster-Gratiola officinalis* Bal.-Tul. 1963 and *Carici praecoci-Alopecuretum pratensis* associations, latter subassociation *typicum* with occurrence of *Thalictrum flavum* and *Leucojum aestivum).*

Site 6: Alluvial meadow cut twice annually, but rarely flooded (*Carici praecoci-Alopecuretum pratensis* association, subassociation *typicum* with *Colchicum autumnale, Galium verum, Symphytum officinale, Sanguisorba officinalis, Inula salicina*).

Site 7: Uncut area near Devinska Nova Ves (suburb of Bratislava) with the forest-steppe vegetation, *Crataegus* surrounded by agricultural phytocoenoses and by alluvial meadows (*Carici praecoci-Alopecuretum pratensis,* subassociation with *Filipendula vulgaris* and *Serratulo-Festucetum commutatae* Bal.-Tul. 1963 association on gravelly outcrops and sandy alluvial sediments with occurrence of *Galium verum, Sanguisorba officinalis, Inula salicina, Rumex acetosa, Centaurea jacea, Fragaria viridis, Aristolochia clematitis*).

Site 8: Alluvial meadow near Devinska Nova Ves, cut twice annually and partly flooded. Highly modified by application of liquid manure. There is a depauperate community of plant species (*Carici praecoci-Alopecuretum pratensis,* subassociation *typicum*).

Site 9: Alluvial meadow near Devinska Nova Ves modified by cattle grazing with a depauperate community of plants, partly flooded annually (*Carici praecoci-Alopecuretum pratensis,* subassociation *typicum* with *Galium verum, Rumex crispus, Cirsium arvense*).

The lower Morava floodplain was entirely flooded at the beginning of August 1991, with water level reaching about 2.5 m above ground elevation.

Table 1. General survey of Lepidoptera species found on the Morava River alluvia (EC = Ecological Characteristics: X = xerothermophil, M = mesophil, H = hygrophil, U = ubiquist).

		Study Area								
Taxon	**EC**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Incurvaroidea										
Adelidae										
Adela reaumurella (L., 1758)	M				2					
Tortricoidea										
Tortricidae										
Aphelia viburnana (D. et. S., 1775)	M							+		
Aphelia paleana (Hb., 1793)	M							+		
Agapeta zoegana (L., 1767)	X					+				
Olethreutes rivulana (Sc., 1763)	M							+		
Epiblema uddmanniana (L., 1758)	X		+							
Dichrorampha gueneeana (Obr., 1953)	X					+				
Pterophoroidea										
Pterophoridae										
Pterophorus pentadactyla (L., 1758)	X		2					+		
Pyraloidea										
Pyralidae										
Hypochalcia ahenella (D. et S., 1775)	X							+		
Tachycera advenella (Gm. et Znk., 1818)	X		+							
Elophila nymphaeata (L., 1758)	H			2						
* *Chrysoteuchia culmella* (L., 1758)	M					4	2	17	7	9
Crambus pascuella (L., 1758)	X, M							+		
Crambus lathoniella (Znk., 1817)	M							+		
Crambus perlella (Sc., 1763)	M					4			4	4
Agriphila tristella (D. et S., 1775)	X, M							7		2
* *Agriphila inquinatella* (D. et S., 1775)	X			2	2	2		7		2
Platytes cerussella (D. et S., 1775)	X							+		
* *Evergestis aenealis* (D. et S., 1775)	X			2						
* *Pyrausta despicata* (Sc., 1763)	X				2					
* *Loxostege sticticalis* (L., 1761)	X							7		4
Ecpyrrhorrhoe rubiginalis (Hb., 1796)	X							+		
* *Sitochroa verticalis* (L., 1758)	X			4	9			7		4
* *Psammotis pulveralis* (Hb., 1796)	H				2					2
Pleuroptya ruralis (Sc., 1763)	X, M		2							
Zygaenoidea										
Zygaenidae										
* *Adscita statices* (L., 1758)	H							9		
* *Zygaena loti* (D. et S., 1775)	X							4		
Zygaena viciae (D. et S., 1775)	M							+		
* *Zygaena filipendulae* (L., 1758)	M							2		
* *Zygaena angelicae* O., 1808	X							4		
Hesperoidea										
Hesperiidae										
* *Erynnis tages* (L., 1758)	X, M		2				26	33		
* *Pyrgus malvae* (L., 1758)	X, M	2	+				+	+		
Carterocephalus palaemon (Pallas, 1771)	M, H						+			
Heteropterus morpheus (Pallas, 1771)	H			+						
* *Thymelicus sylvestris* (Poda, 1761)	M	4	+		2			13		4
* *Thymelicus lineolus* (O., 1808)	M	2	+		2		+	20		4
Hesperia comma (L., 1758)	M	2						+		
* *Ochlodes venatus* (Br. et Grey, 1853)	M		+				+	2		

Papilionoidea										
Papilionidae										
* *Zerynthia polyxena* (D. et S., 1775)	X		4					11		
* *Papilio machaon* L., 1758	X, M	9	+	20	4	11	11	15	2	+
* *Iphiclides podalirius* (L., 1758)	X		+		9		9	11	2	+
Pieridae										
Leptidea sinapis (L., 1758)	M							+		
* *Pieris brassicae* (L., 1758)	U		+					2		
* *Pieris rapae / napi* (L., 1758)	U	80	67	83	54	63	83	93	80	65
* *Pontia daplidice* (L., 1758)	X	9	9	17			11	+	4	4
* *Anthocharis cardamines* (L., 1758)	X, M	4	2				+		2	2
* *Colias hyale* (L., 1758)	M			33		7	15	17	9	22
* *Colias alfacariensis* Ribbe, 1905	X			4			2	4	+	9
Colias chrysotheme (Esper, 1781)	X							+		
* *Colias crocea* (Fourcr., 1785)	X, M			20			4	7	+	
* *Colias erate* (Esp., 1804)	X			17		2	2	2	4	2
Gonepteryx rhamni (L., 1758)	M		+							
Nymphalidae										
* *Apatura ilia* (D. et S., 1775)	M				4			2		
* *Inachis io* (L., 1758)	U	2	+				+	9	4	7
* *Vanessa atalanta* (L., 1758)	U		+		9	2	+	2	2	4
* *Cynthia cardui* (L., 1758)	U		+		4		7	4	9	2
* *Aglais urticae* (L., 1758)	U		+				+	2	4	4
* *Polygonia c-album* (L., 1758)	M		4					4		
Araschnia levana (L., 1758)	M		+				+		+	
* *Issoria lathonia* (L., 1758)	X, M			2		7	7	4		+
* *Clossiana selene* (D. et S., 1775)	M							4		
Clossiana dia (L., 1767)	X, M		+				2		+	
* *Mellicta athalia* (Rott., 1775)	M							2		
Satyridae										
* *Melanargia galathea* (L., 1758)	X, M		+				+	30	+	
Minois dryas (Sc., 1763)	X							+		
* *Maniola jurtina* (L., 1758)	U		2				17	48	+	11
* *Aphantopus hyperanthus* (L., 1758)	M		15				9	22		
* *Coenonympha pamphilus* (L., 1758)	U	67	39	28	22	17	46	52	+	17
* *Coenonympha glycerion* (Bkh., 1788)	M, H	22	2	+		2	4	13		
Pararge aegeria (L., 1758)	M								+	
* *Lasiommata megera* (L., 1767)	X, M						2	+	+	
Lycaenidae										
Fixsenia pruni (L., 1758)	X		+							
* *Lycaena phlaeas* (L., 1761)	M		+	+	22	9	9	11		17
* *Lycaena dispar* (Haw., 1803)	H		2	17			2	+		
* *Lycaena tityrus* (Poda, 1761)	M, H		+	7	11	20	11	28		
* *Everes argiades* (Pallas, 1771)	X, M						11	2		
Everes decoloratus (Stdgr., 1886)	X						+			
* *Celastrina argiolus* (L., 1758)	X, M		4		+	4	4	+		+
Maculinea teleius (Brgstr., 1779)	H			2						
* *Lycaeides argyrognomon* (Brgstr., 1779)	X			2				+		2
Aricia agestis (D. et S., 1775)	X						+	+		
* *Polyommatus icarus* (Rott., 1775)	X, M	7		9	4	9	35	41	2	
Geometroidea										
Geometridae										
* *Timandra griseata* W. Pet., 1902	X, M		7	7		4				
* *Scopula immorata* (L., 1758)	X		4					4		
* *Scopula virgulata* (D. et S., 1775)	X, M							4		
* *Scopula immutata* (L., 1758)	M							7		
* *Idaea serpentata* (Hufn., 1767)	X, M							7		

* *Idaea subsericeata* (Haw., 1809)	X							9		
* *Idaea aversata* (L., 1758)	M							9		
Lythria purpuraria (L., 1758)	X			2						
* *Lythria rotaria* (F., 1798)	X	4				7		4		4
* *Catarhoe cuculata* (Hufn., 1767)	X		4							
* *Epirrhoe alternata* (Müller, 1764)	X		4				+	4		
Minoa murinata (Sc., 1763)	X			+				+		
* *Lomaspilis marginata* (L., 1758)	M		4				+			
* *Semiothisa clathrata* (L., 1758)	X		4	13	7		2		4	4
* *Ematurga atomaria* (L., 1758)	X	4	+	2		7	9	13	4	4
Siona lineata (Sc., 1763)	X							+		
Sphingoidea										
Sphingidae										
Agrius convolvuli (L., 1758)	X						+			
Macroglossum stellatarum (L., 1758)	X						+			
Hyles euphorbiae (L., 1758)	X						+			
Noctuoidea										
Arctiidae										
* *Diacrisia sanio* (L., 1758)	X			2			+	2		
Syntomis phegea (L., 1758)	X, M				+					
Noctuidae										
Polypogon tentacularia (L., 1758)	X							+		
* *Euclidia glyphica* (L., 1758)	X							20		
Deltote bankiana (F., 1775)	M, H							+		
* *Emmelia trabealis* (Sc., 1763)	X					2				
* *Macdunnoughia confusa* (Stph., 1850)	X			2				2		
* *Autographa gamma* (L., 1758)	X		+	2			7	4	9	
Phlogophora meticulosa (L., 1758)	M, H								+	

RESULTS AND DISCUSSION

Table 1 presents the survey results of the Lepidoptera species found on the Morava floodplain. We have found 111 species in the region, but species not recorded during transect counts marked by a + . All the found species were used to construct the dendrogram of species similarity, using Soerensen's index following the Complete linkage clustering method of Podani (1993). The summary numbers of individuals of different species (68 species marked with an asterisk in Table 1) in the course of the periods 1992–1994 (27 samples from each site, 9 samples each year) were used for the Shannon and Weaver diversity and the Pielou equability (evenness) indices that are given in Fig. 2. The samples of Lepidoptera were from the same or similar date of each year with the differences between triplets of corresponding dates not exceeding 8 days.

Numerical classification according to species similarity shows that the Lepidoptera communities from non-flooded or rarely flooded sites with the plant community at drier elevations (sites 2, 6, and 7) form a separate group (Fig. 2). The community from the driest site (site 7) with forest-steppe vegetation has the highest diversity (H′ = 2.944) and high evenness (equability) (e = 0.760). This corresponds with the high species richness on this site, 78 species (Table 1). The Lepidoptera communities of the damp sites (1, 3, 4, 5, 8, and 9) form a single group. Within this group the communities of sites 8 and 9, however, differ considerably from the others. They inhabit sites affected by negative anthropogenic factors, this is, intensively managed

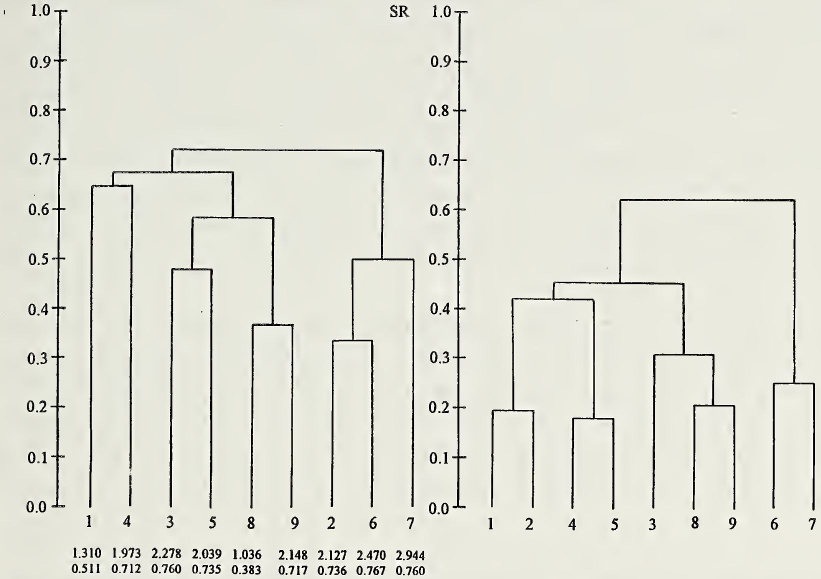

Fig. 2. Dendrograms of classification of Lepidoptera communities in individual study sites according to species presence/absence (to the left) and according to frequency of species (to the right). Diversity and equability values of these communities are given under the left dendrogram.

meadows. The community of Lepidoptera from site 8 with a depauperate plant community and application of liquid manure shows the lowest diversity (H′ = 1.036) and evenness (e = 0.383). In contrast the community from site 9 with many ruderal flowering plants (*Asteracae*) for food sources for adult butterflies has relatively high diversity (H′ = 2.148) and evenness (e = 0.717).

The Lepidoptera communities of the more flooded sites, 3 and 5, form a distinct group. These communities have high evenness, e = 0.760 and 0.735, respectively. Communities from sites with the same plant association (1 and 4) form another separate group, but are similar to each other at a low level (Fig. 2).

The hierarchical classification (Podani 1993; Fig. 2) used the Complete linkage clustering method and Similarity ratio index for making the dendrogram based on the frequency of 78 species (given in Table 1) which were derived from all 46 samples from each site.

The classification shows that the Lepidoptera communities of the driest sites, 6 and 7, form a conspicuous grouping (Fig. 2). The communities of the intensively managed meadows, sites 8 and 9, form a separate group together with the community of regularly flooded meadow, site 3. All these sites, 3, 8, and 9, are extensive open wet meadows without shrubs and trees. Lepidoptera communities of the narrow areas (1, 2, 4, and 5) surrounded by zones of a transitional character (e.g., shrubland) or by different habitat type (e.g., banks, high *Phragmites australis* stands, etc.) form yet another separate group.

According to the IUCN classification, five of the species found are listed as vulnerable: *Heteropterus morpheus, Zerynthia polyxena, Iphiclides podalirius, Fixsenia pruni, Lycaena dispar.* In addition two species are listed as endangered: *Colias chrysotheme* and *Maculinea teleius. Zerynthia polyxena, Papilio machaon* and *Iphiclides podalirius* are protected by law. The greatest number of Lepidoptera occurred on site 7 where not only the xerothermic species occur, but many hygrophilous species immigrate from the nearby wet habitats as well.

According to an ecological classification of lepidopterous species given by Blab and Kudrna (1982), Koch (1984) and original data, the species spectrum shows that xerothermophilous species predominate in the investigated region (40.5%) (Table 1). This appears to be a result of the study region, altitude 138–145 m, with poor sandy soil, being located in the warmest region of Slovakia (Kulfan & Kulfan 1992). Some Lepidoptera found are known to prefer sandy soil, e.g., *Lythria rotaria.* Many butterflies, as *Minois dryas* and *Colias chrysotheme* fly to these sites from nearby habitats of xerothermic character with the forest-steppe vegetation, especially from the adjacent slopes of Devinska Kobyla, a part of Little Carpathian mountains.

The following species found in this study are useful indicators: *Zerynthia polyxena, Iphiclides podalirius, Colias chrysotheme, Melanargia galathea, Minois dryas, Erynnis tages, Agriphila inquinatella, Loxostege sticticalis, Zygaena loti, Z. angelicae, Scopula virgulata, S. immutata, Idaea* spp. and *Euclidia glyphica.* These species indicate relatively well preserved xerothermic habitats with forest-steppe vegetation characterized by *Crataegus* over uncut grassland on slightly elevated places as gravelly and sandy alluvial sedimentary outcrops, exemplified by site 7.

Heteropterus morpheus, Colias hyale, Lycaena dispar, and *Maculinea teleius* indicate extensive wet meadows, cut twice annually and frequently flooded, as site 3.

Psammotis pulveralis, Elophila nymphaeata, Coenonympha glycerion, Lycaena tityrus, and *Phlogophora meticulosa* indicate boggy habitats at sites 1, 3, 4, 5, and 9.

Two species from the family Nymphalidae, *Cynthia cardui* and *Aglais urticae,* reached their highest abundance on sites 8 and 9 that were modified by extensive application of liquid manure and by cattle grazing. The abundance of flowering weeds on site 9 especially attracted adults of these butterflies.

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Effectiveness of caterpillar defenses against three species of invertebrate predators

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Abstract. The efficacies of larval defenses against invertebrate predators representing different (but overlapping) foraging guilds were compared by offering 34 species (287 individuals) of lepidopteran larvae to *Paraponera clavata* ants, *Apiomerus pictipes* bugs, and *Polistes instabilis* wasps. Overall, the ants were the most likely to eat caterpillar prey, and the wasps were the most cautious. Larval chemistry and diet breadth were significant predictors of rejection by the group of predators; chemically defended specialist herbivores were better protected than generalist herbivores without known chemical defenses. These results provide evidence for the potential importance of predators in maintaining diet breadth of phytophagous insects, and they suggest that plant chemistry is part of a mechanism for restricting diet breadth. Other important larval defenses included size, morphology, and coloration. Large prey (heavier than 1 g) were less acceptable than smaller prey (lighter than 200 mg) for the wasps and bugs but not for the ants; hairs deterred predation by the ants and bugs but not by the wasps; and brightly colored caterpillars were frequently rejected by the wasps but not by the ants and bugs.

Key Words. Caterpillars, defenses, diet breadth, predation, *Apiomerus pictipes, Polistes instabilis, Paraponera clavata,* plant secondary compounds, Lepidoptera, specialization, tropics

INTRODUCTION

Faced with a deluge of special cases that often appear to be a morass of contradictions and confusion, ecologists frequently attempt to generalize about predominant forces or patterns that are manifested by specific experiments and observations. A few prominent examples in research on Lepidoptera include: attempts to use specific studies of oviposition patterns (particularly those of lepidopteran pest species) to construct a diet-choice theory for all phytophagous insects (e.g., Courtney & Kibota 1990); attempts to identify the most important processes which organize communities by examining particular systems of predators, herbivores and plants (e.g., Karban 1989); and attempts to explain the high incidence of dietary specialization in lepidopteran larvae by examining known feeding patterns (e.g., Ehrlich & Raven 1964). These generalizations, which arose from

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multiple-species pattern analyses as well as from reductionist (single-species or single-system) approaches, have contributed significantly to a theoretical framework for a large number of studies on Lepidoptera.

In light of these and many other studies which provide good data for generalizations, it is surprising that there is a dearth of attempts to characterize important components of lepidopteran larval defenses, either by conducting multiple-species experiments or through literature reviews (Witz 1990, Dyer & Floyd 1993, Dyer 1995; also for adult Lepidoptera see Maclean et al. 1989). While multiple-species approaches are generally not as thorough as experiments examining the effectiveness of a particular defense in one species, they allow for different generalizations on insect defenses which can ultimately provide a framework for both basic and applied research questions with specific systems. For example, Bernays and Cornelius (1989) demonstrated that a number of species of leaf rollers were extremely palatable to ants; their generalization that trade-offs could exist between chemical defense and concealment from predation provides an impetus for quantitative genetics experiments examining the potential for such trade-offs in specific systems.

Two important groups of general hypotheses about larval defenses which I attempt to address in this study are: 1) hypotheses about the effectiveness of a suite of defenses against specific predatory guilds or against single species, and 2) hypotheses about effectiveness of specific defenses against a suite of predatory guilds or against multiple species. A related question which I address involves generalizations about the importance of biotic interactions (particularly natural enemies: Brower 1958, Bernays & Graham 1988) and plant chemistry (Dyer 1995) in influencing herbivores' diet breadths. Recent studies have demonstrated that certain specialist herbivores are better protected than certain generalists against various invertebrate predators (Bernays 1988, Bernays & Cornelius 1989, Dyer & Floyd 1993, Dyer 1995), which suggests that natural enemies could be important in the maintenance of narrow diet breadth or could be a selective force in the evolution of dietary specialization. In this study, I further test this natural enemy hypothesis, and I also explore the possibility that plant chemistry mediates the evolution of differences in defensive capacity between specialists and generalists. Chemistry might provide such a mechanism if specialized herbivores tend to evolve the ability to sequester plant defensive chemicals and use them as defenses against their natural enemies.

In order to generalize about the efficacies of various defenses against different predators and about the importance of biotic interactions and plant chemistry in the evolution of dietary specialization, I offered specialist and generalist lepidopteran larvae (caterpillars) with a wide variety of potential defensive qualities to three predators representing different predatory guilds: an assassin bug, *Apiomerus pictipes* (Reduviidae); a paper wasp, *Polistes instabilis* (Vespidae); and the giant tropical ant, *Paraponera clavata* (Formicidae). Specifically, I asked the following questions: 1) Are different predator guilds deterred by different types of defenses? 2) What are the most effective defensive mechanisms of lepidopteran larvae against a suite of predators? 3) Are specialist herbivores better protected than generalists against a suite of predators? 4) Are noxious prey chemicals effective defenses against a suite of predators?

The prey used in my experiments were larvae in 13 different families of Lepidoptera that were native to a variety of micro-habitats in Costa Rica. These caterpillars exhibited a wide variety of antipredator mechanisms which could be compared. *Apiomerus pictipes* is a common sit-and-wait predator that ranges from Colorado (USA) to Columbia (Johnson 1983). It is solitary, visually oriented, and quickly kills prey by inserting its mouthparts and sucking, leaving behind a dry carcass. *Polistes instabilis* is a common foraging predator found from Costa Rica to Southern Brazil and Argentina (Richards 1978). It is a solitary (i.e., it does not recruit), visually-oriented predator, and it kills prey by biting rather than stinging. Each wasp extensively chews the prey before returning to the nest to distribute ingested fluids and solid caterpillar remains to the other adults and larvae (West-Eberhard 1983). *Paraponera clavata* is a foraging predator common in lowland rainforests and found from Nicaragua to the Amazon (Janzen & Carroll 1983). It is a chemically-oriented predator that forages independently or in groups and that kills prey by using its powerful sting, using its mouthparts and cooperating with nestmates (pers. obs.). All three predators commonly prey on caterpillars (pers. obs., West-Eberhard 1983, Johnson 1983) and are sympatric with all the caterpillars used in my study.

MATERIALS AND METHODS

I conducted all experiments and most collecting in June and July, 1993 at the following sites in Costa Rica: Palo Verde National Park, Lomas Barbudal National Park, and private land near Lomas Barbudal. These sites are located in the Guanacaste province of Costa Rica and are characterized by dry forest (sensu Holdridge et al. 1971) and marsh (at Palo Verde).

Collecting

I collected most caterpillars at Palo Verde and Lomas Barbudal. I also bought several species of caterpillars that are known to occur in Guanacaste from *Finca Mariposa*, a commercial butterfly farm in La Guacima.

I either identified caterpillars to the lowest taxon possible using Stehr (1993), or if sufficient numbers of caterpillars were available, I reared them to the adult stage for identification. I deposited voucher specimens of most caterpillars and adults at both the Instituto Nacional de Biodiversidad (INBio) in Costa Rica and the University of Colorado Entomology Museum, Boulder (Table 1).

For host plant data, I identified plant families on which I found caterpillars and held the caterpillars in captivity for several days to verify that they actually were using their presumed host plants as food resources. If possible, I collected enough plant material for identification to lower taxa by park naturalists or I dried and pressed them for identification by other tropical botanists. Voucher specimens for some host plants are at the University of Colorado Herbarium, Boulder (Table 1).

Table 1a. Generalist caterpillars offered to *P. clavata*, *P. versicolor*, and *A. pictipes* and the host plants upon which the caterpillars were found.

Caterpillar[a]	**Predators**[b]	**Host Plants**[c]
Arctiidae (5, 5, 3) CU:LS93GAT	A(Y), B(Y), W(Y)	(Annonaceae)* *Costus* sp. (Costaceae) *Siparuna pauciflora* (Monimiaceae) *Welfia georgii* (Palmae) *Adiantum* sp. (Polypodiaceae) *Myriocarpa longipes* (Urticaceae)*
Arctiidae (5, 5) CU:PV93AWB	A(N), B(Y)	*Protium panamense* (Burseraceae) (Compositae) *Hernandia* sp. (Hernandiaceae) *Nectandra hypoleuca* (Lauraceae) *Colubrina spinosa* (Rhamnaceae) (Rubiaceae)
Eois sp. (Geometridae) (3, 3) CU:TBG92	A(N),B(N)	(Araceae)* (Leguminosae) *Piper urostachyum* (Piperaceae) *Sabicea* sp. (Rubiaceae)
Pero sp. (Geometridae) (5, 3, 5) CU:LS93ATB	A(N), B(N), W(N)	(Annonaceae)* *Diffenbachia* sp. (Araceae) *Costus* sp. (Costaceae) *Erythrina* sp. (Leguminosae) *Pentaclethra macroloba* (Leguminosae) *Hampea appendiculata* (Malvaceae)
Geometridae (5, 3, 5) CU:BTB92	A(N), B(N), W(N)	*Richeria dressleri* (Euphorbiaceae) *Ardisia* sp. (Myrsinaceae) *Passiflora* spp. (Passifloraceae)* *Colubrina spinosa* (Rhamnaceae) *Citrus* spp. (Rutaceae) (Solanaceae) (Violaceae)
Gonodonta sp. (Noctuidae) (5, 3, 3) IN:GON92	A(N),B(N),W(N) TASTY	(Brassicaceae) (Compositae) *Wissadula excelsior* (Malvaceae) *Calathea* sp. (Marantaceae) *Pithecellobium* sp. (Mimosaceae) *Ficus* sp. (Moraceae) *Solanum* sp. (Solanaceae) *Myriocarpa longipes* (Urticaceae)*
Pantographa limata (Pyralidae) (5, 3, 5) CU:LS93SIM	A(N),B(N),W(N) TASTY	*Costus* sp. (Costaceae) *Manihot esculenta* (Euphorbiaceae) *Hamelia patens* (Rubiaceae) *Paullinia pterocarpa* (Sapindaceae) *Cestrum* sp. (Solanaceae)* (Solanaceae) *Goethalsia meiantha* (Tiliaceae)* *Luehea seemannii* (Tiliaceae)* *Myriocarpa longipes* (Uritcaceae)*

Antheraea polyphemus (Saturniidae) (3, 3) IN:SAT92	A(N),W(Y)	*Godmania aesculifolia* (Bignoniaceae)* *Solanum* sp. (Solanaceae)* *Luehea* sp. (Tiliaceae)* [Plus 18 additional families reported in Tietz 1972]
Automeris rubrescens (Saturniidae) (3, 3) CU:PV93IOT	A(N),W(Y)	*Cordia alliodora* (Boraginaceae) *Rourea glabra* (Connaraceae) *Cassia* sp. (Leguminosae)* *Inga* sp. (Leguminosae) [Plus 5 additional families reported in Janzen 1984]
Automeris zugana (Saturniidae) (5, 3) CU:93IOM	A(N),W(Y)	*Cydista heterophylla* (Bignoniaceae)* *Cassia* sp. (Leguminosae)* *Lonchocarpus* sp. (Leguminosae)* (Sapindaceae) *Solanum hazenii* (Solanacae) [Plus 2 additional families reported in Janzen 1984]
Citheronia lobesis (Saturniidae) (5, 3, 3) CU:PV93HHD	A(N),B(Y),W(Y)	(Anacardiaceae) *Cydista heterophylla* (Bignoniaceae)* *Godmania aesculifolia* (Bignoniaceae)* *Cochlospermum vitifolium* (Cochlospermaceae)* [Plus 4 additional families reported in Janzen 1984]
Erinnyis ello (Sphingidae) (4, 3) CU:PV93ELL	A(N),W(Y)	(Bignoniaceae) *Manihot esculenta* (Euphorbiaceae) *Sapium* sp. (Euphorbiaceae) *Cissus microcarpa* (Vitaceae) [Plus 2 additional families reported in Tietz, 1972 and 1 additional family reported in Janzen, 1984]

Table 1b. Specialist caterpillars offered to *P. clavata*, *P. versicolor*, and *A. pictipes* and the host plants upon which the caterpillars were found.

Caterpillar[a]	**Predators**[b]	**Host Plants**[c]
Euchaetes sp. (Arctiidae) (3,3) CU:PV93BOA	B(Y),W(Y)	*Asclepias curassavica* (Asclepiadaceae)*
Arctiidae (3) CU:PV93MHA	W(N)	*Cydista heterophylla* (Bignoniaceae)*
Hesperiidae (3) IN:PV93HES	W(Y)	*Solanum* sp. (Solanaceae)*
Limacodidae (3,3)	B(Y),W(Y)	*Quercus oleoides* (Fagaceae)

Lymantriidae (3, 3) CU:PV93040	B(Y),W(N)	*Cassia* sp. (Leguminosae)*
Lymantriidae (3, 3) IN:LS92LYM	B(Y),W(Y)	*Godmania aesculifolia* (Bignoniaceae)*
Megalopygidae (3, 3) CU:PV93MGT	B(Y),W(Y)	*Ceiba pentandra* (Bombacaceae)
Azeta versicolor (Noctuidae) (3, 3, 3) CU:PV93010	A(N),B(N),W(N)	*Siparuna pauciflora* (Monimiaceae)
Diphthera festiva (Noctuidae) (3) IN:PV93NOC2	W(Y)	*Solanum* sp. (Solanaceae)
Caligo memnon memnon (Brassolinae) (5, 3, 5) CU:LS93CAL	A(Y),B(Y),W(Y) NASTY	*Heliconia imbricata* (Heliconiaceae)
Agraulis vanillae (Nymphalinae) (3) CU:LS93AGV	W(Y)	*Passiflora* sp. (Passifloraceae)*
Aeria eurimedia agna (Ithomiinae) (4, 3, 3) CU:LS93AEA	A(N),B(N),W(Y)	(Apocynaceae)
Morpho peleides limpida (Morphinae) (5, 3, 4)	A(Y),B(Y),W(Y) NASTY	*Lonchocarpus oliganthus* (Leguminosae)*
Adelpha fessonia (Nymphalinae) (5, 3, 4) CU:LS93ADF	A(N),B(N),W(N) TASTY	*Randia armata* (Rubiaceae)*
Marpesia petreus (Nymphalinae) (5, 3, 3)	A(N),B(Y),W(Y)	(Anacardiaceae)
Papilio cresophantes (Papilionidae) (5, 3, 3) CU:LS93PAC	A(Y),B(Y),W(Y) NASTY	*Citrus limon* (Rutaceae)*
Papilio anchisiades idaeus (Papilionidae) (5, 3, 5) CU:LS93PAP	A(Y),B(Y),W(Y) NASTY	*Citrus limon* (Rutaceae)*

Anteos clorinde (Pieridae) (5, 3, 3) CU:LS93ANT	A(N),B(N),W(N) NEUTRAL	*Cassia fruticosa* (Leguminosae)*
Pyralidae (3, 3) CU:PV93FNT	B(Y),W(Y)	*Bombacopsus quinatum* (Bombacaceae)
Saturniidae (3, 3) CU:PV93013	A(Y),W(Y)	*Ceiba pentandra* (Bombacaceae)
Manduca sexta (Sphingidae) (5, 3, 3) CU:LS93THW	A(Y),B(Y),W(Y)	*Solanum* sp. (Solanaceae)
Sphingidae (3) CU:PV93003	W(Y)	*Piper* sp. (Piperaceae)

[a] Those species that I could not identify past the family level are identified by the family. Sample sizes (number of caterpillars offered to ants, bugs, and wasps, respectively) are indicated in parentheses underneath each species. Voucher specimen codes are included under those species for which I had appropriate replicates to keep a voucher. CU = University of Colorado Entomology Museum, Boulder; IN = Instituto Nacional de Biodiversidad, Costa Rica.
[b] Not all caterpillar species were available for all predators; this column indicates to which predators each species was offered. A = ants, B = bugs, W = wasps. The predators' average responses (rejection) are indicated in parentheses after the letter indicating the predator. Y = Rejected more than half of the time, N = Not rejected more than half of the time. If extract data were available, the level of the "chemistry" category is also included in this column.
[c] Caterpillars were reared on host plants on which they were found. Although there are other reported hosts for some species, none of them are known to feed on plants in more than 2 families. Asterisks (*) indicate those species for which voucher specimens are available at the University of Colorado Herbarium, Boulder.

Experiments with wasps

I offered caterpillars to wasps throughout the day and at 5 different sites. Three of the sites were areas where wasps were frequently found foraging along the side of a dirt road within and just outside of Lomas Barbudal. The other two sites were two different trees in Palo Verde which contained many wasp nests. Caterpillars offered to wasps foraging along the road were placed on the ground amidst vegetation where the wasps were foraging. Caterpillars offered to wasps in the trees were placed in small, clear plastic cups which were suspended with string from branches of the trees. If the caterpillars crawled out of the cups before being encountered by a wasp, they were placed back into the cup. Depending on availability, I offered 3–5 individuals of each caterpillar species (32 species) to the wasps (see Table 1), and each site received only 1 individual of each species. Each caterpillar was independently offered at a different spot along the road or in the tree, and the order of presentation was haphazard (often depending on when caterpillars were found). No site received more than 4 caterpillars in a single day.

I observed all caterpillar-wasp interactions until either most of an entire caterpillar was carried away by wasps or at least 3 wasps had encountered and rejected it. Rejections consisted of a wasp approaching the caterpillar and either touching it or coming within about 20 cm without attacking; 20 cm is a distance which is well within the field of vision of wasps (Spradbery 1973).

Experiments with bugs

Fourteen assassin bugs were collected at the 3 experimental sites and were kept in 17 cm × 13 cm × 7 cm plastic boxes containing paper towels and twigs. When not being used for experiments, twice a week the bugs were fed a drab, glabrous noctuid caterpillar (voucher: PV93NOT at the University of Colorado Museum, Boulder) which was abundant and which was palatable to various wasps, ants and mantids (pers. obs.).

Three to five replicates of 24 species of caterpillars were offered to the bugs (Table 1), and no bug received more than 6 total caterpillars or more than 1 replicate per species. Caterpillars were placed in the plastic boxes containing bugs and were left with the bugs for 24 hours. The bugs would either attack the caterpillar within an hour or they would ignore it, which constituted a "rejection."

Experiments with ants

Data were used from caterpillars offered to *P. clavata* in a larger study (Dyer 1995). In that study, caterpillars were offered to 5 ant colonies, and the numbers of ants (within a colony) rejecting individual caterpillars were classified into the categories "no rejections" (0 ants rejecting the caterpillar), "some rejections" (fewer than 7 ants rejecting the caterpillar), and "completely rejected" (8 or more ants rejecting the caterpillar). Because the wasps and bugs either rejected or accepted prey as opposed to having inconsistent responses within a colony (hence, "some rejections"), I reclassified the ant rejection category to make it comparable to data for the bugs and wasps. Caterpillars receiving fewer than 5 rejections were considered to be "not rejected," while caterpillars receiving 5 or more rejections were considered to be "rejected." This was an arbitrary categorization, but it effectively split the "some rejections" category in half and made the *P. clavata* responses comparable to data for the bugs and wasps.

Statistical analyses

I scored each caterpillar species for the following categorical variables: a) caterpillar diet breadth — generalist or specialist; b) caterpillar coloration — brightly colored, visually cryptic, or other; c) caterpillar morphology — spines, hairs, or glabrous; d) caterpillar size — small, medium, or large; and e) caterpillar chemistry — palatable extract or deterrent extract.

For the diet breadth variable, I used a taxonomic definition of specialization. Caterpillars known to feed on fewer than 2 families of plants (according to Tietz 1972, Janzen 1984, DeVries 1987, Marquis 1991, and personal communication with various naturalists), or caterpillars of unknown diet breadth that were found feeding on only 1 plant species, were classified as "specialists" (22 species; 9 of which had unknown diet breadths). Since most herbivores at La Selva are monophagous or oligophagous (Marquis and Braker 1994), I assumed that it was unlikely that unknown caterpillars would be erroneously classified as specialists. Caterpillars found feeding on plants in greater than 3 families were classified as "generalists" (12 species; most fed on plants in greater than 6 families).

The coloration and morphology variables were based on visual inspection of the caterpillars. "Spiny" caterpillars had sclerotized spines at least 2 mm long. Caterpillars with hairs or with hairs and spines were rated as "hairy" only if more than 50% of their cuticle was covered with secondary setae that were at least 5 mm long. "Glabrous" caterpillars had no hairs or spines.

The size statistic was based on the weight (in mg) of a caterpillar just before it was offered to a predator. Levels of size categories were: "small" (weight $\leq$ 200 mg), "medium" (200 mg $<$ weight $\leq$ 1000 mg), and "large" (weight $>$ 1000 mg). The size categories were pooled in the preceding manner based on examination of a frequency histogram of all the weights.

For the chemistry variable I used results from a bioassay done with crude caterpillar extracts offered to *P. clavata* (Dyer 1995). Data for this variable were only available for 8 caterpillar species (see Table 1). The levels of this variable were: "nasty" (caterpillars with deterrent extracts), "tasty" (caterpillars with extracts which attracted ants), and "neutral" (caterpillars with neutral extracts). This variable was included to examine the defensive efficacy (against all three predators) of chemicals found in caterpillars without the confounding effects of morphological and behavioral features.

I used logit analyses to study the relative importance of these caterpillar characteristics as determinants of predator rejections (see Christensen 1990 for a thorough discussion of logit models). All of the caterpillar characteristics which I examined may act as important anti-predatory traits (reviewed by Edmunds 1974, DeVries 1987, Evans and Schmidt 1990). For all logit models I used the maximum likelihood method for parameter estimation of linear models and Chi-square statistics for hypothesis testing (see SAS 1990). All of the models were nonhierarchical because I either obtained significant highest-order associations in the saturated models, or because I had specific hypotheses that I wanted to test. Since the models were nonhierarchical, I used the Newton-Raphson algorithm for parameter estimation and model testing (SAS 1990). I assigned values of 1×10^{-20} to cells that contained "sampling zeroes" (sensu Bishop et al. 1975), while cells that contained "structural zeroes" (sensu Bishop et al. 1975) were automatically deleted (see SAS 1990).

To avoid running a large model containing many cells with zeros or small values, it was necessary to use more than one model. I chose variables for models that addressed specific questions which I wanted to ask with my experiments; in addition, examination of frequency tables for all combinations of variables helped form decisions for appropriate models (see Tabachnick and Fidell 1989). Variables that were not significantly associated with rejection in 2-dimensional frequency tables (using a conservative criterion of $P < 0.001$ because of the large number of tests) were not included in the models.

I ran two logit models which included data from all the predators. Model 1 addressed these questions: 1) Are caterpillars' levels of rejections dependent on the

Table 2. Summary of two-dimensional tables with predictors versus rejections.

Predator	Predictor	χ^2	DF	P
ALL	Chemistry	84.5	2	0.000
(n=287)	Diet Breadth	29.6	1	0.000
	Predator	34.9	2	0.000
	Size	31.6	2	0.000
	Morphology	25.3	2	0.000
	Coloration	10.0	2	0.007
ANTS	Chemistry	36.2	2	0.000
(n=103)	Diet Breadth	17.8	1	0.000
	Size	1.9	2	0.386
	Morphology	11.3	2	0.003
	Coloration	0.97	2	0.617
BUGS	Chemistry	24.0	2	0.000
(n=76)	Diet Breadth	4.5	1	0.035
	Size	28.7	2	0.000
	Morphology	29.5	2	0.000
	Coloration	2.5	2	0.297
WASPS	Chemistry	25.4	2	0.000
(n=108)	Diet Breadth	4.5	1	0.033
	Size	24.6	2	0.000
	Morphology	0.24	2	0.885
	Coloration	16.7	2	0.000

type of predator?, 2) Are the presence of unpalatable chemicals in caterpillars likely to make predators reject them more frequently?, 3) Which predictor of rejection (chemistry or predator) is more reliable?, and 4) Are there interactions between rejections, type of predator, and extract palatability? Model 2 addressed these questions: 1) Are specialists rejected more frequently than generalists against a variety of predators?, 2) Is diet breadth a better predictor of rejection than type of predator?, and 3) Are there interactions between rejections, diet breadth, and type of predator?

For the wasps and bugs I also ran a logit model for data specific to each predator. Each model asked questions about associations between caterpillar characteristics and rejections by the predator. The bug model included morphology and size as predictors. The wasp model included coloration and size as predictors. Models examining predictors of ant rejections are reported elsewhere (Dyer 1995).

RESULTS

I used results from 108 individuals of 32 caterpillar species offered to the wasps and results from 76 individuals of 24 caterpillar species offered to the bugs. For the ant data, I only used data for caterpillar species that were also offered to either the wasps or bugs; this subset of the data included

Table 3. Summary of log-linear models.

Model[a]	Likelihood ratio probability[b]
Models using all predators	
1. Chemistry (5.38 ***)	0.589
2. Diet Breadth (-5.67 ***)	0.905
Predator (5.56 ***)	
Model for bugs	
3. Size (3.44 ***)	0.594
Morphology (3.0 *)	
Model for wasps	
4. Size by Coloration (-2.85 ***)	0.290
Coloration (2.56 *)	

[a] The variables shown are significant predictors of rejections from the most parsimonious model that fit the data. Predictor variables were ranked by standardized parameter estimates, which are given in parentheses along with asterisks to indicate significance of the estimate (* denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.005$).

[b] The likelihood ratio probability is a goodness-of-fit test for the overall model, and p-values above 0.05 indicate a good fit (SAS 1990). P-values reported here are for the most parsimonious models.

103 individuals of 23 caterpillar species. χ^2 values from the 2-dimensional tables of defenses and rejections are summarized in Table 2.

For the combined predators, Model 1 revealed a significant ($\chi^2 = 36.0$, DF = 2, $P < 0.0001$) chemistry effect on rejections. Chemistry was a more reliable predictor than type of predator, which was not significant ($\chi^2 = 0.41$, DF = 2, $P = 0.814$; Table 3). The predators rarely rejected caterpillars with neutral and tasty extracts, while 98% of caterpillars with nasty extracts were rejected (Fig. 1). There were no significant interactions between chemistry and predators—all predators were deterred by the caterpillars with observed chemical defenses.

Model 2 for the combined predators revealed a significant association between predator and rejection ($\chi^2 = 34.68$, DF = 2, $P < 0.0001$) and an association between diet breadth and rejection ($\chi^2 = 28.86$, DF = 1, $P < 0.0001$). Predator was a more reliable predictor than diet breadth (Table 3) and there were no interactions between the two predictors. Ants were the most likely to eat caterpillars, and the wasps were the most cautious (Fig. 2). The association between diet breadth and rejection reflects the fact that specialists were rejected more frequently than generalists (Fig. 3).

The logit model for the bugs revealed a significant association between size and rejection ($\chi^2 = 11.95$, DF = 2, $P = 0.0025$) and a significant association between morphology and rejection ($\chi^2 = 8.78$, DF = 2, $P = 0.012$). Size was a more reliable predictor than morphology (Table 3) and there were no interactions between the two predictors. As the mean size of caterpillars increased, the levels of rejection also increased (Fig. 4). Caterpillars with hairs were rejected more frequently than those with other morphologies — particularly caterpillars with spines which were never rejected (Fig. 5).

The logit model for the wasps revealed a significant interaction between size, coloration, and rejection ($\chi^2 = 17.43$, DF = 2, P = 0.0002) and a significant association between coloration and rejection ($\chi^2 = 8.05$, DF = 2, P = 0.0179). The interaction was a more reliable predictor than coloration (Table 3). Brightly colored caterpillars of all sizes were better protected than caterpillars with other colorations (Fig. 6); however, if the caterpillars were large, their coloration was not important (100% of the large caterpillars were rejected by the wasps — Fig. 4).

DISCUSSION

To some extent, the predators evaded characterization by generalizations such as, "hairs are a good defense against invertebrate predators." Predators varied in their propensities to reject, and each predator was influenced by a different assemblage of caterpillar defenses. However, there were results which can be generalized for a variety of invertebrate predators (based on the wide behavioral and taxonomic differences between the three predators) and results that can be generalized for specific predatory guilds represented in this study.

The best generalizations about caterpillar defenses against invertebrate predators come from examining the results of the models that included all predators. Chemistry and diet breadth were both important predictors of rejections when considering the suite of predators and when including the variation in predators' inclination to reject prey. Specialists and caterpillars with deterrent extracts were rejected more frequently than other caterpillars by the predators, and since these predators represent very different guilds, it may be reasonable to conclude that these qualities would protect caterpillars against many different types of invertebrate predators. Examples of the guilds that were covered by these predators include: solitary predators (*P. instabilis* and *A. pictipes*), recruiting predators (*P. clavata*), sit-and-wait predators (*A. pictipes*), flying predators (*P. instabilis*), visually oriented predators (*P. instabilis* and *A. pictipes*), chemically oriented predators (*P. clavata*), sucking predators (*A. pictipes*), chewing predators (*P. instabilis*), stinging predators (*P. clavata*), nocturnal predators (*P. clavata*), and diurnal predators (*P. instabilis* and *A. pictipes*). One caveat to broad interpretation of these results is that these predators are not necessarily representative of their foraging guilds; *P. clavata*, for example, is much more likely to indiscriminately accept prey than other members of the tribe Ectatommini (Dyer and Folgarait, unpub. data). Thus, the results from this study do not indicate that prey protected against these three predators should be equally protected against any representatives of their respective foraging guilds, rather they illustrate the effectiveness of narrow diet breadth and defensive chemistry against very different types of predators.

The importance of diet breadth and chemistry as predictors of rejection for this group of predators are also consistent with another generalization:

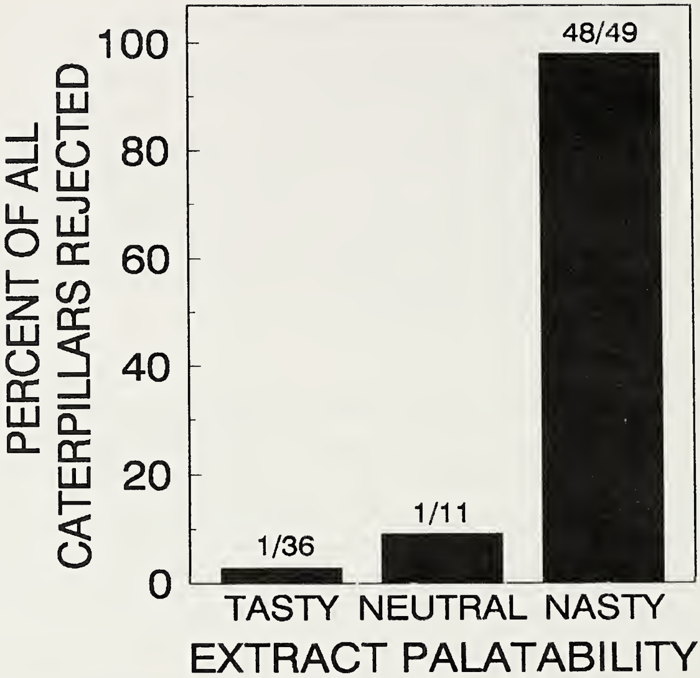

Fig. 1. The association between palatability of caterpillars' chemical extracts and percentage of rejections by all the predators. The *y*-axis represents the percentage of individual caterpillars (n = 96 individuals; 8 species) with specific palatabilities that were rejected by all 3 predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular palatability) is in the denominator.

both predation and plant chemistry could affect herbivores' diet breadth. A scenario by which this could happen is as follows: 1) An herbivore overcomes a specific plant defense and in the process loses access to other plants because of trade-offs in physiological abilities to utilize plants with different chemical compounds (Ehrlich & Raven 1964). 2) As the herbivore becomes more specialized as a result of step 1, it also sequesters secondary compounds either casually (because it is eating fewer plants; Jones et al. 1989) or because of specific physiological adaptations (Bowers 1990). 3) Specialization is further maintained by predators because specialists are better chemically protected than more generalized herbivores (Dyer 1995). Steps 2 and 3 are consistent with results from these experiments because herbivores with specialized diets were better protected against a group of predators, chemistry was an important component of their defense, and there is evidence that some of the species used in my experiments sequester noxious compounds from their host plants (Dyer 1995).

The results unique to specific predators reveal prey preferences that could be common responses for their respective guilds. Size, for example, was

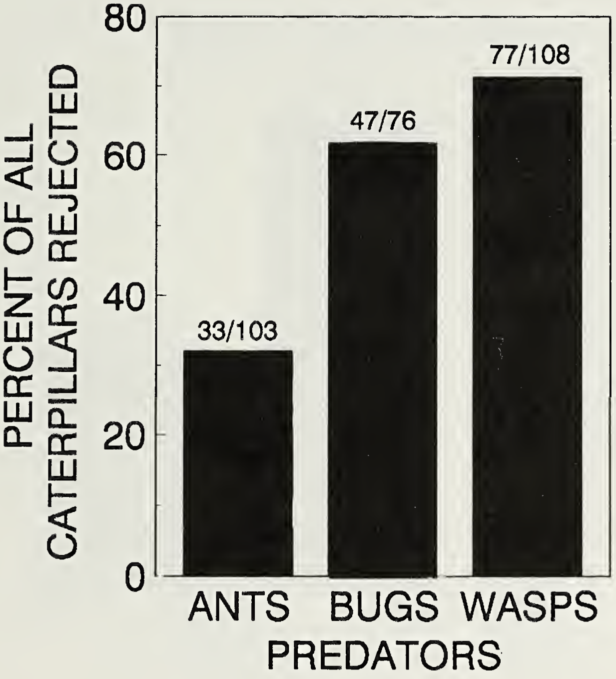

Fig. 2. Percentages of all caterpillars rejected by each predator. The *y*-axis represents the percentage of individual caterpillars (n = 287 individuals; 34 species) rejected by each of the 3 predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (to that particular predator) is in the denominator.

important for the two solitary predators (the bugs and wasps) but not for the ants which could recruit other ants and easily subdue larger prey items. It is generally assumed that prey size is an important limitation for invertebrate predators (Cohen et al. 1993, Reavey 1993), but this assumption may vary with the degree of predators' social cooperation. The differences between the solitary (wasps and bugs) and recruiting (ants) foragers were actually quite dramatic; the bugs and wasps barely touched large prey items (many of which were generalists which probably were not otherwise defended very well), while the ants attacked them as voraciously as caterpillars of any other size. The size categories were not ambiguous, in that all of the predators would be in the same category as the "small" prey, since their mass varies from 50–200 mg, while the "large" caterpillars had masses over 9 g.

Hairs were an important deterrent for the bugs which have mouthparts specialized for sucking. Hairs are probably a significant deterrent for most hemipteran predators because they prevent insertion of a bug's proboscis (pers. obs., also see Bowers 1993). Alternatively, hairs may function by warn-

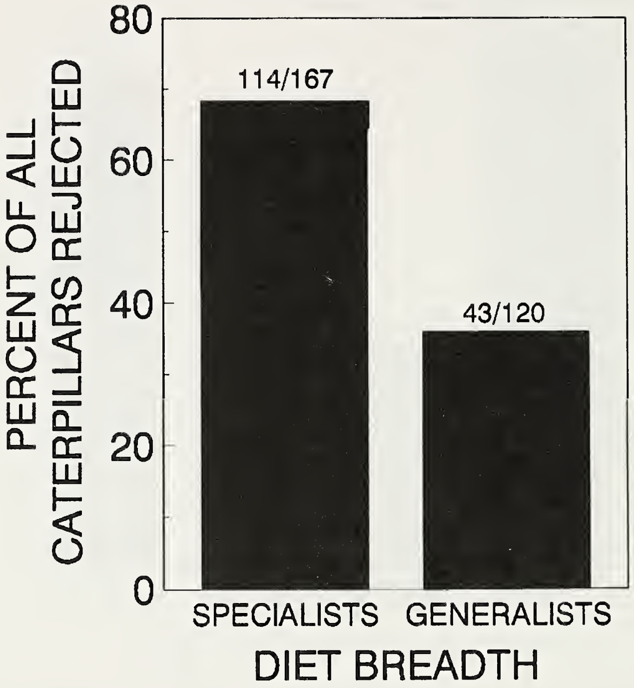

Fig. 3. The association between diet breadth and percentage of rejections by all the predators. The *y*-axis represents the percentage of all generalist or specialist caterpillars (n = 287 individuals; 34 species) that were rejected by the 3 predators (ants, bugs, and wasps). Although not all caterpillar species were offered to all predators, the predators are treated as a group. The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular diet breadth) is in the denominator.

ing the caterpillar of a predator's advance before it actually has a chance to catch the caterpillar (Tautz & Markl 1978). Indeed, many hairy caterpillars (particularly arctiids) are fast, and an "early warning system" such as hairs extending far from the body may make it difficult for sit-and-wait predators to successfully attack them. It is not as clear, however, why the hairs were effective against the ants but not against the wasps. One explanation could be that wasps, which can fly and are more maneuverable, are able to pluck hairs (without the prey escaping) from caterpillars more effectively than ants (Bowers 1993). I have observed wasps and ants plucking hairs from prey with varying degrees of success.

Coloration was important for wasps, but it was not important for ants which are often chemically oriented. Wasps were deterred by brightly colored prey which supports general theories about aposematism (see Cott 1940). Bugs, on the other hand, which are also visually oriented (Johnson 1983), were not deterred by brightly colored prey. A correlation between palatability

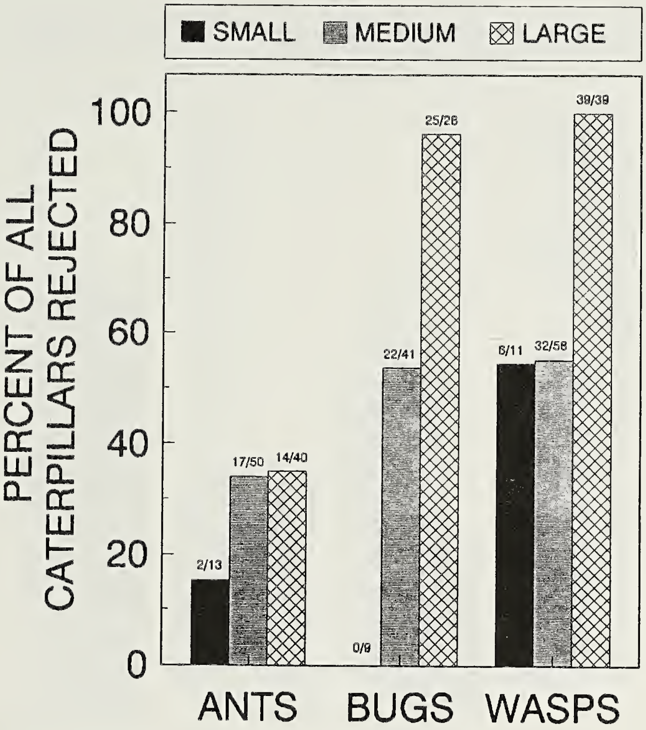

Fig. 4. The association between size and percentage of rejections by the 3 different predators. The *y*-axis represents the percentage of all caterpillars (n = 287 individuals; 34 species) of each particular size that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (of that particular size) is in the denominator.

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and coloration is widely assumed to exist in the animal kingdom (e.g., Cott 1940, Edmunds 1974, Harborne 1989), and coloration has even been used as an indicator of palatability (Sillen-Tullberg 1988). It is therefore noteworthy that for two of the three invertebrate predators used in my experiments, bright coloration is not correlated with unpalatability.

As with most studies of community patterns, there were several major limitations to this study which prevent me from concluding with grand generalizations. With regard to questions about the relative effectiveness of various caterpillar defenses, I had to ignore many important defenses such as symbioses with ants (e.g., DeVries 1991), aggregation (Bowers 1993), and other behavioral defenses (Edmunds 1974, DeVries 1987, 1994, Evans & Schmidt 1990). It is therefore impossible to conclude that any defense examined in this study is the "most important." Second, the relatively small taxonomic sample size (number of individual species representing each family) of this study makes it impossible to determine if a characteristic typi-

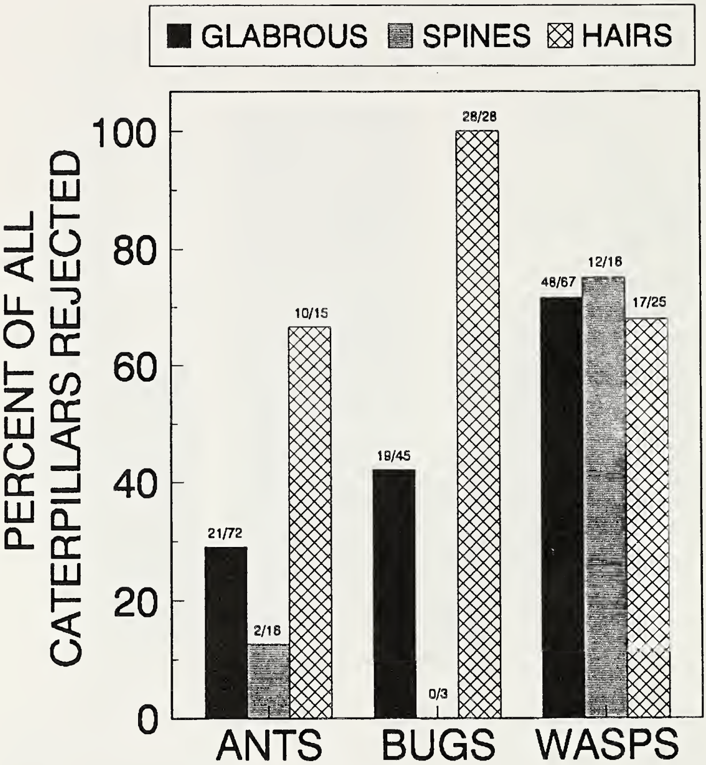

Fig. 5. The association between morphology and percentage of rejections by the 3 different predators. The *y*-axis represents the percentage of all caterpillars (n = 287 individuals; 34 species) of each particular morphology that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular morphology) is in the denominator.

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cally associated with a specific taxon is an effective defense or if some correlated trait of that taxon is responsible. For example, comparisons of hairy and glabrous caterpillars could just be comparisons of traits correlated with hairy and glabrous families (e.g., Arctiidae vs. Pyralidae), because not all the families used in my experiments included all of the possible morphologies. I addressed this problem to some extent in another study with larger sample sizes (Dyer 1995), and found that defenses were effective despite taxonomic affinity.

With regard to questions about the evolution of specialization, multi-species comparisons, such as this study, are not particularly useful in terms of providing evidence for natural selection on particular characteristics, since protection from natural enemies could be a consequence rather than a cause of specialization. Actual tests of predation as a selective pressure on diet

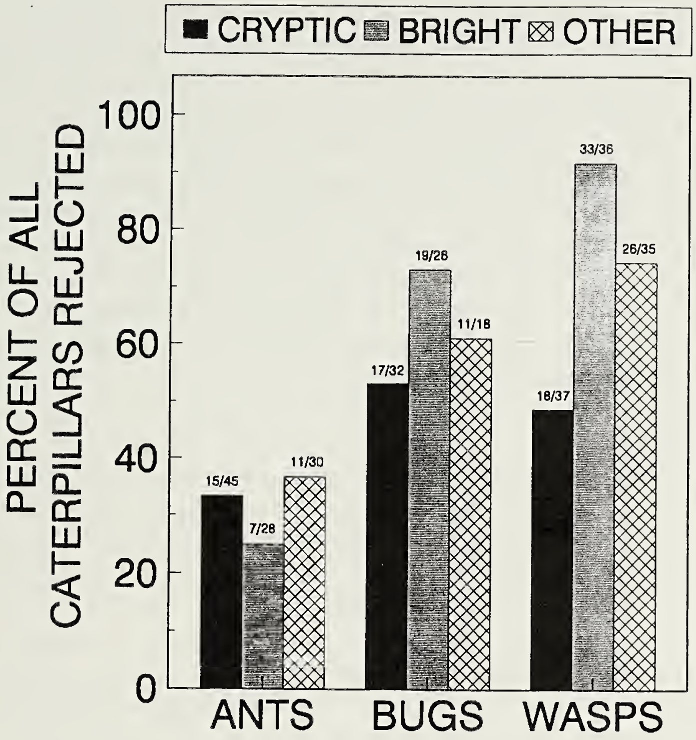

Fig. 6. The association between coloration and percentage of rejections by the 3 different predators. The *y*-axis represents the percentage of all caterpillars (n = 287 individuals; 34 species) of each particular morphology that were rejected by each of the 3 different predators (ants, bugs, and wasps). The numbers above each bar indicate the sample size; the number of caterpillars rejected is in the numerator, and the total number of caterpillars offered (with that particular coloration) is in the denominator.

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breadth would require studying intraspecific variation (see Futuyma and Moreno 1988).

Despite these limitations, a few reasonable generalizations can be made which address my original questions. 1) Predators from different guilds are deterred by different defenses, but there are some antipredator mechanisms that may function against many different guilds. 2) Narrow diet breadth and the utilization of noxious chemicals are significantly associated with rejection by a suite of predators. 3) Generalist predators are probably important in the maintenance of narrow diet breadth in caterpillars.

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Cooperation vs. exploitation: interactions between Lycaenid (Lepidoptera: Lycaenidae) larvae and ants

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Abstract. The larval stages of many lycaenid species are myrmecophilic, i.e. they are associated with ants. We revised the literature and categorized these associations as neutral (nonexistent, commensalistic), cooperative (mutualistic, mutualistic inquiline), and parasitic (food competitor, cleptoparasitic, predaceous symphile, or synechthran). The relationships were also noted as being facultative or obligate. Within several of the lycaenid taxa there has been a change in the diet from phytophagy to aphytophagy associated with a change from cooperative to exploitative behavior towards ants. A relatively low number of species, however, seem to have followed the route from cooperative (mutualists) to exploitative behavior (cleptoparasites, predaceous symphiles, synechthrans) even though the latter may give higher returns for less investment. Even neutral behavior (no relation with ants, commensals) is more probable than exploitative behavior. We suggest that this pattern reflects both the constraints produced by the species specific nature of exploitative interactions and the stability of cooperative interactions in evolutionary terms. We suggest that a "reverse evolution" from obligatory to facultative relationships is evolutionarily unlikely, a phenomenon which may be explained by negentropy criteria or the irreversible nature of evolution.

INTRODUCTION

Many species of lycaenids are myrmecophilic, i.e., they are associated with ants. Through these associations with ants, lycaenid larvae have developed a number of morphological and behavioral adaptations. Many species of larvae have evolved what have been termed myrmeocophilous organs, one of the most important of these being the nectary organs which are found on the seventh abdominal segment and secrete a substance containing sugars and amino acids when solicited by the ants (Malicky 1970, Maschwitz et al. 1975, Pierce 1983, Cushman et al. 1994).

Apart from their morphological adaptations lycaenid larvae are unusual with respect to their diet. They may feed on lichens, homoptera, or ant brood rather than on angiosperms, which is the normal food of lepidopterous larvae. Many of the interactions involving lycaenid larvae and ants have been described (Kitching 1987; Fiedler & Maschwitz 1988, 1989a, Elmes et al. 1991) and a exhaustive revision of these was undertaken by Fiedler (1991b). Lycaenid-ant interactions have been classified as mutualistic/para-

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sitic, facultative/obligate and phytophagous/aphytophagous. Although some authors (Henning 1983) have given finer classifications, the full range of possible associations have not been taken into account. For example, *Maculinea* spp. and *Liphrya brassolis* are both classed as "parasites" even though they have completely different relations with their ant hosts at a behavioral level which implies different evolutionary pathways towards each of these two types of relation; *Maculinea* spp. are attended, for example *M. alcon, M. rebeli* (Cottrell 1984, Elmes et al. 1991), or ignored, for example *M. arion, M. teleius* (Cottrell 1984), by the ants whilst *Liphrya brassolis* is attacked (Johnson & Valentine 1986).

Several authors have studied the relative importance of cooperation vs. exploitation using different models and have shown that in theory, "cooperation rather than "exploitation" dominate in the Darwinian struggle for survival" (Nowark & May 1992, Nowark et al. 1996, Sigmund 1992). Empirical evidence suggests that in the Lycaenidae this dominance of cooperation over exploitation may be true (Pierce 1987, Fiedler 1996).

Using data in the literature, most of it summarized by Fiedler (1991a, b), on the types of interactions between lycaenid larvae and ants, the myrmecophilous organs on the lycaenid larvae, the degree of relationship (facultative or obligate) and the diet of the larvae, we tentatively propose a more detailed classification of "types of interaction." In each case we noted the presence or absence of the nectary organs, larval diet (spermatophytes, algae, lichens; homoptera; ants; homoptera honeydew; ant regurgitations), and type of interactions with ants. Using this information we classified eight types of interactions the larvae may have with the ants. We then use this classification to describe the diet changes that have occurred both between and within subfamilies (from phytophagy to aphytophagy) and discuss these diet changes in the context of the relative importance of cooperative/exploitative behavior of the larvae towards their ant partners.

A truly phylogenetic system of the Lycaenidae is still not available, thus the diet changes we describe cannot yet be confirmed since without a sound phylogeny the directionality of such changes is difficult to assess. Nevertheless, it is widely considered that phytophagy is a primitive trait in lycaenids (and butterfly larvae as a whole) (Cottrell 1984, Fiedler 1991b), thus we feel justified in our assessments of possible evolutionary change from phytophagy to aphytophagy in the Lycaenidae. The higher classification of the Lycaenidae we adopt is the same as that used by Fiedler (1991b), based on Eliot (1973), with modifications by Scott and Wright (1990). The discussion about whether or not the Riodinidae (or Riodininae) form a monophyletic group together with the Lycaenidae is still very much alive (Robbins 1988, De Jong et al. 1996, Weller et al. 1996), but since the myrmecophilous organs of the Riodinidae are clearly analogous but not homologous with those of the Lycaenidae (DeVries 1990) we do not further discuss the Riodinidae here.

TYPES OF INTERACTION BETWEEN LYCAENID LARVAE AND ANTS

The range of types of relationships that the ants may share with lycaenids were classified as follows. It must be emphasized that these are "types of behavioral interactions," not "types of larvae." Thus a larva that is neutral at one stage of its life cycle may be parasitic at another, as in *Maculinea* spp. (Cottrell 1984). Parasitic larvae such as *Maculinea rebeldi* or *M. alcon* may be generally regurgitation feeders (cleptoparasites) but during times of food shortage may also prey on eggs and ant brood (Elmes et al. 1991).

Relationship not recorded

Larvae which have unknown relationships with ants. (Relationships recorded with a question mark by Fiedler [1991a, b].)

Neutral relationships

The ants neither gain nor lose from the interaction with the lycaenid larvae. The larvae, however, may neither gain or lose (No relationship) or may gain (Commensal) from the relationship. It is very difficult to assess with the data available which larvae are in "No relationship" with the ants, and which are "Commensals." The discussion about whether the larvae enter into "enemy free space" or not must depend on studies of particular lycaenid larvae and their relation with ants. Whether or not the ants protect the larvae in any way from other predators depends on factors such as time of occupancy of ants at the site, whether or not they have antagonistic relations with the larvae, and whether they influence in the rates of predation or parasitism of the larvae. Since the subject of whether and which of these larvae benefit from the presence of ants is in many cases ambiguous we have lumped "No relationship" and "Commensal" into the same category of Neutral relationship. Nevertheless, it is useful to define the two sub-categories, as they may represent the transition from a completely myrmecoxenous state to the beginnings of an association with ants.

No relationship. The larvae do not interact with ants mutualistically, parasitically, or commensally. Thus neither the ants nor the larvae gain from the relation. The larvae may avoid encounters with ants using specific defensive tactics such as *Eumaeus atala* (Bowers & Larin 1989) or they may be rarely found by ants. The point is that they do not enter into ant-inhabited "enemy free space" (Atsatt 1981). In the Curetinae, ants sometimes encounter larvae and then lick up plant sap at feeding damage, or feed at extra floral nectaries (DeVries et al. 1986, Fiedler et al. 1995). The evidence is ambiguous, however, as to whether or not the larvae benefit from the relation.

Commensalistic. In these associations, unlike the "No relationship" associations, the larvae benefit from the relation, whilst the ants remain unaffected. Thus they gain a twofold advantage (avoidance of ant attacks and entering into "enemy free space"). Commensalistic relations have been described in the Liptenini where the larvae are strictly associated with ant columns on tree trunks where they feed on lichens or algae. The data are, however, scanty and the proportion of Liptenini in these types of relationships is unknown (Downey 1962, Atsatt 1981, Callaghan 1992). The larvae

Table 1. Number of species and relative proportions of neutral, cooperative, and exploitative interactions found between lycaenid larvae and ants: a) within the subfamilies of the Lycaenidae, b) within the Lycaeninae.

a)	**Poritinae**	**Miletinae**	**Curetinae**				**Lycaeninae**		
	Liptenini	Miletini	Liphryini	Curetini	Total	%*		Grand Total	%*
Not recorded	0	0	0	0	0		122	122	—
Phytophagous									
Neutral	60	0	0	7	67	64.4	215	283	30.8
Cooperative	0	0	0	0	0		574	574	62.5
Aphytophagous									
Exploitative	0	28	9	0	37	35.6	24	61	6.7
Total	**60**	**28**	**9**	**7**	**104**	**100**	**935**	**1039**	**100**

b)			**Lycaeninae**				
	Aphnaeini	Lycaenini	Theclini	Eumaeini	Polyommatini	Total	%*
Not recorded	4	0	0	104	14	122	—
Phytophagous							
Neutral	5	38	44	101	27	215	26.5
Cooperative							
Facultative	18	0	57	111	284	470	
Obligate	49	0	19	2	34	104	
Total Cooperative	67	0	76	113	318	574	70.5
Aphytophagous							
Exploitative	4	0	4	0	16	24	3
TOTAL	**80**	**38**	**124**	**318**	**376**	**936**	**100**

*The last column (%) refers to the relative proportion of lycaenid larvae in a given type of interaction with ants with respect to the total number of larvae. Larvae with a relation "not recorded" are NOT taken into account.

supposedly gain from the relation in that the presence of ants reduces attacks from predators and parasites (Atsatt 1981) whilst the ants remain unaffected since the larvae do not compete in any way with food or other resources. Nonetheless, Callaghan (1992) described larval behavior in 12 species from the tribe Liptenini where the larvae seem to have strictly defensive relationships with ants, thus suggesting that the ants may not be protective elements in this case and that the relationship between them and the larvae is rather antagonistic. Nevertheless, detailed studies are required in order to establish exactly what is the relationship between the ants and certain Liptenini larvae. There are also certain species in the Lycaeninae that can be classed as being commensalistic because they are or appear to be associated with ants, but apparently do not possess a nectary organ and thus presumably do not provide the ants with a substantial food resource, for example *Aloeides dentatis* (Henning 1983).

Mutualistic (Cooperative)

This follows the standard definition of mutualism in the literature whereby both the ants and the lycaenid larvae benefit from the association. The larvae secrete a sugary nectar which the ants imbibe (Fiedler & Maschwitz 1988, 1989a, Cushman et al. 1994, Fiedler & Saam 1995). The ants in return protect the larvae from predators and parasites (Pierce & Mead 1981, Pierce et al. 1987, Baylis & Pierce 1991) Under this definition a larva is mutualistic if it has a functional nectary organ, if the diet is phytophagous and if it is associated with ants. Mutualists may be facultative or obligate, where the term obligate is defined as complete dependency on a specific genus of ants (Fiedler 1991b, 1994). Mutualists as defined here are only found in the Lycaeninae (Table 1).

Mutualistic inquiline. Here we define a new type of interaction which is a subdivision of the mutualists. In this case the larvae are attended by ants as for the mutualists, but furthermore they shelter either in pavilions constructed by the ants or in the ant nests themselves. The larvae, however, remain phytophagous, leaving the shelters to feed on their hostplant. Examples of species which exhibit "inquiline behavior" are *Anthene emolus* (Fiedler & Maschwitz 1989a) and *Paralucia aurifera* (Cushman et al. 1994). It must be emphasized again that it is the interaction that is important not the species. Thus "inquiline behavior" may be a rare occurrence in a species or a life history trait. The importance of this category is that it suggests a possible intermediate stage between free-living mutualists and parasites which live in the ant colony and feed on the ant brood.

Parasitic (Exploitative)

In these cases the lycaenid larvae benefit from the association whilst the ants are disadvantaged. We divide the parasitic larvae in four subgroups; food competitors, cleptoparasites (after Hoelldobler & Wilson 1990), predaceous symphiles and synechthrans (after Wasmann 1894).

Food competitors. Here we define a type of interaction in which the larvae feed on Homoptera (and Homoptera secretions), which have a trophobiotic relationship with ants such as many species from the Miletinae (Kitching 1987, Maschwitz et al. 1985, 1988). This definition differs from that of Maschwitz and Fiedler (1988) who defined homopterophagous lycaenid larvae as "indirect parasites." We suggest, however, that "food competitors" is a more precise definition. The food competitors may be further divided into "stealthy competitors," which are not tolerated by the ants and feed inside shelters or cover themselves with bits of their prey to protect themselves from ant attack, for example, *Spalgis* spp., and "symphilic cleptoparasites," which are ignored or even sometimes attended by the ants, for example, *Miletus* spp. (Cottrell 1984, Fiedler 1991b).

Cleptoparasites. The larvae are food robbers (*Euliphyra* spp. [Dejean & Beugnon 1996]) or feed on oral regurgitations from ants. Oral regurgitation feeders may be either free-living (*Spindasis takanonis*) or may inhabit the nests of the ants (*Niphanda fusca*) (Cottrell 1984). Fiedler (1991b) defined ant regurgitation feeders as "parasites," nevertheless Hoelldobler and Wilson (1990) define "food robbers" which rob the ants of a food resource and the regurgitation feeders which receive nutrients that would normally be destined for the ant brood (oral regurgitations) as cleptoparasitism (cleptobiosis in their terms). Cleptoparasitic behavior has been reported from both the Lycaeninae and Miletinae.

Predaceous symphile. The larvae spend all or part of the larval phase inside the nests of their host ant, feeding on ant brood. By means of putative pheromone secretions the larvae are accepted by the ants as ant brood whilst they remain in the ant nest (Jackson 1937, Cottrell 1984, Thomas et al. 1989). This definition applies to lycaenids such as *Maculinea arion, M. teleius,* and *Lepidochrysops* spp., described simply as "parasites" in the literature, for example (Cottrell 1984, Elmes et al. 1991).

Synechthran (following Wasmann 1894). These species of lycaenid also feed on ant larvae, but their relation with the ants has a completely different behavioral base than that of the predaceous symphiles. The larvae are not welcome guests in the ant nests; rather they are treated as intruders and attacked by the adult ants. *Liphyra brassolis* (Johnson & Valentine 1986) is apparently the only known case which falls in this category in the Lycaenidae.

CHANGES IN THE DIET WITHIN SUBFAMILIES

Changes in the diet within a subfamily have taken place in the Lycaeninae from angiosperms to ant brood, Homoptera and regurgitations from ants, and in the Miletinae from Homoptera, to honeydew, ant regurgitations, or ant brood.

Changes in the diet in the Lycaeninae

Within the Aphaenini, Theclini, and Polyommatini there has been a change in the diet from phytophagy to aphytophagy, the aphytophagous larvae feeding on Homoptera (food competitors) or oral regurgitations from the ants (cleptoparasites), but sometimes on ant larvae or pupae (predaceous symphiles). The phytophagous species in the Lycaeninae are either commensals (e.g., *Aloeides dentatis;* all examples taken from Fiedler [1991b] unless otherwise stated), mutualists, mutualistic inquilines, or have no relation with ants. Their behavior towards the ants is thus neutral or cooperative. The aphytophagous species, however, all exploit their ant hosts. Food competitors and/or cleptoparasites may be found in the Aphnaeini, (*Spindasis nyassae, S. takanonis, Axiocerses harpax* and *A. pseudo-zeritis,* oral regurgitations), in the Theclini (*Shirozua jonasi,* oral regurgitations) and the Polyommatini (*Niphanda fusca,* oral regurgitations, *Triclema lamias,* Homoptera and three *Maculinea* spp.). These species have nectary organs and sometimes also tentacle organs (except *S. jonasi,* which has neither). There are predaceous symphiles in the tribes Theclini: *Acrodipsas cuprea, A. myrmecophila, A. illidgei*; Polyommatini: two *Maculinea* spp. and nine *Lepidochrysops* spp.; and Aphnaeini: *Cigaritis acamas* (Sanetra & Fiedler 1996). As far as is known, all species possess a nectary organ, except *Cigaritis acamas* which also has eversible tentacles. The *Maculinea* spp. are generally specific to one ant species, at least within the same geographical region (Thomas et al. 1989). *Lepidochrysops* spp. are almost certainly species specific (Cottrell 1984), although there is little information as regards the remaining genera, what evidence there is points to host-ant specificity (Cottrell 1984).

Changes in the diet within subfamilies in the Miletinae

In the Miletinae there have been changes in the diet of the larvae from Homoptera to other food sources(all examples taken from Fiedler [1991b] unless otherwise stated). Although the scarcity of data on this tribe does not permit conclusions to be drawn we can state that in all cases studied the behavior of the larvae towards the ants is exploitative. In the Miletini there are several species reported to feed on Homoptera honeydew, these include *Miletus chinensis, Taraka hamada, Logania malayica, L marmorata* (also Homoptera) (Fiedler 1993), *Allotinus unicolor* (also Homoptera) (Maschwitz et al. 1985, Fiedler & Maschwitz 1989b) and *Lachnocnema bibulus* (also ant regurgitations). *Thestor* spp. (Miletini) are suspected of predating on ant brood. In the Liphyrini *Euliphyra mirifica* and *E. leucyania* feed on oral regurgitations from ants and *Liphrya brassolis* (Liphyrini) feeds on ant brood. These species do not possess nectary or tentacle organs. Of these, *Lachnocnema* is not specific as regards the ant host, but *Thestor, Miletus, Euliphyra,* and *Liphyra* are species specific.

DISCUSSION

Facultative and obligate relations in the Lycaeninae

Regarding the subfamily Lycaeninae, Fiedler (1991b) discusses the possible evolutionary development from facultative mutualisms to obligate relations of various types (including mutualists, inquilines, cleptoparasites, predaceous symphiles) or alternatively an evolutionary decrease in the interactions with ants (secondary myrmecoxeny). He states that there "is yet no evidence that a reverse evolution from obligatory towards facultative myrmecophily has ever occurred within the Lycaenidae, although such would be possible from theory." We propose that the theory of negentropy provides a possible explanation for the lack of evidence for this "reverse evolution." This proposal assumes that the higher the order or complexity of an organism, including in the concept of complexity higher specializations that may involve loss or simplifications of certain structures, the lower will be the probability state of the system and the longer the evolutionary time to produce the given state. Thus the further down a certain evolutionary pathway an organism finds itself the fewer available choices it will have to return back along that pathway (Zotin & Konoplev 1978, Jaffé 1984, Jaffé & Hebling-Beraldo 1993, Jaffé & Fonck 1994). We argue that obligate myrmecophiles are more "complex" in that they have more finely tuned adaptations in their associations with ants than facultative myrmecophiles. Thus in this case negentropy is expressed as specificity of communication with ants. (For a discussion on lycaenid/ant communication see Fiedler et al. [1996].) For example, the predaceous symphiles are often associated with one or a few ant species, which implies the development of brood pheromone mimics, that are specific to a single (or a few closely related) ant species (Thomas et al. 1989), probably from facultative relations where the larvae are attractive to many species of ant. A reversal of this trend would imply a loss of specificity and thus of complexity, which would revert and thus probably reduce the adaptive gains made in the first place. This negentropic assumption does not exclude the possibility of posterior losses as has taken place in the secondarily myrmecoxenous species, but predicts that these reversions should be rare and should have specific biological explanations, as the evolutionary process is strongly irreversible (Jaffé 1996).

Cooperation vs. exploitation in lycaenid/ant relations

From Table 1, we may conclude that the majority of the lycaenid butterflies maintain neutral (no relationship, commensalistic) or cooperative (mutualistic) interactions with ants, rather than exploitative (cleptoparasite, predaceous symphile, synechthran) ones (Pierce 1987, Fiedler 1996). This fact seems remarkable considering that exploitative behavior may give higher nutrient returns for less investment to the lycaenid larvae. In subfamilies without a nectary organ, i.e. where cooperative behavior has not appeared (Table 1a), 64.4% of species show neutral behavior (no relation or commensal), representing the subfamilies Poritiinae (60 species) and Curetinae (7 species) and only 35.6% of the species show exploitative behavior (cleptoparasites or synechthrans) representing the Miletinae (37 species). In the Lycaeninae with 818 species (Table 1b, excluding species for which no information is recorded), cooperative behavior dominates, with 70.5% of the larvae being mutualists as opposed to 3% being cleptoparasites or predaceous symphiles. In this subfamily, 26.5% of the species have no relation with ants are or commensals, showing that even neutral behavior is more likely than exploitative behavior. Taking the Lycaenidae as a whole (Table 1a final column), 62.5% show cooperative behavior, 6.7% exploitative behavior and 30.8% neutral behavior towards the ants. Although these percentages may vary as more Lycaenid species are investigated, we suggest that the relative proportions between exploitative larvae and cooperative/neutral larvae should remain roughly the same.

Thus, where cooperative (mutualistic) behavior is possible in the Lycaenidae this is the most probable evolutionary outcome, and where it is not likely, neutral behavior is more probable than exploitative behavior. The preponderance for mutualistic interactions over exploitative relations in Lycaenidae lead us to suppose that cooperation must have either a higher probability to evolve or to be maintained during evolution or both. Thus, we postulate that cooperation is an evolutionarily more probable strategy compared to exploitative behaviors. We propose different, but not necessarily contradictory, explanations for this pattern:

1) A model of cooperation between species as a stable strategy was developed by Axelrod and Hamilton (1981) using the Prisoners Dilemma game. They showed that if the probability that two individuals will continue to interact is great enough then cooperation may be evolutionarily stable. Since then several authors have modeled cooperation vs. exploitation using dif-

ferent versions of the Prisoners Dilemma and have shown that in theory, "cooperation rather than exploitation can dominate in the Darwinian struggle for survival" (Nowark & May 1992, Nowark et al. 1996, Sigmund 1992). Empirical evidence suggests that the Lycaenidae larvae benefit from the association (Pierce et al. 1987, Robbins 1991, Fiedler & Hoelldobler 1992, Wagner 1993) and there is evidence showing that both partners benefit (Fiedler & Maschwitz 1988, 1989a, Cushman et al. 1994, Fiedler & Saam 1995). Cooperation in lycaenid/ant interactions is not necessarily a fixed strategy (Bronstein 1994, Noe & Hammerstein 1994, 1995) and a coalition may end or change when it becomes unproductive for one or both partners (Enquist & Leimar 1993). For example, ants abandoned *Polyommatus coridon* larvae when the secretions from the nectary gland were artificially eliminated (Fiedler & Maschwitz 1989c). Leimar and Axen (1993) showed that the amount of nectar secreted by larvae of *P. icarus* varied according to the level of ant attendance and the larva's need for protection. A model of mutualism, commensalism and parasitism as evolutionarily stable strategies in lycaenid/ant relations was developed by Pierce and Young (1986). This model assumes that the ants enhance both the population growth rate and the equilibrium density of the larvae by increasing the realized fecundity of individual butterflies and by increasing juvenile survival, whereas the larvae enhance the equilibrium density of the ants by increasing ant food supply. Under these assumptions (albeit largely unverified) Pierce and Young (1986) were able to demonstrate that all three types of relation were evolutionarily stable strategies. Nonetheless, although all three strategies are evolutionarily stable, not all have the same odds of appearing during evolution and of avoiding extinctions in evolutionary history. Cooperative strategies possess economic advantages which decrease their probabilities of extinction and thus increase their odds of being fixed in the genetic repertoire of more species. That is, cooperation is a highly probable strategy in addition of being evolutionarily stable.

2) There are three possible strategies for exploitative behavior which the larvae could take; a "synechthran" approach where the larvae fend off ant attack whilst predating on ant brood, a "stealthy" approach, whereby the larvae avoid ant attack, and a "symphilic" approach whereby the larvae deceive the ants by mimicking ant brood. Thus, ants either ignore the larvae or attend them as they predate on Homoptera or ant brood. Examples of the first approach could be *Liphrya brassolis* which has an armor shaped carapace in order to withstand ant attack. This type of defense does not, however, seem to have developed in lycaenid taxa other than the Liphyrini. Examples of the second "stealthy" approach may be found in the genera *Taraka, Spalgis,* and *Feniseca* (Miletini) where the larvae occupy silken tents or burrows, or cover themselves with remains of their prey to avoid ant attack (Cottrell 1984, Kitching 1987). The third "symphilic" approach involves the development of a chemical mimicry system with the larvae mimicking their homopteran prey, adult ants or ant brood. The possibility that lycaenid larvae are chemical mimics has been studied for *Aloeides dentatis,* a non-

mutualistic inquiline and *Lepidochrysops ignota*, a predaceous symphile (Henning 1983). In both species, larval epidermal glands produced a secretion that appeared to mimic the brood pheromones of the host ants, although Henning (1983) did not identify the chemical compounds involved. It is also supposed that *Maculinea* spp. mimic the brood pheromones of their *Myrmica* ant hosts (Thomas et al. 1989), although chemical analyses have not been undertaken as yet. In the Miletini many lycaenid larvae such as *Miletus* spp., *Lachnocnema bibulus* are attended by ants even though they do not give any reward (Cottrell 1984). All of these strategies; the "synechthran" approach, the "stealthy" approach and the "symphilic" approach carry with them certain disadvantages. The carapace used by *Liphyra brassolis* may not be 100% effective against all ant species, with the larvae possibly incurring high mortality rates as a result. This restricts the larvae to only associating with *Oecophylla* spp. The stealthy larvae may still be attacked by ants in spite of their protective burrows. The symphilic larvae are constrained by having to penetrate the complex chemical communication systems of ants, which are highly species specific. In this sense it is notable that the larvae mimic the brood of the ants rather than the adult ants. In the genus *Myrmica* (usually hosts for larvae of *Maculinea* spp.)' the brood odor is not specific to one species and *Myrmica* brood are transferable between the nests of different species (Brian 1975, Howard et al. 1990), although Thomas et al. (1989) point out that these ants are far more discriminatory under conditions of stress.

3) As far as the "symphilic" or "mimicry" approach to exploitative behavior is concerned, lycaenid larvae mimics are normally specific to one species of host ant (Cottrell 1984; Thomas et al. 1989), which is probably due to a specificity in the chemical signals the ants use to recognize nest companions and brood (Hoelldobler & Carlin 1987). Although this species specificity of the lycaenid larvae towards their ant hosts may have led to a diversification of some genera (e.g., *Maculinea*, *Lepidochrysops*), this diversification is far lower than that of cooperative taxa, a finding that contradicts the hypotheses of Pierce (1984) who argued that species specificity should amplify the species diversity of the Lycaenids (see also discussion in Fiedler 1991b). Nonetheless, being associated with only one species of ant carries with it certain ecological disadvantages for the lycaenid larvae such as constraints on their distribution caused by a patchy distribution of their host ant species (Jordano et al. 1992), problems of host encounter in areas with a highly diverse ant fauna, and nutritional constraints (Fiedler 1991b). For the predaceous symphiles exploitative behavior also carries with it a high risk. Their host ants are generally tolerant of intruders in times of plenty, but when food reserves are low they become increasingly intolerant and will even eat their own brood (Thomas et al. 1989). The lycaenid larvae must therefore be under extreme pressure to mimic their hosts as closely as possible and it is not surprising that so few species have developed this type of relation.

4) We may speculate that parasites normally have much shorter life cycles

than their hosts, as for example viral or bacterial parasites on insect or mammal hosts. Thus, cooperative mechanisms are more likely to act in interactions between two species with equivalently long life cycles. The lifespans of ant workers and butterflies have roughly the same order of magnitude (they are measured in months). Even ant colonies do not live much longer, as in most species, the mean life span of queens and colonies is a few years. Thus exploitation of one by the other is evolutionarily unlikely.

In conclusion, a relatively high proportion of species seem to employ cooperative or mutualistic behavior in their associations with ants rather than exploitative or selfish behavior. We suggest that this pattern reflects the extraordinary stability of cooperative interactions in evolutionary terms, at least as regards lycaenid/ant interactions.

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A revision of *Mesogona* Boisduval (Lepidoptera: Noctuidae) for North America with descriptions of two new species

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Abstract. The North American species of *Mesogona* Boisduval are revised. *Pseudoglaea* Grote, 1876a is treated as a synonym of *Mesogona*. Three species of *Mesogona* occur in North America, two of which are described as new. All are found in western North America: *M. olivata* (Harvey, 1874) occurs from British Columbia south to California and Texas, while *M. subcuprea* n. sp. and *M. rubra* n. sp. are restricted to Washington, Oregon, and California. The adults and genitalia of these species are described and illustrated. A key for identification of the adults is presented. The larva of *M. rubra* is illustrated.

INTRODUCTION

Members of *Mesogona* Boisduval, 1840 are stout-bodied medium-sized moths. They occur in a variety of habitats ranging from wet forest to semiarid steppe. The adults are active in the Fall at about the time leaves of deciduous trees and shrubs turn color. Their eggs are laid in the Fall and hatch in the Spring. The known larval foodplants include a diverse assortment of woody plants.

There are five species in this genus, two in Eurasia and three in North America. Until now, only one of the North American species, *olivata* Harvey, 1874, was described. It was placed in the monotypic genus *Pseudoglaea* Grote, 1876b. The two other North American species were recognized recently from material collected in Washington and Oregon. The relationship of the Nearctic species to *Mesogona*, previously thought to be restricted to Europe, became evident because one of the undescribed species resembles *M. acetosellae* (Denis & Schiffermuller 1775), the genotype of *Mesogona*. Closer comparison of the Palaearctic *M. acetosellae* to the Nearctic species shows that they are structurally similar and thus congeneric. This revision is limited to the North American *Mesogona* species because the Palaearctic species are well known (Fibiger 1993).

Mesogona Boisduval

Mesogona Boisduval, 1840:144.

Type species: *Noctua acetosellae* [Denis & Schiffermuller], 1775, by subsequent designation by Blanchard, 1840:512.

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Pseudoglaea Grote, 1876b:18, **new synonomy**

Type species: *Choephora blanda* Grote, 1876a, by subsequent designation by Grote, 1895:95.

Description. Adult: Eyes naked, lashed. Palpi upturned with porrect third segment, the first and second segments bearing long loose scales, the third segment closely scaled. Frons smooth. Antennae ciliate. Thorax untufted, covered with hairlike scales. Prothoracic tibia unarmed, slightly longer than first tarsal segment; meso- and metathoracic tibiae with several loose rows of stout setae ("spines") in addition to the tibial spurs. Tarsal segments with stout setae laterally. Male abdomen with basal coremata in all known species. **Male genitalia** (Figs. 11–14)**:** Uncus narrow, curved. Tegumen broad, with penicillus lobes. Juxta flat, widest ventrally. Valve long and narrow, slightly constricted mesially; cucullus rounded, with a weak corona; sacculus with a costal process (sensu Forbes 1954), ⅔–1 × as wide as valve, extending to base of harpe; harpe nearly cylindrical, 1.5–2 × as long as valve width, parallel to valve at base, curved posterodorsad distally; digitus absent. Aedeagus with dorsal and ventral extensions onto base of vesica; vesica 1–2.75 × as long as aedeagus, coiled or T-shaped and bent, surface minutely granulose and armed with two to three fields of cornuti, portion of vesica bearing cornuti either flat, slightly raised, or a small diverticulum; the cornuti are fragile and entire cornuti or fragments are often left in the female corpus bursae following copulation. **Female genitalia** (Figs. 15–18)**:** Bursa copulatrix uni- or bisaccate; corpus bursae curved toward right anteriorly, with 1–3 signa, posterior corpus bursae (*M. acetosellae*) or appendix bursae heavily sclerotized; appendix bursae (if present) broadly joined to corpus bursae posteriorly, extending to the right and anteriorly; ductus seminalis joined to posterior corpus bursae (*M. acetosellae*) or to apex of appendix bursae. Ductus bursae ⅔–1 × as long as bursa, joined to it posterodorsally; ostium bursae weakly sclerotized. Anterior apophyses ½–⅔ as long as posterior apophyses. Ovipositor lobes triangular, covered with long and short hairlike setae.

Discussion: McDunnough (1927, 1928) recognized the close relationship of *M. olivata* and *M. acetosellae*, but retained *Pseudoglaea* because of differences in the lengths of the distal spines of the first tarsal segments of the first legs ("tarsal claws") of these species. The link between the Old and New World species is more evident now since *M. acetosellae* (Fig. 9) is similar to the recently discovered *M. subcuprea* n. sp. (Fig. 6), and both of these species lack the long "tarsal claws" of *M. olivata*.

The most closely related genus is *Eucirroedia* Grote, 1875 from the eastern United States and southern Canada. This monotypic genus (type species *pampina* Guenée, 1852) differs from *Mesogona* by the following character states: 1) the vestiture of thorax has a median crest, absent in *Mesogona*; 2) the mid and hind tibiae bear only two weak spines while those of *Mesogona* have multiple stronger spines; 3) the forewing is falcate and scalloped while that of *Mesogona* has a slightly convex crenulate outer margin; 4) the harpe of the male valve is expanded and flattened subapically and pointed distally while that of *Mesogona* is uniform in width; 5) the juxta has a membranous dorsomedian cleft, absent in *Mesogona*; 6) the bursa copulatrix is long and narrow while that of *Mesogona* is ovoid or bisaccate.

The species of *Mesogona* have often been placed in Noctuinae, as defined by Hampson, due to the presence of tibial spines (Hampson 1903, McDunnough 1928, Fibiger 1993). They are more closely related to a group of genera referred to as the "winter moths" (Xylenini, in part), including *Eucirroedia, Metaxaglaea* Franclemont, and *Epiglaea* Grote. *Mesogona olivata* is correctly placed in Xylenini by Franclemont and Todd (1983). In this list Xylenini is placed in the Cucullinae (as defined by Hampson). Hampson's subfamily concepts are now recognized to be unnatural. Recent reevaluation of the subfamilies in the trifid noctuids, outlined in Poole (1994), indicates that *Mesogona* is a member of the subfamily Noctuinae which has been expanded to include a large number of species previously included in other subfamilies.

The distribution of the species of *Mesogona* is disjunct. The Palaearctic species occur predominantly in Europe with the range of *M. acetosellae* extending east to the Altai Region of Siberia (Fibiger 1993), while the Nearctic species are restricted to western North America. In Europe, larval foodplant records include *Quercus* species for *M. acetosellae* and *Salix* species for *M. oxalina* (Hübner, [1803]) (Fibiger 1993).

Key to adults of North American species of *Mesogona*

1.a. Hindwing gray or with gray suffusion; vesica of aedeagus with two distal bands of short thin cornuti (Fig. 11b); appendix bursae overlapping corpus bursae ventrally (Fig. 15); widely distributed in western North America .... *olivata*
1.b. Hindwing uniform copper-colored or reddish, without gray scales; vesica with stout cornuti; appendix bursae not overlapping corpus bursae ventrally; restricted to the west coast states 2
2.a. Thorax and forewings yellow-brown, with orbicular and reniform spots strongly outlined; vesica shaped like a lopsided T with median and subapical cornuti (Fig. 12b); appendix bursae not overlapping corpus bursae (Fig. 16) .... *subcuprea*
2.b. Thorax and forewings brownish red to pink, with faint or absent forewing spots; vesica coiled with one stout basal cornutus and two subapical bands of long cornuti (Fig. 13b); appendix bursae overlapping corpus bursae dorsally (Fig. 17) .... *rubra*

Mesogona olivata (Harvey), **new combination**
(Figs. 1–5, 11, 15; Map 1)

Glaea olivata Harvey, 1874:120, TL — California. Grote 1880:155, Smith 1893:221, Dyar 1903:181.

Choephora blanda Grote, 1876a:86, TL — Washington Territory and Vancouver Island, [British Columbia].

Pseudoglaea blanda (Grote) Grote, 1876b:18, Smith 1893:210, Dyar 1903:178, Anderson 1904:29, McDunnough 1927:65, Jones 1951:52, Franclemont & Todd 1983:145.

Pseudoglaea taedata Grote, 1876b:18, TL — Texas. Smith 1893:210, Dyar 1903:178, McDunnough 1927:65, Jones 1951:52, Franclemont & Todd 1983:145.

Cerastis olivata (Harvey) Grote, 1878:181.

Pseudoglaea decepta Grote, 1881:271, TL — Colorado. Smith 1893:210, Dyar 1903:178, Jones 1951:52, Franclemont & Todd 1983:145.

Metalepsis blanda (Grote) Dyar, 1903:132.

Metalepsis taedata (Grote) Dyar, 1903:132.

Metalepsis decepta (Grote) Dyar, 1903:132.

Mythimna blanda (Grote) Hampson, 1903:608, pl. 76, fig. 19; Barnes & McDunnough 1917:47.

Mythimna taedata (Grote) Hampson, 1903:608; Barnes & McDunnough 1917:47.

Mythimna decepta (Grote) Hampson, 1903:608; Barnes & McDunnough 1917:47.

Spectraglaea olivata (Harvey) Hampson, 1906:439, pl. 106, fig. 14.

Mesogona olivata (Harvey) Barnes & McDunnough, 1916:161.

Mythimna olivata (Harvey) Barnes & McDunnough, 1917:47, Blackmore 1927:19.

Pseudoglaea olivata (Harvey) McDunnough, 1927:65, McDunnough 1938:67, Jones 1951:52, Franclemont & Todd 1983:145.

Description. Adults (Figs. 1–5): Males and females identical in habitus. Distal spines of first tarsal segment of prothoracic leg twice as long as proximal spines. Ground color of head, dorsal antennae, thorax, and forewings variable, ranging from dull tan to reddish brown, gray-brown, or cream; median area of forewing and postmedian space at costa darker; palpi with mixture of ground color and dark scales; abdomen fuscous. Forewing length: 15–20 mm. Forewing 2 × as long as wide; margin crenulate; lines double, smooth, pale filled; basal line sinuous, evident only near costa; antemedian line oblique, undulating, bent basad at costa, outer line dark; median shade absent; postmedian line smooth, laterally convex, inner portion dark, strongest in interspaces; subterminal line sinuous, indistinct, a series of dark spots between veins; terminal line thin and dark; orbicular and reniform spots large, pale with darker filling; claviform spot absent. Hindwing variable, fuscous gray to reddish, always suffused with gray scales, with darker terminal area and faint discal spot, fringe lighter. **Male genitalia** (Fig. 11): Valves as in generic description; costal lobe of sacculus triangular. Vesica 2.75 × as long as aedeagus, shaped like a lopsided T beyond basal twist with short extension ventrad and to the right and longer distal portion curved dorsad and to the left, two long fields of fine cornuti on distal ⅓, the proximal end of the field of larger cornuti is raised from adjacent vesica surface. **Female Genitalia** (Fig. 15): Corpus bursae approximately 2 × as long as wide, ante-

Map 1. Map of part of western North America showing distribution of examined material of *M. olivata*.

rior ½ curved dorsad and to the right, with single long dorsal and ventral signa; appendix bursae cone-shaped, curving anteriorly to overlap ventral corpus bursae. Anterior ⅔ of ventral ductus bursae with a sclerotized band.

Type Specimens: *Choephora blanda* Grote was described from two syntypes. One specimen was located, a male in the BM(NH) labeled: Vancouver I, Grote Coll 82-54 / 4425 Vancouver Island / *Choephora blanda* Type. Grote / *Pseudoglaea blanda* Grote / Syntype / Noctuidae Brit. Mus. slide No. 4925 male. It lacks antennae as is mentioned in the description. This specimen is here designated lectotype. The holotypes of *Glaea olivata* Harvey, *Pseudoglaea taedata* Grote, and *Pseudoglaea decepta* Grote are also in the BM(NH). Photographs of these type specimens and their genitalia have been examined.

Diagnosis: This species is variable in color and size. The range of color is depicted in the illustrated specimens. Individuals from semi-desert locales tend to be pale while those from more mesic forest are darker. Most specimens are brownish (Figs. 1–3), but reddish morphs (Figs. 4, 5) also occur and can be common. *M. olivata* is most easily separated from both other species by the presence of gray scales on its hindwings, but can also be determined without dissection by the presence of long distal spines on the first segment of the prothoracic tarsi. These are nearly equal in length to the proximal spines in the other species. Both this species and *M. rubra* n. sp. differ from *M. subcuprea* n. sp. in having the distal cornuti of the vesica in two bands. These are thin in *M. olivata* and stout in *M. rubra.* Also, the latter species has a coiled vesica while that of *M. olivata* is somewhat T-shaped. The female genitalia of *M. olivata* differ from the other species in that the anterior portion of the appendix bursae overlaps the ventral corpus bursae.

Early stages: The larva has been described by Crumb (1956). It is a general feeder on deciduous shrubs and trees. Crumb lists poplar, oak, hazel, *Amelanchier* Medic., alder, antelope brush, *Symphoricarpos* Duhamel, and *Berberis* L. as foodplants. It has also been reared from *Quercus garryana* Dougl. and *Ceanothus velutinus* Dougl. in Oregon (J.C. Miller, pers. comm.) and *Quercus agrifolia* Nee. in California (J. Powell, pers. comm.).

Distribution and flight period: This common species occurs from southern coastal and interior British Columbia south through California, Colorado, and Texas (Map 1). It most likely also occurs in northern Mexico. The distribution records suggest that it is most common in the western portion of its range. It occurs most often in dry open forest but also lives in shrub steppe and mesic forest habitats. *M. olivata* is sympatric with both other species. Adults have been collected from late August to November, with the earliest flight in the northern part of its range.

Mesogona subcuprea Crabo & Hammond, **new species**

(Figs. 6, 12, 16; Map 2)

Description. Adults (Fig. 6)**:** Males and females identical in habitus. Spines of first tarsal segment of prothoracic leg nearly equal. Head, palpi, dorsal antennae, thorax, and ground color of wings light yellow brown; proximal antennae and terminal space of forewing slightly lighter; abdomen reddish. Forewing length: 19–21 mm. Forewing broader than in *M. olivata,* outer margin prominently crenulate; lines and spots similar to *M. olivata*; orbicular and reniform prominent with filling darker than ground color. Hindwing light copper-colored, slightly glossy, with faint median shade and discal dot. **Male genitalia** (Fig. 12)**:** Valves as in generic description; costal lobe broad, nearly obsolete. Vesica 2× as long as aedeagus, shaped like a lopsided T beyond basal twist with short extension dorsad and toward right and longer distal portion curved ventrad, cornuti divided into a patch of equal length spines on a median diverticulum and a large subapical patch with multiple minute and several massive rod-like spines. **Female genitalia** (Fig. 16)**:** Corpus bursae 2.5× as long as wide, anterior ⅓ bent 90° to the right, with 1 long dorsal and 1 short ventral signa; appendix bursae dorsoventrally flattened and heavily sclerotized with irregular ridges, extending first posteriorly and to the right and then anteriorly to project to right of median corpus bursae without overlap; ductus seminalis joins right anterior appendix bursae. Anterior ½ of ventral ductus bursae with broad sclerotized band.

Type specimens: Holotype, ♂: WASHINGTON: Kittitas Co.: Reecer Cr. at Johnson Cyn., 900 m, 47.16°N 120.62°W, 4.IX.1989, Lars Crabo. Paratypes, 32♂, 22♀: WASHINGTON: Same data as type locality: 17.IX.1988 (2♂), 4.IX.1989 (4♂, 5♀), 1.IX.1990 (1♀), 4.IX.1994, Troubridge & Crabo (8♂, 11♀); Klickitat Co.: Lyle, 4 mi [6.4 km] N., 1500' [457 m], 12.VIII.1960, D.F. Hardwick (6♂, 2♀); Toppenish, 29 mi [46.7 km] S., 1800' [549 m], 23.VIII.1960, D.F. Hardwick (10♂, 3♀); Yakima Co.: Tieton River valley, Oak Creek at Tieton River, Elev. 525 m, 46.72°N 120.81°W, 7.IX.1990, L.G. Crabo, riparian with Garry Oak (1♂); Kusshi Canyon, 17.IX.1949, E.C. Johnston (1♂).

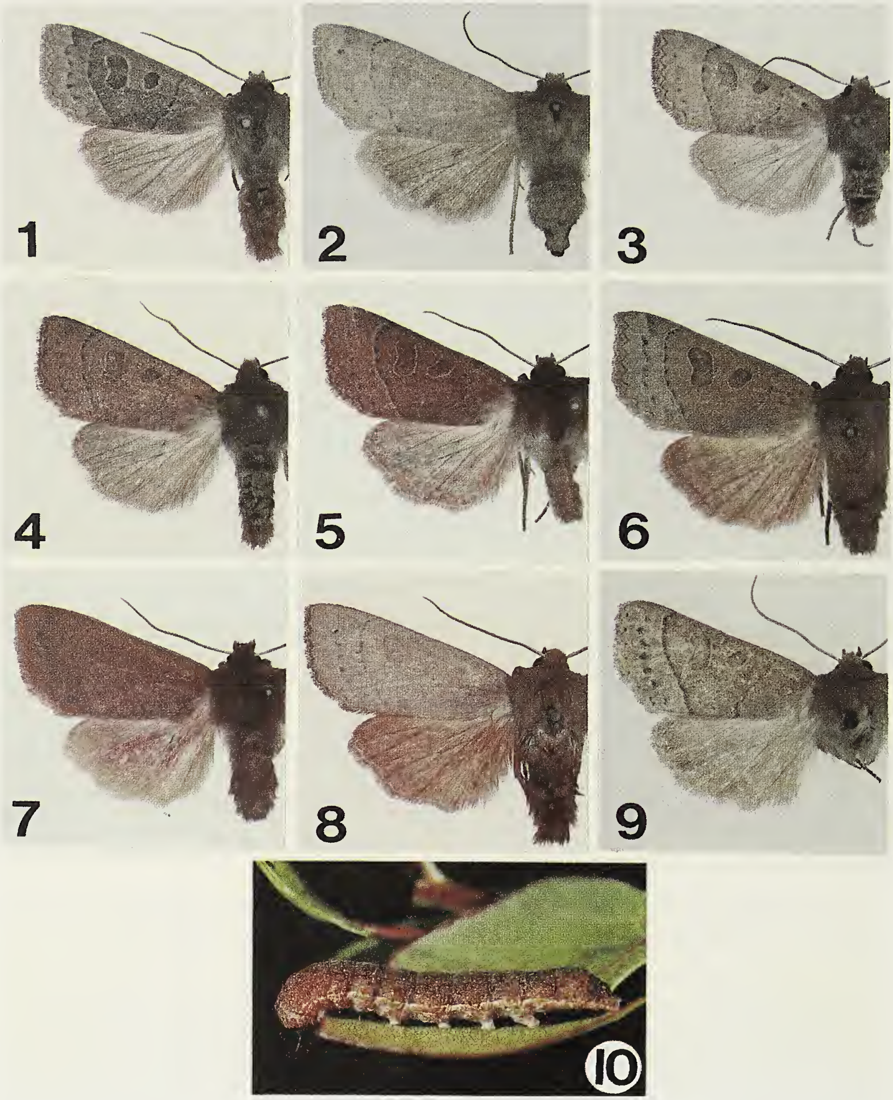
We restrict the type series to specimens from Washington state. The holotype is in the Canadian National Collection (CNC). Paratypes are in, or will be deposited in, the CNC, the United States National Museum (USNM), University of California (Berkeley), University of California (Davis), Oregon State University (Corvallis), and the personal collections of Lars Crabo (Bellingham, Washington) and Jim Troubridge (Langley, British Columbia).

Diagnosis: This species is less variable than *M. olivata* or *M. rubra.* It can be identified by the combination of yellow-brown ground color and light copper-colored hindwings. It is the only North American species with a median patch of spines on the male vesica and no overlap of the appendix bursae and corpus bursae of the female genitalia.

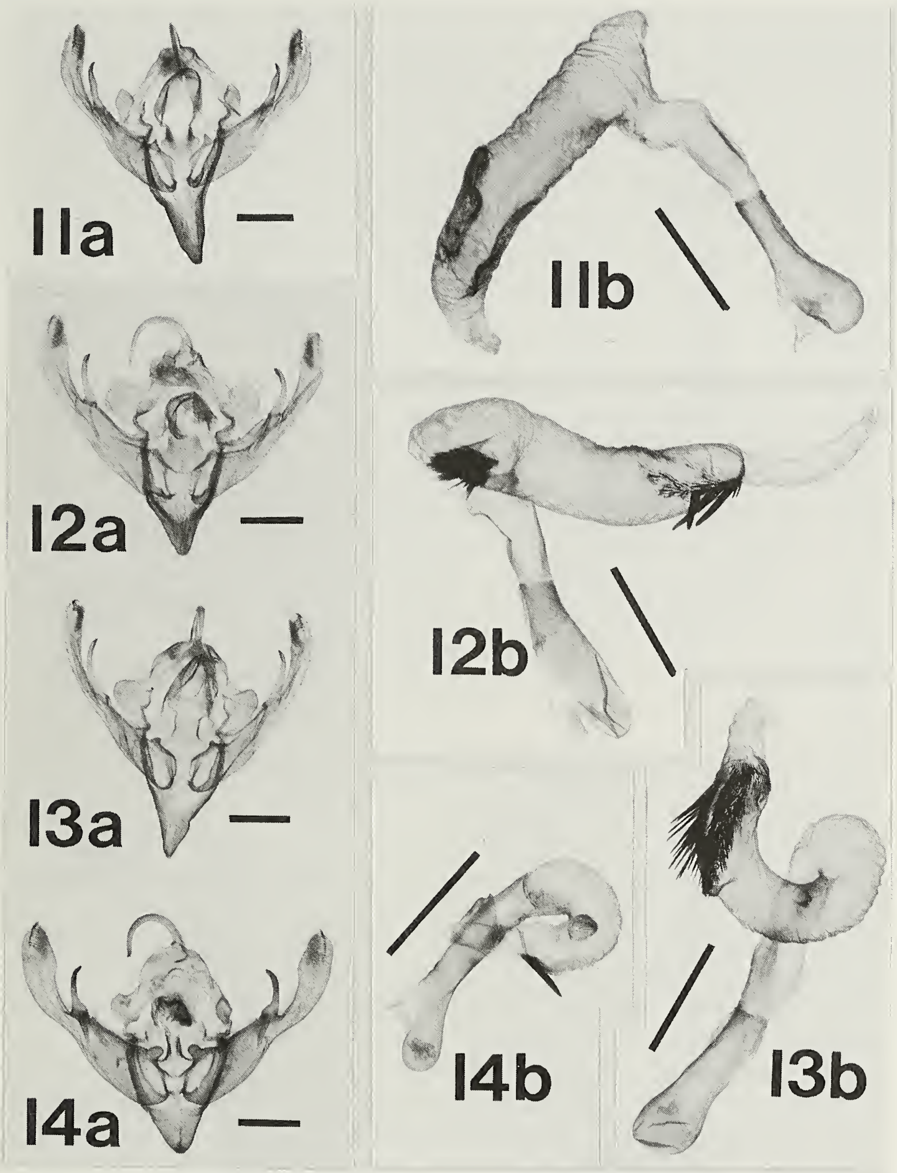
M. subcuprea superficially resembles *M. acetosellae* (Fig. 9) which occurs in Eurasia. The male genitalia of *M. acetosellae* (Fig. 14a) differ from those of the North American species by having a more massive valve with a large rounded costal lobe of the sacculus. Its vesica (Fig. 14b) is most like that of *M. subcuprea.* Both species have a median patch of cornuti on a diverticulum, while the other species have two distal patches and no diverticula. Furthermore, both *M. acetosellae* and *M. subcuprea* have at least one massive spine in the subapical group. The female genitalia of *M. acetosellae* (Fig. 18) differ from all of the North American species by having a unisaccate bursae copulatrix.

Early stages: The larva of *M. subcuprea* has been reared on *Quercus agrifolia* at Big Creek, Monterey County, California (J. Powell, unpub. data) and *Q. dumosa* Nutt. from the San Gabriel Mountains, Los Angeles County, California (label data, L. Crabo collection), but has not been described. It is closely associated with oak at many localities, but must also feed on other genera since oaks are absent from the type locality.

Distribution and flight period: *M. subcuprea* is known from the east slope of the Cascade Mountains and the eastern Columbia Gorge in Washington, from the Willamette Valley and the Klamath Mountains in Oregon,



Figs. 1–10. Adults and larvae of *Mesogona*. 1) *M. olivata* ♂, British Columbia, Okanogan Falls, near Vaseaux Lk. 2) *M. olivata* ♀, California, Mono Co., Benton Insp. Sta. 3) *M. olivata*, male, Washington, Grant Co., 1.5 mi [2.4 km] N. of Wanapum Dam on Hwy. 243, 225 m. 4) *M. olivata* ♂, Oregon, Douglas Co., Umpqua River valley, Thorn Prairie, 1040 m. 5) *M. olivata* ♂, Washington, Skagit Co., Anacortes, S. slope of Sugarloaf, 900' [274 m]. 6) *M. subcuprea* ♂, paratype, Washington, Kittitas Co., Reecer Creek at Johnson Canyon, 900 m. 7) *M. rubra* ♂, paratype, Washington, Skamania Co., Big Lava Bed, 3000' [914 m]. 8) *M. rubra* ♂, California, B.T.I. Exp. For., Grass Valley. 9) *M. acetosellae* ♂, Digne, Gallia mer. 10) Last instar larva of *M. rubra*, Oregon, Josephine Co., Cave Junction.



Figs. 11–14. Male genitalia of *Mesogona* species. Vesica of aedeagus has been everted (bar = 1 mm for genital capsule; 2 mm for aedeagus). 11) Male genitalia of *M. olivata*, Oregon, Douglas Co., Umpqua River valley, Thorn Prairie, 1040 m (a = valves; b = vesica). 12) Male genitalia of *M. subcuprea*, Washington, Kittitas Co., Reecer Creek at Johnson Canyon, 900 m (a = valves; b = vesica). 13) Male genitalia of *M. rubra*, paratype, Washington, Cowlitz Co., N. shore Lewis River between Yale Lake and Swift Creek Reservoir, 580' [177 m] (a = valves; b = vesica). 14) Male genitalia of *M. acetosellae*, Digne, Gallia mer. (a = valves; b = vesica).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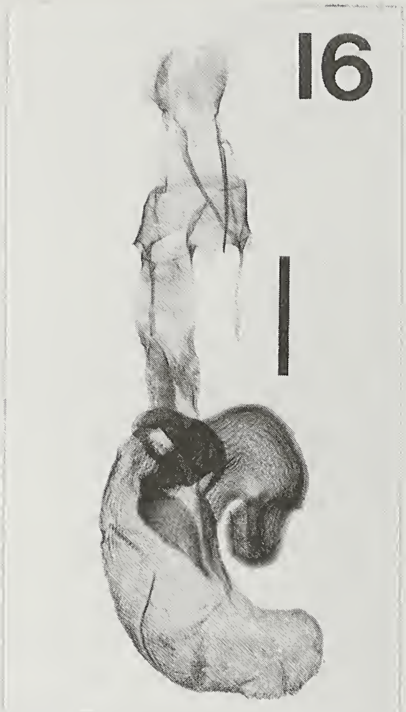
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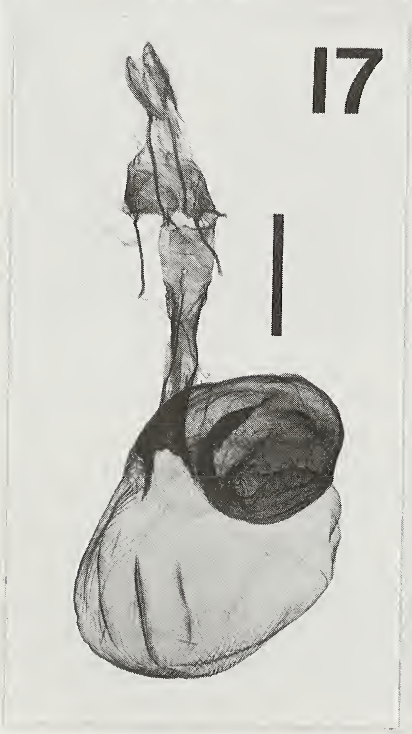
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and from the Klamath Mountains, the Sierra Nevada, and Coast Ranges south to Los Angeles in California (Map 2). Adults have been collected from mid August until early October. It emerges approximately one week earlier than *M. olivata* at the type locality. Adults come to light, but are more attracted to sugar bait at some localities.

Comments: Grote's original description of *Choephora blanda*, including "forewings... yellowish fawn..." and "hindwings silky reddish... with a trace of median line" could pertain to either *M. subcuprea* or some specimens of *M. olivata*. This hindwing description is especially suggestive of *M. subcuprea* although some specimens of *M. olivata* have reddish hindwings with gray scales. The Vancouver Island syntype of *blanda*, designated lectotype above, is a typical *M. olivata* with fuscous hindwings and two subapical bands of cornuti on the vesica. The other syntype from Washington Territory could not be located in collections containing Grote type specimens (J.D. Lafontaine, pers. comm.) and is presumed lost. It is likely that the lost syntype was also a *M. olivata* despite the suggestive description since the Vancouver Island specimen and *M. subcuprea* are dissimilar and would probably have been recognized as different species by Grote.

M. subcuprea is moderately common in collections, especially in material from California, but has been confused with the more common *M. olivata*.

The name *subcuprea* refers to the copper color of the hindwings of this attractive species.

Mesogona rubra Hammond & Crabo, **new species**
(Figs. 7, 8, 10, 13, 17; Map 3)

Description. Adults (Fig3. 7, 8): Males and females identical in habitus. Spines of first tarsal segment of prothoracic leg nearly equal. Ground color of head, palpi, dorsal antennae, thorax, abdomen, and forewings uniform brownish red, appearing nearly immaculate. Forewing length: 18–21 mm. Forewing 2 × as wide as long; margin undulating; lines double, inconspicuous, evident mostly as the pale filling; basal line and median shade obsolete; antemedian line oblique, undulating, bent slightly basad at costa; postmedian line forming a laterally convex arc, its inner line absent or evident as small dark dots in interspaces opposite cell; subterminal line sinuous, a series of faint dark dots between veins; terminal line dark, barely evident; orbicular and reniform spots faint, pale, similar in shape to those of *M.*

Figs. 15–18. Female genitalia of *Mesogona* species (bar = 2 mm). 15) Female genitalia of *M. olivata*, Washington, Kittitas Co., Reecer Creek at Johnson Canyon, 900 m. 16) Female genitalia of *M. subcuprea*, paratype, Washington, Kittitas Co., Reecer Creek at Johnson Canyon, 900 m. 17) Female genitalia of *M. rubra*, California, Diablo, 3 mi [4.8 km] NE, 2100' [640 m]. 18) Female genitalia of *M. acetosellae*, PODOLE POLUDN., str, KOP u Bedrykowce, Koroszów.

Map 2. Map of Pacific Coast states showing distribution of examined material of *M. subcuprea*.

Map 3. Map of Pacific Coast states showing distribution of examined material of *M. rubra*.

olivata but filled with ground color. Hindwing immaculate, uniform red with a slight sheen, terminal area and fringe lighter in some specimens.

Male genitalia (Fig. 13): Valves as in generic description; costal lobe small and rounded. Vesica 2.5 × as long as aedeagus, coiled 360°, first ventrad and toward right and then leftward to project to left of distal aedaeagus, with a small flattened basal cornutus, distal ⅓ with two large fields of cornuti containing both minute hairs and long spines, the latter as two longitudinal bands one with longer spines than the other, the proximal portion of the band of shorter spines elevated from surrounding vesica like the end of an anvil. **Female genitalia** (Fig. 17): Corpus bursae rounded, slightly wider than long with blunt extension posteriorly to the right, with 1 long dorsal and 2 long ventral signa; appendix bursae bulbous, slightly rugose, extending anteriorly and dorsally to overlap right side of dorsal corpus bursae; ductus seminalis joined to left anterior appendix bursae. Anterior ⅔ of ventral ductus bursae with a thin sclerotized band.

Type specimens: Holotype, ♂: OREGON: Linn-Lane Co. [Lane County]: H. J. Andrews For., 11 mi [17.7 km] NE. Blue River, September 3, 1986 / J.C. Miller LEPSTUDY, HJA Admin. site, 1500' [457 m] elev., ex. UV light trap / 1. Paratypes, 26♂, 5♀: OREGON: Lane Co.: Florence, 10.IX.1960, Blk. Lt. Trap, K. Goeden (2♀), 1.IX.1995, J. Troubridge (10♂); 0.2 mi [0.3 km] E. of S. Fk. McKenzie R. on Rd. to Cougar Reservoir, 44.15°N 122.25°W, 350 m, 14. IX .1991, L.G. Crabo, powerline cut/manzanita (1♂); Lincoln Co.: Newport, 15.IX.1961, Blk. Lt. Trap, K. Goeden (1♂); Linn Co.: Santiam Pass, Hwy. 20, 16.IX.1993 / 3-1-A (1♂), 29.IX.1993 / 3-1-B (1♂), 9.IX.1993 / 3-1-B (1♂), 22.IX.1993 / 3-1-B (1♂), 10.IX.1993 / 3-1-B (1♂), 15.IX.1993 / 3-1-B (1♂); Linn-Lane Co. [Lane Co.]: same as type locality, September 2, 1986 (1♂), September 11, 1986 (1♂), September 1, 1987 (1♂); Linn-Lane Co.: H.J. Andrews, [larva collected] 8.IV.1986, reared (1♀), [larva collected] 8.IV.1986, ex. *Arctostaphylos columbiana*, 86-49 (1♀), [larva collected] 8.IV.1986, ex. *Arctostaphylos columbiana*, 86-50 (1♀); WASHINGTON: Cowlitz Co.: N. shore Lewis R. between Yale L. and Swift Creek Res., 46.05°N 122.25°W, 580' [177 m], 30.VIII.1994, A. & L. Crabo, small lava bed/manzanita (2♂); S. Cascades, Dry Cr. 300 m E. of FR81, 1 mi [1.6 km] N. of Merrill L., 46.11°N 122.32°W, 1620' [494 m.], 30.VIII.1994, leg L.G. Crabo, pumice with lodgepole pine (2♂); Skamania Co.: E. side of Big Lava Bed on FR66, 2 mi [3.2 km] S. of South Prairie, 45.89° N, 121.72° W, 3000' [914 m], 29.VIII.1994, A. & L. Crabo, Lava flow, Lodgepole pine (1♂).

We restrict the type series to specimens from Lane County, Oregon and north in Oregon and Washington. The holotype will be deposited in the CNC. Paratypes are in, or will be deposited in, Oregon State University (Corvallis), USNM, University of California (Davis), and the personal collections of Lars Crabo (Bellingham, Washington) and Jim Troubridge (Langley, British Columbia).

Diagnosis: Most individuals of this species are easily recognizable by the combination of red forewings and immaculate red hindwings. Populations of *M. rubra* from Lane County, Oregon northward are uniformly of the deep red to brownish red color morphs. The populations in California and southwestern Oregon are quite variable, with pink morphs (Fig. 8) common along with the red morphs. These vary from pale whitish pink to a darker pinkish gray. Some of the light-colored individuals resemble *M. subcuprea*, but lack the well-defined orbicular and reniform spots on the forewing of this species. Some red *M. olivata* morphs are also similar to *M. rubra*, but have gray hindwings and more distinct forewing markings. *M. rubra* is the only North

American species with a coiled male vesica and dorsal overlap of the appendix bursa with the corpus bursae in the female.

Early Stages: The larva of *M. rubra* (Fig. 10) is reddish brown in ground color with a finely mottled pattern, and has a pale lateral stripe. This coloration blends with the reddish bark of *Arctostaphylos*. By contrast, the larva of *M. olivata* reared from *Ceanothus velutinus* is pale whitish gray in ground color with fine black lines and dots, and has a broad white lateral stripe (J.C. Miller, pers. comm.). Larvae of *M. rubra* have been beaten from and reared to adults exclusively on *Arctostaphylos columbiana* Piper in Lane County, Oregon and an *Arctostaphylos* species, possibly *A. cinerea* Howell, in Josephine County, Oregon (J.C. Miller, pers. comm.). The larvae have been collected during April and May. It probably utilizes *A. nevadensis* Gray in Washington sites where *A. columbiana* does not occur. However, it is probably host restricted to certain species of *Arctostaphylos*, since it has never been collected along the east slope of the Oregon Cascades in habitat with *A. patula* Greene.

Distribution and flight period: This species occurs in the Cascade Mountains north to Skamania County, Washington, in the Klamath Mountains, on the Pacific coast from central Oregon to central California, and in the Sierra Nevada (Map 3). It is sympatric with both other species at many localities, including with *M. olivata* at the type locality. *M. rubra* occurs in dry forests with *Arctostaphylos* species, including lava flows in the Washington and Oregon Cascades and forested dunes on the Oregon coast. It flies from late August to mid October.

The red color of this species resembles the bark of the foodplant. This feature is shared by some of the other Noctuid moths which feed on *Arctostaphylos* and madrone (*Arbutus menziesii* Pursh. — both Ericaceae) which both have reddish brown bark. These include *Orthosia mys* (Dyar), *O. pulchella* (Harvey), and *O. transparens* (Grote). This is likely a protective adaptation, although it is not known that the moths rest on the plants during the day.

Comments: This species is moderately common in California collections but has been confused with *M. olivata*. It was first recognized as distinct from *M. olivata* during a Lepidoptera survey of the H.J. Andrews Experimental Forest (USDA) performed by Jeffrey C. Miller of Oregon State University.

The specific epithet refers to the prominent red color of this species.

Acknowledgements: J. Donald Lafontaine searched North American collections for the type specimen of *Choephora blanda*, arranged for photographs of all *Mesogona* types in the British Museum (Natural History) to be sent to the senior author, made specimens in his care available for study, recorded locality records for *Mesogona* specimens from the United States National Museum, and provided encouragement. This study would not have been possible without his help. Jim Troubridge photographed the adults and genitalia. Jeffrey C. Miller provided the photograph of the larva of *M. rubra*. Eric Metzler (Columbus, Ohio), Jerry Powell (University of California, Berkeley), Steve Hayden (University of California, Davis), Ron Robertson (Santa Rosa, California), Jon Shepard (Nelson, British Columbia), and Jim

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The endangered quino checkerspot butterfly, *Euphydryas editha quino* (Lepidoptera: Nymphalidae)

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Abstract. With the listing of the quino checkerspot butterfly, *Euphydryas editha quino*, as a federally endangered species, research into its ecology and conservation is necessary to allow for recovery planning and management. We review systematics, distribution, natural history, and conservation prospects, with reference to pertinent literature about other *E. editha* subspecies. Additional information is presented from museum specimens and ongoing research on the species.

Keywords. Quino checkerspot butterfly, *Euphydryas*, endangered species, conservation

INTRODUCTION

The quino checkerspot butterfly, *Euphydryas editha quino* (Behr) 1863 (QCB or *quino*), was listed as an endangered species on January 16, 1997 (62 Federal Register 2313). The basis for the listing was habitat loss, degradation, and fragmentation, recognizing additional negative effects from fire management practice. All factors are the results of intensive human economic development of ever diminishing resources. Recent loss of the distribution area of *quino* was estimated as 50–75%, with "seven or eight populations" known in the United States with "all but three populations" consisting of fewer than five individuals (Nelson 1997). Surveys over the past year indicate that although QCB may not seem in as dire circumstance as the listing package indicated, with at least two robust metapopulations found in two counties and numbering thousands of individuals, we believe the species was correctly assessed as near extinction. QCB appears headed toward becoming the "passenger pigeon" butterfly — a once common widespread species crashing to extinction over a few decades. This would be especially remarkable because an average female QCB lays over 500 eggs in a season compared with two eggs for the passenger pigeon. We summarize herein all pertinent data regarding QCB, discuss our reasoning for projecting its imminent disappearance in the absence of substantial effort, and emphasize the rather unique event this disappearance will be among the set of all U.S. endangered butterfly species.

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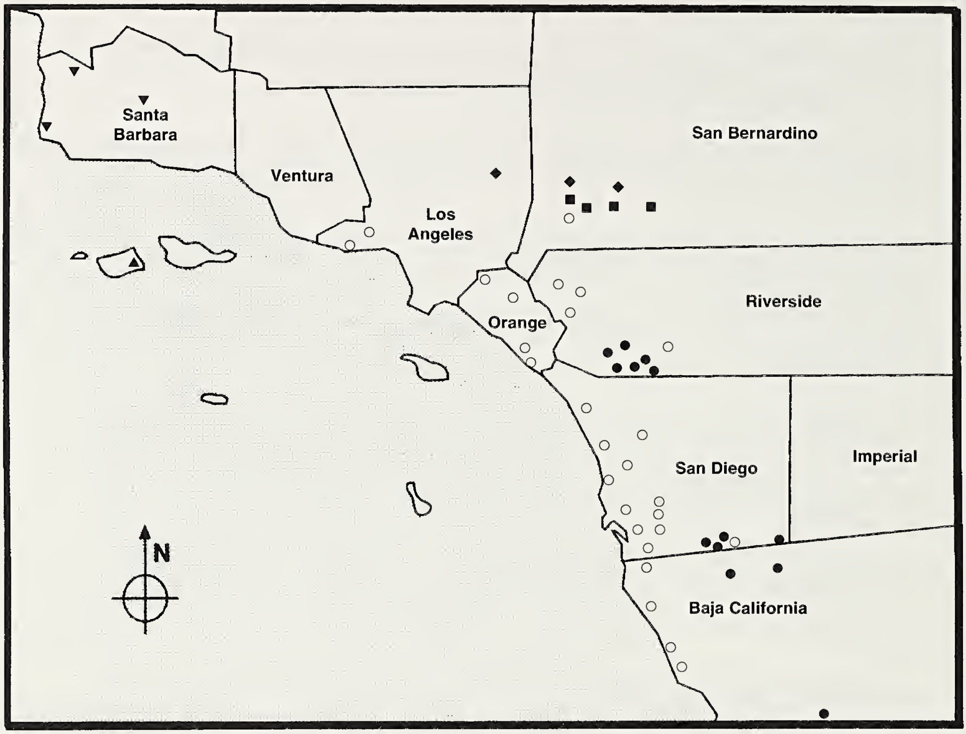

Fig. 1. Historic and current distribution of Quino checkerspot butterfly in southern California and Baja California, showing distribution of nearby subspecies of *Euphydryas editha*. Legend: ○ *quino* pre-1990, ● *quino* post-1990, ▲ *insularis*, ■ *augustina*, ◆ new subspecies, ▼ *editha.*

SYSTEMATICS

The QCB is one of over 20 recognized subspecies of *Euphydryas editha* (Miller & Brown 1981). *Euphydryas editha quino* is the most southwesterly distributed taxon and is parapatric with three other subspecies (Fig. 1): *editha* (Boisduval) 1852, *augustina* (W.G. Wright) 1905, and a new subspecies on the desert slopes of the Transverse Range to the southern Sierra Nevada. A fourth subspecies, *insularis* (Emmel & Emmel) 1974, occurs in southern California on Santa Rosa Island.

In adult appearance the QCB is distinguishable from all other subspecies by size and relative cover of red, yellow, black, and white scaling forming both upper- and underside maculation (Fig. 2). In nominotypical *editha*, black scaling predominates on the uppersides of the wings, covering approximately 50% of the wing surface, with cream spots covering about 25–30% and orange/red scaling covering about 20–25% of the wing surface. *E. e. quino* is similar to nominotypical *editha* in size, but differs in that the orange/red scaling is increased and cream spots are slightly larger. *E. e. augustina* is markedly smaller than *quino* and is similar in maculation to *quino* except that there is greater development of orange/red scaling in *augustina.* The desert slope Transverse Range segregate is intermediate in size between *quino* and *augustina*, and tends to have greater development of both orange/red and cream scaling than either of these taxa. *E. e. insularis* is similar to nominotypical *editha* in size but differs from that subspecies by greater development of black scaling and greater reduction of the orange/red scaling relative to the cream scaling.

There are additional defining larval characteristics, but these have not been systematically described for all subspecies (D. Murphy & G. Pratt, unpub. data). Foodplant utilization by QCB in the wild is restricted to *Plantago erecta* E. Morris, possibly *P. ovata* Forsskal [=*P. insularis* Eastw.], and *Castilleja exserta* (A.A. Heller) Chaung & Heckard [=*Orthocarpus purpurascens* Benth.]. Among *E. editha* subspecies, this foodplant utilization pattern is shared with nominotypical *editha* and *insularis*. In a study that did not include *insularis*, Baughman et al. (1990) presented genetic evidence that *quino* is more closely related to *editha* than other subspecies.

A contrasting view of *E. editha* was given by Scott (1986), who recognized only three subspecies: *editha, nubigena,* and *beani,* and stated that "Dozens of localized races have been named, but they all fit into these three ssp." In our opinion Scott's view under-represents variation (see also Baughman & Murphy, in press).

There have been two recent nomenclatorial changes with the taxon. The first was assignment of *editha* to the genus *Occidryas* (Higgins 1978). However, the erection of *Occidryas,* although accepted by a few uncritical authors (e.g., Miller & Brown 1981), was unsubstantiated by morphological or genetic evidence. All objective authorities synonomized it to *Euphydryas.* The other matter was recognition of *quino* as the correct available name for the taxon which earlier had been referred to as *wrighti* (Emmel et al., in press, a). Although Gunder (1928) associated the name *quino* with the *Euphydryas chalcedona* complex, a critical examination of Behr's description as well as the geographic parameters of collecting in the 1860s places *quino* with the *E. editha* species complex. A neotype for *quino* has been designated and the type locality fixed as San Diego, San Diego County, California.

The following summarizes the nomenclatorial treatment of *quino* and the three other named subspecies in southern California (format based on Miller & Brown 1981).

EUPHYDRYAS Scudder

editha (Boisduval) *MELITAEA*.

a. ***e. editha*** (Boisduval) *MELITAEA*. Ann. Soc. Ent. France, (2) 10:304 (1852). Type locality restricted to Twin Peaks, San Francisco, California, and lectotype designated, in U.S. National Museum, by Emmel et al. (in press, b).

= *bayensis* Sternitzky. Canadian Ent., 69:204–205 (1937). Type locality

Hillsborough, San Mateo Co., California. Syntypes in California Academy of Sciences, San Francisco.

b. ***e. augustina*** (W.G. Wright) *MELITAEA*. Butts. W. Coast: 154 (1905). Type locality San Bernardino Mtns., San Bernardino Co., California. Holotype in California Academy of Sciences, San Francisco.

c. ***e. insularis*** T. Emmel & J. Emmel. J. Res. Lepid., 13:131–136 1974(1975). Type locality Santa Rosa Island, Santa Barbara Co., California. Holotype in Los Angeles County Museum.

d. ***e. quino*** (Behr) *MELITAEA*. Proc. California Acad. Nat. Sci., 3:90 (1863). Type locality restricted to San Diego, San Diego Co., California, and neotype designated, in California Academy of Sciences, San Francisco, by Emmel et al. (in press, a).

= *augusta* (W.H. Edwards) *MELITAEA*. Canadian Ent., 22:21–23 (1890). Type locality vic. San Bernardino, San Bernardino Co., California. Lectotype in Carnegie Museum, designated by F.M. Brown, Trans. American Ent. Soc., 92:371 (1966).

= *wrighti* (Gunder). Pan-Pac. Ent., 6:5 (1929). Type locality San Diego, San Diego Co., California. Holotype in American Museum of Natural History, New York.

The name *augusta* has been applied to the *E. editha* populations in the San Bernardino Mountains since Comstock's publication of *The Butterflies of California* in 1927. However, examination of the lectotype specimen as well as consideration of the type locality (vicinity of San Bernardino, specifically Little Mountain northwest of the city; see Coolidge 1911, for a description of a day collecting on Little Mountain with W.G. Wright, during which he was told that this was the type locality for *Melitaea augusta*) clearly places the low elevation, phenotypically large *augusta* with *quino*. The name *augustina* is based on an aberrant specimen from the San Bernardino Mountains; because Wright considered it a new variety (his term for subspecies), the name can be used in a subspecific sense for the small phenotype, higher elevation San Bernardino populations of *E. editha*.

Populations of *E. editha* on the desert slope of the Transverse Ranges (San Bernardino and Los Angeles counties) that use *Castilleja plagiotoma* Gray as a larval host represent an undescribed subspecies; this taxon is being described by Baughman and Murphy (in press).

In spite of the importance of *E. editha* to population biology theory, there has been no recent revision of the overall species group. However, the patterns of variation and approximate phylogenetic relationships of the taxa surrounding *E. editha quino* are fairly well defined. Because of the sensitivity of *E. editha* senso lato to a suite of anthropocentric environmental im-

Fig. 2. *Euphydryas editha quino* and parapatric subspecies. Columns across: ♂ upperside, ♀ upperside, ♂ underside, ♀ underside. Top row: *editha,* ♂ CA: San Luis Obispo Co., Foothill Rd. near Los Osos, 29.IV.1976, ♀ same. Second row: *quino,* ♂ CA: San Diego Co., hills S of Lake Jennings, 25.III.1981, ♀ CA: San Diego Co., Dictionary Hill, 23.III.1975. Third row: new species, ♂ CA: San Bernardino Co., near Bowen Ranch SE of Hesperia, 14.IV.1987, ♀ same. Bottom row: *augustina,* ♂ CA: San Bernardino Co., Cienega Seca Crk., ♀ same. *E. e. insularis* is illustrated in Emmel & Emmel (1975).

Table 1. Localities for *Euphydryas editha quino* and most recent date of collection or observation. A list of museum specimens is available from the authors upon request.

Mexico	
Estrado de Baja California	
N of Ensenada	1935
Las Animas Canon	1935
Mosquito Springs	1936
Rodriguez Dam, Tijuana	1977
S of Salsipuedes	1979
N of Sordo Mudo	1979
Table Mt. (near Rosarita Beach)	1979
Turn off to Ojos Negros	1981
Valle de La Trinidad, Aquaito Spring	1994
N of El Testerazo	1996
S of El Condor	1996
California	
San Diego County	
San Francisquita Pass	1914
Warner's Dam	1916
South San Diego	1917
Santa Fe Ranch	1930
Lake Hodges	1932
Rancho Santa Fe	1933
Alta Vista	1934
Adobe Falls, San Diego	1948
Division Street, San Diego	1948
Vista	1951
Dehesa	1957
San Miguel Mt.	1957
El Cajon	1958
La Presa, San Diego	1958
Miramar	1960
Mission Gorge	1960
Tecate Mt.	1961
Fletcher Hills near El Cajon	1963
Sweetwater Dam/Reservoir	1969
Encanto	1969
Kearney Mesa	1969
Paradise Mesa, National City	1969
Spring Valley	1969
SE of El Cajon	1970
Proctor Valley	1971
Otay Lake	1973
Mt. Palomar	1975
San Diego	1976
Chula Vista	1978
Little Cedar Canyon	1979
Mesa E of Otay Reservoir	1979
Otay Mesa	1980
Dictionary Hill	1981
Brown Field	1997
Otay Mt., ridge S of O'Neal Canyon	1997
South Otay Mt., Marron Valley	1997
Jacumba	1997
North slopes of Tecate Peak	1997
Riverside County	
Sage	1951
Lake Elsinore	1983
Gavilan Hills	1985
Murrieta Hot Springs	1997
Aguanga	1997
Oak Mountain	1997
Temecula	1997
Lake Skinner	1997
Orange County	
Hills E of Orange Co. (Irvine) Park	1917
Anaheim	1930
Laguna Lakes	1931
Hills N of Orange Co. (Irvine) Park	1934
Dana Point	1936
Irvine Park	1937
Hidden Ranch	1967
Los Angeles County	
Tapia Camp, Santa Monica Mts.	1947
Pt. Dume	1954

pacts now entrained, it would be well to document geographic variation patterns and correlated natural history characteristics into a formal revision as quickly as possible.

DISTRIBUTION

The few known persistent populations of the QCB are large in area, distributed as complex metapopulations. In attempting to reconstruct historic QCB distribution, this hypothesis implies that specimens collected prior to 1940 most likely represent samples of extensive, and not small refugial, populations. Maps of presumed historic vegetation communities (e.g., Küchler 1977) and documented specimen localities indicate that the QCB may have had an almost continuous distribution across cismontane southern California from the westernmost Santa Monica Mountains, where dense but local concentrations of *Plantago erecta* still persist, across the Los Angeles plain and margins of the Transverse Ranges into the desert in upper Anza-Borrego and thence south into Baja California to about the northern San Pedro Martir (Fig. 1; Table 1). It was abundant on coastal bluffs in Point Dume in western Los Angeles County, Orange County (John Johnson, in litt. 1989 and see Orsak 1977), and the northern Baja California coast (Brown et al. 1992). All the coastal bluff populations have probably been destroyed with the possible exception of refugial colonies in the inaccessible coastal region between Ensenada and Cabo Colonet. During the past 20 years most of the coastal Baja terraces have been converted to high density agriculture.

By reasonable extrapolation, the first European missionaries to southern California made large negative impacts that are now immeasurable. In addition to direct land conversion, they caused many destructive secondary effects including introduction of grazing animals and many preadapted invasive Mediterranean plant and invertebrate species, introduction of destructive agricultural practices, general resource depletion, and modification of native American lifestyles. With open grass- and forb lands in the general scrub communities taking the brunt of habitat destruction, the QCB from that moment forward likely suffered more than any butterfly species of southern California. The importance of harvested *Plantago erecta* as a major grain resource of Native Americans provides some insight as to the quantities of this plant that were available, but are now more restricted. From the initial missionary invasion in the 1770s, the tide of acculturated humanity has unceasingly brought on natural habitat degradation by outright destruction, fragmentation, soil ecosystem disturbance, and explosions of nonnative species. Nevertheless, as recently as the early 1900s, two flora of Los Angeles reported that *P. erecta* was "Very common on dry plains and in the foothills throughout our range [Los Angeles and Orange counties]" (Abrams 1903) and "On dry hillsides throughout the south; the common species" (Davidson & Moxley 1923).

Any reconstruction of the former distribution of QCB is complicated by relying on museum specimens, which provide only presence data, and then only for localities frequented by collectors. Our recent discovery of populations across the southern slope of Otay Mountain and north of Tecate Peak indicates that previous collection localities were far from exhaustive. Casual collections rather than systematic surveys are the norm for our knowledge of historic butterfly distributions. The geographic extent of collection records, taken with the historic abundance of foodplant, leads to the presumption that *quino* was once commonly, if patchily, distributed from Point Dume to Ensenada and inland up to 60 miles (100 km).

Recently, Parmesan (1996) surveyed *Euphydryas editha* populations across the entire species range, sans the Rocky Mountain populations, to test the hypothesis that global warming should cause "net extinctions to increase in the south and at low elevations and to decrease in the north and at high elevations." After censusing 151 previously recorded populations, she concluded that there indeed was a correlation, acknowledging that the relationships expected were complex, particularly with regard to habitat destruction and its effect on recolonization. Given the complex population structure of *E. editha*, and our observation that human impacts were almost always involved in local extirpations in southern California (even for those areas that may seem to still have "suitable habitat"), the role of global warming as the proximate cause of extinction of *E. e. quino* populations must be carefully evaluated. We suspect that warming is perhaps an exacerbating factor, but that increased extinction rates in southern California are primarily caused by more direct anthropogenic forces.

NATURAL HISTORY

The studies of Paul Ehrlich and his many students and colleagues have produced a large body of information about *Euphydryas editha* as a species, mostly concerning the bay checkerspot, *Euphydryas editha editha* [=*bayensis*] (BCB). Most of this work is applicable to the QCB (e.g., Ehrlich 1965, Labine 1965, Ehrlich et al. 1975, 1980, Ehrlich & Murphy 1987, Ehrlich & Wheye 1984, 1986, 1988, Launer & Murphy 1994, Murphy et al. 1983, Murphy & Weiss 1988, Singer 1971, 1983, Singer & Thomas 1992, Baughman et al. 1990, Dobkin et al. 1987, White 1986, Weiss et al. 1987, 1988).

Life cycle

The QCB is univoltine with adults usually flying from late February into April (but see anomalies in phenology below). Females usually mate only once, and are "plugged" by males, which inhibits multiple copulations (Labine 1964). Shortly thereafter gravid females begin laying egg masses of 120–180 eggs (Ehrlich et al. [1975] record a minimum of 39 eggs per mass for *quino* in the field), which hatch in 7–10 days. Murphy et al. (1983) experimentally demonstrated in BCB that nectar feeding is essential to maximize egg mass production beyond the initial two masses, and in all cases subsequent egg number per mass decreased. Total egg production ranged from about 400–800 per female. The emergent prediapause larvae undergo two or three obligate moults, depending perhaps on the quality of the foodplants, and then enter an obligate diapause as either third or fourth instar larvae (G. Pratt, unpub. data). The prediapause larvae are gregarious, usually spinning a communal web, whereas postdiapause larvae are solitary.

Surviving larvae break diapause after winter rains of the next season are sufficient to germinate and establish foodplant. These postdiapause larvae go through three to perhaps seven or more additional instars and then pupate, usually among low plants near the ground or under rocks if such occur (G. Pratt, unpub. data, White 1986). Pupae mature and eclose in about ten days. Once larvae enter diapause their survival rates likely increase given that postdiapause larvae can repeat diapause at least once, and perhaps several times (D. Murphy & G. Pratt, unpub. data). There is also variation in larval coloration that may be geographic. White (1986) discusses several less studied aspects of the life history of *E. editha* subspecies.

Because of their dependence on annual foodplants that senesce and dry rapidly following the last rain of a season, prediapause larvae are the stage most susceptible to mortality. If neonate larvae cannot find foodplant within 10 cm of the egg masses, they will starve (Singer 1972, Singer & Ehrlich, 1979). Singer found approximately 99% mortality in the prediapause cohort leaving little room for other factors, at least in the seasons of the years studied. Singer and Ehrlich concluded that the major population regulators were density independent, highly variable weather conditions. Prediapause larvae (BCB) survived under three different conditions: 1) if eggs were laid when *P. erecta* would remain green for five more weeks, 2) if eggs were laid on *P. erecta* in soil tilled by pocket gophers (*Thomomys bottae*), which plants have deeper root systems and are generally more robust (see Hobbs & Mooney 1985), or 3) if larvae were able to locate the larger secondary foodplant *Castilleja exserta* (Singer 1972, Ehrlich et al. 1975).

Foodplants and nectar sources

Under field conditions the QCB essentially is restricted to the two larval foodplants, *Plantago erecta* and *Castilleja exserta*, throughout its range. Where present, *Plantago ovata* may be used although these plants are not usually abundant in QCB territory. *P. ovata* may be a long-naturalized exotic species from the Mediterranean region (Dempster in Hickman 1993). One larva was observed on *Keckiella antirrhinoides* (Benth.) Straw (G. Ballmer, unpub. data), a plant not common in QCB range. In the laboratory females oviposit and larvae feed on other *Plantago, Keckiella,* and *Penstemon*, including plant species found at QCB localities that are not used in nature. Although the patterns of *Euphydryas editha* oviposition choice and larval foodplant specificity have been elucidated in geographical context by Singer (1971, 1982, 1983), the physiological significance remains unknown. Experimental trials have not been conducted on *quino* to determine host preference.

Nectar sources are almost entirely small annuals that flower in synchrony with appearance of adult QCB. These include *Lasthenia* spp., *Cryptantha* spp., *Gilia* spp., *Linanthus dianthiflora, Salvia columbariae,* and annual *Lotus* spp. Most perennial plants are not in flower during the average QCB flight period. However, we observed QCB nectaring at *Eriodictyon* spp. late in the season.

Phenology and microclimate

Murphy and Weiss (Murphy & Weiss 1988, Weiss & Murphy 1988; see also Weiss et al. 1993) provided a detailed study of fine scale distribution of the BCB in terms of relative densities of both larvae and adults to slope and exposure (microtopography) and the resultant microclimates produced by insolation effect. They showed that the distribution of larvae, which were highly clumped, changed between years depending on weather patterns, and also moved in response to climatic factors. Position of larvae across the

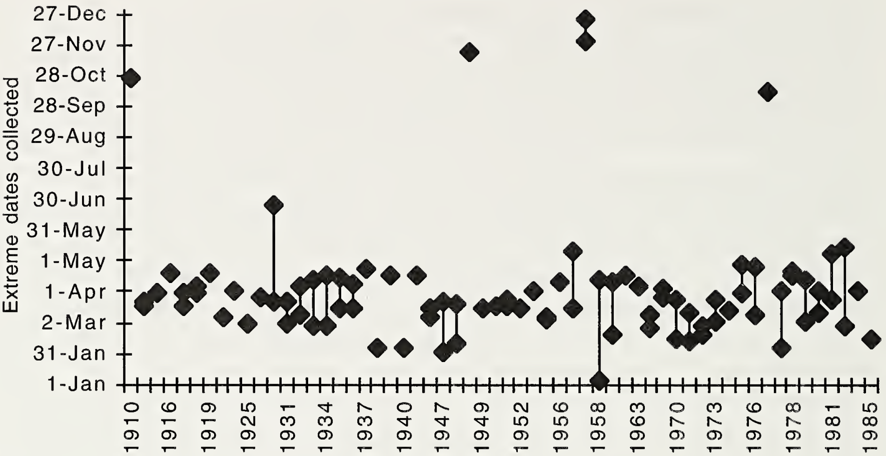

Fig. 3. Extreme collection dates of *Euphydryas editha quino* from museum specimens. Lines connect dates assumed to be within the same flight season. Note the fall emergence of adults in 1910, 1948, 1957, and 1976. All of these years had significantly greater than normal rainfall in September and October; 1957 and 1976 were El Niño years.

microclimatic strata affected their phenology and the timing of adult emergence. They also determined during the four-year study that population density centers shifted, with resultant variability in rates of postdiapause larval development to pupation and eclosion. The complex pattern of adult emergence, oviposition, and foodplant status (senescence) is described in terms of "phasing" to weather patterns in any season (Dobkin et al. 1987). These results illustrate that persistence of complex metapopulations depends on maintaining large and variable habitats with a broad range of microenvironments that may not be obvious at a glance.

Adults usually fly from February through April, but substantial variation has been recorded. Known adult flight dates are shown in Fig. 3, tabulated from museum specimens. Late fall adult emergence in 1910, 1948, 1957, and 1976 is correlated with significantly greater than normal rainfall during September and October (measured in San Diego) of those years, which may or may not be associated with an El Niño/Southern Oscillation event (1957 and 1976 were El Niño years). These extreme emergence dates suggest that larval phenology is plastic; larvae are able to break diapause virtually anytime in response to rain sufficient to establish foodplant. However, early adult emergence dates also require sufficiently warm weather as to not slow larval development. Dobkin et al. (1987) suggested that El Niño years were in fact detrimental to *editha,* because larval development and subsequent adult emergence were delayed by the cool, damp thermal regime more than foodplant vigor was prolonged — the butterfly and the foodplant were "out of phase." For El Niño, this condition may have been unique to the Jasper Ridge colony studied, because the serpentine soil is extremely porous and excess rainfall drains quickly. Drought, too, was shown to be detrimental to *editha* populations (Ehrlich et al. 1980, Ehrlich & Murphy 1987). In sum, weather conditions may cause the time of adult flight to vary anywhere from October to June.

Predators, parasitoids, and disease

Quantitative data on predation are available for the BCB, where mortality from parasitism in mature larvae was about 5% and in pupae about 50% (Weiss et al. 1988, White 1986). The only QCB data are for 200 larvae collected at Lake Skinner, of which three were parasitized by tachinid flies (K. Osborne, pers. comm.). No other field data concerning predation or disease are available, although ground dwelling larvae must be vulnerable to a number of spiders, ants, and carabid beetles. Nothing is known about QCB diseases.

Mating behavior and hilltopping

Mating behavior is an important factor in population dynamics. At locations with high population densities of the QCB, mate locating usually involves actively flying males seeking perched females. Females rest on the ground or low plants near where they eclosed, with wings spread, awaiting males. At locations where there is topographic relief combined with dispersed nectar and foodplant resources, females frequently move to high points, ridges and hilltops, where they encounter perching males (see Ehrlich & Wheye 1984, 1986, 1988). Here, males await females and usually defend small territories.

The latter phenomenon, hilltopping, has been described and documented for butterflies by Shields (1967) and is defined as "a phenomenon in which males and virgin or multiple-mating females instinctively seek a topographic summit to mate." According to this theory, high ground, ridges, hilltops, or even rock formations serve as visual beacons for sexual encounters. Larval foodplant or adult nectar sources may or may not be present, but males usually defend perches and/or patrol territory. At sites where both nectar and foodplant resources are also associated with "hilltops," butterfly occurrence is adventitious and is not necessarily hilltopping unless mating can be shown to be the purpose of butterfly presence. Nor is it the case where hilltop presence is the result of "random" movement across high ground. Unequivocally discriminating mate location from resource occurrence (and resource seeking) on "hilltops" requires statistical analysis. Shields provided quantitative data for one species, *Papilio zelicaon*, whereas a summary table of species he presents as hilltopping (including *quino*) is not supported by documented evidence. Regardless, however, there is a clear tendency among many volant insects to congregate at high ground regardless of sex or resources (see refs. in Shields 1967).

While Ehrlich and Wheye (1984, 1986, 1988) presented evidence supporting hilltopping in *E. editha*, Singer and Thomas (1992) disagree. They argue that hilltopping, defined as a behavioral preference for a resource, cannot be distinguished using measures of resource use (e.g., sex ratio on hilltops). Rather, to show hilltopping, one must observe a tendency in individual males or virgin females to move toward hilltops, or a trend for mating location to be closer to hilltops than emergence location, neither of which has been shown for any *E. editha* subspecies (Singer & Thomas 1992). Singer and Thomas' argument does not suggest that butterflies are not found on hilltops; it only questions the explanation for their presence. However, determination of the ecological and evolutionary role of the distribution of *E. editha*, especially *quino*, on hilltops is of important conservation value. If indeed *quino* congregate on hilltops to mate, the conservation value of those hilltops will be great.

Our observations across southern San Diego County during spring 1997 (Pratt et al. 1997) provided evidence of QCB using hilltops, although insufficient data were collected to prove hilltopping as prescribed by Singer and Thomas (1992). Our survey team found virtually all QCB as "hilltoppers" in the sense of appearing to be concentrated on ridges and peaks. Across the slopes of Otay Mountain and Tecate Peak, individuals (mostly ovipositing females) were found infrequently on lower slopes in comparison with ridges. By contrast, QCB populations across extensive flat grasslands, as in the vicinity of Murrieta, are found where there is little or no relief that provides hilltops (G. Ballmer, pers. comm.). There are also large expanses of *Plantago erecta* and *Castilleja exserta* with abundant nectar from sites where the species has been extirpated (Gavilan, March AFB, etc.), sites both with and without relief. Dense, shrub-covered areas, including high relief sites, do not have QCB populations. Thus the determination of whether a specific upland, ridge, rock outcrop, or hill serves for hilltopping behavior remains subject to interpretation and depends on the areography of the *quino* aggregates in question, their place in the vegetation matrix, and population density.

Population cycles and structure

Long-term studies initiated by Paul Ehrlich on the BCB in 1959 provided quantitative data showing large fluctuations in population density from year to year. As his work progressed it became apparent that the fluctuations were caused primarily by weather patterns, principally rainfall quantity and timing. After the major drought years, populations crashed, then variably recovered with return of favorable rains (Ehrlich et al. 1980). In the past two years, however, his major study population at Stanford's Jasper Ridge seems to have been extirpated. Although there are only anecdotal records on the QCB, cyclic fluctuations have been recorded.

The late John Johnson (in litt. 1989) observed *quino* for over 60 years in Orange County and noted significant changes in densities over time. The QCB was collected in abundance at Irvine County Park between 1917 and 1922 and then apparently almost disappeared until 1928. In 1933 and 1934 the species was again common, but vanished thereafter and was never seen again. A nearby colony about 0.5 miles (0.8 km) southwest of Hidden Ranch in Black Star Canyon, Santa Ana Mountains, was known from the 1920s to 1930s. After two decades without records James Mori found the butterfly abundant in March 1967. A severe fire in November 1967 burned the area and the butterfly has not been seen since. Two large reservoirs were constructed near Irvine Park and the whole area has been subjected to ever-increasing trampling over the 30 years since Mori found the last QCB in this part of the Santa Ana Mountains.

Harrison (Harrison et al. 1988, Harrison 1989) has proposed a metapopulation model for the BCB, a description which probably also fits the QCB. A metapopulation is a set of populations that are usually demographically independent (as Ehrlich found among the three populations of BCB at Jasper Ridge, 1965), but that are "interdependent over ecological time" (Harrison 1988). The evidence from *editha* is that local populations vary independently and occasionally suffer extinctions, but are recolonized from other populations. At Morgan Hill, there is a "reservoir" population that is large, stable, and much less likely to suffer extinction, even during a bad year. Surrounding smaller patches are periodically recolonized from the reservoir population. Because of the sedentary nature of *E. editha*, these small patches of once-occupied habitat may remain unoccupied for long periods before being recolonized (Harrison 1989).

Current data are insufficient to describe conclusively the population structure of *quino*, but observed patterns and anecdotal evidence suggest that it is similar to that of BCB. The distribution observed during 1997 surveys on Otay Mountain was patchy, with the butterfly exploiting temporally limited resources in some localities (post-fire chaparral, see below). Localities are separated by several to tens of kilometers, and can be assumed to be demographically isolated. The existence of a reservoir population has yet to be shown. QCB could have a true metapopulation structure (small patches, low dispersal) or a core-satellite structure typified by a reservoir population and smaller outlying habitats.

In the Gavilan Hills, Riverside County, anecdotal accounts of *quino* abundance and distribution seem to be consistent with a core-satellite population structure. At one location, on private land near Harford Spring Park, *quino* was abundant and always present, according to accounts from collectors reaching back to the 1930s. QCB were also found on outlying patches as far as 5 miles (8 km) distant (G. Pratt, unpub. data), but never in the numbers or consistency as adjacent to Harford Spring Park. In 1984 the landowner disked the presumptive reservoir population, completely destroying its habitat value. The butterfly subsequently disappeared in the surrounding region.

Plant community associations

The QCB is not associated with a single plant community, as are many butterflies, but instead with open spaces within several communities. Furthermore, QCB resource and climatic requirements are met, over the long term, by dynamic relationships that we can only generally recognize and at present describe rather imprecisely. The butterfly is found within several plant community types from scrub on coastal bluffs, through coastal sage scrub, chaparral, oak woodland, to desert pinyon-juniper woodland. In all these communities, however, it is only found in openings within the dominant plant community where there is sufficient local cover of the larval foodplants, which usually co-occur with the annual forbs that provide most nectar for adults. Sufficient foodplant density has yet to be determined; at Lake Skinner, QCB have occupied areas with foodplant densities as low as one plant per square meter (K. Osborne, pers. comm.). The butterfly does not occur in extensive open grasslands, nor does it occur in dense (without small clearings) coastal sage scrub, chaparral, or oak woodland. Plant community structure, and not dominant species composition, is the critical factor for QCB populations. The optimum habitat for oviposition and larval development consists of patchy shrub or small tree landscapes with openings of several meters between large plants. Landscapes with alternating open swales and dense shrub patches also provide habitat.

Among known colonies, there is usually some topographic relief such as raised mounds, low to high hills, slopes, and ridges. The species was common on Otay Mesa before urbanization; the natural landscape was one of vernal pool depressions alternating with a relief of mima mounds. Prior to widespread habitat destruction, the species was apparently abundant on coastal bluffs, which were characterized by sparse low vegetation.

Plant community identity as normally construed (i.e., dominant cover) is less helpful in defining *quino* habitat than is consideration of larval foodplant abundance and distribution, nectar source availability, and microtopography. In addition, cryptobiotic crusts and episodic disturbances such fire and light grazing contribute both to creating and maintaining suitable habitat.

Cryptobiotic crusts. In surveys for stands of *Plantago erecta* on Otay Mountain, we observed that the species was correlated with the presence of undisturbed cryptobiotic crusts (also called cryptogamic or microbiotic crusts, St. Clair & Johansen 1993). Cryptobiotic crusts are formed in soils in arid environments by blue-green algae, lichens, mosses, and other lower plant species, as well as fungi and bacteria (Belnap 1993). Research has shown that cryptobiotic crusts increase the ability of the soil to hold moisture and decrease its susceptibility to erosion through the adhesive qualities of mucilaginous polysaccharides exuded by certain blue-green aglae and fungi (Belnap & Gardner 1993). They also improve the availability of essential minerals (N, P, K, Ca, Mg, Fe) for higher plants and provide conditions that promote mycorrhizal associations (Harper & Pendleton 1993). Crusts are easily disturbed by trampling, especially by cattle. At Otay Mountain, we observed that *P. erecta* and other native annual species (e.g., *Lasthenia* sp., *Castilleja* sp., *Lepidium* sp.) were more often found in areas that had crusts intact, as identified by their characteristic patina and the presence of small mosses. In general, the proportion of native to exotic plant species was observed to be larger in areas with intact crusts. We speculate that crusts serve the role of "gatekeeper," allowing the germination of native species and perhaps inhibiting exotic species. However, crust areas have more "bare" ground (actually occupied by lichens, small mosses, algae, etc.) than non-crust areas, a characteristic preferred by the QCB. Cryptobiotic crusts are also usually darker (and thereby warmer) than surrounding soils (Harper & Pendleton 1993), making them attractive locations for QCB thermoregulation. The combination of native annuals (foodplant and nectar sources) and open ground may be encouraged by different edaphic factors (e.g., high clay content) in other areas. The BCB is found in grasslands defined by serpentine soils, which, much like crusts, support sparse native vegetation.

Grazing. In areas of heavy grazing, the annual plant cover at Otay Mountain was largely dominated by *Erodium* spp. (mostly *E. botrys*). In grazed areas, *Plantago erecta* was absent, all available space being preempted by the prostrate storksbills. *P. erecta* tended to occur in areas that would be less accessible to cattle, such as steep or rocky areas. Our observations about cryptobiotic crusts suggest a pathway of replacement wherein trampling by cattle disrupts the crusts, allowing establishment of the exotic *Erodium*, which in turn excludes *P. erecta.* Cattle also disperse *Erodium* seeds, thus further facilitating the invasion. Such animal-mediated disturbance has been implicated elsewhere in the spread of alien plants (Schiffman 1997a), and the quantity of seed dispersed by cattle has been shown to be enormous (Malo & Suárez 1995). However, light grazing may serve to maintain QCB habitat by promoting forb-dominated, intermediate successional grassland stages, as discussed for the southern habitat patches of the BCB by Murphy and Weiss (1988). But too much grazing has been implicated in local extirpations (Murphy & Weiss 1988). Light grazing by native ungulates was historically present throughout the QCB range, and emulation of it may indeed be necessary to maintain stable habitat areas. Also, regular disturbance by fossorial rodents may have contributed to maintaining areas dominated by annuals (Schiffman 1997b, Longcore, in prep.). Such disturbance by pocket gophers has already been shown to contribute to foodplant quality and BCB larval survival (Hobbs & Mooney 1985, Ehrlich & Murphy 1987).

Fire. Areas on the western side of Otay Mountain occupied by QCB in 1997 were in early post-burn succession. Adult QCB, *Plantago erecta,* and ample nectar sources were found throughout recently burned areas. QCB distribution was limited by the edge of the burn, which was marked by dense, mature chaparral. Although in some areas *P. erecta* distribution is stable, it can also be found tracking disturbance, with a distribution variable in both space and time. Like other "fire-followers," *P. erecta* grows well following disturbance (usually fire, but also other one-time events), sets large amounts of seed, and then thins out as the canopy is closed by the regenerating shrub layer. The regionally dynamic metapopulation structure of the QCB is adapted to such geographic and temporal variation in foodplant distribution.

The variable and synergistically interacting factors that contribute to appropriate *quino* habitat make defining essential areas for species survival difficult. What is one year closed canopy chaparral may the next year be covered with foodplant and flowering annuals, posing a special challenge to conservation efforts. Protecting sufficient habitat may mean protecting large enough areas to allow for a natural fire regime to maintain a shifting mosaic of habitat patches.

CONSERVATION PLANNING

With exception of the QCB and the BCB, all Nearctic butterflies listed under the Endangered Species Act have restricted distributions and/or highly specific habitat requirements. The threatened Karner blue butterfly (*Lycaeides melissa samuelis*) has a 1,000-mile wide geographic distribution, but is restricted to small dynamic successional habitat patches that support its one foodplant. The highest extinction probability is for species found only at single small sites. One limited catastrophe could destroy them: e.g., Lange's metalmark (*Apodemia mormo langei*) and Palos Verdes blue butterfly (*Glaucopsyche lygdamus palosverdesensis*).

By contrast, the QCB had a large range (ca. 200 × 60 miles [320 × 100 km], now reduced by over half), occurring over a continuum of climatic regimes from wet coastal to high desert; it is still found in several plant communities although it has only two hostplants, and likely maintains substantial genetic variation both hidden and expressed by local ecotypes. The key to its conservation will be management of the surviving populations under the assumption that they conform to a classic metapopulation structure. The fundamental feature of this scenario is the vulnerability of any metapopulation following the permanent loss of any of its demes (subpopulations) or fragmentation that would destroy dispersal patterns that connect them.

To ensure the conservation of the QCB, there must be some critical number of interconnected demes to provide a population structure with sufficient habitat variation that a viable effective population size is always maintained in some part of the metapopulation unit (Murphy & Weiss 1988). Available data do not permit even one metapopulation to be circumscribed even though at present there are three fairly large (each ca. 40–150 square miles [100–390 sq. km]) areas of distribution that may support at least one metapopulation: Otay Mountain, Temecula-Oak Mountain-Anza, and north central Baja. Although small refuge colonies may yet be found in parts of the historic range, as in Orange County and northern San Diego County, these colonies will be at high risk unless appropriate management plans are implemented to assure their survival, which may include providing corridors.

Murphy and Noon (1992), using the northern spotted owl as an example, provided a useful exercise in applying rigorous hypothesis tests to reserve planning. Their approach, which was to identify the minimum number of populations necessary to ensure species persistence, was a pioneering attempt to offset the usual socioeconomic constraints in conservation planning. Their first task was to determine if the data supported rejection of the null hypothesis that the finite rate of population change (λ) was > 1.0. The null hypothesis was rejected, leading to the recognition that their target species was in fact on the path to extinction (data concerning the QCB concur). Murphy and Noon then proceeded to test nine more hypotheses and concluded with a conservation map and strategy that were logically consistent.

Unfortunately, field data currently available are insufficient to provide a testable set of null hypotheses from which to design a reserve and management program for the QCB. The only operable current reserve design approach will be to maintain large contiguous parcels of land that will contain most, if not all, of the remaining metapopulations. The extent to which *quino* can tolerate limited development on these parcels currently cannot be assessed without further research on the autecology of the species. Tentative conservation requirements must include care to not overgraze, attention to the fire regime, and security of core cryptobiotic crust areas to preclude trampling. Whether sufficient land to preserve the species can be set aside, either through public ownership or voluntary conservation agreements with private landowners, remains to be seen.

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Immature stages of high arctic *Gynaephora* species (Lymantriidae) and notes on their biology at Alexandra Fiord, Ellesmere Island, Canada

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Abstract. Two species of *Gynaephora* are found in North America and their geographic ranges overlap broadly in the Canadian Arctic. Despite numerous studies that have addressed aspects of the biology, ecology, and physiology of these species, confusion regarding identification of their immature stages, originating with the original description of the first of the two species discovered, persists even in recent literature. In this paper, for the first time, all immature stages of both species are described and most are illustrated, with emphasis on the differences between the two species that allow for their identification.

Eggs and pupae of the two species are very similar morphologically but usually may be distinguished by association with cocoons and also by size at Alexandra Fiord, Ellesmere Island. In first instar larvae, the cuticle is black in *G. groenlandica* but pale in *G. rossii*; older larvae are readily identified by distinct differences in the color patterns of the larval hairtufts and by the form of the hairs, being spinulose in *G. groenlandica* and predominantly plumose in *G. rossii.* Cocoons usually may be distinguished by color but this feature is variable while the structure of the cocoons, double-layered in *G. groenlandica* and single-layered in *G. rossii,* is definitive.

Field studies conducted at Alexandra Fiord revealed some gaps and inaccuracies in previously published life history information. Egg masses laid on cocoons were found to suffer extensive predation by birds, a source of mortality that was previously overlooked. There appear to be six larval instars in *G. rossii* but seven in *G. groenlandica* rather than six as previously reported. Seasonal activity patterns of larvae were found to differ, with *G. groenlandica* active only in the early part of the growing season and *G. rossii* remaining active in late summer. Foodplant preferences also differed, partly as a result of the different food sources available at different times during the spring and summer. Finally, larval hairs of these species have been found to have urticating properties, causing skin irritation after extensive handling of larvae or cocoons.

Key Words. *Gynaephora groenlandica, Gynaephora rossii,* eggs, larvae, pupae, cocoons, morphology, seasonal activity, foodplants

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INTRODUCTION

The genus *Gynaephora* Hübner (Lymantriidae) is represented in North America by two species, *G. groenlandica* (Wocke [in Homeyer] 1874) and *G. rossii* (Curtis 1835). The geographic distribution of *G. groenlandica* is almost entirely limited to Greenland and islands of the Canadian arctic archipelago; that of *G. rossii* includes most of the North American Arctic (excluding Greenland) and Siberia, with isolated populations occurring in alpine areas of Japan, New England, and the southern Rocky Mountains (Ferguson 1978, Mølgaard & Morewood 1996). *Gynaephora groenlandica* has the distinction of ranging to the most northerly point of land in Canada (Ward Hunt Island, 83°N; Downes 1964) as well as northernmost Greenland (Wolff 1964) and is considered to be a high arctic endemic species (Munroe 1956, Downes 1964) whereas *G. rossii* has a typical arctic/alpine distribution.

Early accounts of arctic *Gynaephora* species are numerous, mostly consisting of descriptions and natural history observations (Curtis 1835, Homeyer 1874, Grote 1876, Packard 1877, Scudder et al. 1879, Skinner & Mengel 1892, Dyar 1896, 1897, Nielsen 1907, 1910, Johansen 1910, Gibson 1920, Forbes 1948, Bruggemann 1958). Later authors emphasized the apparent adaptations of these insects and others to the extreme conditions of the arctic environment (Downes 1962, 1964, 1965, Oliver et al. 1964, Oliver 1968). More recent studies have investigated the biology, ecology, and physiology of arctic *Gynaephora* species in order to elucidate and understand the various ways in which they are adapted to arctic conditions (Ryan 1977, Ryan & Hergert 1977, Schaefer & Castrovillo 1979, Kevan et al. 1982, Kukal 1984, Kukal & Kevan 1987, Kukal, Heinrich & Duman 1988, Kukal, Serianni & Duman 1988, Kukal & Dawson 1989, Kukal et al. 1989, Kevan & Kukal 1993, Kukal 1995, Lyon & Cartar 1996).

Despite the attention that arctic *Gynaephora* species have received, there remains confusion regarding identification of the immature stages. For example, Kevan et al. (1982) ostensibly studied *G. rossii* but published photographs of a larva, cocoons, and even an adult that are clearly *G. groenlandica.* Furthermore, Ryan and Hergert (1977) considered the two species to be "identical in their food choices and development, and almost identical morphologically"; however, there are considerable differences, both morphologically and ecologically. The purpose of this paper is to describe and illustrate the immature stages of *G. groenlandica* and *G. rossii*, with emphasis on differences between the species, and to update information on their natural history as observed at Alexandra Fiord, Ellesmere Island, Canada.

METHODS AND MATERIALS

Fieldwork was conducted at Alexandra Fiord (78° 53′ N, 75° 55′ W) on the east coast of Ellesmere Island from 6.VI.1994 to 15.VIII.1994, from 29.V.1995 to 17.VIII.1995, and from 25.V.1996 to 13.VIII.1996. The study site consists of a small (about 8 km^2) lowland valley bounded by glaciers to the south, upland polar desert and fellfield to the east and west, and the fiord itself to the north. This site has been subject to a considerable amount of ecological research (cf. Svoboda & Freedman 1994) and is described as a "polar oasis," noted for its relatively lush vegetation compared to the surrounding polar desert (Freedman et al. 1994). Populations of both species of *Gynaephora* occur at Alexandra Fiord, although *G. groenlandica* is far more abundant there than is *G. rossii.*

Larvae, cocoons, adults, and eggs of both species of *Gynaephora* were observed and photographed in the field and were collected for rearing and for more detailed examination. Dimensions of eggs and maximum widths of larval head capsules viewed from the front were measured to the nearest 0.05 mm using a stereomicroscope equipped with an ocular micrometer, at a magnification of 20×. Early larval instars were determined by rearing larvae from eggs and measuring head capsules shed at each moult. Head capsule width (HCW) for the final instar was determined by measuring head capsules from larvae that had been killed by parasitoids after spinning cocoons, indicating that they were in their final stadium. Mean HCW for each of the intermediate instars was estimated by extrapolating from the mean HCW of the early and final instars according to the Brooks-Dyar Rule (Dyar 1890, Daly 1985) and these estimates corresponded well with peaks in the distribution of measured HCW for *G. groenlandica.* The distribution of HCW overlapped for these intermediate instars and therefore sample statistics were calculated by dividing the HCW distribution at the low points between peaks. Due to this overlap in HCW between intermediate instars and the very limited number of actual HCW measurements for the intermediate instars of *G. rossii,* the given HCW for these instars should be considered approximations only. Descriptions of the later instars were obtained by measuring the head capsules of larvae examined in detail and assigning these larvae to the appropriate instar. These descriptions were supplemented with field observations of larval phenotypes, especially larvae that were spinning cocoons, indicating that they were in their final stadium. Descriptions of larvae follow the terminology used by Ferguson (1978).

Photographs of larval hairs and portions of cocoons were taken through a stereomicroscope at a magnification of 30×. Maximum lengths and widths of cocoons viewed from above were measured to the nearest millimeter using a plastic ruler; sexes were subsequently determined from the morphology of caudal segments of the pupal exuviae (cf. Fig. 1). Maximum lengths and widths of pupae in ventral view were measured to the nearest half millimeter using a plastic ruler; very few pupae were measured because most were left to develop within their cocoons for other studies. Descriptions of pupae follow the terminology of Mosher (1916) and were formulated to be comparable to those published by Patočka (1991). Measurements are given as mean ± standard deviation, followed by the sample size in brackets, and are rounded off to the level of precision of the original measurements; statistical tests were conducted as described by Zar (1984) before rounding off the data.

Foodplant preferences were determined by recording the plant species and part of the plant eaten by all *Gynaephora* larvae that were observed actively feeding on the tundra in 1995 and 1996; these observations were limited to free-ranging larvae.

RESULTS

Descriptions of Immature Stages

Eggs. Eggs laid in masses covered by hairs rubbed from the abdomen of the female, typically on the cocoon from which the female emerged but also frequently on vegetation or the ground (Plate 1). Eggs of both species smooth, creamy white, and roughly spherical but somewhat flattened.

***G. groenlandica*:** 1.60 ± 0.05 mm in diameter by 1.35 ± 0.05 mm in height (n = 10).

***G. rossii*:** 1.40 ± 0.05 mm in diameter by 1.10 ± 0.05 mm in height (n = 10).

Eggs of *G. rossii* significantly smaller than those of *G. groenlandica* ($t_{(1)18}$ = 15.345, $P < 0.0005$ for diameter; $t_{(1)18}$ = 15.545, $P < 0.0005$ for height), this difference visible even to the unaided eye.

Larvae. Larvae of both species large and very hairy, superficially resembling larval Arctiidae (Plate 2). The following general description, outlining the basic arrangement of verrucae and hairs, applicable to all instars of both species; modifications and species-specific differences described in the subsequent sections. Differences only noted in the specific descriptions; larvae of a given instar correspond to the description given for the previous instar except as described otherwise.

Head capsule black and bearing many hairs. Addorsal, subdorsal, supraspiracular, subspiracular, and subventral verrucae present on mesothorax, metathorax, and abdominal segments 1 through 8. Addorsal verrucae fused with subdorsal verrucae on prothorax and abdominal segment 9. On prothorax, supraspiracular verrucae greatly reduced, sometimes lacking hairs, and subspiracular verrucae enlarged and oriented anteriorly. Except as just noted, all verrucae bearing from one to many hairs. Hairs arising from addorsal and subdorsal verrucae generally thicker than those arising from supraspiracular, subspiracular, and subventral verrucae. Hairs arising from supraspiracular and subspiracular verrucae, and from dorsal verrucae on abdominal segment 9, up to two or three times as long as the longest hairs arising from addorsal, subdorsal and subventral verrucae. Cuticle, including verrucae, entirely black except where noted below. Dorsal glands on abdominal segments 6 and 7 whitish and well developed in all instars except the first.

***G. groenlandica*:** First instar HCW = 0.70 ± 0.05 mm (n = 140). Corresponding to the general description above. Cuticle between verrucae black. Hairs arising from addorsal and subdorsal verrucae black, hairs arising from subspiracular and subventral verrucae brown, and hairs arising from supraspiracular verrucae mixed. All hairs spinulose.

Second instar HCW = 0.95 ± 0.05 mm (n = 85). All verrucae bearing a mixture of black and brownish yellow hairs. Hairs arising from supra-spiracular, subspiracular, and subventral verrucae predominantly yellow. Hairs arising from addorsal and subdorsal verrucae predominantly yellow on mesothorax and metathorax, black on abdominal segments 1, 2, and 8, and yellow on abdominal segments 3 through 5.

Third instar HCW = 1.30 ± 0.05 mm (n = 30). Hairs more dense than in previous instars, beginning to obscure underlying verrucae from which they

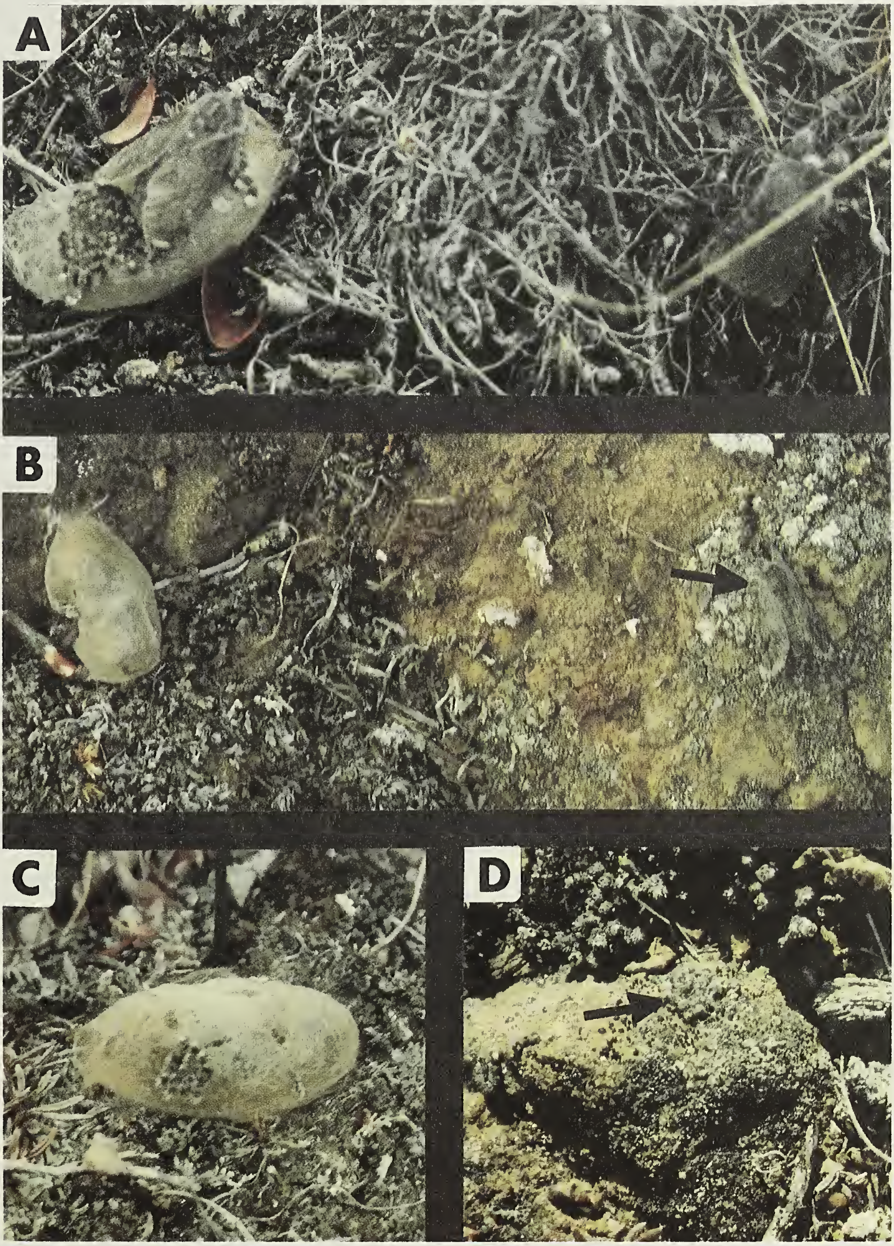

Plate 1. *Gynaephora groenlandica* (A–D). Female ovipositing on the cocoon from which she emerged; male still present to the right (A). Female (arrow) ovipositing on the ground near the cocoon from which she emerged (B). Egg mass partially depredated by foraging birds; note small tears in the cocoon where eggs were removed (C). Egg mass (arrow) on a lichen-covered rock (D).

arise. Predominance of black and yellow hairs in separate tufts, as noted in the second instar, more pronounced.

Fourth instar HCW = 1.85 ± 0.10 mm (n = 46). All hairs brown except the following. Black hairs arising from mesal portions of addorsal and subdorsal verrucae on abdominal segments 1, 2, and 8 forming tufts much denser and somewhat longer than surrounding dorsal hairs. Yellow hairs arising from addorsal verrucae on abdominal segments 3 and 4 forming tufts denser but not longer than surrounding dorsal hairs.

Fifth instar HCW = 2.35 ± 0.15 mm (n = 230); sixth instar HCW = 3.10 ± 0.20 mm (n = 353). Hairs longer and denser than fourth instar, most notably hairs arising from supraspiracular, subspiracular, and subventral verrucae, and dorsal verrucae on abdominal segment 9. Some hairs arising from dorsal verrucae on prothorax and from subdorsal verrucae on mesothorax and metathorax as long as hairs arising from supraspiracular verrucae. Lengths of black and yellow dorsal tufts somewhat variable, sometimes nearly even and sometimes with black tufts distinctly longer than yellow. Black tuft on abdominal segment 8 longer and more slender than those on abdominal segments 1 and 2, resembling more the rudimentary hair pencil that it represents (Plate 2A).

Seventh instar HCW = 3.95 ± 0.20 mm (n = 235). Color pattern of dorsal hairtufts on abdominal segments 1 through 5 somewhat variable. Typically, on abdominal segments 1 through 4, hairs arising from addorsal verrucae black and those arising from subdorsal verrucae black mesally and yellow laterally; occasionally this pattern developed to a lesser extent also on abdominal segment 5. This produces an overall appearance of four, or occasionally five, central black tufts fringed laterally with yellow (Plate 2B). Rarely, the pattern of two black tufts on abdominal segments 1 and 2, followed by two yellow tufts on abdominal segments 3 and 4, retained in this final instar.

With the exception of the distinctive black and yellow tufts, the larval hairs of *G. groenlandica* show considerable variation in overall color, depending on how recently an individual has moulted. Freshly moulted larvae appear silvery brown overall but the brown hairs quickly darken and then very gradually fade to golden yellow (Plate 2C) during the course of the stadium.

***G. rossii*:** First instar HCW = 0.60 ± 0.05 mm (n = 44). Corresponding to the general description above. Cuticle between verrucae pale. Hairs uniformly grey in color. All hairs spinulose.

Second instar HCW = 0.85 ± 0.05 mm (n = 41). Some hairs arising from addorsal verrucae on abdominal segments 1, 2, and 8 plumose. One or two hairs arising from supraspiracular verrucae on each abdominal segment plumose. All other hairs spinulose. Cuticle generally somewhat paler between verrucae.

Third instar HCW = 1.25 ± 0.05 mm (n = 26). Hairs more dense than in previous instars, beginning to obscure underlying verrucae from which they arise. Some hairs arising from addorsal verrucae on mesothorax and metathorax, as well as abdominal segments 1, 2, and 8, plumose. Some hairs arising from subdorsal verrucae and most hairs arising from supraspiracular and subspiracular verrucae on all segments except prothorax plumose. Other hairs spinulose, either black or yellow, those arising from thoracic verrucae and from addorsal verrucae on abdominal segments 3 through 5 predominantly yellow.

Fourth instar HCW approximately 1.75 mm. Grey plumose hairs denser and more prominent, otherwise very similar to third instar.

Fifth instar HCW approximately 2.50 mm. Some to most hairs arising from all verrucae plumose. Hairs arising from addorsal and subdorsal verrucae quite uniform in length, giving a "clipped" appearance in lateral view. Hairs arising from supraspiracular and subspiracular verrucae up to twice as long as those arising from dorsal verrucae. Longer plumose hairs grey, shorter spinulose hairs black or yellow, as in the third and fourth instars.

Sixth instar HCW = 3.55 ± 0.20 mm (n = 202). All hairs black except as noted in the following. Thoracic verrucae bearing a mixture of black and yellow hairs not forming distinct tufts. Addorsal and subdorsal verrucae on abdominal segments 1 through 8 bearing dense tufts of relatively short hairs, those arising from addorsal verrucae and the mesal portion of subdorsal verrucae black, and those arising from the lateral portion of the subdorsal verrucae yellow. This produces the appearance of a black tuft fringed laterally with yellow on each abdominal segment, the pattern becoming less distinct caudally. Variable numbers of longer grey plumose hairs arising from all verrucae, usually obscuring the pattern of black and yellow tufts to some extent, sometimes completely, and giving the impression of lint accumulated among the larval hairs (Plate 2D). In rare individuals, grey plumose hairs replaced by black spinulose hairs which do not obscure the pattern of black and yellow tufts (Plate 2E). Rearing of such larvae produced either adults of *G. rossii* or adults of the tachinid parasitoid *Chetogena gelida* (Coquillett), which is extremely host-specific to larvae of *G. rossii*, at least at this site (Morewood, unpub. data).

In general, larvae of *G. rossii* smaller than larvae of *G. groenlandica* and with much shorter hairs of more uniform length. Pattern of black and yellow dorsal hairtufts quite different in the two species and not obscured by other hairs in *G. groenlandica* but usually obscured at least partially by grey plumose hairs in *G. rossii*. Long spinulose (Plate 3A) or plumose (Plate 3B) larval hairs characteristic of *G. groenlandica* and *G. rossii*, respectively, producing a contrast in overall appearance and also quite distinct when viewed under magnification. These hairs also readily distinguished after they have been incorporated into cocoons (Plate 3C&D).

Cocoons. Cocoons spun on the surface of the tundra and anchored to the substrate, not concealed in any way but rather located in exposed sites with maximum insolation, on substrates of vegetation, litter, bare soil, or rock. Cocoons of *G. groenlandica* much larger than those of *G. rossii* (Plate 3E), mainly due to the difference in structure (see below).

***G. groenlandica*:** Cocoons constructed in two distinct layers with a consid-

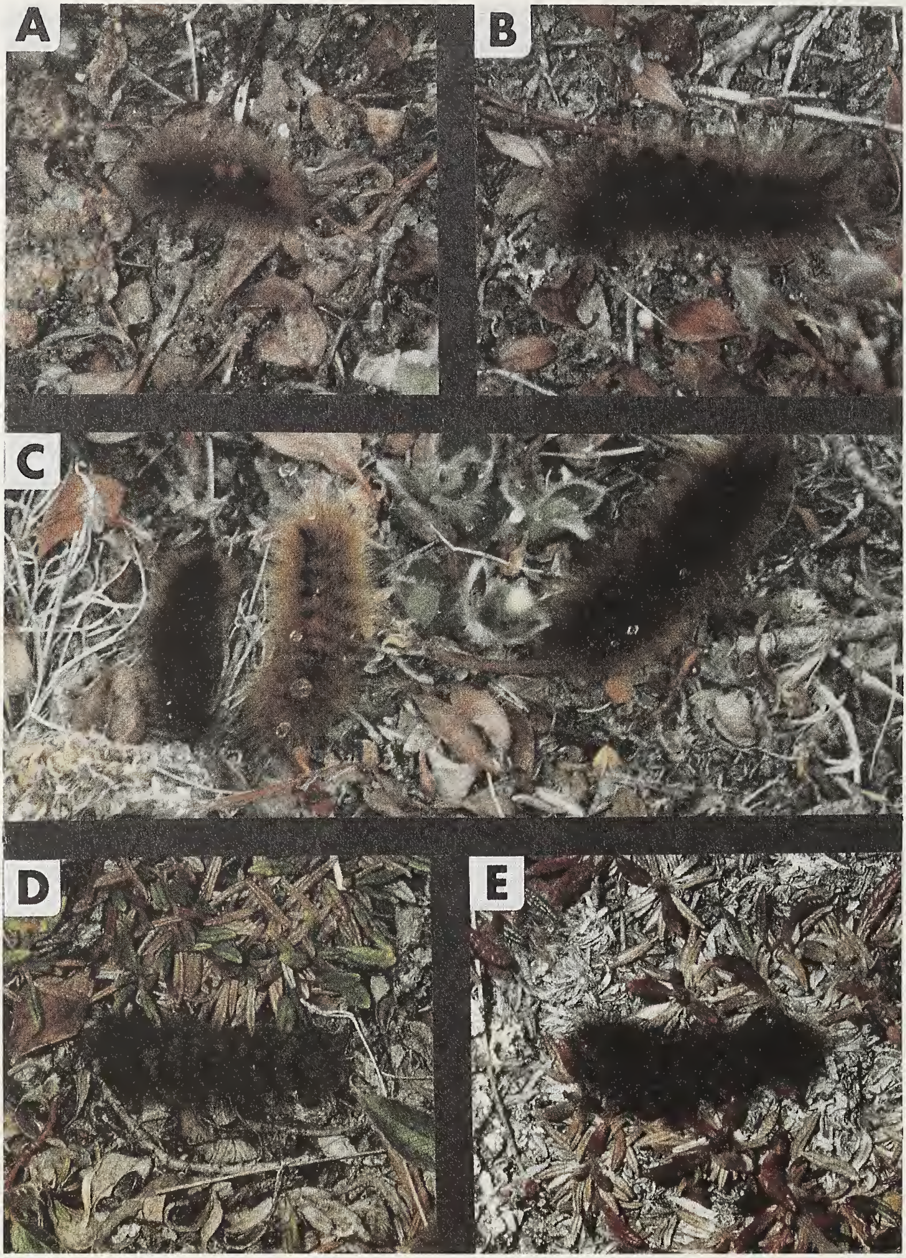

Plate 2. *Gynaephora groenlandica* (A–C) and *Gynaephora rossii* (D–E). Fifth instar larva (head to the right) with the characteristic black and yellow dorsal hairtufts and rudimentary dorsal posterior hair pencil (A). Seventh instar larva (head to the left) with the four black dorsal hairtufts typical of the final instar (B). Larvae showing the range of color of larval hairs with the most recently moulted larva on the left (C). Typical larva, showing grey tufting produced by the plumose larval hairs (D). Larva lacking grey plumose hairs (E).

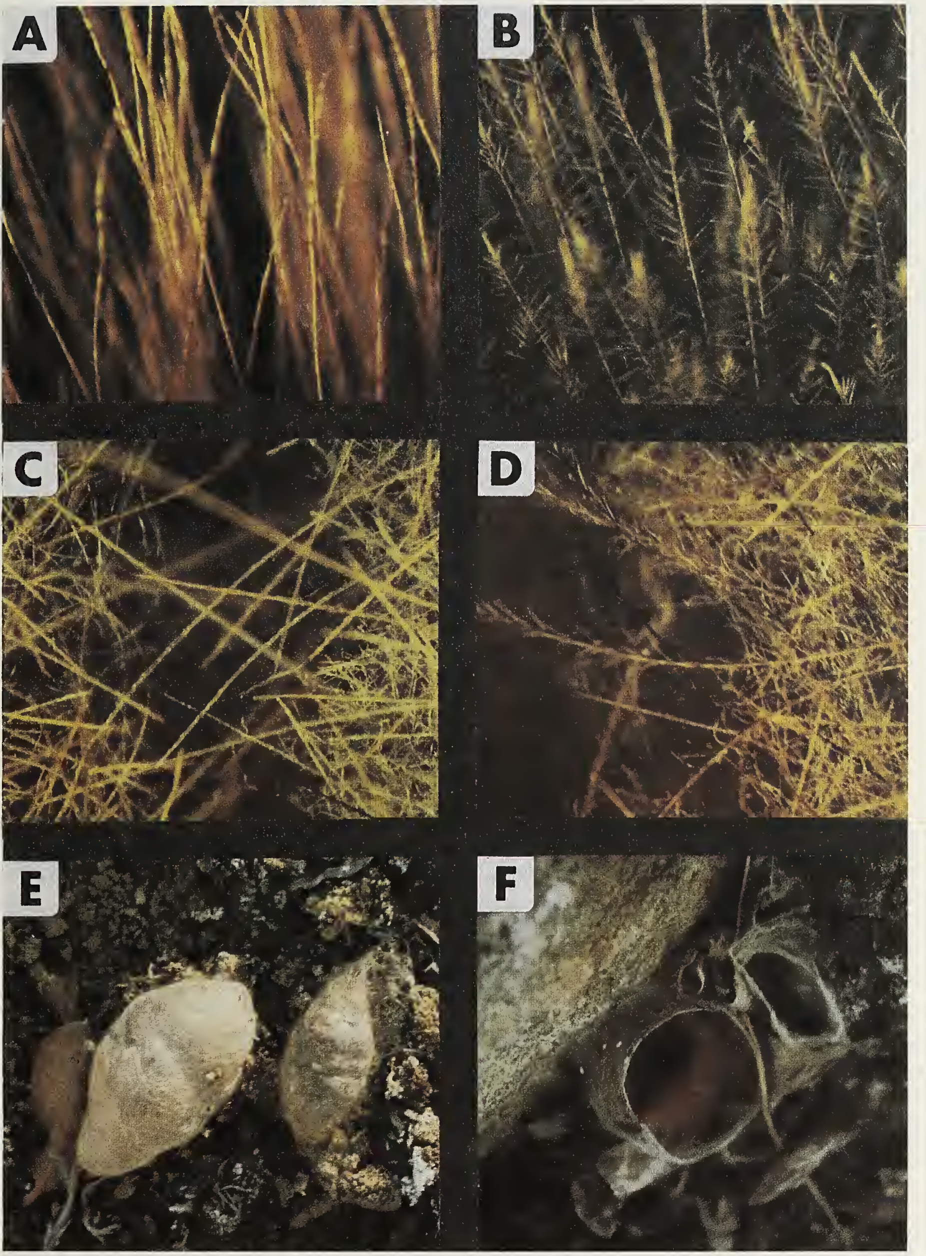

Plate 3. *Gynaephora groenlandica* (A, C, E, F) and *Gynaephora rossii* (B, D, E). Spinulose larval hairs (A). Plumose larval hairs (B). Portions of the outer (right) and inner (left) layers of the pupal cocoon (C). A portion of the pupal cocoon (D). Complete cocoons of *G. groenlandica* (left) and *G. rossii* (right) (E). Larval hibernacula; the opening in the occupied hibernaculum was the result of removing an overlying rock (F).

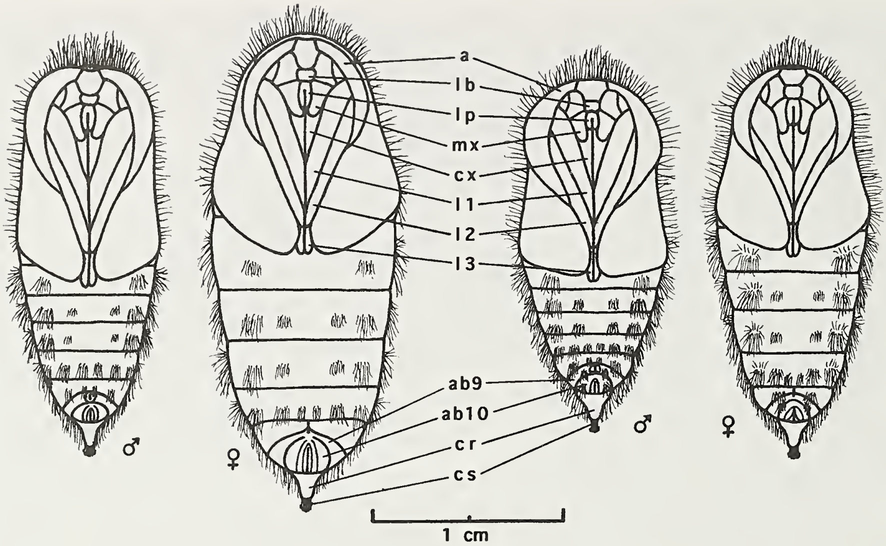

Fig. 1. Pupae of *Gynaephora groenlandica* (left) and *Gynaephora rossii* (right) in ventral view. Abbreviations: a = antenna, ab = abdominal segment, cr = cremaster, cs = cremastral setae, cx = coxa of the prothoracic leg, l1 = prothoracic leg, l2 = mesothoracic leg, l3 = metathoracic leg, lb = labrum, lp = labial palp, mx = maxilla.

erable air space between the layers. Outer layer ovoid, dimensions 32 ± 3 mm in length by 19 ± 2 mm in width (n = 279), comprised of a thin layer of silk with some larval hairs, cream colored to deep yellow or grey, depending on the number and relative proportions of black and yellow larval hairs incorporated and the extent of weathering. Inner layer oblong-ovoid, dimensions 28 ± 3 mm in length by 13 ± 1 mm in width (n = 279), comprised mainly of larval hairs tied together with silk and correspondingly deeper in color than the outer layer. Cocoons of females, with outer layer dimensions of 34 ± 3 mm by 20 ± 2 mm and inner layer dimensions of 30 ± 2 mm by 14 ± 1 mm (n = 124), significantly larger ($t_{(1)277} = 6.463$ for outer length, 3.576 for outer width, 12.970 for inner length, 9.770 for inner width; $P < 0.0005$ in all cases) than those of males, with outer layer dimensions of 31 ± 3 mm by 19 ± 2 mm and inner layer dimensions of 26 ± 2 mm by 13 ± 1 mm (n = 155).

***G. rossii*:** Cocoons constructed in a single layer roughly equivalent to the inner cocoon of *G. groenlandica*, oblong-ovoid, dimensions 26 ± 2 mm in length by 13 ± 1 mm in width (n = 56), comprised of a single layer of silk with many larval hairs incorporated, dark grey to light grey, depending on the extent of weathering. Cocoons of females, with dimensions of 27 ± 2 mm by 13 ± 1 mm (n = 17), significantly larger ($t_{(1)54} = 2.852$, $0.0025 < P < 0.005$ for length; $t_{(1)54} = 2.143$, $0.01 < P < 0.025$ for width) than those of males, with dimensions of 25 ± 2 mm by 12 ± 1 mm (n = 39).

Pupae. Pupae of both species (Fig. 1) reddish-brown, darkening to black as the pharate adult matures but often retaining some areas of reddish-brown cuticle, most notably along caudal margins of abdominal segments. Very hairy; hairs arising from scars of larval verrucae, brown to golden yellow and always simple, not plumose or spinulose. Dorsal hairs long, dense, and erect; ventral hairs much shorter, sparser, and recumbent. Labrum trapezoidal with rounded corners, caudal margin varying from straight to strongly concave. Maxillae short, slightly longer than labial palps; coxae of prothoracic legs distinctly visible caudad of maxillae. Prothoracic legs (excluding coxae) border on each other for about as long as length of maxillae. Antennae short, extending only about halfway to caudal margin of wings. Wingtips separated by ends of metathoracic legs. Ventral surface of abdominal segments 9 and 10 tapering steeply towards cremaster. Cremaster short and conical, somewhat flattened dorsoventrally, apex rounded and bearing a group of short, hooked setae.

***G. groenlandica*:** Pupae with dorsal hairs up to 4 mm in length and ventral hairs up to 2 mm in length. Hairs usually absent from ventral surface of abdominal segment 9 and always absent from ventral surface of abdominal segment 10. Maxillae usually curving mesad and often meeting beyond ends of labial palps. Ventral surface of cremaster with fine longitudinal grooves in females, less apparent in males. Female pupae, with dimensions of 24.0 ± 2.0 mm in length by 9.5 ± 0.5 mm in width (n = 3), significantly larger ($t_{(1)4} = 3.255$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 7.071$, $0.001 < P < 0.0025$ for width) than male pupae, with dimensions of 19.5 ± 1.0 mm in length by 7.5 ± 0.5 mm in width (n = 3).

***G. rossii*:** Pupae with dorsal hairs up to 3 mm in length and ventral hairs up to 1.5 mm in length. Hairs always present on ventral surface of abdominal segment 9 and usually present on ventral surface of abdominal segment 10. Maxillae roughly straight or slightly curved mesad but never meeting beyond ends of labial palps. Ventral surface of cremaster smooth. Female pupae, with dimensions of 19.0 ± 1.0 mm in length by 8.0 ± 0.5 mm in width (n = 2), larger than male pupae, with dimensions of 17.0 ± 1.0 mm in length by 7.0 ± 0.5 mm in width (n = 3), the difference statistically significant for length ($t_{(1)3} = 2.402$, $0.025 < P < 0.05$) but not for width ($t_{(1)3} = 2.049$, $0.05 < P < 0.10$), probably due, at least in part, to the small sample size.

Pupae of *G. groenlandica* generally larger than those of *G. rossii*, the difference being more pronounced for females ($t_{(1)3} = 3.349$, $0.01 < P < 0.025$ for length; $t_{(1)3} = 5.563$, $0.005 < P < 0.01$ for width) than for males ($t_{(1)4} = 3.545$, $0.01 < P < 0.025$ for length; $t_{(1)4} = 2.121$, $0.05 < P < 0.10$ for width). Considerable variation was seen among individuals in exact shapes and relative dimensions of morphological features, even in the small number of pupae examined in detail. Therefore, differences between species, as described above, were limited to those most consistent and clearly visible; nonetheless, these differences should be regarded with caution.

Differences between *G. groenlandica* and *G. rossii* in the immature stages are outlined in Table 1. Voucher specimens, including eggs, most larval

Table 1. Morphological differences between high arctic *Gynaephora* species in the immature stages. For measurements, the full range found in this study is given.

Stage **Morphological feature**	*G. groenlandica*	*G. rossii*
Eggs		
Diameter (mm)	1.55–1.70	1.35–1.45
Height (mm)	1.30–1.40	1.05–1.15
Larvae		
Head capsule width (mm)		
First instar	0.60–0.80	0.55–0.65
Second instar	0.90–1.05	0.75–0.90
Third instar	1.15–1.40	1.20–1.35
Fourth instar	1.50–2.00	ca. 1.75
Fifth instar	2.00–2.70	ca. 2.50
Sixth instar	2.70–3.60	2.90–4.15
Seventh instar	3.35–4.45	N/A[1]
Cuticle between verrucae		
First instar	black	pale
Second instar	black	paler than verrucae
All subsequent instars	black	black
Form of larval hairs		
First instar	all spinulose	all spinulose
Second instar	all spinulose	some plumose
All subsequent instars	all spinulose	many plumose
Color of larval hairs		
First instar	black and brown	uniformly grey
All subsequent instars	varying shades of brown with distinct dorsal tufts of black and yellow	longer plumose hairs grey, shorter hairs black and yellow
Cocoons		
Color	cream to deep yellow, occasionally grey	grey
Outer layer		
length (mm)	25–40	21–30
width (mm)	14–26	11–16
Inner layer		
length (mm)	19–35	N/A[1]
width (mm)	10–17	N/A[1]
Pupae		
Length (mm)	19.0–26.0	16.0–19.5
Width (mm)	7.5–9.5	7.0–8.0

[1] N/A = not applicable; these stages or structures do not occur in *G. rossii.*

instars, pupae, cocoons, and adults of both species, have been submitted to the Canadian National Collection of Insects, Ottawa, Ontario.

NATURAL HISTORY

Both species spin cocoons and pupate, adults emerge, mate, and lay eggs, and eggs hatch all within a single summer season lasting little more than two months; however, larval development is spread over a number of years with larvae overwintering in each stadium (Kukal & Kevan 1987; Morewood & Ring, submitted).

Fully grown larvae begin spinning cocoons very soon after becoming active in the spring. An exceptionally heavy snow accumulation in east-central Ellesmere Island during the winter of 1994–95, combined with a relative lack of wind, left the Alexandra Fiord lowland covered by a near-complete blanket of snow at the end of May. Judging by the extremely limited extent of snow-free ground and the subsequent rate of snowmelt, larvae found active upon our arrival 28.V.1995 could not have been active for more than a few days prior; however, some of these larvae had begun spinning cocoons as early as 29.V.1995. Cocoons may be completed within one day or may require two or three days for completion. Similarly, pupation may occur within one day of the cocoon being completed or may be delayed for two or three days. Pupal development, from pupation to adult emergence, of *G. groenlandica* required 15 ± 5 days (n = 53) in the field in 1995; only two *G. rossii* could be monitored for the complete period of pupal development and these required 10 and 16 days. The variation in time required for these developmental stages is due, at least in part, to variations in weather conditions, with cool and/or cloudy weather retarding activity and development.

Adults of both sexes have fully developed wings and males are strong fliers; however, females fly very little and when they do, scarcely get off the ground. Normally a female remains on her cocoon until she attracts a male and, once mated, will often lay a mass of eggs there (Plate 1A). Additional eggs are laid nearby on vegetation or on the ground, with no apparent discrimination among potential oviposition sites, and some females leave their cocoons even before laying their initial egg masses (Plate 1B). Of nine initial egg masses laid in the field in 1996, four were laid on cocoons whereas five were not. Eggs laid on cocoons are very conspicuous and suffer heavy predation by birds (Plate 1C), primarily snow buntings (*Plectrophenax nivalis* Linnaeus), by far the most abundant breeding birds at Alexandra Fiord (Freedman 1994). Of 39 egg masses found on cocoons during the summer of 1994, 26 showed signs of predation and a further 11 were completely removed before they could be protected with netting; only two egg masses were protected before apparently suffering any predation. In contrast, egg masses laid on the ground are quite cryptic (Plate 1D) and none of these egg masses were found to suffer any predation.

Embryonic development, as measured from the day that an initial egg mass was laid to the day that the first larvae eclosed, for *G. groenlandica* was 28 ± 5 days (n = 10) in the field in 1995; for *G. rossii* only one female was observed to lay an egg mass in the field and this required 31 days to begin hatching. Upon hatching, neonates usually eat a portion, often most but rarely all, of the chorion from which they emerged.

With the exception of neonates, larvae of *G. groenlandica* are active for only a relatively short portion of the growing season, after which they spin hibernacula and become dormant until the following spring. Regular surveys, combined with incidental observations, indicated that the bulk of the larval population was active only until the third week of June in 1994, the fourth week of June in 1995, and the second week of July in 1996 due to a very late and prolonged snowmelt. Very few *G. groenlandica* larvae were found active on the tundra after 1.VII.94, 15.VII.95, and 19.VII.96, and none were found after 1.VIII.94, 31.VII.95, and 4.VIII.96. In contrast, larvae of *G. rossii* remain active late in the growing season, with active larvae observed regularly on the tundra until and including 15.VIII.94, 17.VIII.95, and 13.VIII.96, our last days of fieldwork each year. In all three years, with the exception of fully grown larvae that were spinning cocoons in June, more *G. rossii* larvae were found active in August than in June and July combined.

Gynaephora larvae were observed feeding on 11 different species of plants, representing seven different plant families (Table 2). For *G. groenlandica*, *Salix arctica* represented 87% of the feeding observations, most of these being buds and expanding leaves, with *Dryas integrifolia* representing 7%, *Saxifraga oppositifolia* representing 3%, and the remainder represented by single or very few observations. The few feeding observations for *G. rossii* were almost evenly split between *S. arctica* and *D. integrifolia*, with a single observation of a larva feeding on developing fruits of *Cassiope tetragona* on the tundra (Table 2).

Hibernacula of *Gynaephora* larvae are spun with silk, much like pupal cocoons except that no larval hairs are incorporated and the structure consists of a single layer in both species. Larvae that are confined within enclosures on the tundra generally spin hibernacula in clumps of vegetation or in litter and incorporate litter into the structure, making it extremely cryptic. Such hibernacula are rarely found on the open tundra, probably due to their cryptic nature; however, hibernacula are commonly found beneath or between loosely piled rocks (Plate 3F).

Larvae and cocoons of *Gynaephora* generally may be handled with impunity; however, the larval hairs can cause skin irritation. Extensive work dissecting parasitoid-killed larvae or tearing open cocoons, which contain larval hairs, resulted in small (1–2 mm diameter) itchy blisters, particularly on the sensitive skin between the fingers, and these blisters persisted for many days.

DISCUSSION

Identification of Immature Stages

Confusion concerning identification of immature stages of North American *Gynaephora* species dates back to the original description of *G. rossii.* Curtis (1835) described an adult male in some detail and provided a color illustration that leaves no doubt that the species was *G. rossii.* In contrast, his descriptions of immature stages were rather cursory; however, the "two tufts of black hair on the back [of the caterpillar], followed by two of orange" are unmistakably those of *G. groenlandica.* His description of the cocoons is unfortunately too generalized to assign to either species. The original description of *G. groenlandica,* on the other hand, includes a mention of "the characteristic *Dasychira*-caterpillar hairtufts on the back and the *end segment*" (emphasis added) typical of the larvae of this species (Homeyer

Table 2. Plants on which *Gynaephora* larvae were observed feeding at Alexandra Fiord, Ellesmere Island, during the spring and summer of 1995 and 1996.

Plant species	**Number of observations**	
Part eaten	***G. groenlandica***	***G. rossii***
Salix arctica Pallas (Salicaceae)		
Buds (unopened)	99	0
Expanding leaves	166	1
Developing catkins	48	0
Mature leaves	6	2
Senescent leaves	0	3
Dryas integrifolia M. Vahl (Rosaceae)		
Leaves	24	5
Flower petals	1	0
Saxifraga oppositifolia Linnaeus (Saxifragaceae)		
Flowers	9	0
Leaves	3	0
Oxyria digyna (Linnaeus) Hill (Polygonaceae)		
Leaves	1	0
Arctagrostis latifolia (R. Brown) Grisebach (Gramineae)		
Leaves	1	0
Festuca brachyphylla Schultes (Gramineae)		
New shoots	1	0
Luzula confusa Lindeberg (Juncaceae)		
Leaves	2	0
Flower head	1	0
Luzula arctica Blytt (Juncaceae)		
Leaves	1	0
Flower stalk	1	0
Potentilla hyparctica Malte (Rosaceae)		
Flower	1	0
Vaccinium uliginosum Linnaeus (Ericaceae)		
Leaves	1	0
Cassiope tetragona (Linnaeus) D. Don (Ericaceae)		
Developing fruits[1]	0	1
Total number of observations	**366**	**12**

[1] Developing fruits were also accepted as food by *G. rossii* larvae held in the laboratory; foliage and mature fruits were not.

1874). Packard (1877) described all stages of what he thought was *G. rossii*, based on specimens collected in northern Greenland. These descriptions are fairly accurate for *G. groenlandica* and Packard himself noted that the adults differed from the description of *G. rossii* given by Curtis (1835) in that their hind wings had no "broad, blackish margin," which is perhaps the most obvious difference between adults of *G. groenlandica* and *G. rossii* (cf. Plate 1 in Ferguson 1978). The brief descriptions published by Scudder et al. (1879) as representing *G. rossii* are inadequate for identification of the species; however, they did note that the original "description of the larva does not well accord with the present specimen." It may be that neither Packard (1877) nor Scudder et al. (1879) knew of *G. groenlandica*, considering that the description of this species was published in 1874 in Germany and therefore may not have been available to them.

As early as 1875, *G. rossii* had been found above treeline on Mount Washington, New Hampshire, and recognized as the same species as had been described from the Arctic (Grote 1876). Later, Dyar (1896) described larvae from the same locality and noted that they differed from the descriptions published by both Curtis (1835) and Packard (1877). The following year, he received larvae from Greenland that agreed with Curtis' description, obtained an adult *G. groenlandica* from one of them, and concluded that "Curtis must have mixed the species" (Dyar 1897).

Despite Dyar's conclusion and his fairly detailed descriptions of the larvae of *G. rossii* (Dyar 1896) and *G. groenlandica* (Dyar 1897), misidentifications and confusing information may be found in much more recent published literature, as noted in the introduction to this paper. In addition, Ryan (1977) and Ryan and Hergert (1977) presented a photograph of a number of specimens from Truelove Lowland, Devon Island, that included both species of *Gynaephora*, but the adults were not shown associated with their cocoons. Both "light and dark color cocoons" were illustrated and Ryan and Hergert (1977) stated that "both forms [were] found with each species"; however, they made no mention of the structure of the cocoons and submitted only a single specimen (a *G. groenlandica* female with the cocoon from which it emerged) to the Canadian National Collection of Insects. As described above, cocoons of both species may be light or dark in color, depending on the extent to which larval hairs of different colors are incorporated into the cocoon and the extent to which the cocoons are weathered, but the structure of the cocoon is species-specific. Descriptions of larvae provided by Ferguson (1978) are accurate, even though they were based on extremely limited material; however, they may give the impression that the differences between the two species are rather subtle when in fact these differences produce a distinctive appearance for each species that is discernible even from a distance.

Pupae of *G. groenlandica* and *G. rossii* have not been described previously, but both species may be identified to genus using the key to genera provided by Patočka (1991). They also fit the generic description of *Gynaephora* pupae except that their antennae are apparently much shorter than those of the European species *Gynaephora selenitica* (Esper), as described and illustrated by Patočka (1991). The diagrams presented here (Fig. 1) are composites that attempt to illustrate "typical" pupae for both sexes of both North American species; however, a considerable amount of individual variation was seen, even among the small number of pupae examined. The only differences between species that were obvious and consistent were overall size and the length of hairs (which may be related to overall size), the presence or absence of hairs on the ventral surface of abdominal segments 9 and 10, and possibly the form (curved or relatively straight) of the maxillae.

It should be noted that the size differences between the two species may not be consistent across their entire range. In fact, the adults illustrated by Ferguson (1978) clearly show that *G. rossii* may be larger than *G. groenlandica* from different localities. The fact that *G. rossii* were found to be consistently smaller than *G. groenlandica* in the current study may reflect the fact that this population of *G. rossii* is in the extreme northern portion of the species' range whereas Alexandra Fiord is more central in the distribution of *G. groenlandica*.

Despite the confusion that is apparent in the literature, most of the immature stages of arctic *Gynaephora* species can be identified to species quite readily and with little more than a cursory examination. The occasional lack of grey plumose hairs in *G. rossii* larvae may cause some confusion and may be responsible for a report of "morphs intermediate between the two ... species" (Kukal 1994), although the supposed intermediate morphs were not described in that report. The species may be reliably separated by differences in the patterns of black and yellow hairtufts and the much longer overall hairs of *G. groenlandica*. Furthermore, there is strong evidence that they are reproductively isolated at the level of mate recognition and therefore do not produce hybrids (Morewood, submitted). We hope that the descriptions and illustrations provided here will help to prevent future misidentifications.

Natural History

Gynaephora species are among the most conspicuous insects on the high arctic tundra and observations on their natural history have been recorded ever since the early arctic expeditions of European explorers. The first comprehensive study of *G. groenlandica* was conducted by Kukal (1984) and later published by Kukal and Kevan (1987). That study provided a significant advance in knowledge of the natural history of this species; however, it did contain some gaps and inaccuracies due, in part, to the fact that it was conducted during a single summer season (see also Morewood & Ring, submitted).

Kukal and Kevan (1987) identified mortality factors and estimated mortality rates for most of the life stages of *G. groenlandica*; however, the only mortality factor they identified for eggs was "inviability." With respect to eggs, their study included only "six females observed in nature [which] remained on their cocoons and deposited all of their eggs there" and they concluded that the "eggs hatched within several days of their deposition" without presenting any relevant data (Kukal & Kevan 1987). They apparently found no other eggs masses in the field and this may be due to the facts that eggs are often laid after the female has left her cocoon, such eggs are extremely cryptic, and egg masses laid on cocoons are extremely vulnerable to predation by birds. Egg masses on cocoons are likely to be removed before they are found and, considering the rate of predation recorded in 1994, it seems likely that very few eggs laid on cocoons would escape predation long enough to hatch.

It has been known for some time that larvae of *G. groenlandica* limit their activity to the early part of the growing season (Kukal & Kevan 1987). In contrast, the fact that larvae of *G. rossii* are active late in the growing season has not been reported previously from the Arctic, although Schaeffer and

Castrovillo (1979) reported larvae of *G. rossii* to be active and feeding in September on both Mt. Katahdin, Maine, and Mt. Daisetsu, Japan. This contrast in seasonal activity may have significant consequences for the respective life cycles of the two species and there are indications that it is consistent across the Canadian Arctic. We collected *Gynaephora* larvae in the vicinity of the Muskox River on north-central Banks Island in early August of 1993 and this collection consisted of approximately two dozen larvae of *G. rossii* but only a single larva of *G. groenlandica.* In addition, researchers working on the Fosheim Peninsula of west-central Ellesmere Island in 1996 observed larvae of *G. groenlandica* in abundance in late June and early July but larvae of *G. rossii* only in early August (A. Lewkowicz, Department of Geography, University of Ottawa, pers. comm.).

Larvae of *Gynaephora* are clearly opportunistic feeders, accepting a wide variety of plant species as food, but do show definite preferences in their choice of foodplants. Curtis (1835) originally reported that larvae of *G. groenlandica* (reported as *G. rossii*) fed mostly on *Saxifraga tricuspidata* Rottböll and *S. oppositifolia,* but the preference of this species for *Salix* has since been noted repeatedly (Wolff 1964, Kukal & Kevan 1987, Kukal & Dawson 1989). The relatively few feeding observations for *G. rossii* in this study probably underestimate the variety of plants that these larvae actually eat, even at Alexandra Fiord. This widely distributed species has been reported to feed on many different plants, ranging from sedges to broad-leaf trees (Schaefer & Castrovillo 1979 and references cited therein) and it has been suggested that some isolated alpine populations show preferences for ericaceous plants, which predominate in alpine habitats (Schaefer & Castrovillo 1979).

One of the hypotheses proposed to explain why larvae of *G. groenlandica* cease feeding and become dormant so early in the growing season is that they restrict their feeding activity to the early portion of the season when the available food has the greatest nutritional value and become dormant when the benefits of continued feeding on foodplants of declining quality are outweighed by the metabolic costs of remaining active (Kukal & Dawson 1989). This hypothesis is supported by observations that larvae of *G. groenlandica* feed primarily on buds, expanding leaves, and developing catkins of *S. arctica* (Kukal & Dawson 1989; this study), a food source that rapidly declines in nutritional value as the leaves and catkins mature (Kukal & Dawson 1989, Dawson & Bliss 1993, Klein & Bay 1994). This may be considered an adaptation of this species for making the most efficient use of available food sources, given the constraints of the high arctic environment to which it is endemic. In contrast, larvae of *G. rossii* remain active late in the growing season and appear to be less particular about seeking out food sources of maximal nutritional value; however, the fact that *G. rossii* larvae consumed developing fruits, but not foliage or mature fruits, of *C. tetragona* suggests a similar selection of optimal food sources available later in the summer.

The distinct double-layered structure of the cocoons of *G. groenlandica* may again represent an adaptation to its high arctic environment, allowing the crucial life stages of pupation and reproduction to be completed within the very short growing season. These cocoons are thought to act as "microgreenhouses" and temperatures within them have been shown to be higher than both ambient temperatures and surrounding substrate temperatures (Kevan et al. 1982, Kukal 1984). Furthermore, it has been recently reported that cocoons of *G. groenlandica* significantly enhance the rate of pupal development but that those of *G. rossii* do not (Lyon & Cartar 1996). The similar pupal development times in both species found at Alexandra Fiord might be accounted for by the difference in size of pupae of the two species at this site. Without a development-enhancing cocoon like that of *G. groenlandica*, a decrease in size of *G. rossii* in the northern portion of its range may be necessary for this species to complete pupal development quickly enough to reproduce and still leave time for the resulting eggs to hatch before winter closes in.

In a recently published study of hibernacula and winter mortality, Kukal (1995) apparently contradicts her previous assertion (Kukal, Serianni & Duman 1988, Kukal & Dawson 1989, Kukal 1990, 1991, 1993, Danks et al. 1994) that larvae of *G. groenlandica* move down close to the permafrost when they become dormant in early summer. It is noteworthy that within at least some of the cages used for that study, there were deep crevices in the tundra but the larvae chose to remain on the surface and construct their hibernacula in the vegetation and litter. The significance of this is that, although it may be argued that *G. groenlandica* larvae undergo "voluntary hypothermia" by virtue of the fact that they no longer thermoregulate by basking (cf. Kukal, Heinrich & Duman 1988), temperatures within such hibernacula track ambient temperatures fairly closely (Kukal 1995). Ground-level temperatures, both ambient and within hibernacula, often exceed 20°C and even approach 30°C during sunny weather (Morewood, unpub. data). Metabolism of poikilothermic organisms in general is directly related to temperature and this has been shown experimentally for larvae of *G. groenlandica* (Kukal & Dawson 1989). The hypothesis that larvae of *G. groenlandica* move close to the permafrost where "the larval body temperatures range between 0–5°C" (Kukal 1990) and thus reduce maintenance metabolism and conserve energy reserves during their summer dormancy (Kukal 1990, 1991, 1993, Danks et al. 1994) must be re-evaluated in the light of more recent discoveries regarding the location of, and temperature conditions in, larval hibernacula.

Finally, the urticating nature of the larval hairs of *Gynaephora* has not been reported in previously published literature but has been experienced by other fieldworkers and may be much more severe than the small itchy blisters recorded in this study. Reactions experienced by other researchers working with *Gynaephora* in the field include large blisters covering most of the hands and extensive swelling and itching of the hands (B. Lyon, Department of Biological Sciences, University of Calgary, pers. comm.). It is not known whether there is any chemical basis for these urticating properties and it may be that the irritation is a simply mechanical effect of the barbed hairs, as has been reported for the similar, although not closely-related, larvae of *Lophocampa argentata* (Packard) (Arctiidae) (Silver 1958). As noted above, the severity of reported reactions to *Gynaephora* varies widely among different individuals and therefore researchers who plan extensive work involving exposure to the larval hairs would be well-advised to exercise caution.

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Notes on *Boloria pales yangi*, ssp. nov., a remarkable disjunction in butterfly biogeography (Lepidoptera: Nymphalidae)

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Abstract. A population of *Boloria pales* (Denis & Schiffermüller) was found at an alpine area in Taiwan, far away from the nearest population in western China and farther south than any previous record of the genus *Boloria*. The taxon is considered a new subspecies and is described herein.

Key Words. *Boloria pales*, disjunction, biogeography, Taiwan, China

INTRODUCTION

The genus *Boloria* (sensu Scott 1986, D'Abrera 1992) is composed of approximately 30 species of small nymphalids favoring either damp and wet habitats or rocky slopes (Shepard 1975), distributed in boreal and arctic parts of the Holarctic region. The recognized southernmost limit of this genus was 30° N for *B. pales* (Denis & Schiffermüller) in the Palaearctic (BMNH specimens) and 35° N for *B. chariclea* (Esper) in the Nearctic (Scott 1986).

Two male specimens of this genus were collected by Prof. C.T. Yang from an alpine area in the central part of Taiwan at approximately 24° N. These specimens represent the first record of *Boloria* outside the Holarctic, and are herein classified as a subspecies of *B. pales* (Denis & Schiffermüller). This discovery is significant for three reasons: 1) This is unquestionably the southernmost record for the genus and the first record of *Boloria,* a typical Holarctic genus, in the Oriental region. 2) The closest *B. pales* colony to Taiwan is found in the Sichuan province of western China, about 2000 km distant (Fig. 1). This large disjunction suggests that the Taiwan population is a relict left from a glacial period of the Pleistocene. 3) It is striking that such a unique species has been found in a well-collected island.

The specimens from Taiwan most closely resemble *B. pales palina* Fruhstorfer in western China, but has distinctive characters on wing patterns and male genitalia. We describe these specimens as a new subspecies here.

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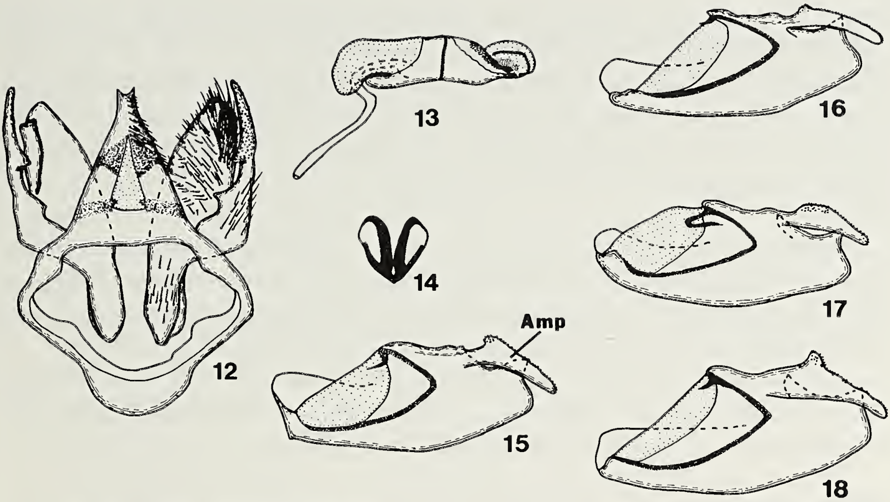
Fig. 1. Known geographical distribution of *Boloria pales* in East Asia and neighboring areas; squares denote confirmed sites from specimens examined from BMNH, NCU, and NTU; circles represent province records based on BMNH specimens.

Boloria pales* subspecies *yangi Hsu & Yen, **ssp. nov.** (Figs. 2, 3, 12–15)

Male. Forewing length 18.0 mm (n = 2). Head: hairy, covered with buff orange hairs on vertex and frons. Eyes semi-oval, naked. Labial palpus hairy, porrect, pointed, yellow proximally, buff orange distally. Thorax: black, covered with pale buff orange hairs. Legs hairy, buff orange. Forewing: termen slightly concave. 12 veins, R1 independent, other R veins all extending from Rs. M2 slightly bent toward M1; base of M3 strongly curved posteriorly. Upperside color pale buff orange with pale black markings. Six black, round postdiscal spots with posterior three indented. Submarginal spot black, prominent, fused with postdiscal spot series anteriorly. Marginal markings obscure. Discal spots prominent, wider than postdiscal spots. Black markings in discoidal cell composed of a distal bar, a medial bar, and two proximal dots. Basal area covered by extensive pale black scaling. Underside pale buff with pale black markings. Cinnamon-rufous bar edged by creamy yellow patches present near apex. Fringe uniformly orange. Hindwing: nine veins, all separate. M3 bent near base. Humeral vein a short bar, perpendicular to Sc + R1. Upperside pale buff orange with pale black markings. Six round postdiscal spots arranged into an arch. Submarginal spot series prominent, triangular. Marginal markings more prominent than forewing. Discal spots narrow. Basal area with extensive pale black scaling extending distally covering distal end of discoidal cell and discal band in

Figs. 2–11. *Boloria* specimens. 2–9: *Boloria pales* from various geographical regions. 2, 3) Taiwan; 4, 5) Sichuan, western China; 6, 7) Kazakhstan; 8, 9) Southwestern France. 10, 11) *Boloria napaea* from Switzerland.



Figs. 12–18. Male genitalia of *Boloria* specimens. 12–15: *Boloria pales yangi* Hsu & Yen. 12) Tegumen + valvae, dorsal view; 13) Phallus, lateral view; 14) Juxta, posterior view; 15) Left valva. 16–18: Left valva of *Boloria pales* from various geographical regions. 16) Sichuan, western China; 17) Kazakhstan; 18) southwestern France. "Amp" denotes ampulla.

Cu cells. Underside coloration variegated. Basal area cinnamon-rufous surrounded by three silvery white lunules. Single prominent silvery white dot present at base of cell Cu2; another small silvery white dot in discoidal cell. Discal area forming a tawny band unevenly delimited distad by short black lines. Yellow scalings present in anterior part of discal band. Postdiscal area pale cinnamon-rufous with a series of amber-colored round spots. Silvery white lunules present distally in cell Sc + R1, Rs, and Cu2. Extensive yellow scaling present in cell M3 and posterior edge of cell M2. Marginal spots silvery white edged proximally by amber-colored scalings. Fringe uniformly orange. Abdomen: Black covered with pale buff orange hairs, ventrally with extensive pale yellow scaling toward distal end. Genitalia (Figs. 12–15): Sclerites of 9th + 10th segments ring-shaped with a medial triangular membranous area dorsad. Uncus narrow, elongate, bifurcate distally. Saccus broad, short. Valva broad, somewhat rectangular in shape; ampulla elongate with minute teeth dorsad, forming downcurved arm with a wart-like dorsal process at basal ¼; harpe simple, setose, with distal end nearly straight; cucullus forming a prominent, densely setaceous triangular tooth dorso-distally. Phallus stout, short, with phallobase about as long as aedeagus. Distal end of vesica forming two vertical semicircular lobes; both lobes spinulose externally but asymmetrically. Bulbus ejaculatorius subterminal. Juxta forming thin, flat lobe with deep dorsal cleft mesad.

Female. Unknown.

Diagnosis. *B. pales yangi* Hsu & Yen is similar to *B. pales palina* Fruhstofer (Figs. 4, 5) of western China, but differs from it by the following characters: 1) discal spots broader than postdiscal spots on forewing upperside,

2) fringe uniformly colored instead of checkered, 3) basal area of hindwing underside without yellow scaling.

Biology. Host plant and early stages in Taiwan unknown. Larvae of populations in Europe utilize *Viola* spp. (Violaceae) (Higgins & Riley 1983). According to Wang and Huang (1993), 15 *Viola* species are known to occur in Taiwan with six species found in the vicinity of the type locality of *B. pales yangi.*

Type data. Holotype: ♂, 24°15′N, 121°14′E. TAIWAN: [Taichung Hsien], Lishan, 10.V.1964. Coll. C.T. Yang; paratype: 1♂, same data as holotype. Both holotype and paratype deposited in the Insect Museum, National Chung-Hsin University, Taichung, Taiwan, R.O.C. (NCU).

Comparative material was from the collections of the Natural History Museum, London, U.K. (BMNH), Insect Museum, National Taiwan University, Taipei, Taiwan, R.O.C. (NTU), and NCU.

DISCUSSION

The population of *B. pales* in Taiwan appears more closely related to those in western China than to those in central Asia and Europe. Two possible synapomorphies shared by the specimens from Taiwan and western China are: 1) Reduced yellow scaling at basal area on hindwing underside (Figs. 3, 5); 2) ampulla of valva narrow with the dorsal process wart-like, present at basal ¼, abruptly narrowed down toward the base (Figs. 15, 16). The specimens of *B. pales* from central Asia (Figs. 6, 7) and Europe (Figs. 8, 9), as well as *B. napaea* (Hoffmannsegg) (Figs. 10, 11), the sister species of *B. pales,* all have extensive basal yellow scaling on hindwing underside (Figs. 7, 9, 11) and a robust ampulla on which a large dorsal process is present at basal ½ and attenuates toward the base (Figs. 17, 18; for *B. napaea* see Higgins 1975).

Acknowledgements. We thank Chung-Tu Yang and Cheng-Tse Yang (NCU) for permission to examine the material deposited in NCU. We are grateful to Philip R. Ackery of Natural History Museum, London, Robert Alexis of Belgium, and Iv Bereznoi of Russia for assistance on material from other regions. We also thank Raina Takumi, University of California, Berkeley for reading the manuscript.

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Yania gen. nov. and *Yania sinica* sp. nov. from Sichuan, China (Lepidoptera: Hesperiidae)

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Abstract. *Yania* gen. nov. and *Yania sinica* sp. nov. (Hesperiidae) are described from Sichuan, China. *Yania* can be placed in the *Ancistroides* group of the Hesperiidae and can be distinguished from all the known genera of this group by the following combination of characters: 1) club of antennae very gradually marked, 2) both wings with vein 5 nearer to vein 4 than to vein 6, 3) without secondary sexual characters, 4) forewing with vein 2 nearer to wing-base than to vein 3, 5) male genitalia with uncus deeply bifid, uncus longer than tegumen, and 6) the clasp a very simple structure.

The new species described here was recognized when I sorted the butterflies I collected from Qingchenshan, Sichuan during the summer of 1991. Most specimens from the Qingchenshan Mountains were somewhat damaged when captured or when spread. Consequently, the unique holotype of this new species lost its labial palpi and the antennae are broken at the tip (one broken below the apiculus). However, its wing venation, genital structure, and other features indicate that it belongs to a new genus.

Yania Huang, **new genus**

Type species *Yania sinica* Huang

Male

Antennae. Half as long as costa; club very gradually marked, not constricted before apiculus.

Body. Thin, weak; abdomen slightly longer than dorsum of hindwing.

Forewing. No prominent hyaline spots. Dorsum quite longer than termin. Vein 2 arising before the origin of vein 11 and nearer to wing-base than to the origin of vein 3. Vein 5 slightly closer to vein 4 than to vein 6 at its origin. Vein 11 originates midway between veins 10 and 12.

Hindwing. Costa slightly longer than dorsum. Discocellular cell slightly shorter than half the length of hindwing. Vein 7 arising beyond the origin of vein 2. Vein 5 well defined, not oblique and very slightly closer to vein 4 than to vein 6 at origin.

Secondary sexual characters. Absent.

Male genitalia. Uncus much longer than tegumen and deeply bifid. Gnathos slightly shorter than uncus. Saccus significantly longer than

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tegumen and sharply pointed at tip. Clasp very simple in structure, without a style from valva or harpe.

Etymology. The name *Yania* is a feminine noun based upon the given name of my younger sister, Yan Huang.

Yania sinica Huang, **new species** (Figs. 1–6)

Male. Eyes smooth and blackish brown when dried. Frons nearly twice as wide as eye, densely clad with black hairs mixed with some yellow.

Labial palpus. Unknown (both palpi missing from the holotype).

Antennae. 9.5 mm long (about half the length of forewing); club weakly and gradually marked, segments becoming broader on apical ⅓ of antennae with the thickest portion only twice as thick as shaft; club densely clad with blackish scales as well as shaft on upperside, but with pale yellow scales on underside in contrast with shaft; number of nudum segments in the apiculus unknown as the apiculus is broken at the tip, the remaining nudum segments all in bent-over portion of club, and club not constricted before apiculus (Fig. 3).

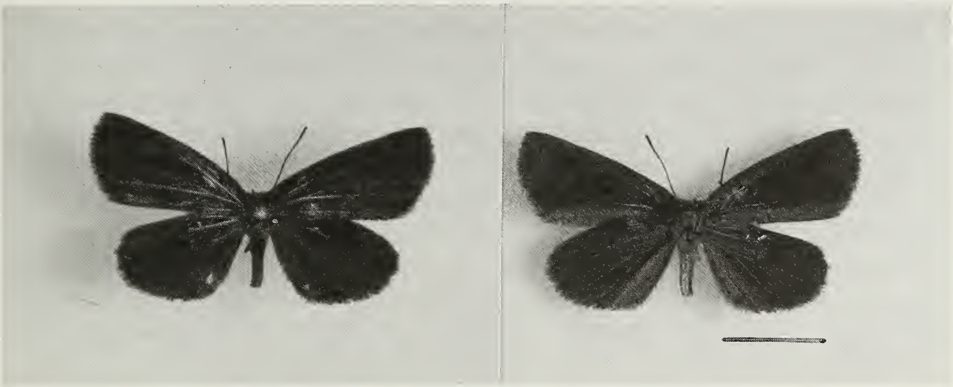
Thorax. Clad with darker brown scales and scattered long yellow hairs.

Abdomen. Thin and weak, slightly longer than dorsum of hindwing, densely clad with dark brown scales above, but with longer yellow and brown scales beneath mixed with scattered yellow hairs.

Legs (Fig. 4). Densely covered with dark brown scales above, yellowish scales beneath; fore and mid femora not apparently clad with hairs, hind femora densely clad with long yellowish hairs beneath; tibial epiphysis reddish, wicker-leaf-shaped and somewhat distorted, nearly ⅓ times as wide as fore tibiae, originating from the basal ⅔ of fore tibiae and surrounded with long yellow and black scales; all tibiae without spines or hair-brushes, only sparsely clad with few long yellow hairs; mid tibiae with terminal pair of spurs which are densely clad with brown scales and blunt at tip, the inner one (just on the inside of tibiae) slightly longer than the outer: hind tibiae with two pairs of spurs, the upper pair somewhat shorter than the lower; all tarsi clad with three rows of reddish spines below, which are as long as the scales on tarsi, without any hairs; claws as in *Astictopterus jama.*

Wing markings. Ciliae of both wings on both sides dark brown, concolorous with ground color of wings. Upperside: Both wings unmarked, uniform dark brown in color, without secondary sexual characters. Veins not marked in color. Underside: Both wings ground color dark brown as on upperside, with a yellowish cast. Some veins thinly clad with yellow scales. Costal and apical areas of forewing and basal half of hindwing sparsely clad with scattered yellow scales. Posterior marginal areas of both wings somewhat paler than other areas in color, otherwise as upperside.

Wing shape and wing venation (Fig. 5). Forewing. Length: 19.5 mm. Dorsum quite longer than termin. Vein 2 much closer to wing base than to vein 3 at its origin. Vein 5 slightly closer to wing base than to vein 3 at its origin. Vein 5 slightly closer to vein 4 than to vein 6 at its origin. Vein 11 beyond



Figs. 1–2. *Yania sinica* ♂ holotype. 1) Left: upperside. 2) Right: underside. Scale 1 cm.

vein 2 at origin and about midway between veins 10 and 12. Hindwing. Costa slightly longer than either termin or dorsum. Vein 5 well marked, not oblique, very slightly closer to vein 4 than to vein 6 at its origin. Vein 7 midway between veins 2 and 3 at origin.

Male genitalia (Fig. 6). Uncus nearly twice as long as tegumen, deeply bifid in dorsal view, its two arms running parallel with each other. Gnathos significantly longer than tegumen, nearly as long as the uncus arms. Saccus also long and sharply pointed at tip in both dorsal and lateral views. Clasp nearly rectangular in shape, with distal margin nearly plain and flat, only bearing a small tooth in the middle, posterior angle well produced, with a sharply pointed process. Juxta as *Ancistroides nigrita.* Aedeagus nearly as long as clasp, without cornuti, its suprazonal portion nearly as long as subzonal portion.

Female. Unknown.

Type data. Holotype: ♂ (Figs. 1, 2). Qingchengshan, Sichuan, China, 1500m. 12.VII. 1991. Leg. H. Huang. Deposited in the Biological Laboratory of Qingdao Education College, Qingdao, Shandong Province, China.

DIAGNOSIS AND DISCUSSION

Yania clearly belongs in the subfamily Hesperiinae by exhibiting a hind tibia without erectile hair tufts, an abdomen without specialized scales, and a forewing lacking a costal fold. According to W.H. Evans (1949:2–4), Hesperiinae is composed of eight generic groups: *Heteropterus, Astictopterus, Isoteinon, Ancistroides, Plastigia, Hesperia, Taractrocera,* and *Gegenes. Yania* can be distinguished immediately from the *Hesperia, Taractrocera,* and *Gnegnes* groups by an antennal club that is not constricted before the apiculus and by a hindwing vein 5 that is well marked. *Yania* is differentiated from the *Heteropterus* group in having the hindwing cell less than half the wing length, antennae not short and legs normal (fore tibia with prominent epiphysis, mid tibia not spined, and hind tibia with prominent upper spurs). *Yania* is distinct from *Plastingia* with hindwing vein 5 closer to vein 4 than 6 and its wings not obviously produced. *Yania* differs from the *Isoateinon* group with the hindwing median vein not co-linear with vein 4 and vein 2 before the origin of vein 7. It would be difficult to infer to which of the remaining groups, *Astictopterus* or *Ancistroides, Yania* is most closely related since Evans only used the state of the second palpus segment — erect or porrect — as

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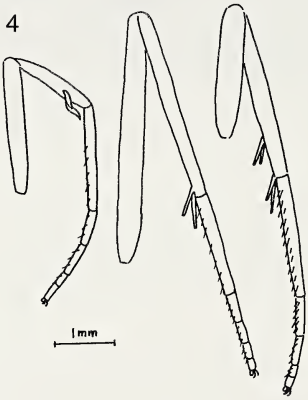

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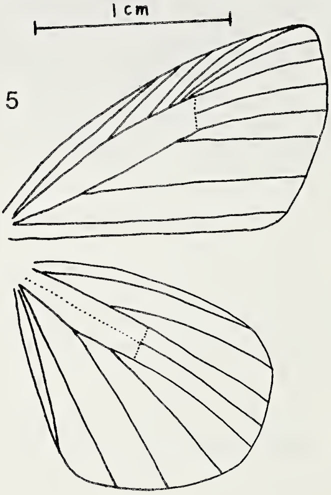

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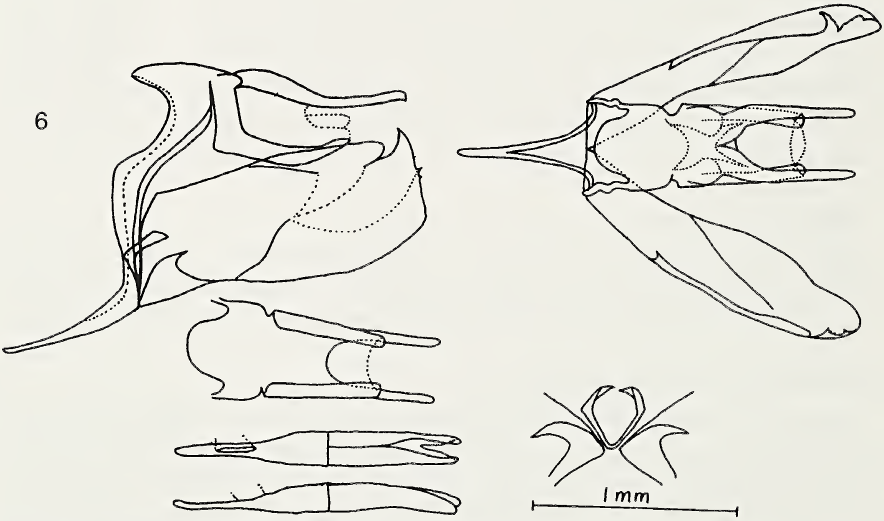

Fig. 3. Antennae of *Yania sinica.*

Fig. 4. Legs of *Yania sinica* (left to right): fore leg, mid leg, hind leg.

Fig. 5. Wing venation of *Yania sinica.*

Fig. 6. Male genitalia of *Yania sinica* consisting of lateral view of genital capsule with left valva and aedeagus removed; dorsal view of gential capsule with juxta and aedeagus removed; ventral view of gnathos and uncus; dorsal view of aedeagus; lateral view of aedeagus; and juxta in posterior view.

the key for separation (palps of the unique holotype of *Yania sinica* are missing). However, Eliot (in Corbet & Pendlebury 1992:363) questioned the taxonomic value of palpi and rearranged the Hesperinae accordingly. The *Astictopterus* group was suppressed, the *Ampittia* and *Hesperia* subgroups placed into the *Halpe* group, and the genera *Astictopterus* and *Arnetta* placed into the *Astictopterus* and *Plastingia* groups respectively. The latter rationale is provided by wing venation and male genitalic character states. The *Halpe* group differs from the *Ancistroides* group of Eliot (including *Astictopterus*) in that forewing vein 2 arises opposite or beyond the origin of vein 11 and the uncus of the male genitalia is broader in dorsal aspect. It follows then that *Yania* be placed in the *Ancistroides* group of Eliot which comprises eight Asian genera: *Iambrix, Idmon, Koruthaialos, Psolos, Astictopterus, Ancistroides, Notocrypta,* and *Udaspes.*

The phylogenic relationships between *Yania* and these eight genera are of interest. According to Eliot's key, mainly based on wing venation and wing markings, *Yania* can be distinguished from *Notocrypta* and *Udaspes* in the first dichotomy by a forewing without large hyaline spots; from *Iambrix, Idmon, Koruthaialos,* and *Psolos* in the second dichotomy by both wings having vein 5 downcurved at its origin and closer to vein 4 than vein 6; from *Astictopterus* in the third dichotomy by forewing vein 11 about midway between veins 10 and 12; leaving *Ancistroides* the closest allied genus to *Yania.* However, *Yania* shares other characters which appear as important as veins 5 and 11 for generic classification. These include body aspect and the hindwing dorsum shorter than the costa, which place *Yania* closest to *Astictopterus* and differing from the other seven genera. With the forewing vein 2 closer to the wing base than to vein 3 at its origin, *Yania* resembles *Notocrypta* and *Udaspes.* With regard to male genitalia the most important character for determination of generic classification appears to be the degree to which the clasp is specialized. Secondary characters are relative length of the uncus to the tegumen, length and shape of the gnathos, and least important the shape of the uncus. I propose this hierarchy from experience with treatment of the well defined subgeneric groups. Thus, within the *Halpe* group, all genera can clearly be placed into two subgroups by specialization of the clasp: the *Halpe* subgroup has the cuiller of the clasp longer and more complex (usually with heavy and branching teeth) than in the *Ampittia* subgroup.

Although the shape of the uncus is variable within related genera, the character is usually stable within a single genus. The relative length of the uncus to the tegumen is of greater supergeneric value than uncus shape alone. For example, the two closely related genera, *Iambrix* and *Idmon,* both have a long uncus, but in one the uncus tapers to a long point, in the other the uncus is deeply bifid. Accordingly, *Yania* resembles *Iambrix* and *Idmon* in male genitalia.

In the following key for separating genera of the *Ancistroides* group, I employ male genitalia as the main character. However, since the discovery of *Yania,* it is not possible to decide which vein — 2, 5, or 11 — is more important for inferring phylogeny. For this reason, the subgroups which Eliot (1992:37) divided the group have been disregarded.

KEY TO THE GENERA OF THE *ANCISTROIDES* GROUP

1 (6) Male genitalia with uncus substantially longer than tegumen. (Male clasp very simple in structure. Forewing vein 11 midway between veins 10 and 12.) .... (*Iambrix* subgroup)

2 (5) Forewing vein 5 midway between veins 4 and 6 at origin. Forewing vein 2 closer to vein 3 than wing base at origin. Male forewing usually without brand. Body robust.

3 (4) Male genitalia with uncus tapered to a long point. Underside hindwing with silvery-white spots. .... *Iambrix*

4 Male genitalia with uncus deeply bifid. .... *Idmon*

5 Both wings vein 5 slightly closer to vein 4 than 6. Forewing vein 2 closer to wing base than to vein 3 at origin. Male without brand. Body thin. .... *Yania*

6 Male genitalia with uncus slightly longer than tegumen.

7 (12) Forewing vein 11 midway between veins 10 and 12. Male clasp with cuiller not forked with harpe, or bearing a style from valva or from cuiller. .... (*Ancistroides* subgroup)

8 (11) Forewing vein 2 closer to wing base than to vein 3.

9 (10) Hindwing cell half wing length. Antennae longer than half length of forewing costa. Upperside hindwing unmarked. .... *Notocrypta*

10 Hindwing cell shorter than half the wing length. Antennae shorter than half length of forewing costa. Upperside hindwing with large white discal area. .... *Udaspes*

11 Forewing vein 2 closer to vein 3 than to wing base at origin. .... *Ancistroides*

12 Forewing vein 11 bowed toward or briefly touching or anastomosing with vein 12 and remote from vein 10. Male clasp with cuiller forked with harpe and without style from valva. .... (*Astictopterus* group)

13 (14) Both wings vein 5 slightly downcurved at origin, closer to vein 4 than 6. Male without secondary sex characters. Body weak. .... *Astictopterus*

14 Both wings vein 5 midway between veins 10 and 12. Males with secondary sex characters. Body robust.

15 (16) Forewing origin vein 4 midway between veins 3 and 5. .... *Koruthaialoa*

16 Forewing origin vein 4 closer to 5 than 3. .... *Psolos*

SUGGESTED PHYLOGENY

Yania appears to represent a mixture of all genera of the *Ancistroides* group, which I interpret to make it ancestral for the group. *Yania* shows more apparent primative characters than any other genus in the group: structure

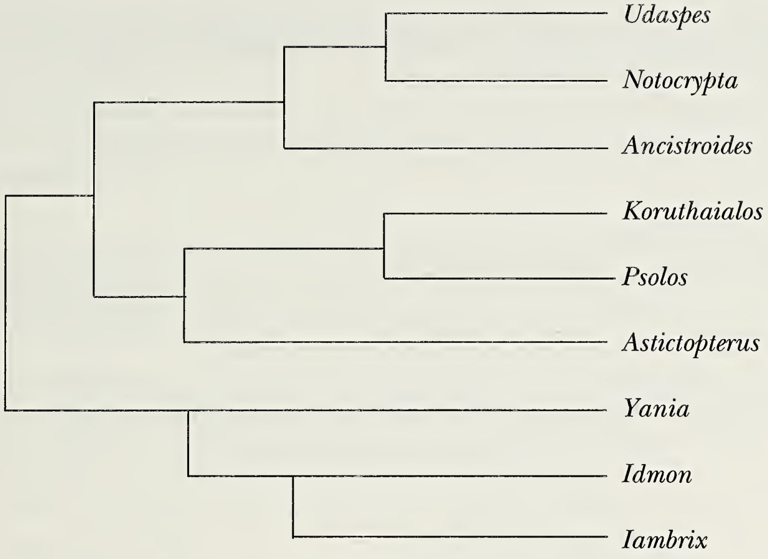

Fig. 7. Suggested phylogeny of *Ancistroides* group.

of the male genitalia is simple, veins 11 and 12 of the forewing are not joined, the antennal club is formed gradually, and secondary sex characters are absent. I lastly present the following hypothetical phylogenetic tree based on my intuitive evaluation of the selected diagnostic characters (Fig. 7).

Acknowledgments. I wish especially to thank two anonymous reviewers for suggestions that materially helped my presentation including substantive editing in English.

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Journal of Research on the Lepidoptera 34:154–160, 1995(1997)

A commentary on the recent book, Butterflies of Costa Rica and their natural history: vol. 2

"Books are not made to be believed, but to be subjected to inquiry"
— Umberto Eco

Although it was ordered and paid for in 1996, my copy of the new Costa Rican riodinid field guide (DeVries, P.J., 1997. Butterflies of Costa Rica and their natural history: vol. 2, Riodinidae. Princeton University Press, 288 pages, 25 plates; ISBN: 0-691-02890-7) arrived but a few weeks ago — a lag of over nine months. I've heard rumors that the delay was due to unforeseen technical difficulties stemming from the vagaries of the publishing business. But in America tardiness seems to be the corporate standard. As Fats Waller once philosophically opined, "you pays your money, and you takes your chances." But what of that. The book arrived and could now be perused in my spare moments.

A quick glance through the riodinid book revealed a similar layout to the previous volume. A further riffle showed what appeared to be a substantial consignment of information on riodinid butterflies, some technical photos, tables with numbers, and to my satisfaction, the color plates appeared to be useful for identifying riodinid specimens in the collection.

Carrying the volume to the study I pulled out a few specimens and compared them to the plates. I was pleased to find that the plates were adequate for this task. After identifying a number of specimens and writing the names carefully on individual labels I decided to read a little about one particularly odd looking species, *Syrmatia nyx,* on Plate 9. Great Scott!, I exclaimed, as my whiskey glass crashed to the floor and the dog yelped from its slumbers by the fire. Imagine my shock at finding that not only the facing plate for number 9, but indeed all of the facing plates were devoid of page numbers for the species accounts. I resolved to get to the bottom of this. Pouring myself another stiff whiskey to stem the tide of annoyance, and another for the dog to soothe its agitation, I mounted my inquiry by lunging to the index. There I found the answer I was looking for — page 165, and so turning to the proper page I read the information about the odd little *Syrmatia nyx.*

This archaic method of finding out information from the index was inconvenient, even if it did work for the odd little riodinid. This, however, did not solve the problem for all of the other species treated in the book. Something had to be done. Much to the exasperation of the dog's liver I set to work, and the epistle presented here was born after a good many whiskeys and words of opprobrium shouted into the night. That is to say, users of the new riodinid volume may find the following table useful; it provides the page numbers in the text for the species illustrated on the plates. The user can now annotate the page numbers directly on the facing plates in the book, as I have done on my copy. Furthermore, I have noted in **bold face** some errors or inconsistencies between the plates, the index, and the species accounts.

One hopes that my missive here will be useful to current book owners, and that the publisher will eventually correct these omissions in future editions of the book.

— Reginald B. Swinethrottle

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15) Theope herta, p. 246
16) Theope barea, p. 246
17) Theope barea, p. 246
18) Theope barea, p. 246
19) Theope acosma, p. 244
20) Theope acosma, p. 244
21) Theope decorata, p. 245 (should be **thestias decorata**)
22) Theope decorata, p. 245 (should be **thestias decorata**)
23) Theope eudocia, p. 244
24) Theope eudocia, p. 244

Plate 25

1) Metacharis onorata, p. 163 (should be **umbrata**)
2) Metacharis onorata, p. 163 (should be **umbrata**)
3) Theope guillaumei cecropia, p. 245
4) Theope lycaenina, p. 247
5) Theope lycaenina, p. 247
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7) Brachyglenis esthema, p. 157
8) Brachyglenis esthema, p. 157
9) Brachyglenis nr dodona, p. 158 (should be **nr dodone**)
10) Brachyglenis nr dodona, p. 158 (should be **nr dodone**)

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Manuscript format: At the time of initial submission, **two** copies *must* be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. If possible italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All **measurements** must be metric. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (e.g. 6.IV.1995). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

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COVER: Quino checkerspot butterfly, *Euphydryas editha quino*

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Differences in lifetime reproductive output and mating frequency of two female morphs of the sulfur butterfly, *Colias erate* (Lepidoptera: Pieridae)

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Abstract. Both female morphs of the sulfur butterfly *Colias erate* were captured in the field and dissected to investigate whether differences of reproductive output are affected by mating frequency between them. Lifetime mating frequency of the yellow morph was significantly lower than that of alba. In every female the immature egg load decreased with age. During their life span the monandrous yellow morph laid about 550 eggs, with the monandrous alba producting about 400 eggs. Polyandrous alba laid more eggs than either the monandrous or polyandrous yellow morphs. Thus, multiple mating is important for alba to increase its reproductive output, supporting the field observation that alba effectively attracts males.

INTRODUCTION

Some butterfly species show wing color polymorphism, such as *Papilio polytes* (Watanabe 1979, Uesugi 1992) and *Lycaena phlaeas* (Brakefield & Shreeve 1992). Komai and Ae (1953) reported that the Japanese sulfur butterfly, *Colias erate*, exhibits a sex-limited wing color dimorphism in females with yellow (ancestral) and white (alba) morphs. Both morphs occur sympatrically although the yellow morph is never more abundant than alba (e.g., Watanabe & Nakanishi 1996), unlike most American *Colias* species. Gilchrist and Rutowski (1986) explained the adaptive significance of alba from the viewpoint of reproductive success.

Emmel (1972) hypothesized that female-limited dimorphism is balanced by differential mate selection by males. Ley and Watt (1989) studied female limited dimorphism and concluded that the dimorphism is balanced by differential predation on the morphs. The persistence of the two morphs in time, however, suggests that they are equally fit. Other studies on *C. erate* (e.g., Watanabe et al. 1997) demonstrated a higher frequency of mate attraction by the alba morph which would give them a fitness advantage. The latter observation predicts that the yellow morph must have a compensatory advantage beyond mating that equalizes their lifetime fitness. Mating behavior of female morphs has been reported for some *Colias* species in America (e.g., Gilchrist & Rutowski 1986, Graham et al. 1980). Our study focuses on the lifetime reproductive success of the two morphs.

Recent studies have shown that female butterflies may engage in polyan-

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dry to obtain sperm and/or nutrients that are ejaculated from males (e.g., Boggs & Gilbert 1979). When a mated female accepts subsequent males the last male's sperm has precedence (e.g., Watanabe 1988). In *C. erate* Watanabe & Nakanishi (1996) pointed out that females are polyandrous. However, there is no report on the lifetime reproductive success of the two morphs of this species from the viewpoint of female polyandry. In this paper, we examine how frequently females in the field mated during their life span, and then estimated the fecundity for each morph.

MATERIALS AND METHODS

The data were obtained mainly from the summer generations of *C. erate* in Shirouma of Nagano Prefecture, which is located in a cool temperate zone of Japan. The details of the study area have been described elsewhere (e.g., Watanabe & Nakanishi 1996). The habitat consisted of rice fields and five ski slopes where nectar sources and larval food plants were abundant.

We collected females engaged in various activities including feeding, roosting, flying, copulating and ovipositing on calm sunny days from late July through mid-August of 1989 to 1994 (n=34 days). When females were captured, their abdomens were amputated and immersed in 50% ethyl alcohol. Forewing length of each was also recorded. The age of each female was estimated mainly by wing wear condition, and rated among 1 to 5 age classes (Watanabe & Nakanishi 1996).

Thirty seven *C. erate* larvae (mainly 3rd to 5th instar) were collected on a ski slope during late June 1993. They were reared on clover at 25 °C in the laboratory (16L/8D). All pupated and eclosed; 22 out of 37 were female. Immediately after emergence, their abdomens were amputated and immersed in 50% ethyl alcohol. All abdomens were dissected and examined for male spermatophores in the bursa copulatrix. Eggs in the ovaries were also counted and classified into three groups (mature, submature and immature), as has been done with the other pierid butterflies (Ando & Watanabe 1992, 1993, Watanabe & Ando 1993, 1994). Most statistical comparisons were done with a Mann-Whitney U-test, except for the Kendall test on mating frequency in relation to age.

RESULTS

Females immediately after emergence

No diseased individuals or parasitic wasps were noted in the 37 field captured larvae. Among the 22 females of the 37 emergences, the size was not significantly different for the two morphs (Table 1). Females of both morphs carried more than 750 immature eggs and 40 submature eggs. No mature eggs were found in either morph. Therefore, if no more immature eggs were added during her life span, as in *Pieris rapae* (Watanabe & Ando 1993), the fecundity of *C. erate* females would be about 800 for either morphs. Since adult size and fecundity are largely dependent upon the quality and quantity of food during the larval stage, we assume that each larva had consumed similar quantities of food.

Of 474 albas captured in the field, 5 were virgin, while we found no virgin yellow morphs. Such virgin albas were considered freshly eclosed. Table

Table 1. Fecundity and size for two morphs of female *C. erate* at emergence reared in the laboratory, comparing those of field-captured alba having no spermatophore (±SD).

	Yellow	Alba	Field-captured virgin alba
Number of females	6	16	5
Forewing length (mm)	29.8±1.52	30.0±1.34	29.4±1.33
Number of immature eggs	794.2±93.57	766.8±41.87	688.8±188.82
Number of submature eggs	40.3±6.11	37.8±8.66	99.2±78.32
Number of mature eggs	0.0±0.00	0.0±0.00	3.8±5.02
Total number of eggs	821.0±209.22	795.6±178.55	791.8±253.11

Table 2. Forewing length for two morphs of female *C. erate* captured in the field (mm ± SD).

	Age class	Alba	Yellow	Mann-Whitney U-test
Monandrous	I	29.5±0.97(139)	29.4±1.16(43)	U=96.5, n.s.
	II	29.7±1.59(79)	29.1±1.31(25)	U=86.0, n.s.
	III	29.4±1.94(48)	29.0±1.69(19)	U=16.0, n.s.
	IV	30.0±1.35(9)	29.1±2.86(4)	U=7.0, n.s.
	V	30.2 (1)	28.8±0.77(3)	U=11.0, n.s.
Polyandrous	I	29.6±1.81(19)	30.3±1.44(5)	U=9.0, n.s.
	II	29.5±1.38(31)	29.7±0.96(12)	U=43.5, n.s.
	III	30.5±1.31(55)	29.9±1.49(30)	U=142.0, n.s.
	IV	29.6±1.51(48)	30.3±0.48(14)	U=18.0, n.s.
	V	30.2±1.12(17)	29.6±0.10(5)	U=4.0, n.s.

( ):Sample size

Table 3. Frequency distributions of the number of spermatophores in the bursa copulatrix of females in two morphs of *C. erate* captured in the field.

Morph	Number of Spermatophores	Age class				
		I	II	III	IV	V
Alba	0	5	0	0	0	0
	1	143	79	48	10	1
	2	22	28	51	34	13
	3	0	3	6	15	2
	4	0	0	0	3	2
	Total	170	110	105	62	18
	Mean	1.13	1.30	1.60	2.05[a]	2.27[b]
Yellow	0	0	0	0	0	0
	1	43	28	21	5	3
	2	5	12	29	13	7
	3	0	0	1	2	0
	4	0	0	0	0	0
	Total	48	37	49	21	10
	Mean	1.10	1.32	1.63	1.80[a]	1.70[b]

Mann-Whitney U-test, a: $U=818.0$, $P=0.05$; b: $U=126.0$, $P=0.03$

1 gives their fecundity. The number of immature and submature eggs per female was not significantly different from reared females, although wild females carried a few mature eggs.

Table 2 gives forewing length of field captured specimens. The difference between morphs was not significant in each age class and body size was not correlated with their age class. Watanabe and Nakanishi (1996) showed that the population structure of this species was similar for each year in the same study area.

Spermatophores in the bursa copulatrix of field-captured females

We dissected 474 alba and 166 yellow morphs in this study. No seasonal effect on mating frequency was found, as in *P. rapae* (Watanabe & Ando 1993). Table 3 shows that the youngest alba (age class I) had a single spermatophore in the bursa copulatrix, while 5 were virgin, and 14 had been polyandrous. The average number of matings was 1.1 for age class 1. The number of matings for alba increased with age (Kendall Test, $\tau=1.000$, $P<0.01$). The average number of matings in alba exceeded 2. Although the number of matings for the yellow morph increased with age (Kendall Test, $\tau=0.800$, $P<0.05$), their mating frequency was significantly lower than for alba by age class 4 ($U=818.0$, $P=0.05$) and age class 5 ($U=126.0$, $P=0.03$). Therefore, the yellow morph mated less than alba over their life (less than 2).

Figure 1 shows the change in the number of immature eggs with mating frequency. Every female carried a decreased load of immature eggs within

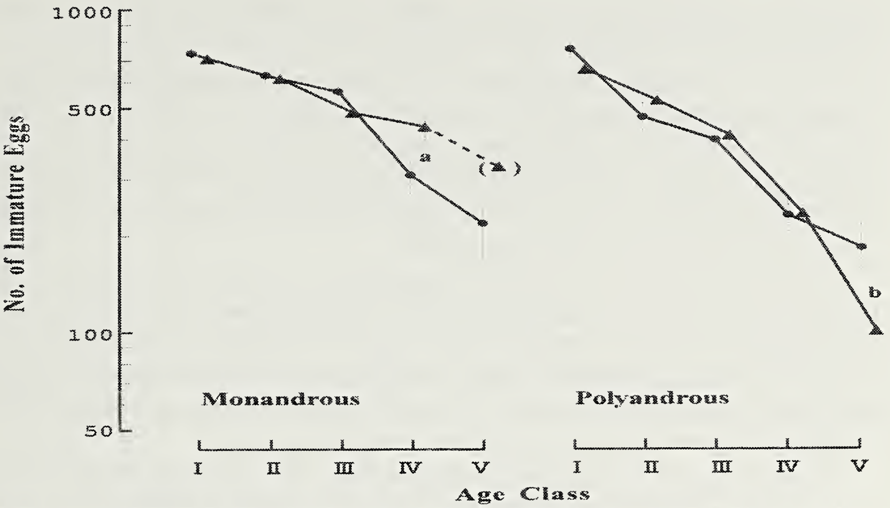

Fig. 1 Changes in the number of immature eggs of respective age (I, II, III, IV, and V) in relation to mating frequency in wild females of *C. erate*. Circles and triangles indicate the data for yellow morph and alba, respectively. Each bar represents SE. a and b are the results from Mann-Whitney U-test for P=0.04 (U=10.0) and P=0.03 (U=58.0) respectively. Parentheses show one sample.

its age class. We never observed fused eggs in the ovaries, suggesting that eggs were not consumed for somatic maintenance. If no immature eggs were added during adult stage, the decreasing number of immature eggs assumed due to oviposition.

For monandrous females, there was a significant difference in number of immature eggs carried by age class 4 among alba and yellow morphs (U=10.0, P=0.04). Because virgin females revealed about 750 immature eggs, about 550 eggs were laid by yellow morph and about 400 eggs by alba during their life span. Thus when monandrous, a yellow morph female lays more eggs than an alba morph.

In polyandrous females, alba lays more eggs than the yellow morph (U=58.0, P=0.03, in the age class 5), with alba laying about 650 eggs and the yellow morph laying about 550 eggs, a similar number to the monandrous yellow morph.

DISCUSSION

Colias species are widely used for studies of butterfly biology (e.g., fecundity in Stern & Smith 1960; thermoregulation in Watt 1968, 1973), including reports showing that pteridine or nitrogen pigments on the wings are important for their reproductive success. Watt et al. (1989) showed that population structure of *Colias* species co-existing with another pierid butterfly, *Pieris napi*, influenced the frequency distribution of wing color morphs in the *Colias.* Boggs and Watt (1981) also described the effect of mating frequency on population structure.

We have examined the biology of *C. erate* in Japan (population density in Watanabe & Nakanishi 1996; courtship behavior in Watanabe et al. 1997), in which the yellow morphs never outnumbered albas in any age class. Only for *C. scudderi,* the alba outnumber yellow morph in North America (Graham et al. 1980), but no relationship between the fecundity and the mating frequency has been demonstrated.

Over a period of six years, we examined in excess of 700 females of *C. erate* in our study area. Here the number of matings increased with age class, though about half the females were captured young. Braby (1996) pointed out that the mean number of spermatophores correlated significantly with age class (based on wing wear) in field females of bush brown butterflies, *Mycalesis* spp.

Positive correlations between mating frequency and population density have been noted in some butterfly species (e.g., Pliske 1973). Such studies suggest that at high density competition among males for females becomes more intense and the number of matings increases. Although Watanabe and Ando (1993) showed for *P. rapae* that the number of active males searching for mates differed between years, male density did not affect the number of matings by females. Thus females must exhibit mate choice (Rutowski 1978). For *C. erate* alba, the increasing tendency in the number of matings with age class was similar for *P. rapae,* while the yellow morphs were apt not to re-mate at older ages (age class 3, 4, and 5) than albas.

There were a relatively few mature eggs and a small number of submature eggs in the ovaries of young virgin alba, in which fecundity was estimated at about 800. Although we have no data on the fecundity of virgin yellow morphs from the field, laboratory populations indicated that females of both morphs have similar fecundities. The immature eggs loaded in virgin females of *C. erate* was the highest among other pierid butterflies inhabiting the study area, *P. rapae* (Watanabe & Ando 1993) and *P. melete* (Ando & Watanabe 1993).

Watanabe and Ando (1994) pointed out that monandrous females of *P. rapae* laid fewer eggs than polyandrous females. Multiple spermatophores have been shown to increase female reproductive output in some butterfly species (e.g., Watanabe 1988, Wiklund et al. 1993). However, in the yellow morph of *C. erate* females, mating frequency did not correlate with the number of eggs laid during their life span. In other words, the yellow morph does not need the extra spermatophores for oviposition, suggesting that one mating provides a female with enough sperm to fertilize all of the eggs (e.g., Suzuki 1978), and that spermatophores are not available energy for egg production (e.g., Svärd & Wiklund 1988). In fact, we observed small but intact shaped single spermatophores in older yellow morphs. Since the yellow morph might be mimetic to males to avoid further matings (unpublished data), they may have evolved an increased reproductive output without multiple matings.

Watanabe et al. (1997) showed that males persistently courted albas and sometimes harassed copulating pairs involving an alba rather than an yellow morph in the field. In the present study, alba tended to re-mate and polyandrous alba laid significantly more eggs than the monandrous females, suggesting an increase of fitness as in the case of many butterfly species (e.g., Oberhauser 1989, Wiklund et al. 1993). Therefore, it is likely that alba effectively attract males in morphology to increase their reproductive output.

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Oviposition, host plant choice and survival of a grass feeding butterfly, the Woodland Brown (*Lopinga achine*) (Nymphalidae: Satyrinae)

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Abstract. Oviposition, host plant choice and survival on different plants of a grass-feeding butterfly, *Lopinga achine*, were studied in the field and in the laboratory. Grass-feeding butterflies are generally thought to be non-specific in their host plant choice. This seems not to be true for *L. achine*. Females were selective in their host plant choice and preferred to oviposit near *Carex montana*, although they do not attach their eggs to any plant. *Carex montana* was also generally preferred by the larvae in laboratory experiments among the plants available in the field. However, the larvae preferred three species that they seldom encounter in the field (*Agrostis capillaris, Phleum pratense* and *Poa pratensis*) before *C. montana* when they were offered these four species. Most of the larvae found in the field (>80%), were found on *C. montana*. The larvae survived significantly better on *C. montana* than on six other species in rearing experiments. The results indicate that host plant choice occurs in two steps in *L. achine*: 1) the females choose a patch to drop the egg to the ground, usually in the vicinity of a *C. montana* plant 2) the newly hatched larva moves to the host plant. The apparent dependence of the Swedish mainland *L. achine* population on a single host plant has important conservation implications.

KEY WORDS: *Lopinga achine*, Satyrinae, host plant choice, performance, larvae, conservation, *Carex montana*.

INTRODUCTION

Lopinga achine Scopoli (Nymphalidae: Satyrinae) is one of the threatened Swedish butterflies that may disappear from the Swedish mainland without conservation measures. The species is classified as endangered in three European countries and as vulnerable in four (Heath 1981). It is one of the few Swedish species on the Bern Convention list (Council of Europe 1993) of endangered flora and fauna in Europe. The species is local throughout its distribution area from the south of Fennoscandia through central Europe to North and Central Asia and Japan (Kudrna 1986). In Sweden it lives in two areas, in the province of Östergötland, where I am studying it, and on the island of Gotland in the Baltic (Henriksen & Kreutzer 1982).

Little is known about the host plant of *L. achine*. The female drops the eggs to the ground and does not attach them to plants. Consequently it is difficult to ascertain its host plants (Karlsson & Wiklund 1985). At least 15 species or genera within Poaceae and Cyperaceae are suggested as host plants in the literature (Nordström 1955, Henriksen & Kreutzer 1982; Karlsson & Wiklund

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1985; Ackery 1988; Lepidopterologen-Arbeitsgruppe 1988; Jutzeler 1990;). Only three of the plants seem to be confirmed by larval findings in the field. One larva was found on *Carex alba* Scop. and one on *C. montana* L. (Cyperaceae) (Ebert & Rennwald 1991) and larvae (numbers not stated) were also found on *Brachypodium sylvaticum* (Huds.) PB (Poaceae) (Lepidopterologen-Arbeitsgruppe 1988).

Knowledge about host plants is still poor in many butterfly species, especially in grass-feeding ones (Thomas 1984). Grass feeding butterflies are generally thought to be unspecific in their choice of oviposition site (Wiklund 1984), but the studies of this are few in number. Our present knowledge of host-plant choice and oviposition in butterflies is based primarily on studies of Pieridae, Heliconiidae, *Papilio* spp. and *Euphydryas* spp. (e.g. Thompson & Pellmyr 1991, Renwick & Chew 1994). Many butterfly species have been shown to be more specific in their choice of habitat in the young stages than first had been suspected. Therefore it is necessary to know the exact needs of the immature stages to make conservation successful (Thomas 1984, Thomas 1991, New et al. 1995).

The aim of this investigation is to study the host plant choice of *Lopinga achine* and to determine its degree of specificity.

MATERIALS AND METHODS

Study animal and study site

L. achine fly in one generation in June-July and hibernates in the larval stage. The typical habitat in Östergötland, where I study it, is partly open oak woodland (*Quercus robur* L.) (Fagaceae) with hazel (*Corylus avellana* L.) (Corylaceae). This habitat is a successional stage lasting 30-50 years before the canopy closes if not grazed. The habitat on Gotland is different, being partly open coniferous forest with a well-developed scrub layer of *Frangula alnus* Mill. (Rhamnaceae), *Sorbus aucuparia* L. (Rosaceae), *S. intermedia* (Ehrh.) Pers. and *Juniperus communis* L. (Cupressaceae). According to inventories up to 1997, *L. achine* lives in 49 populations in Östergötland in a small area (21 x 10 km) and most of the populations have contact with each other according to mark-recapture work. The matrix is usually open fields or spruce plantations. Most populations are small, some hundreds of adults. Four populations may comprise two to three thousand adults.

Oviposition

Ovipositing females were followed in the field in areas of high adult density. I used binoculars to be able to observe the females from a distance in order not to disturb them. Immediately after oviposition the exact place was marked and all Poaceae, Juncaceae and Cyperaceae species within 15 cm were recorded. Plant names follow Mossberg (1992). All females I saw ovipositing did so sitting on the vegetation. The oviposition place is henceforth referred to as an “oviposition point”. The observations were mainly (48 out of 84 egglayings) made in the largest population and the rest in nine other populations.

Plant species at randomly selected points were checked in the same manner as the oviposition points. These “random points” were placed at approximately the same distance from the edge (one meter zones) between forest and open areas as the oviposition points to avoid vegetation differences due to influence from the forest.

For example, a oviposition point 1.7 meters from the edge of the glade in the forest has a corresponding random point between 1-2 meter from the edge.

Larval host-plant choice in the laboratory

The larval host-plant choice was tested in the laboratory using different grasses and sedges (Table 1.) during the season when larvae normally feed. The laboratory temperature varied between 22° and 25°C and there was limited daylight (50-80 lux) from a small window above the petri dishes. Plant leaves were cut in 25 mm long pieces and placed in a circle with the cut ends towards the centre of a petri dish (9 cm diameter). Each plant species was represented by one piece, except the thin *Deschampsia flexuosa* (L.) Trin. (Poaceae) with several pieces in each place. Moist filter paper covered the bottom in the dish. The leaves rested against a roll of paper at the edge of the dish to prevent them from laying flat on the bottom. During all the trials, only two larvae made no choice.

Eggs were collected from 20 females caught in the wild and kept together in a cage. All of them laid eggs and the collected eggs was a mixture from these 20 females. A newly hatched larva arising from each of these eggs was placed in the middle of each petri dish with a fine brush. After 72 hours, the plant species were ranked according to larval preferences: plants with the largest area eaten of was ranked as number one, that with the second largest area eaten as number two and so on to the last one.

Host plant choice in the field

In the glades where I had found the largest numbers of flying adults, I systematically searched through every plant in the families Poaceae, Juncaceae and Cyperaceae for larvae in a zone six meters out in the open glade and six meters under the tree and bush cover. I noted the species upon which they were found. This was done in four populations in the autumn (20.IX.90-3.X.90) and spring (22.V.91-6.VI.91).

Rearing experiments on different plant species

In 1989-90 I reared larvae on five putative hostplants: *Calamagrostis arundinacea, Carex montana, Deschampsia cespitosa, Melica nutans* and *Poa nemoralis.* The larvae originated from the eggs from the captured females mentioned earlier. The larvae were reared outdoors in 18 x 18 x 18 cm cages with net sides. Each cage contained 10 larvae and the plants stood in water. The plants were changed every third day for the first two weeks, and then weekly or when deteriorated. The cages were moved into the laboratory in November and kept at 4°C until March. In February, the larvae were offered pieces of the plants that had green shoots in the field. Survival and weight (0.1 mg) were followed up to and including adult eclosion. Pupae were not weighed in order not to disturb them so the last weighing before weighing the adults was of mature larvae. The newly hatched larvae were too small to be weighed individually so 57 were weighed together and the average was used as a starting weight. Adults were weighed one day after eclosion.

In the second experiment (1991-92), the larvae were reared in round plastic cages 10 cm high and 11 cm in diameter, with a net lid. The larvae came from 20 females caught in the wild and kept individually and the offspring were mixed as evenly as possible. Five larvae were reared in each cage. The plants roots were submerged in water through a hole in the bottom of each cage. The plants were changed whenever they showed signs of deterioration. Seven plants (Poaceae and Cyperaceae) were tested: *Agrostis capillaris* L., *Calamagrostis arundinacea, Carex montana, Dactylis glomerata, Deschampsia cespitosa, Milium effusum* L., *Phleum pratense* L. Survival was followed up to

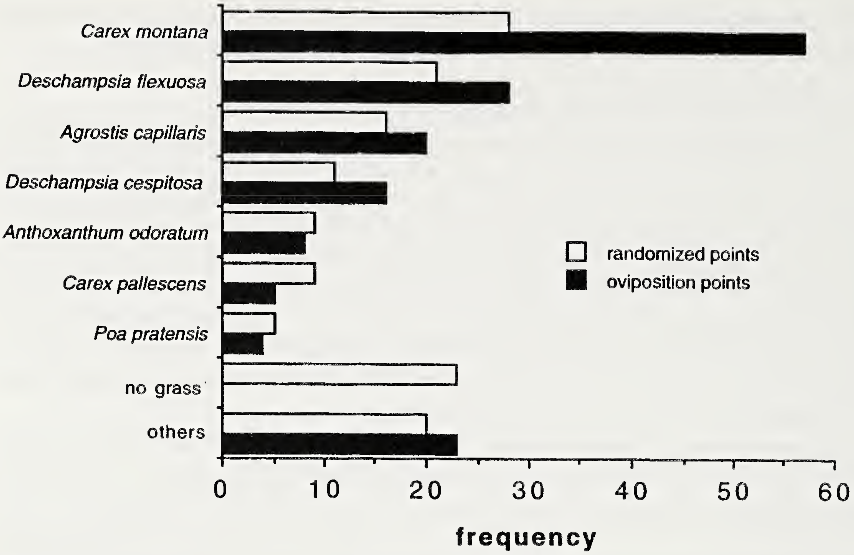

Fig. 1. Grass and sedge species within 15 cm from oviposition points of *Lopinga achine* and within 15 cm from randomly selected points (n=84 in both cases). Plant species with less than five occurrences among the randomly selected points are pooled as "others." These species are also grouped as "others" at the oviposition points.

and including adult eclosion. The entire experiment including hibernation was conducted outdoors.

Statistics

All statistics were calculated using Statview 4.01 for Macintosh (Haycock et al. 1992).

RESULTS

Oviposition

The plant frequency in the randomly chosen points was significantly different from the frequency in the oviposition points (χ^2=35,7; p<0,0001; df=8) (Fig. 1). Females preferred to oviposit near *Carex montana.* No female oviposited at points lacking grasses or sedges although 23 of the 84 randomly selected points lacked grasses and sedges. Therefore I excluded these 23 points and tested whether the frequency of *C. montana* differed between oviposition points and the 61 randomly selected points with grasses and sedges. The difference is significant (χ^2=7.0, p<0.01, df=1), 57 out of 84 females (68%) oviposited within 15 cm from *C. montana,* but it occurred at only 28 of the 61 randomly selected points (46%) with grasses and sedges.

Larval host plant choice

The newly hatched larvae clearly preferred some plants to others in all seven experiments (Table 1). *Carex montana* was preferred in four of five trials

Table 1. Ranking of host plants by choice of newly hatched *Lopinga achine* larvae in seven laboratory experiments. Mean rank among the plants are given in parenthesis and the differences between the plant species in each experiment were tested by the Friedman test (tied p-values). Empty places mean species not included in the experiment.

	Exp no 1	Exp no 2	Exp no 3	Exp no 4	Exp no 5	Exp no 6	Exp no 7
Number of replicates (larvae)	20	20	20	19	21	29	20
Friedman test	**p=0.004**	**p<0.001**	**p=0.003**	**p<0.0001**	**p=0.012**	**p<0.0001**	**p<0.0001**
Agrostis capillaris							1 (3.025)
Anthoxantum odoratum						7 (4.793)	
Carex montana	1 (1.675)	1 (2.475)	1 (1.875)			1 (2.741)	4 (4.175)
Carex pallescens						5 (4.259)	5 (4.525)
Calamagrostis arundinacea		5 (4.550)		2 (2.684)		3 (3.828)	6 (4.875)
Dactylis glomerata		7 (4.600)	2 (2.725)	3 (2.711)	3 (2.429)	2 (3.448)	
Deschampsia cespitosa		5 (4.550)	3 (2.750)	4 (3.053)	4 (3.143)	6 (4.741)	
Deschampsia flexuosa	3 (2.525)						
Melica nutans	2 (1.800)	3 (3.875)			1 (2.167)		
Milium effusum						4 (4.190)	6 (4.875)
Phleum pratense							2 (3.225)
Poa annua		2 (3.575)	3 (2.750)	1 (1.553)	2 (2.262)		
Poa nemoralis		4 (4.375)					
Poa pratensis							3 (3.300)

where it occurred. However, *A. capillaris, Phleum pratense* and *Poa pratensis* were preferred to *C. montana* in one trial. Other preferred species were *M. nutans* and *P. annua. Deschampsia flexuosa* and *D. cespitosa* were generally disliked. The larvae refused to eat *D. flexuosa* completely.

Field observations of 97 larvae in the autumn confirmed the results of the larval host plant choice experiments. *Carex montana* was used by 82 larvae (85%), and nine were found on the low preferred host, *D. cespitosa.* One larva were found on each of *P. pratensis* , *Festuca rubra* L. (Poaceae), *Luzula pilosa* (L.) Willd (Juncaceae) and an unidentified Poaceae. Two were found on non-host material. The difference between *C. montana* frequency in ovipositions (57 of 84) and larval occurrence (82 of 97) is significant (χ^2=7.0, p=0.008, df=1).

The result was almost the same in the spring. *C. montana* was used by 71 larvae of 86 (83%), and 10 used *D. cespitosa.* The other larvae were found on non-host material or when pupating.

Rearing experiments

The larvae grew slowly until hibernation started in October in the third instar (Fig. 2a). They grew fast in spring (March-June) to the fourth (most of the males) or fifth instar (most of the females) and pupation. The larvae were left undisturbed and eating for a week before they were weighed in the spring which is the reason for the apparent weight gain during hibernation. Adult weights among females reared on different plant species differ significantly (p=0.007, F=4.68; df_1= 4, df_2=21, single-factor ANOVA). However, it is only the groups reared on *C. montana* and *D. cespitosa* that differ in a *post hoc* test (p=0.017, Scheffé´s F). Male groups do not differ significantly from each other (p=0.62, F=0.665, df_1=4, df_2=34, single-factor ANOVA) (Fig. 2a).

There are significant differences in survival in the first experiment between larval groups feeding on *C. montana* and those feeding on *D. cespitosa, M. nutans* and *P. nemoralis* (χ^2, p<0.02 three pairwise comparisons, df=1 in each comparison) but not between *C. montana* and *C. arundinacea* (χ^2=2.92, p=0.09, df=1) (Fig. 2b). Larval mortality was highest during the first 50 days (July-August) and after hibernation. In the second rearing experiment, the survival on *C. montana* was significantly higher than on all the other species (χ^2, p<0.02 six pairwise comparisons, df=1 in each comparison) (Fig. 3). The survival on *D. cespitosa* and *C. arundinacea* was low compared to the results in the first rearing experiment. There is also a tendency for increased mortality during the first days of this trial and again after hibernation but it is not as clear as in the first trial.

Mean time to eclosion for males varied between 334 days (*P. nemoralis*) and 338 days (*M. nutans*) (Fig. 4). Mean time to eclosion for females varied between 341 days on *D. cespitosa* and 348 days on *C. montana.* There are significant differences between times to eclosion between females (p=0.006, F=4.93, df_1=4, df_2=21, single-factor ANOVA) but not for males (p=0.154, F=1.79, df_1=4, df_2=34, single-factor ANOVA).

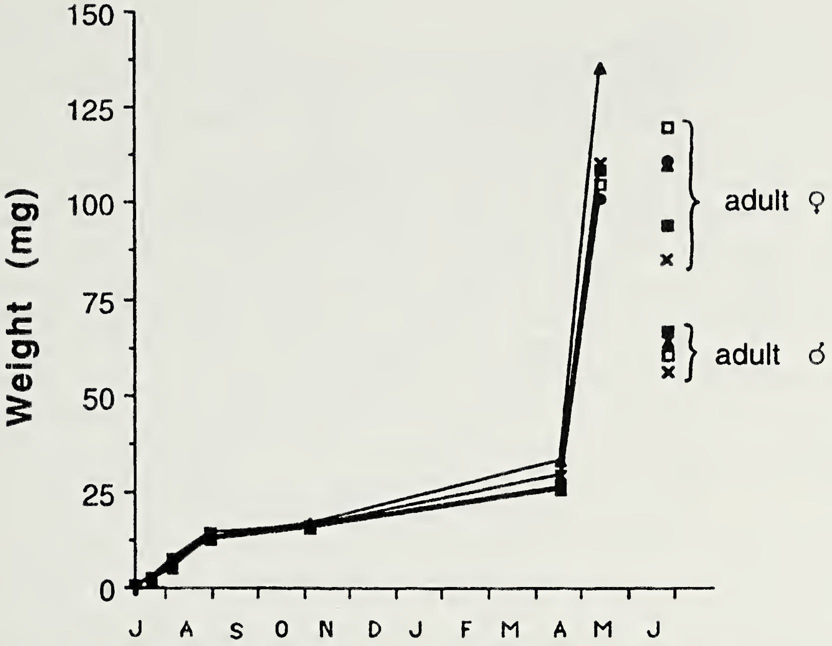

Figure 2a. Mean weight increase of *Lopinga achine* larvae and mean of adult weights at eclosion after development on five different grass species. Measures of spread are omitted for clarity. The largest SEs are ±15,5% for larvae and ±10,9% for adults. See Figure 2b number of larvae.

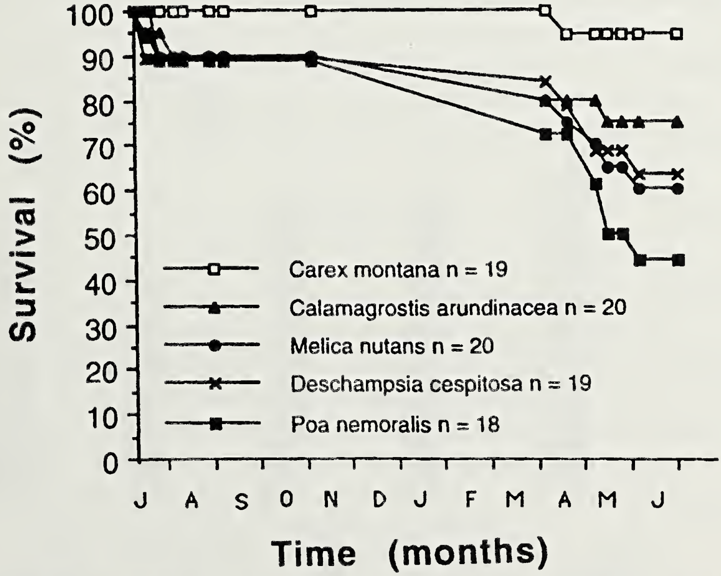

Figure 2b. Survival of *Lopinga achine* larvae to adult butterflies on five different plant species. The experiment was done 1989-1990 and started 8.VII outdoors but hibernation took place in the laboratory November-March. n = number of larvae.

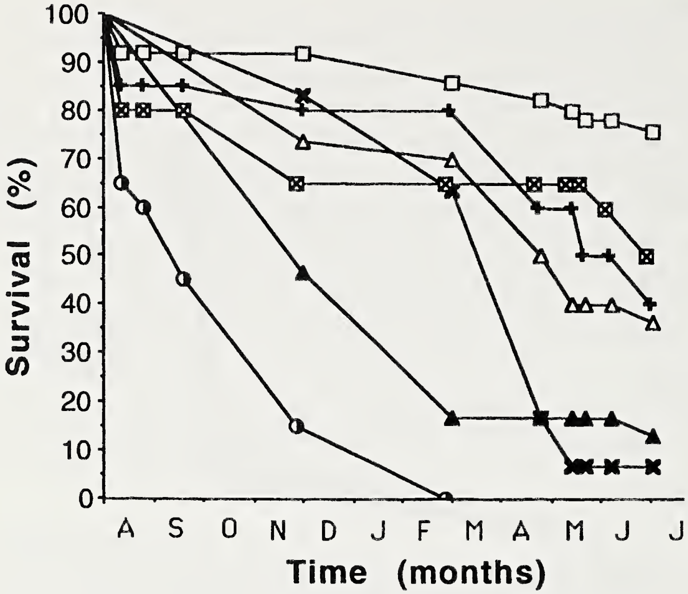

Figure 3. Survival of *Lopinga achine* larvae to adult butterflies on seven plant species. The experiment was done outdoors and started 4.VIII.1991. Plant species in decreasing order of butterfly survival: *Carex montana* (n=50), *Phleum pratense* (n=20), *Agrostis capillaris* (n=20), *Dactylis glomerata* (n=30), *Calamagrostis arundinacea* (n=30), *Deschampsia cespitosa* (n=30), *Milium effusum* (n=20). n = number of larvae reared.

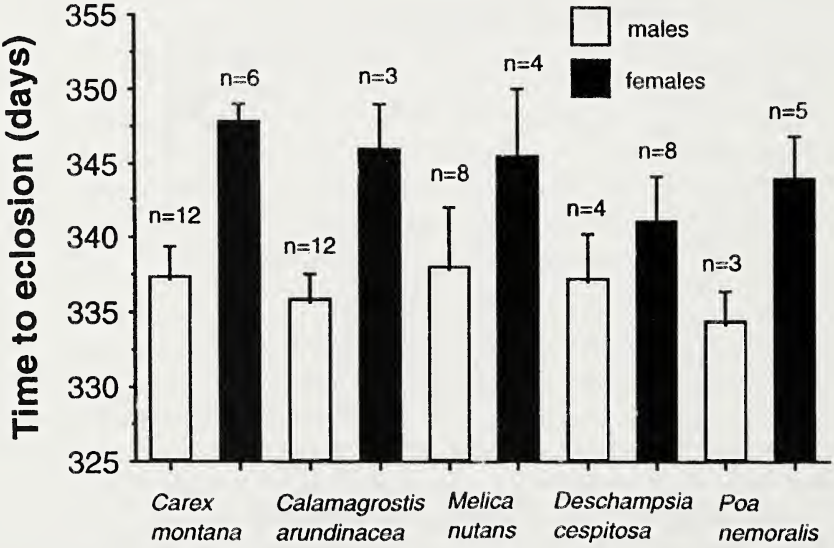

Figure 4. Mean development time to eclosion (±S.E.) of *Lopinga achine* males and females on five grass species. n = number of butterfly specimens.

Discussion

It is clear that *L. achine* females prefer to oviposit near *C. montana* (Fig. 1), even though they do not attach their eggs to that plant. This selective oviposition behaviour contrasts to the suggestions of Wiklund (1984) that the satyrines that do not attach their eggs do not bother much about were they drop them. Polyphagy or superabundant host plants are suggested as reasons for the behaviour (Wiklund 1984, Thompson & Pellmyr 1991). Neither seems to be true for *L. achine* populations in Östergötland when looking at the selective host plant choice and the difference in survival on different plants. It is important to note that *C. montana* is not superabundant in large areas of the *L. achine* sites even though the species was the most common grass species in the areas were the females oviposited. This indicates that the females first make a habitat choice. After the habitat choice, the host plant choice seem to occur in two steps in *L. achine*: 1) the females choose a patch to drop the egg to the ground 2) the newly hatched larvae moves to the host plant (only tested under laboratory conditions).

Lopinga achine females show the characteristic fluttering flight before landing and oviposition (Porter 1992). This indicates that the female do not drop the egg without regard to the environment. During this flight the females may use shapes (Vaidya 1969, Stanton 1982), colour (Saxena & Goyal 1978) and odour (Petersen 1954, Feeny et al. 1989) to locate host plants. Wing fluttering increased in *Papilio polyxenes* in the presence of host plant odours (Feeny et al. 1989). Many species also use contact stimuli (Chew & Robbins (1984) and references therein) before they oviposit. This does not seem to be the case in *L. achine* females as they sometimes oviposited in a tussock of *C. montana* when sitting on other plants growing together with *C. montana*, for example *Lathyrus linifolius* (Reichard) Bässler (Fabaceae). The search for ovipositing places may also involve microclimatic conditions (Thomas et al. 1986, Petersen 1954) and levels of shade (Greatorex-Davies et al. 1993).

In many species it is the female who selects host plant by her oviposition. The newly hatched larvae cannot exercise host-plant preference in many species, as they lack sufficient powers of movement to leave the plant on which the eggs were laid (Singer 1971, Saxena & Goyal 1978, Ohsaki 1979, Singer et al. 1994). However, the larva of *L. achine* must make the final choice itself since the female drops the egg to the ground, although near a host plant. The larva is quite able to choose (Table 1zx). It is also able to starve longer than the newly hatched larva of *Papilio machaon* whose female glues the egg to the host plant (Karlsson & Wiklund 1985). They stated that the ability of the *L. achine* larvae to endure starvation may be regarded as an adaptation to the females way of oviposition.

However, the plant species they can choose among are determined by the egg laying females (Fig. 1). That is probably one reason why larvae mostly occur on *C. montana*, even though they preferred *A. capillaris, P. pratense* and *P. pratensis* to *C. montana* in the experiments where all four species were offered (Table 1). The larvae seldom encounter the three grasses in the field except for *A. capillaris* (Fig. 1), but this grass was often represented by just one or two leaves in the vicinity of the egg. Another reason for the significantly higher larval occurrence on *C. montana* (83-85%) in the field compared to ovipositions (68%), may be due to lower mortality of larvae on *C. montana* compared to other species. The larva may also be able to move longer than 15 cm, the distance arbitrarily chosen when checking plant species at oviposition points. About 10% of the larvae found in the field occurred on *D. cespitosa* but the larvae rated this species low in the choice experiments (Table 1). In the second rearing experiment it also caused high mortality (Fig. 3). However, it relatively often occurred at the oviposition points (Fig. 1). Its tussocks are large so it may be difficult to leave it if the egg hatches in the tussock. The development to adult may succeed on it (Fig. 2b, 4).

The developmental time does not seem to be important for host-plant choice in *L. achine.* The females on the preferred species, *C. montana,* had the longest time to adulthood (Fig. 4). Development time can be important if the time available for larval growth is limited (Nylin 1988).

Summarising, *L. achine* larvae survived and succeeded best on *C. montana,* and the plant species was also preferred by egg-laying females and newly hatched larvae in choice experiment among the plants available in the field (Table 1, Fig. 1, 2a,b, 3). The good correspondence between oviposition and performance in *L. achine* indicate that the generalist behaviour suggested for satyrines (Bink 1985) does not seem to be true for *L. achine.* The correlation between oviposition preference and performance in phytophagous insects varies much. Many studies have reported a good correspondence (e.g. Papaj & Rausher 1987, Nylin & Janz 1993) but many have also reported low correlations (e.g. Courtney 1981, Rausher 1979, Larsson & Strong 1992).

Carex montana is probably also the host plant for *L. achine* populations on the island of Gotland. *Carex montana* is very common in the woods that are habitat for *L. achine* there. *Lopinga achine* larvae from Gotland survived better on *C. montana* than on *D. glomerata* why Karlsson & Wiklund (1985) suggested *C. montana* as the major host plant. However, *C. montana* cannot be the single host plant for *L. achine* since the populations in Finland occur in areas without it (Hultén & Fries 1986). *L. achine* also completed the life cycle on many of the other plant species in my experiments, even though the success rate was lower. Different populations of butterflies may evolve different host plant preferences as in the satyrid *Satyrodes eurydice* Johansson (Shapiro 1974) and the nymphalid *Euphydryas editha* Boisduval (Singer et al. 1994), especially when living in different habitats.

The dependence of at least the Swedish mainland *L. achine* populations, on a single host plant has important conservation implications. In the future, the relations between the butterfly and the host plant may be studied to understand the reasons for the geographic distribution and to determine if there is a need for habitat management to ensure long-term survival.

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The effect of environmental conditions on mating activity of the Buckeye butterfly, *Precis coenia*

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Abstract. The readiness of males of *Precis coenia* to court females depends on time of day, temperature, and light level. Courtship activity has a temperature optimum and, at that optimum, increasing light level dramatically enhances courtship activity. High light level appears to be critical for courtship activity, and high temperature cannot substitute for high light level. The requirement for high light intensities may be related to the behavior of males that chase females from preferred territorial perches on bright patches of exposed substrate.

Key Words: light level, temperature, courtship, *Precis coenia*

INTRODUCTION

Some years ago, when we first started to raise Buckeye butterflies (*Precis coenia* Hubner) for our experiments on the development of wing patterns (Nijhout, 1991), we encountered considerable difficulties in getting this species to mate in cages in the laboratory. Our early experimental work was done with animals produced from eggs of gravid females caught in the field. None of the standard measures to enhance mating in the laboratory such as confining the adults with various species of host plants, enlarging the mating cage, and modifying temperature and humidity, appeared to provide the necessary conditions to induce courtship and mating.

Our observations of mating activity in the field confirmed the reports by Scott (1973, 1975a,b) that courtship and mating are most frequently observed during the warmest part of the day. At these times male buckeyes perch preferentially on bright patches of sand and from those perches chase passing females. We attempted to mimic these conditions by placing our mating cages in front of a south-facing window at mid-day, and found that this immediately induced courtship behavior in males. We found that *P. coenia* would mate readily and successfully even in cages as small as 10 x 10 x 10 cm as long as they were placed in direct sunlight. It was not clear, however, whether the increased light level or the increased temperature in the mating cage was the primary stimulus for courtship and mating. Below we present an analysis of the independent effects of temperature and light level on mating activity.

MATERIALS AND METHODS

Larvae of *Precis coenia* were reared in the laboratory on artificial diet and long

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day (16L: 8D with the lights-on signal at 6 am EST) conditions at 27 °C. Our laboratory colony was derived from animals collected in the Sandhills of North Carolina (Sandhills Wildlife Management Area, Richmond County). Freshly emerged adult butterflies were sexed by using characters of the prothoracic legs, and labeled on the ventral hind wing with a permanent fine tip laboratory marker. Males and females were separated and animals of each sex were grouped in separate Plexiglas cages measuring 45 x 50 x 60 cm.

Observations were made during the months of June and July 1996. For each observation session, 10 males and 5 females aged between 4 to 8 days after emergence were randomly selected from the holding cages and transferred to an observation cage (Plexiglas, 25 x 30 x 25 cm, except for some observations in the greenhouse when a wire mesh cage was used, as noted below). The data presented below are based on 6 to 10 observations sessions under each set of environmental conditions. Observation sessions were 45 minutes long. Preceding each observation session the mating cage was placed into the test environment for a 30 minute equilibration period.

Observations were made at three times of day (10 am, 12 pm, 3 pm EST), at three different temperatures, and at three different light levels. Target temperature values were 25 °C, 33 °C, and 40 °C. Due to uncontrollable drafts and imprecise temperature regulation in the greenhouse actual temperature values around these targets ranged from 23.0-28.8 °C, 30.0-38.0 °C, and 38.0–42.6 °C during the observation period. Target light level values were 2.3, 53, and 280 lux, with actual values ranging from 2.1-2.6, 49-56, and 100-430 lux around those targets due to variation in solar irradiance and physical setup of the mating cages. Precision Instruments incubators were used to provide the 33 and 40 °C temperatures under low and intermediate light intensities. Light level of 2.3 lux was provided by a 15 watt incandescent bulb, while values of 53 lux were provided by a 500 watt halogen bulb. Temperature was measured with a Yellow Springs Instrument Co., Inc. Tele-thermometer Model 46TUC. Light levels were measured with a Weston Illumination Meter, Model 756. To enable observation while maintaining the necessary temperatures, the door frame of the incubator was covered with a clear plastic sheet secured with magnets. A clear plastic tray containing one inch of a 10% $CuSO_4$ solution was placed between the cage and halogen lamp (about 6 inches from the light) as a heat absorbing filter. To achieve low and medium light intensities at 25 °C, we used the same lights in a temperature controlled room. The highest light level we used, 280 lux, is representative of the level of sunlight. It was impossible to achieve this level with artificial lights, so measures at high light intensities were made in a climate-controlled greenhouse. In the center of the greenhouse temperatures fluctuated between 32-34 °C. A wire mesh cage (45 x 45 x 45 cm) was used for observations centered around 33 °C. By placing the wire mesh cage near the cooling cells of the greenhouse, a temperature of 25 °C could be accurately maintained. To maintain 40 °C, a Plexiglas cage was placed in a sunny location; sliding vents were used to manually adjust the temperature inside the cage.

Assay of Mating Behaviors. Courtship and mating behavior in *Precis* in captivity consist of four distinctive behaviors: nudging, chasing, head dipping, and abdomen curling. These differ slightly from the general nymphalid courtship behavior

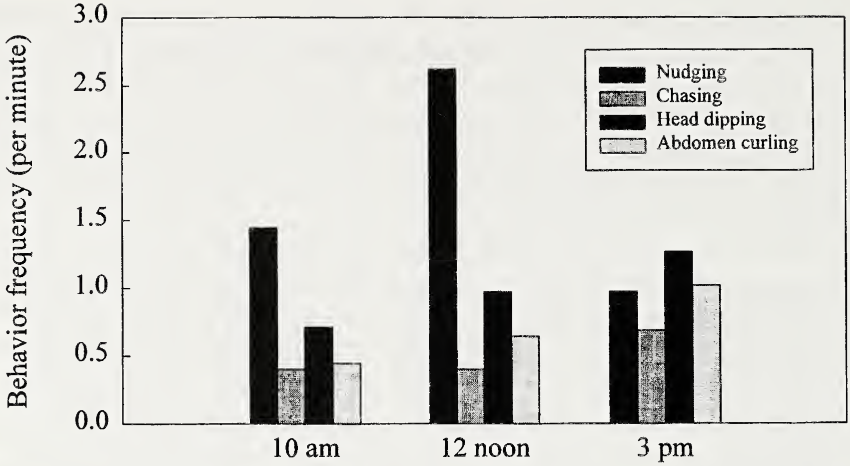

Figure 1. Mean frequency of individual courtship behaviors at each of different times of day, at the intermediate temperature of 33 °C and the high light level of 280 lux.

patterns described by Scott (1975b). Nudging is defined as the brushing of the legs of a hovering male butterfly against the wings of a perched butterfly. Often, a nudging male will land on or next to the perched butterfly. Males do not appear to distinguish between males or females at this stage in the courtship. Chasing is the pursuit, on foot, of another butterfly. Head dipping is defined as the dipping of the head under the abdomen or wing area surrounding the abdomen of the approached butterfly. This seems to serve to raise the female's abdomen into a position that the male can easily couple with. Abdomen curling consists of lateral curling of the male's abdomen towards another butterfly in an attempt to copulate. The frequencies of each of these behaviors during each 45 min observation period was scored in order to obtain a quantitative estimate of the effects of the three environmental variables on mating activity.

RESULTS

Mating activity consistently reached a maximum at intermediate temperatures and high light intensities. Frequencies of individual mating behaviors under these conditions are shown in Figure 1. The proportion of different acts was not significantly different at 10 am and 12 noon (Chi-square, $P>0.95$), while the proportions of the different acts at 3 pm differed significantly from those at the two earlier times (Chi-square, $P<0.0003$). This difference appears to be accounted for entirely by a decrease in the frequency of nudging. At 3 pm the nudging events were significantly less frequent per unit time than they were earlier in the day (t-test, $P<0.0033$), whereas the frequencies of the intermediate and later courtship events did not differ significantly from their frequencies earlier in the day. This observation suggests that in the afternoon courtship becomes more efficient in the sense

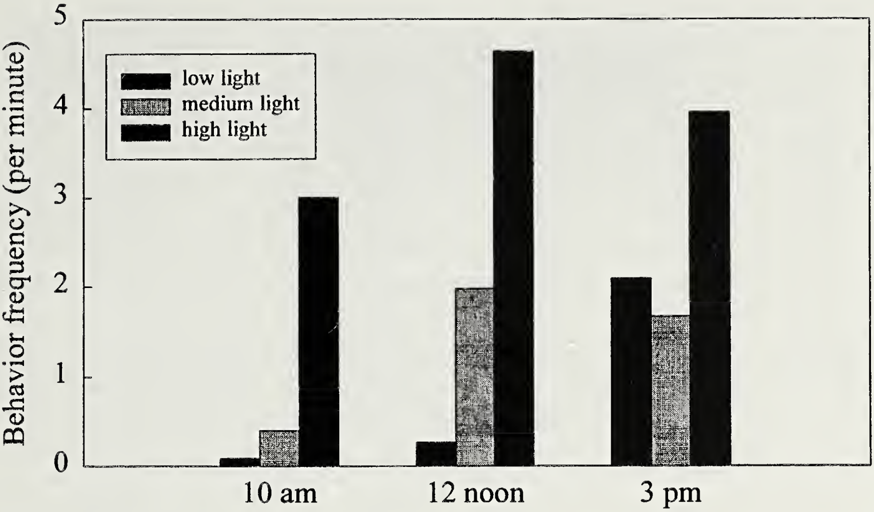

Figure 2. Mean frequency of total courtship activity at three different times of day and three different light intesities (all data shown is at 25 °C).

that a larger proportion of individuals that begin courtship are able to take it to completion.

High light intensity dramatically increased mating activity at all times of day (Figure 2). At 10 am and 12 noon a stepwise increase in light intensity significantly increased mating activity ($P<0.003$ for all pairwise comparisons). At 3 pm mating activity at low and medium light intensities were not significantly different from each other but mating activity increased significantly at the highest light intensity ($P<0.0004$).

The Combined Response to Temperature and Light Level. The overall mating activity was assessed as the sum of all observed courtship events. These are graphed in Figure 3 as a function of both temperature and light level at three different times of day. Contours were calculated using SigmaPlot (Jandel Co.). In view of the fact that the numerical tally of mating activity is dominated by early courtship events (nudging, see Figure 1), the overall mating activity was also estimated based on the intermediate and late courtship events alone (Figure 4). Both measures of mating activity revealed a qualitatively similar pattern. At 10 am, mating activity increased when temperature and light level increased. The effect of increasing temperature was more pronounced at high light intensities than at low light intensities, while the effect of light level was most pronounced at intermediate to high temperatures (Figures 3a, 4a). At 12 pm and 3 pm, by contrast, there was a distinct optimal temperature for mating activity (32–34 °C; Figures 3b,c, 4b,c). At 12 pm, increasing light level had a stimulatory effect on mating activity at optimal temperatures and below, whereas at temperatures above the optimum, light level had little effect on mating activity (Figure 4b). At 3 pm, light level affected mating behavior only within the

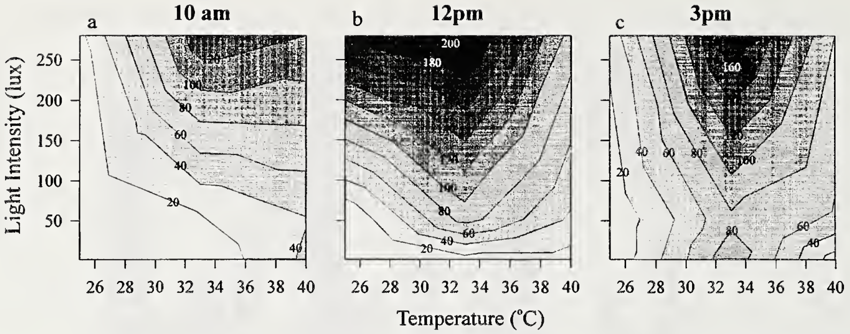

Figure 3. Mating activity at different times of day as a function of both temperature and light level. Mating activity (numbers on contours) was scored as the sum of the frequencies of all 4 of the courtship behaviors (Fig. 1) during a 45 min observation period.

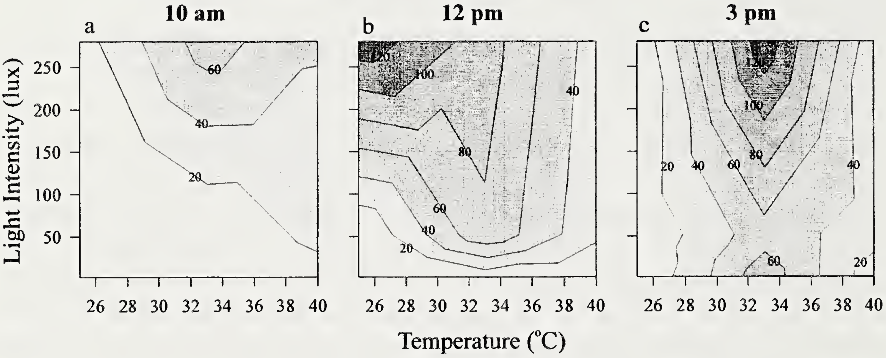

Figure 4. Mating activity at different times of day as a function of both temperature and light level. Mating activity (numbers on contours) was scored as the sum of the frequencies of the three late stages in courtship (chasing, head dipping, abdomen curling) during a 45 min observation period.

optimal temperature range, whereas light level had little or no effect on mating activity at temperatures below or above the optimum (Figure 4c).

Analysis of significance of pairwise comparisons of the data presented in Figures 3 and 4 revealed the following. In Figure 3, pairs of points that differ by more than 55 events (approximately 3 contour intervals) are significantly different from each other (t-test, P<0.05), both within and between panels. In Figure 4, pairs of points that differ by more than 26 events (slightly greater than 1 contour interval) are significantly different from each other (t-test, P<0.05), both within and between panels.

Discussion

The mechanisms that regulate mating behavior result in dramatically different responses to temperature and light level as time of day progresses.

Maximum mating activity always coincided with temperatures of 32–34 °C and high light level (280 lux), regardless of time of day. The relative frequency of nudging, the earliest event in courtship behavior, peaked at 12 pm, while the relative frequency of abdomen curling, the final event preceding copulation, was greatest at 3 pm. Therefore, although total courtship activity at noon was greater than at 3 pm, the final stages of courtship, and presumably mating success, were relatively more frequent at 3 pm.

Rutowski (1991) has outlined three hypotheses to explain why males court preferentially at certain times of day. First, limited thermoregulatory capacity may restrict mating activity to periods when the environmental temperatures are neither too high nor too low. Second, mating may be timed to coincide with female emergence times. Third, mating may be timed so as to minimize interference between species. Our results illuminate the first of these hypotheses, but show that mating activity is not constrained strictly by temperature. Although male *Precis coenia* clearly have an optimal mating temperature of 32–34 °C, exposure to this temperature alone did not result in maximum levels of mating activity. Mating activity at 12 pm and 3 pm was consistently higher than at 10 am. Time of day, therefore, affects mating behavior independently of temperature. Light level also has an independent effect on mating behavior. Within the optimal temperature range, high light level increases mating activity at all three times of day, whereas at non-optimal temperatures the effect of light level depended on the time of day.

Scott (1975b) has noted that in nature, mating activity of *Precis coenia* occurs mostly in late morning and early afternoon. Our results suggest that, given the right combination of temperature and light level, mating behavior can occur at most times of day, although the interaction of light level, temperature, and time of day ensure that the bulk of mating activity is most likely to occur in the early afternoon.

If light level is low, little mating activity occurs, even at optimal and higher temperatures. It is not clear at present why light level should have such a great effect on mating activity. It is possible that high light level acts indirectly, by elevating the male's body temperature. This would imply that the optimal body temperature is substantially higher than the 32–34 °C optimal environmental temperature we measured. Optimal body temperatures for flight in insects range from 35 to 42 °C (Heinrich, 1993), so it is conceivable that mating activity could also require such high body temperatures. However, if the effect of light level was mediated through an elevation of body temperature, one would expect high light intensities to be more effective at inducing mating activity at temperatures below the environmental optimum than at temperature above the optimum. The apparent temperature optima in Figures 3 and 4 would then be expected to be a function of light level, with a lower temperature optimum at high light intensities and a higher temperature optimum at low light levels. Instead, the temperature optima are unaffected by light level (except for a single instance at low temperatures: Figure 4b), suggesting that these two environmental variables do not interact, and that light level seems to be important for reasons other than radiational heating.

One explanation for the evolution of high light level as a cue for mating may be found in the fact that mating activity of the *Precis coenia* population we studied occurs preferentially in open habitats on exposed patches of sand. Such bright areas in the landscape serve as perching territories for males (Scott, 1975b, and personal observations), and from these territories males chase passing insects, including females and other males. Males are chased away, and females, if receptive, land nearby and courtship begins (Scott, 1975b). It is possible that the selection of perching territories is guided primarily by brightness of the substrate. If the acquisition of such a territory is important for mating success, then it seems reasonable to suppose that a response to high light levels as a stimulus for courtship may have evolved in association with the behavior by which males select especially bright perching territories from which to chase passing females.

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Nymphalid butterfly communities in an amazonian forest fragment

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Abstract. Species diversity and abundance of fruit-feeding nymphalid butterflies were studied in an Amazon rain forest fragment. Butterflies were caught in baited traps in twelve areas, selected to sample a gradient of increasing disturbance. Measurements of six parameters of vegetation structure were also taken to estimate the disturbance. A total of 90 butterfly species were trapped. The greatest alpha diversities were found at the edge of the forest and in areas of intermediate disturbance. Canonical Correlation Analysis (CCA) showed that the composition of the species assemblages of nymphalids was related to vegetation structure variables, especially girth at breast height and number of tree morpho-species. The butterfly fauna appeared more similar in forested areas than in the disturbed ones. Some species were suggested as habitat indicators and the value of this guild of fruit-feeding butterflies in conservation programs is discussed.

KEY WORDS: Butterflies, nymphalids, diversity, community structure, disturbance, rain forest fragment, direct gradient analysis, Brazil.

INTRODUCTION

One of the main objectives of community ecology is the synthesis of the roles of physical and biological factors that determine species abundance and distribution within and among natural communities. After MacArthur and MacArthur (1961) found a relationship between bird diversity and high vegetation diversity, ecologists verified that habitat complexity is an important factor for the structuring of local communities. Habitats that are structurally more complex and heterogeneous offer more niches, and therefore support a greater number of species (spatial heterogeneity, Pianka 1966). In addition this idea, Connell (1978) suggested that high diversity in tropical forests is maintained by disturbances, such as tree falls. Considering such dynamics, the forest can be seen as a mosaic of gaps in different successional stages, with different local communities, and a high regional diversity.

Although biogeographic and historical conditions are extremely important factors in structuring communities (Slansky 1972, Ricklefs 1987, Leps and Spitzer 1990, Brown 1982, Brown 1991, Thomas 1991, Gaston 1996), local factors also affect local butterfly diversity (Emmel and Leck 1969, Montesinos 1985, DeVries 1994, Kitahara and Fujii 1994, Sparks and Par-

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ish 1995). Many studies have shown that tropical butterfly communities also respond to physical factors of the habitat, such as topography, stratification, gaps, edges, urbanization and habitat disturbances (Ruszczyk 1986, DeVries 1988, Raguso and Llorente-Bousquets 1990, Brown 1991, Hill et al. 1992, Pinheiro and Ortiz, 1992, Hill et al. 1995, Spitzer et al. 1997). As such, multivariate analysis has proven to be an important tool when investigating the relationships between species assemblages and environmental variables (Leps and Sptizer 1990, Kremen 1992, Ramos 1992, Väisänen 1992, Spitzer et al. 1993, Spitzer et al. 1997, Blair and Launer 1997).

The objectives of this study are (1) to measure neotropical nymphalid butterfly diversity along a gradient of disturbance, (2) to explore the species-environment relationships through a direct gradient analysis and (3) identify the most important butterfly species and vegetation variables, which could be used in conservation monitoring programs.

METHODS

Study site. This study was conducted in a forest fragment at the boundary of the eastern Amazon (5°01´S, 47°32´W; 260 m), a region where the natural landscape has been greatly modified by human activity. The study site was about 50 km north of the transition to Cerrado. The fragment has about 1,000 ha of primary forest with several levels of disturbance, surrounded by secondary forest in several succesional stages, eucalyptus monocultures and cattle pasture. I selected 12 sample units (SUs) throughout a disturbance gradient: forest understory (FU1, FU2, FU3), forest roads (FR1, FR2, FR3), edge (EDG), highly disturbed forest understory (DFU), highly disturbed forest road (DFR), 4-year-old secondary forest (SF4), 2-year-old secondary forests (SF2) and *Eucalyptus pellita* monoculture (EUC).

Data collection. I made lepidoptera collections between June 1990 and July 1991. For each of 12 SUs, three fruit-baited traps were set in line, suspended 1.0-1.7 meters above the ground, and 25 meters apart from one another. For each collection, the traps were visited for 14 consecutive days. The banana and sugar cane bait was kept moist for the duration of the trapping period. The disturbance level of each SU was estimated using vegetation parameters obtained through the point-centered method (Müller-Dumbois and Ellemberg 1974), with 21 quartered points established per SU, only for trees up to 20 cm of circumference at breast high. This method was chosen for its simplicity and common use in phytosociological surveys. The following vegetation variables were used: average *girth at breast hight* (GBH); estimated average *tree height* (THG); n*umber of tree morpho-species* (NMS) estimated by rind and leaf characteristics, with the help of a local guide; *tree density* within 100 m^2 (DEN); average *horizontal cover* (HOC), estimated at each sample point by an observation made on a 50 cm square carton held 10 m from the observer in each quarter. Cover was estimated to be within one of four categories (0-25%, 25-50%, 50-75% and 75-100% vegetation cover); average *vertical cover* (VEC), estimated by the four previously mentioned vegetation cover categories, apllying a 10 cm square frame held at a distance of 60 cm from the observer at an angle of approximately 20° in relation to zenith.

Table 1. Alpha diversity of fruit-feeding butterfly species in twelve sample units of an Amazonian forest fragment.

	Forest understory			Forest road			Edge	Disturbed forest		Secondary forest		Eucalyp monoc	
	FU1	FU2	FU3	FR1	FR2	FR3	EDG	DFU	DFR	SF4	SF2	EUC	**Total**
Number of individuals (N)	63	43	97	114	111	106	334	267	571	490	744	604	3544
Nymphalinae richness	3	5	6	11	13	12	15	16	19	17	16	12	29
Satyrinae richness	13	11	15	14	16	13	27	14	20	19	20	17	41
Brassolinae richness	1	1	2	0	1	1	5	2	4	3	2	2	6
Charaxinae richness	0	2	3	2	3	6	6	6	6	7	3	3	13
Total species richness (S)	18	20	27	28	34	33	54	39	50	47	42	34	90
Species diversity (H´)	2.27	2.76	2.60	2.79	3.08	3.06	3.38	3.06	3.19	3.00	2.28	2.09	3.26

Data analysis. The butterfly alpha diversity of each SU was quantified by the species richness (S) and Shannon-Wiener index (H'). To evaluate environmental effects on the butterfly community I ran a Canonical Correspondence Analysis (CCA), using the program CANOCO (TerBraak 1988). The vegetation parameter estimates of habitat disturbance were used as environmental variables in the CCA. The variable tree height was removed from the analysis due to its high value of inflation, and high colinearity with the other variables. The significance of species-environment relationships was tested using a Monte Carlo test.

RESULTS

A total sample effort of 2,016 trap days (=3 traps x 12 SUs x 56 days) resulted in 3,544 individuals collected, representing 90 species of five subfamilies of Nymphalidae. The five most abundant species were *Paryphthimoides phronius, Yphthimoides* sp1, *Yphthimoides disaffecta, Hermeuptychia hermes* and *Cissia penelope,* all belonging to the subfamily Satyrinae, representing 45.3% of the total number of individuals collected. A complete list of species abundances in each SU can be seen in Appendix 1. The total butterfly diversity in the rain forest fragment sampled was H´ = 3.258.

An analysis of alpha diversity showed that edges and areas of intermediate disturbance presented higher species richness and diversity (Table 1). Although more disturbed areas, such as eucalyptus monoculture and 2-year-old secondary forest had higher species richnesses than forest, they had lower species diversities, due to the high dominance of the Satyrinae species. This pattern was not found when other groups were considered separately: Satyrinae and Brassolinae had higher species richnesses in the disturbed areas, with a peak of the edge; Charaxinae and Nymphalinae had higher species richnesses in the road, edge and disturbed forest areas.

The CCA ordination diagram shows the relationships between butterfly species, sample units and environmental variables (Figure 1). By comparing the arrow lengths, one may evaluate the significance of the constraining vegetation variables. The arrow points roughly in the direction of the maximum variation in the value of the corresponding variable. The spe-

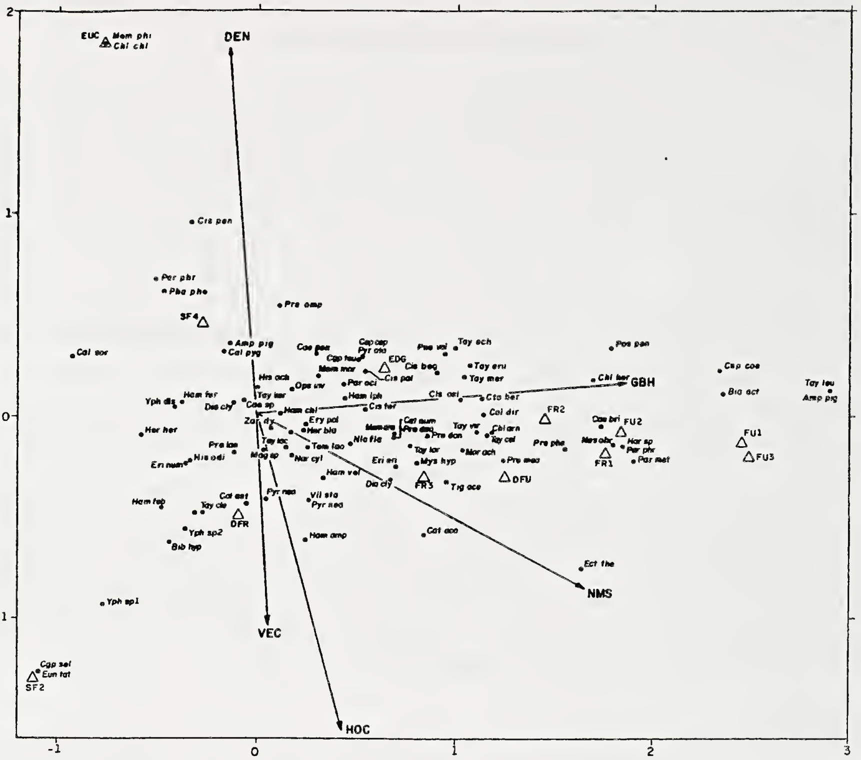

Figure 1. CCA ordination of the fruit-feeding butterfly communities in an Amazonian forest fragment, with respect to five vegetation variables (arrows). The species are abreviated according to the first three letters of their generic and the first three letters of their specific names (see Appendix 1 for full names). The vegetation variables are: average girth at breast height (GBH), estimated average tree height (THG), number of tree morpho-species (NMS), tree density within 100 m^2 (DEN), estimated average horizontal cover (HOC) and estimated average vertical cover (VEC). The sample units are forest understory (FU1, FU2, FU3), forest roads (FR1, FR2, FR3), edge (EDG), highly disturbed forest understory (DFU), highly disturbed forest road (DFR), 4-year-old secondary forest (SF4), 2-year-old secondary forests (SF2) and *Eucalyptus pellita* monoculture (EUC).

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cies far from the origin are rare and less important to analysis. The Monte Carlo permutation test showed that those species are significantly related to supplied vegetation variables (99 permutations, $P < 0.01$).

In the first CCA axis, girth at breast height presented the highest absolute value, followed by the number of tree morpho-species, both contributing to the species data fit. This axis clearly shows a gradient of disturbance — preserved areas with a greater richness of large bole trees on the positive side, and disturbed or early succesional ones on the negative side. The ordination also shows how species respond to vegetation variables: with invader species typical of open areas (the small Satyrinae *Hermeuptychia hermes, Yphthimoides sp1, Y. disaffecta, Cissia penelope, Erichtodes numeria* and *Pharneuptychia pharnaces,* and the Nymphalinae *Hamadryas feronia, H. februa* and *Biblis hyperia*) showing negative scores. With positive scores, near the origin, are the heliophyllous species of the disturbed forests, gaps, edges and canopy (*Eryphanis polyxena, Hamadryas iphthime, H. velutina, Memphis morvus, Narope cyllabarus, Nica flavilla, Pareuptychia ocirrhoe, Temenis laothoe* and *Taygetes laches*). The species on the right side of the diagram are typical of the forest understory (*Colobura dirce, Morpho achiles, Nessaea obrinus, Taygetis celia, T. echo* and *T. virgilia*). The second axis was primarily related to tree density and horizontal cover, but did not form a clear gradient. The analysis gave a large weight to some Satyrinae species, such as *Cissia penelope* and *Paryphthimoides phronius,* which had large populations in high tree density eucalyptus monoculture.

Discussion

The forest edge and intermediate disturbance forest presented higher values of butterfly species richness and diversity. These environments, where intense regeneration occurs, have high productivity and maintain high population levels. On the other hand, the disturbance rate is high, thus reducing the effect of competitive exclusion. A number of ecologically based hypotheses have been proposed to explain patterns of species richness and diversity, but not all of them are mutually exclusive (Meffe and Carroll 1997). The productivity-disturbance hypothesis (Huston 1994) combines elements of several other hypotheses, proposing that the high productivity and the disturbance rate conditions of forest edges and gaps result in high species richness. The results of this study tend to agree with this hypothesis. Additionally, the mixture of forest understory umbrophyllous species with open area heliophyllous ones raises the local diversity. The fact that edges, gaps, physiognomic transitions, and disturbed and secondary forests have high diversity has been documented many times elsewhere (Leps and Spitzer 1990, Raguso and Llorente-Bousquets 1990, Hill et al. 1992, Pinheiro and Ortiz 1992, Väinsänen 1992, Spitzer et al. 1993, Spitzer et al. 1997). For sunloving species, drastic changes in light intensity can act as a habitat barrier, while edges, gaps and canopies may be treated as a continuum of sunny, open area. Other species, however, remain restricted to shady environments (DeVries 1988).

The number of tree morpho-species was not a good predictor of the number of butterfly species. Because the group is herbivorous, butterfly - host plant relationships have been explored (Gilbert and Smiley 1978, Erhardt and Thomas 1991), although not always being meaningful (Sharp et al. 1974, Courtney and Chew 1987, Singer and Ehrlich 1991). Besides that, the sampling considered only trees, and did not consider bushes, herbs and lianas that are host plants of several butterflies (DeVries 1987). Although not related with butterfly alpha diversity, the number of tree morpho-species was important in the formation of an environmental gradient, and is related to habitat disturbance.

The ordination diagram shows that the forest assemblages are homogeneous, but among disturbed areas there are great variations in species composition and abundance. A larger constancy of forest communities has been verified for neotropical satyrins (Brown 1991), and butterflies of South-eastern Asia (Leps and Spitzer 1990), but the opposite pattern was found for Notodontidae and Arctiinae in the same forest fragment (Dubois 1993).

Although other butterfly groups such as Ithominae and Heliconinae have been suggested as more efficient indicators (Brown 1991, Beccaloni and Gaston 1995), the use of the fruit-feeding Nymphalidae has its utility in conservation programs (Daily and Ehrlich 1995). The results of the CCA ordination show that butterfly communities have a significant relationship with vegetation variables, and suggest the use of this assemblage as an appropriate indicator of habitat heterogeneity over this spatial scale. CCA can be used to match a species assemblage to environmental factors for which it is a good indicator, and select a subset of species as indicators for more intensive monitoring (Kremen 1992). Since rare species have little weight in the analysis (TerBraak 1988), common species, and not rare ones, should be selected from this guild to be used as indicators. Thus, *Hermeuptychia hermes, Yphthimoides sp1, Y. disaffecta, Cissia penelope, Erichthodes numeria, Pharneuptychia pharnaces, Hamadryas feronia, H. februa* and *Biblis hyperia* may serve as indicators of disturbed environments, and *Colobura dirce, Morpho achiles, Nessaea obrinus, Taygetis celia, T. echo* and *T. virgilia* indicators of more preserved environments.

The use of higher taxa for biodiversity measurements (Williams and Gaston 1994) can be an important management tool for situations where taxonomic identification at the species level is difficult. For the same data set, counting only subfamily abundance, Ramos (1992) obtained similar ordination patterns as when counting species abundance. Another advantage of this fruit-feeding guild is that it can easily be sampled with traps, simultaneously in several points. Using appropriate criteria and guidelines, as suggested by Sparrow et al. (1994), this nymphalid fauna may be an informative species subset for monitoring programs.

The collection of vegetation variables was designed to be as simple as possible. Of course, other local habitat variables that are important for adult butterflies which could have been measured were not quantified. Among the physical and structural variables are the size of the area, topography, temperature, humidity, light, gaps, roosts and dormitories, and ground pattern. Important biological factors for adults include food and ovoposition site availability, predators and mimics.

Local diversity is determined not only by local factors, but also by regional and historical factors (Ricklefs 1987). Aside from the limits of the local habitat structure, the local butterfly assemblage depends on the regional species pool and historical processes such as climatic changes, isolation, extinction and speciation. The rapid fragmentation of the Amazon rain forest may be contributing to butterfly extinctions, especially larger species with scarce resources - Morphinae, Brassolinae and Charaxinae (Brown 1991). Alternatively, the vegetation structure of disturbed forest is suitable for sun-lovers, secondary and opportunistic species that may spread throughout the region. Some of these butterflies are common in open biomes such as the Cerrado. For example, *Hamadryas februa, H. feronia, Erichthodes numeria* and *Hermeuptychia hermes* are as abundant in cerrado *strictu sensu* of central Brazil (Pinheiro and Ortiz 1992) as in the disturbed areas of the fragment studied.

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Appendix 1. Vegetation structure variables and abundance of fruit-feeding butterfly species in twelve sample units of an Amazonian forest fragment. Each species has an abbreviation with the first three letters of the generic and specific names that are used in Figure 1.

		Forest understory			Forest road			Edge	Disturbed forest		Secondary forest		Eucalypts monoculture	
		FU1	FU2	FU3	FR1	FR2	FR3	EDG	DFU	DFR	SF4	SF2	EUC	
	Vegetation structure variables													
	Average tree high (m)	13.8	13.4	18.8	15.7	15.7	13.6	12.4	10.9	10.3	8.1	7.8	16.0	
	Average horizontal cover	3.58	3.30	3.36	3.25	3.44	3.77	3.99	3.39	3.61	4.00	3.79	1.33	
	Average vertical cover	3.52	3.82	3.93	3.11	3.44	1.96	3.52	3.74	2.74	3.30	2.89	2.82	
	Number of tree morfo-species	39	46	49	47	43	38	19	35	33	19	13	1	
	Tree density (tree / 100m2)	7.85	8.57	7.02	4.44	6.33	5.03	4.13	7.59	7.57	7.24	2.16	15.60	
	Average Girth at breast hight	59.1	61.4	73.9	69.4	63.9	61.2	50.8	44.8	38.0	34.0	27.5	34.8	
	Butterfly species													Total
	MORPHINAE													
Mor ach	*Morpho achiles pindarus* Fruhstorfer, 1912	14	4	13	22	15	9	18	25	26	14	3		163
	NYMPHALINAE													
Bib hyp	*Biblis hyperia* (Cramer, 1779)							1	2	14	8	25		50
Cal ast	*Callicore astarte* (Cramer, 1799)									2				2
Cal mai	*Callicore maimuna* (Hewitson, 1858)				1			1	1	1				4
Cal pyg	*Callicore pygas thamiras* (Ménétriés, 1857)										5			5
Cal sor	*Callicore sorana* (Godart, 1832)											1	1	2
Cat aco	*Catonephele acontius* (Linnaeus, 1758)				1					1				2
Cat num	*Catonephele numia* (Cramer, 1775)						1							1
Col dir	*Colobura dirce* (Linnaeus, 1758)	19	5	29	11	10	9	22	44	15	13	2	9	188
Dia cly	*Diaethria clymena* (Cramer, 1775)					1	1	2		12	6	2	4	28
Ect the	*Ectima thecla lirina* Felder & Felder, 1867				1									1
Eun tat	*Eunica tatila* (Herrich-Schäfer, 1885)											4		4

Ham amp	*Hamadryas amphinome* (Linneaus, 1767)					1				1		1		3
Ham chl	*Hamadryas chloe* (Stoll, 1787)							2	6	1	4	2	2	17
Ham feb	*Hamadryas februa* (Hübner, 1823)					1				2	1	7	2	13
Ham fer	*Hamadryas feronia* (Linneaus, 1758)				1	5	16	17	2	23	17	58	48	187
Ham iph	*Hamadryas iphthime* (Bates, 1864)			1	2	3	1	3	5	7	2	1	5	30
Ham lao	*Hamadryas laodamia* (Cramer, 1777)							2	1		2	4		9
Ham vel	*Hamadryas velutina* (Bates, 1865)					1	1	2	9	16	2			31
His ach	*Historis acheronta* (Fabricius, 1775)					1						1	1	3
His odi	*Historis odius* (Fabricius, 1775)						1		1		2	3	1	8
Mys hyp	*Myscelia hypatia* Strecker, 1900	3	1	8	9	7	7	3	30	34	4	1	2	109
Nes obr	*Nessaea obrinus* (Linneaus, 1758)	5	3	8	12	8	1	4		1	1			43
Nic fla	*Nica flavilla* Hübner, 1826		1	1	1	1	7	4	4	14	3		1	37
Pau per	*Paulogramma peristera* Hewitson, 1853								1	2				3
Pyr nea	*Pyrrhogyra neaerea* (Linneaus, 1758)						3		1	2	1	2		9
Pyr ota	*Pyrrhogyra otalis* Bates, 1864							1						1
Tem lao	*Temenis laothoe* (Cramer, 1777)		1	1	1	6	8	10	6	24	12	8	3	80
Tig ace	*Tigridia acesta* Hübner, 1819				2	1		1	12		1			17
Vil sta	*Vila stalachtioides* Bates, 1864								1	2				3
	BRASSOLINAE													
Cal teu	*Caligo teucer* (Linneaus, 1758)			1				1		2			1	5
Cal sel	*Caligopsis seleucida* Hewitson, 1927											1		1
Cat ber	*Catoblepia berecynthia* (Cramer, 1777)		1				1	1						3
Ery pol	*Eryphanis polixena* (Meerb, 1775)	1		1		1		10	11	5	5	6	4	44
Nar cyl	*Narope cyllabarus* Westwood, 1851							2	3	8	3			16
Ops inv	*Opsiphanes invirae* (Hübner, 1808)							4		2	3			9
	CHARAXINAE													
Mem ara	*Memphis arachne arachne* (Cramer, 1777)						1							1
Mem mor	*Memphis morvus morvus* (Fabricius, 1775)					1	2	7	3	3	5		2	23
Mem oen	*Memphis oenomais* (Boisduval, 1870)						1	2	1		2	1		7
Mem phi	*Memphis philumena corita* (Fruhstorfer, 1916)					1								1

Mem ryp	*Memphis ryphea* (Geyer, 1834)												1	1
Pre doo	*Prepona demophoon* Hübner, 1806						1							1
Pre don	*Prepona demophon* (Linneaus, 1758)			3	1		3	3	5	3	3			21
Pre lae	*Prepona laertes* (Hübner, 1811)							3		1	2	2		8
Pre mea	*Prepona meander* (Cramer, 1775)			1					1	1				3
Pre omp	*Prepona omphale* (Hübner, 1819)							1		1	1			3
Pre phe	*Prepona pheridamas* (Cramer, 1777)		1						1					2
Sid mar	*Siderone marthesia* (Cramer, 1777)										1			1
Zar ity	*Zaretis itys* (Cramer, 1777)		1	1	3	2	5	10	3	10	35	11	2	83
	SATYRINAE													
Bia act	*Bia actorion* (linneaus, 1767)	1		2		1								4
Amp pig	*Amphidecta pignerator* Butler, 1867			1										1
Cae bri	*Caeruleuptychia brixia* (Godart, 1821)			4	1		1			1	1			8
Cae pen	*Caeruleuptychia pencillata* (Godman, 1905)							2			1			3
Cae sp	*Caeruleuptychia sp*							6		5	9	2	1	23
Cep coa	*Cepheuptychia coelestes* (Butler, 1860)	1		1										2
Cep cep	*Cepheuptychia cephus* (Fabricius, 1775)							2						2
Chl arn	*Chloreuptychia arnaea* (Fabricius, 1777)			1	1			1	1		1			5
Chl chl	*Chloreuptychia chloris* (Cramer, 1782)												1	1
Chl her	*Chloreuptychia herseis* Ebert, 1960	1	2					1						4
Cis occ	*Cissia occypede* (Fabricius, 1777)		1			1	1	1			1			5
Cis pen	*Cissia penelope* (Fabricius, 1775)				5	6	2	14	11	17	16	13	116	200
Cis pal	*Cissia nr. palladia* (Butler, 1866)				1	1			2	1			2	7
Cis beg	*Cissia "bege"*	1				1		2			1			5
Cis ter	*Cissia terrestris* (Butler, 1866)		1	4	2	3	4	12	13	8	13	2	4	66
Eri eri	*Erichthodes erichtho* (Butler, 1866)					2		1	1	3				7
Eri num	*Erichthodes numeria* (Felder, 1865)							3		7	5	7	2	24
Har bla	*Harjesia blanda* (Möschler, 1876)							1		1				2
Har sp	*Harjesia sp*					1								1
Her her	*Hermeuptychia hermes* (Fabricius, 1775)		2		1	3	1	9		36	34	96	55	237

Mag sp	*Magneuptychia sp*				1		1	1		7	6	1		17
Par met	*Pareuptychia metaleuca* (Boisduval, 1870)			3								1		4
Par oci	*Pareuptychia ocirrhoe* (Fabricius, 1789)	2		3	7	12	5	40	7	23	23	2	14	138
Par phr	*Paryphthimoides phronius* (Godart, 1823)		2	2	1	1		24	2	46	115	82	228	503
Pha pha	*Pharneuptychia phares* (Godart, 1821)											1		1
Pha phn	*Pharneuptychia pharnaces* (Weymer, 1911)							2		1	2	2	6	13
Pse vel	*Pseudodebis velentina* (Cramer, 1782)	1						2						3
Pos pen	*Posttaygetis penelea* (Cramer, 1779)	1												1
Tay cel	*Taygetis celia* (Cramer, 1782)		2	1	1	2		5	2			1		14
Tay cle	*Taygetis cleopatra* Felder, 1862							1				1		2
Tay ech	*Taygetis echo* (Cramer, 1779)	2	2		3					1			3	11
Tay eru	*Taygetis nr. erubescens* Butler, 1868	1		1		1		2	2				1	8
Tay ker	*Taygetis kerea* Butler, 1869					1						1	1	3
Tay lac	*Taygetis laches* (Fabricius, 1793)	3	4	1	9	3	5	33	22	29	22	35	14	180
Tay lar	*Taygetis larua* Felder, 1867	1		1			1	3	3	1		1		11
Tay leu	*Taygetis leuctra* Butler, 1870			1										1
Tay mer	*Taygetis mermeria* (Cramer, 1779)	1	1				1	3						6
Tay vir	*Taygetis virgilia* (Cramer, 1779)	5	7	3	9	6	1	11	8	4	6	2	1	63
Yph dis	*Yphthimoides disaffecta* (Butler&Druce, 1874)		1		4		1	12	9	66	50	78	63	284
Yph sp1	*Yphthimoides sp1*						3	3	5	74	25	268	3	381
Yph sp2	*Yphthimoides sp2*									4	1	2		7

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A Survey of the Butterfly Fauna of Jatun Sacha, Ecuador (Lepidoptera: Hesperioidea and Papilionoidea)

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Abstract. The first extensive butterfly survey of the upper Río Napo basin in eastern Ecuador was conducted from 1990 to 1993. A total of 811 species was recorded at Jatun Sacha Biological Reserve. Based on species richness comparisons with a similar site in southern Peru and extrapolations from ithomiine diversity, Jatun Sacha is estimated to have approximately 1300 species of butterflies. Species richness is compared with two other Amazonian sites (Pakitza, Peru, 1300 species and Cacaulandia, Brazil, 843 species). Species and generic compositions are more similar between Pakitza and Jatun Sacha than Cacaulandia. This similarity may be due to environmental factors. A greater percentage of Nymphalidae and a lower percentage of Hesperiidae and Lycaenidae occur at the two somewhat disturbed sites (Jatun Sacha and Cacaulandia) than the less disturbed site (Pakitza). Of the 228 species common to all three sites, more nymphalid butterfly species were found than expected based on observed species in each family.

Key Words: Butterfly diversity, community similarities, estimations of species richness

INTRODUCTION

The Amazon basin covers an area approximately 6 million square kilometers and houses the world's greatest diversity of plant and animal life (Erwin 1988, Dinerstein et al. 1995). Insects are the most diverse taxon in the neotropics, yet they have been poorly studied in this vast area (National Academy 1992, Lamas 1989 and ref. therein, Raven 1988, Reid & Miller 1989). Even for taxonomically well known insect groups, such as the butterflies, there exist large gaps in our understanding of tropical species richness and factors influencing diversity (DeVries 1994, Ackery 1986). One major hindrance is the lack of basic information available on natural history and species distributions for most Amazonian butterflies (Ackery 1986, DeVries 1994, DeVries et al. 1997). Inventories from specific localities can be useful in investigating changes in species compositions across landscapes, but most of the current faunal information on Amazonian butterfly communities are from Peru (Lamas 1985, 1989, Robbins et al. 1996) and areas in Brazil (Brown 1984, 1991, Emmel & Austin 1990, Mielke 1994). There are few published surveys of butterfly faunas in eastern Ecuador and Co-

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lumbia (Lamas 1981). Therefore our understanding of the patterns of butterfly diversity in these areas is very incomplete.

Biologically significant areas, such as along the eastern base of the Andes, offer the opportunity to research factors influencing diversity and are of particular importance to study. The eastern flank is postulated to be an area very diverse in plant, bird, and butterfly life (Dinerstein et al. 1995, Robbins & Opler 1996, Gentry 1988a). Gentry (1988b) found that areas of high rainfall and weakly defined wet and dry seasons correlated with areas of high plant diversity. In Ecuador the only protected area in this zone is Jatun Sacha Biological Station, located in the upper Napo basin. A flora survey at Jatun Sacha found over 200 species of trees in one hectare plots on the reserve (Neill & Palacios 1989). Surveys of the fauna on the reserve have found high species richness as well, including an extensive bird survey, which has recorded over 500 species (B. Bochan, pers. comm.). This diversity at Jatun Sacha suggests the area might be equally rich in butterflies.

Here I report a survey of the Jatun Sacha butterfly fauna, which can serve as a baseline for studies of diversity patterns at Jatun Sacha. It can also be used for comparative studies with other localities in the region (DeVries 1994, 1996). In this paper I compare and contrast the taxonomic compositions at Jatun Sacha with two other sites in the Amazon basin.

STUDY SITES

Jatun Sacha Biological Station is located 30 km east of the base of the Andes (01° 04'S; 77° 36'W) and lies between the confluence of the Napo and Arahuno rivers, its natural boundaries. Elevation varies from 400m to 450m. The uplands, typified by steep, low hills and narrow ridges with small streams in the valleys, comprise the majority of the land. There is also a small tract (100 hectares) in the Rio Napo floodplain with alluvial soils and seasonal flooding. The Holdridge system would classify the lowland forests of this area as Tropical Wet Forest (Cañadas 1983). Rainfall data, recorded since 1986, averages 3700mm annually, with no definite dry season. However, April through July are generally the wettest months and December through February the driest months. Major floods of streams and rivers occurs throughout the year but are more common during the wetter months. Soil fertility is relatively rich for tropical wet forests, especially in phosphorous and calcium, when compared to other lowland forest sites (Clinebell et al. 1995). Storms are infrequent in the area but often cause multiple treefalls, leaving the forest in various stages of succession (D. Neill & W. Palacios, unpublished).

The land-use patterns in the vicinity of Jatun Sacha have undergone rapid changes in the last decade. Before the early 1980's the area was sparsely populated by native Quichuans and accessed only by rivers. A road built in 1986 bisected the reserve at its northern end along the Río Napo and greatly increased access to the area. The influx of small scale farmers and portable sawmills resulted in deforestation in areas accessible by the road. Currently, tracts of land owned by farmers adjacent to the road typically have 40 to 70 percent of the land cleared. Tracts in the interior are more pristine, from 50 to 100 percent primary forest. Jatun Sacha continues to expand its reserve and purchases lands in a piecemeal fashion as funds and land become available. Thus the reserve is a patchwork of habitats. Its central core is mostly primary forest (70%), and its edges are a mosaic of primary forest, secondary forest, scrub, and pasture land (D. Neill & W. Palacios, unpublished).

A brief description is presented below of the two comparative sites, Pakitza and Cacaulandia. More complete descriptions are available from Erwin (1991) for Pakitza and Emmel and Austin (1990) for Cacaulandia. Pakitza is a biological station in the Reserved Zone of Parque Nacional Manu. It is located in Madre de Dios drainage basin in Peru along the foothills of the eastern Andes in a similar geographical zone as Jatun Sacha. The butterfly survey for Pakitza was comprehensive and yielded 1300 species (Robbins et al. 1996). The survey from Cacaulandia was conducted on a private ranch in Rondonia, Brazil. Located in the rolling hills and flat plains of the Amazon basin, it has both intact forest and disturbed areas. A total of 843 species of butterflies was recorded by Emmel and Austin (1990), although continued surveys have increased this total number to approximately 1500 species (Austin & Emmel 1996, cited as "unpublished data"). The area of Cacaulandia is ecologically less similar to Jatun Sacha than Pakitza, but faces similar pressures from development.

MATERIALS AND METHODS

The survey at Jatun Sacha was conducted from August 1990 to October 1993. Hours in the field devoted to collection varied by month but covered all the months of the year, with the exceptions of December 1990 and 1991, and October, 1992, and data was not gathered to quantify collection effort. Collection was concentrated in a 3 km area surrounding the station facilities. As the reserve accumulated more land, a few specimens were taken in a 10 km area around the station. Specimens were captured with hand held nets, butterfly traps baited with rotting fruits (DeVries 1987, 1988), artificial bait (Lamas et al. 1994), and by rearing field collected larvae. Extensive use of butterfly traps at Jatun Sacha was conducted during an ecological study that examined spatial and temporal diversity of the fruit feeding butterfly community (DeVries et al. 1997). Material from that study is included here. The study took place from August, 1992 to October, 1993 and during that time, baited traps were placed in both the canopy and understory for seven days a month, a total of 105 trap days. Additional sources for species included donated specimens or field records offered from various visiting scientists.

Identifications were conducted by comparison of my material to specimens in the following institutions and museums: Allyn Museum of Entomology of Florida Museum of Natural History, American Museum, Museum of Comparative Zoology, and National Museum of Natural History. Various specialists identified particular taxonomic groups: D. Harvey (Riodinidae), L. Miller (Satyrinae), S. Nicolay (Hesperiidae), and R. Robbins (Lycaenidae). Due to time constraints in the preparation and identification, some specimen determinations are tentative and are des-

Table 1. Taxonomic Compositions of Butterfly Families at Jatun Sacha, Cacaulandia, and Pakitza. Number of species are listed in parenthesis following the percentage of species within each family.

Family	Jatun Sacha	Cacaulandia	Pakitza
Hesperiidae	25% (198)	27% (231)	34% (442)
Papilionidae	3% (26)	2% (18)	2% (26)
Pieridae	3% (27)	4% (29)	2% (26)
Nymphalidae	38% (307)	33% (275)	28% (364)
Riodinidae	24% (194)	24% (203)	20% (260)
Lycaenidae	7% (59)	10% (87)	14% (182)

ignated with question marks. A synoptic collection has been deposited in the Museo de Ecuatoriana Nacional in Quito, Ecuador.

For comparative work among the three sites, the percent of species occurring in each family was tabulated, and a test for homogeneity across the families was calculated using a 2x2 contingency table. To compare similarity in species assemblages between the three sites, coefficient of community indices (Pielou 1974) were calculated in pairwise comparisons between Jatun Sacha and Pakitza, Jatun Sacha and Cacaulandia, and Pakitza and Cacaulandia. Only those identified to species (species similarities) or genus (generic similarities) were used in calculations. Lycaenidae was not used in due to poor taxonomic resolution at the genus level and lack of identifications in the Cacaulandia survey (59 of the 87 species were unidentified). Using these adjusted species numbers, percentages were again calculated for family compositions, which were used in contrasting the expected and observed species common to all three sites.

RESULTS

A total of 811 species were recorded at the reserve by the end of 1993 (Appendix 1). The taxonomic composition of the butterfly fauna is as follows: Hesperiidae, 198 spp. (25%), Papilionidae, 26 spp. (3%), Pieridae, 27 spp. (3%), Nymphalidae, 307 spp. (38%), Riodinidae, 194 spp. (24%), and Lycaenidae, 59 spp. (7%). Within Nymphalidae, 56 species of Ithomiinae are those reported by Beccaloni (1995), who conducted a thorough study of this group. Temporal variations in richness and abundance were generally noted for the butterfly families, although quantitative data was collected only for the fruit-feeding nymphalids. The fruit-feeders were more common during the wetter months (DeVries et al. 1997), and many specimens collected during this period were fresh, indicating a recent emergence. During this same time period, other families were observed to be much less abundant, although certain species could be common (*Eurybia dardus, Urbanus simplicius, "Thecla" tephraeus gr*). Hesperiidae, Riodinidae, and to some extent, Lycaenidae, were more abundant as the rainfall decreased in August and September. Differences were noted in the abundance of families and individual species from year to year,

Table 2. Coefficient of Community Indices for Jatun Sacha, Pakitza, and Cacaulandia.

	Species similarities	Generic similarities
Jatun Sacha-Pakitza	49	81
Jatun Sacha-Cacaulandia	45	75
Pakitza-Cacaulandia	38	6

especially among Riodinidae and Lycaenidae. Some species abundance patterns were irregular. For example, I did not see *Stalachtis euterpe* until January, 1993, when it was common for several months along the ridges in the primary forest. Other examples include *Metacharis regalis* and *Emesis temesa.*

Family compositions varied significantly among the three sites ($p>0.05$). Jatun Sacha and Cacaulandia shared a greater similarity in family compositions than any other pairwise comparisons (Table 1). The combination of Riodinidae and Lycaenidae percentages is nearly identical in all three sites (31% to 34%). However, the percentages of Lycaenidae are considerably lower at Jatun Sacha, and to a lesser extent, Cacaulandia, than at Pakitza. In contrast, Jatun Sacha shared a greater number of species and genera with Pakitza rather than Cacaulandia. Coefficient of community values ranked Jatun Sacha and Pakitza with greatest similarity and Pakitza and Cacaulandia with the least similarity (Table 2). Interestingly, only 228 species were common to all three sites. Of those 228 species, Nymphalidae accounted for 53% (121 species) of the total number. Listed in order of abundance, the numbers of species for the other butterfly families were: Hesperiidae (56), Riodinidae (32), Papilionidae (12), and Pieridae (7). The number of observed overlapping nymphalid species was greater than expected when calculated using the family percentages (minus unidentified species and Lycaenidae). For example, the adjusted family compositions for Nymphalidae range from 33% (Pakitza) to 43% (Jatun Sacha). Using the higher percentage, 98 species of the total 228 were expected to be nymphalids, although 121 were actually found to be overlapping. In contrast, the number of overlapping hesperiid species was lower than expected.

DISCUSSION

The survey conducted at Jatun Sacha was aimed at developing a baseline understanding of the butterfly community of the area. A large portion of the fauna undoubtably remains unsampled. This conclusion is supported by the fact that unrecorded species were collected up to the end of the survey time. In addition, preliminary identifications for certain groups have probably underestimated the number of butterfly species actually collected. Because field collection was not standardized, estimations of the total species richness at Jatun Sacha can not be generated through rigorous statistical programs (DeVries et al. 1997). Nonetheless, some estimation can be made from comparisons of inventories at similar localities, such as at Pakitza. Pakitza and Jatun Sacha are both located along the eastern edge of the lowland rainforest and share similar elevation, temperature, and annual rainfall, although Jatun Sacha is more aseasonal than Pakitza. Given these similar environmental factors, it is estimated that 1200 to 1300 species potentially occur at Jatun Sacha. This estimate is supported by applying the model proposed by Beccaloni and Gaston (1995), in which total ithomiine richness from an area is used to predict overall species richness. Beccaloni and Gaston found that ithomiines were, on average, 4.5% of the total species for an area. Given 58 species of ithomiines at Jatun Sacha, approximately 1300 species of butterflies are predicted to occur there. This suggests that a third of the fauna has yet to be recorded, illustrating the importance of further survey work.

Comparing faunal lists from different study sites is confounded by differences in sampling methods and climatic and ecological factors (DeVries 1994). Misidentifications of species and nomenclature changes can also yield misleading results. All of these factors could have influenced comparisons of the species assemblages between the Jatun Sacha, Pakitza, and Cacaulandia, however differences in sampling methodologies was probably most influential. Much of the early sampling in Cacaulandia was conducted by participants in tour groups who may have selectively collected colorful butterflies over some of the more drab species. Since the initial list of butterflies was published from Cacaulandia (Emmel & Austin 1990), the authors have continued their sampling effort and have documented many more species (Austin & Emmel 1996). Patterns of diversity reported here may change when compared with the forthcoming update to the survey. Sampling at Jatun Sacha used bait traps more extensively than Pakitza or Cacaulandia. At Jatun Sacha, 189 species were trapped at rotting fruit (23% of the butterfly fauna). At Pakitza, 130 species were trapped (10% of the butterfly fauna) (Robbins et al. 1996). The survey at Pakitza was conducted on a larger scale than the other two, with intense collecting and a greater number of experts available to identify species, although field crews varied with each sampling period. These differences in sampling have influenced the species recorded, and consequently, the compositions of the various groups.

Environmental variables, most notably climatic factors, are most often correlated with species richness and diversity (Wright et al. 1993). In this study the hypothesis is supported by the results of the generic and species similarities. Jatun Sacha and Pakitza had the highest coefficient of community. Pakitza and Cacaulandia, although geographically closest among the three sites were actually the most dissimilar. This underscores the importance of local conditions on determining species compositions.

Disturbance is another factor influencing species compositions between the three sites. Forest areas with mild disturbances, such as those that exist in Cacaulandia and Jatun Sacha, can experience increases in butterfly diversity in certain groups, such as Nymphalidae (Brown 1982; but see also DeVries et al. 1997). Butterfly species common to open, disturbed areas are rare or absent at Pakitza (Robbins et al. 1996), but are quite common at Jatun Sacha along the road bisecting the reserve. The low species richness of Hesperiidae and Lycaenidae recorded at Jatun Sacha and Cacaulandia could also reflect disturbance, especially at Jatun Sacha. A lepidopterist who has been collecting in the Upper Napo area since 1978 has noted a great decrease in the species and abundance of the Hesperiidae over the last decade as developmental pressures increased (S. Nicolay, pers. comm.).

From the comparisons of the overlapping species, nymphalid species were most common and found at greater numbers than expected. This suggests broader distributions of nymphalids than other butterfly families. This may be due to the wide dispersing capabilities of many nymphalids, which have been correlated with greater distributions (Hanski et al. 1993). It could also reflect broader hostplant ranges for nymphalids or more specialized, and hence, localized host use by other butterfly families. With our limited knowledge of host use even in well studied areas such as Costa Rica (DeVries 1987, 1996; DeVries et al. 1994), examining these broader biogeographical patterns must await further investigations (but see Ackery 1988).

Human influence outside of Jatun Sacha most likely has impacted the butterfly fauna. Species inventories conducted while the area contains a high percentage of pristine forest could be compared with future inventories in a potentially much more disturbed landscape. Because degradation of the upper Napo basin will continue, there is a critical need for more research. For too many species, little is known beyond their site records. A great deal remains to be discovered to complete our understanding of the butterfly fauna, not only in documentation of the species diversity, but also their ecology, evolution, and population dynamics.

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APPENDIX 1

The following is a list of the butterflies collected at Jatun Sacha Biological Station. A question mark (?) following a name indicates questionable identification of the species. Species designated as "unknown" could not be identified to genus or species. The list follows the higher taxonomic classification of Evans (1951, 1952, 1953, 1955) for Hesperiidae, Tyler *et al.* (1994) for Papilionidae, Klots (1933) for Pieridae, Harvey (1991) for Nymphalidae, Forster (1964) for Satyrinae, and Harvey (1987) for Riodinidae.

Hesperiidae 198

Pyrrhopyginae: 4
Elbella theseus Bell, 1933
Passova passova Evans, 1951
Pyrrhopyge proculus cintra Evans, 1951
Pyrrhopyge aziza lexos Evans, 1951

Pyrginae: 107

Achylodes thraso thraso (Hübner, 1807)
Achylodes busirus heros (Ehrmann, 1909)
Aguna coelus (Cramer, 1782)
Aguna clina Evans, 1952
Aguna arunce (Hewitson,1867)
Anastrus obscurus narva Evans, 1953
Anastrus sempiternus simplicior (Möschler, 1876)
Anisochoria pedaliodina Butler, 1870
Antigonus nearchus (Latreille, 1824)
Antigonus mutilatus Hopffer, 1874
Antigonus erosus (Hübner, 1812)
Astraptes fulgerator azul Reakirt, 1866
Astraptes alardus alardus (Stoll, 1790)
Astraptes talus (Cramer, 1777)
Astraptes fulgor (Hayward, 1938)
Astraptes alector hopfferi (Plötz, 1882)
Astraptes cretatus cretatus (Hayward, 1939)
Astraptes anaphus anaphus (Cramer, 1777)
Autochton neis (Plötz, 1882)
Autochton longipennis (Geyer, 1832)
Bolla mancoi (Lindsey, 1925)
Bolla cupreiceps (Mabille, 1889)
Bungalotis erythus Cramer, 1775
Cabrius procas purda Evans, 1952
Calliades zeutus (Möschler, 1879)
Camptopleura auxo (Möschler, 1878)
Carrhenes fuscescens Mabille, 1891
Celaenorrhinus jao (Mabille, 1889)
Celaenorrhinus shema shema (Hewitson, 1877)
Celaenorrhinus syllius (Felder & Felder, 1862)
Charidia lucaria pocus Evans, 1953
Chrysoplectrum perniciosus perniciosus (Herrich-Schäffer, 1869)
Cycloglypha caeruleonigra Mabille, 1904
Cyclosemia pedro Williams & Bell, 1940
Cyclosemia lathaea Hewitson, 1878
Dyscophellus euribates euribates (Cramer, 1782)
Dyscophellus sp.
Dyscophellus ramusis Stoll, 1781
Ebrietas evanidus (Mabille, 1897)
Ebrietas infanda (Butler, 1876)
Entheus priassus telemus Mabille, 1898
Epargyreus socus dicta Evans, 1952
Eracon paulinus (Cramer, 1782)
Gorgythion begga plauta (Möschler, 1867)
Haemactis sanguinalis (Westwood, 1852)
Helias phalaenoides phalaenoides (Hübner, 1812)
Heliopetes alana (Reakirt, 1868)
Hyalothyrus neleus neleus (Linnaeus, 1852)
Mictris crispus crispus (Herrich-Schäffer, 1869)
Milanion hemes pemba Evans, 1953
Morvina morvus Plötz, 1884
Mylon cajus (Plötz, 1884)
Mylon illineatus illineatus (Mabille & Boullet, 1917)
Mylon menippus (Fabricius, 1776)
Narcosius mura (Williams, 1927)
Narcosius colossus (Herrich-Schäffer, 1869)
Nisoniades castolus (Hewitson, 1878)
Nisoniades bessus hecales (Hayward, 1940)
Ouleus fridericus fridericus (Geyer, 1832)
Ouleus calavius calavius (Godman & Salvin, 1895)
Ouleus matria Evans, 1953
Paches trifasciatus Lindsey, 1925
Pellicia dimidiata dimidiata (Herrich-Schäffer, 1870)
Phanus vitreus (Cramer, 1782)
Phareas coeleste Westwood, 1852
Phocides metrodorus metrodorus Bell, 1932
Plumbago plumbago (Plötz, 1884)
Polyctor polyctor polyctor (Prittwitz, 1868)
Polythrix eudoxus (Cramer, 1782)
Polythrix ceculus (Herrich-Schäffer, 1869)
Porphyrogenes passalus passalus (Herrich-Schäffer, 1869)
Potamanaxas hirta hirta (Weeks, 1901)
Potamanaxas flavofasciata flavofasciata (Hewitson, 1870)
Pyrdalus corbulo (Stoll, 1781)
Pyrgus oileus Linnaeus, 1767
Pythonides assacla Mabille, 1883
Pythonides herrenius Geyer, 1838
Pythonides jovianus jovianus (Stoll, 1782)
Quadrus deyrollei porta Evans, 1952
Quadrus cerialis (Cramer, 1782)
Sostrata festiva (Erichson, 1848)
Sostrata pusilla pusilla (Godman & Salvin, 1895)
Spathilepia clonius (Cramer, 1775)
Spioniades artemidas (Cramer, 1782)
Staphylus balsa (Bell, 1937)
Staphylus lizeri (Hayward, 1938)

Tarsoctenus praecia plutia (Hewitson, 1857)
Tarsoctenus papias Hewitson, 1857
Tarsoctenus corytus corba Evans, 1952
Telemiades epicalus sila Evans, 1953
Telemiades centrides Hewitson, 1870
Telemiades amphion misitheus (Mabille, 1888)
Telemiades penidas (Hewitson, 1867)
Typhedanus undulatus (Hewitson, 1867)
Typhedanus orion (Cramer, 1779)
Urbanus teleus (Hübner, 1821)
Urbanus simplicius (Stoll, 1791)
Urbanus pronus Evans, 1952
Urbanus virescens (Mabille, 1877)
Urbanus viterboana viterboana (Ehrmann, 1907)
Urbanus pronta Evans, 1952
Urbanus esta Evans, 1952
Urbanus doryssus doryssus (Swainson, 1831)
Urbanus dorantes dorantes (Stoll, 1791)
Urbanus albimargo takuta Evans, 1952
Urbanus procne (Plötz, 1881)
Xenophanes tryxus (Cramer, 1782)

Hesperiinae: 87
Anatrytone sarah (Burnes, 1994)
Anthoptus epictetus (Fabricius, 1793)
Arita arita (Schaus, 1902)
Aroma aroma Hewitson, 1867
Artines aepitus (Geyer, 1832)
Callimormus radiola radiola (Mabille, 1897)
Carystina lysiteles Mabille, 1891
Carystoides sicania orbius (Godman, 1901)
Carystoides lila Evans, 1955
Chloeria psittacina Felder, 1867
Cobalopsis potaro (William & Bell, 1931)
Cobalopsis nero (Herrich-Schäffer, 1869)
Cobalus virbius virbius (Cramer, 1777)
Conga chydea (Butler, 1870)
Corticea corticea corticea (Plötz, 1883)
Cymaenes tripunctata alumna (Butler, 1877)
Cymaenes cavalla Evans, 1955
Cynea megalops (Godman, 1900)
Damas clavus (Herrich-Schäffer, 1869)
Decinea percosius (Godman, 1900)
Decinea sp.
Decinea derisor (Mabille, 1891)
Ebusus ebusus (Cramer, 1782)
Eutocus quichua Lindsey, 1925
Eutychide subcordata subcordata (Herrich-Schäffer, 1869)
Eutychide complana (Herrich-Schäffer, 1869)
Flaccilla aecas Stoll, 1781
Hylephila phylaeus phylaeus (Drury, 1773)
Justinia phaetusa phaetusa (Hewitson, 1866)
Lento lento Mabille, 1878
Lycas boisduvalii Ehrmann, 1909
Metron nr. chrysogastra
Mnasilus allubita Butler, 1877
Moeris vopiscus vopiscus (Herrich-Schäffer, 1869)
Moeris striga Geyer, 1832
Molo mango mango (Guenee, 1865)
Molo petra Evans, 1955
Morys geisa geisa (Möschler, 1878)
Mucia sp.
Nastra insignis (Plötz, 1882)
Niconiades nikko Hayward, 1948
Nyctelius nyctelius (Latreille, 1824)
Orses cynisca (Swainson, 1821)
Oxynthes corusca (Herrich-Schäffer, 1869)
Panoquina fusina fusina (Hewitson, 1868)
Panoquina evadnes (Stoll, 1781)
Papias proximus (Bell, 1934)
Papias integra Mabille, 1891
Paracarystus menestries rona (Hewitson, 1866)
Parphorus decora (Herrich-Schäffer, 1869)
Parphorus storax storax (Mabille, 1891)
Penicula crista Evans, 1955
Penicula criska jon Nicolay, 1980
Penicula bryanti (Weeks, 1906)
Perichares philetes dolores (Reakirt, 1868)
Phanes almoda (Hewitson, 1866)
Pompeius pompeius (Latreille, 1824)
Quinta cannae (Herrich-Schäffer, 1869)
Racta sp.
Saliana salius (Cramer, 1776)
Saliana esperi Evans, 1955
Saliana antoninus Latrielle, 1824
Saliana triangularis (Kaye, 1913)
Saturnus tiberius suffuscus (Hayward, 1940)
Sodalia sodalis Butler, 1877
Talides sergestus Cramer, 1775)
Talides sinois sinois Hübner, 1819
Telles arcalaus (Cramer, 1782)
Thargella caura caura (Plötz, 1882)
Thespias dalman Latreille, 1824

Thoon sp.
Thoon ponka Evans, 1955
Thoon taxes (Godman, 1900)
Thoon modius (Mabille, 1889)
Thracides phidon (Cramer, 1779)
Thracides smaragdulus (Herrich-Schäffer, 1869)
Vehilius stictomenes stictomenes Butler, 1877
Vehilius illudens Mabille, 1891
Vehilius vetula (Mabille, 1878)
Vehilius inca (Scudder, 1872)
Venas caeruleans (Mabille, 1828)
Vettius phyllus phyllus (Cramer, 1777)
Vettius richardi (Weeks, 1906)
Vettius artona (Hewitson, 1868)
Vettius marcus marcus (Fabricius, 1787)
Xeniades orchamus orchamus (Cramer, 1777)
Zenis jebus melaleuca (Plötz, 1882)

Papilionidae: 26
Battus crassus crassus (Cramer, 1777)
Battus polydamas polydamas (Linnaeus, 1758)
Battus belus varus (Kollar, 1850)
Eurytides dolicaon ?
Heraclides torquatus torquatus (Cramer, 1777)
Heraclides thoas cinyras (Ménétriés, 1857)
Heraclides isidorus flavescens (Oberthür, 1880)
Heraclides hyppason hyppason (Cramer, 1776)
Heraclides chiansiades chiansiades (Westwood, 1872)
Heraclides astyalus phanias (Rothschild & Jordan, 1906)
Heraclides androgeus androgeus (Cramer, 1776)
Mimoides ariarathes gayi (Lucas, 1852)
Mimoides xynias (Hewitson, 1867)
Mimoides pausanias pausanias (Hewitson, 1852)
Parides anchises drucei (Butler, 1874)
Parides aeneas bolivar (Hewitson, 1850)
Parides vertumnus bogotanus (Felder & Felder, 1864)
Parides neophilus olivencius (Bates, 1861)
Parides erithalion guillerminae (Pischedda & Racheli, 1986)
Parides sesostris sesostris (Cramer, 1780)
Parides lysander brissonius (Hübner, 1819)
Parides chabrias chabrias (Hewitson, 1852)
Protesilaus telesilaus telesilaus (Felder & Felder, 1864)
Protographium agesilaus autosilaus (Bates, 1861)
Protographium thyastes thyastinus (Oberthür, 1880)
Pterourus zagreus neyi (Niepelt, 1909)

Pieridae 27
Aphrissa statira (Cramer, 1777)
Archonias bellona (Cramer, 1776)
Charonias eurytele (Hewitson, 1853)
Cunizza hirlanda (Stoll, 1791)
Dismorphia theucharila (Doubleday, 1848)
Dismorphia amphiona Cramer, 1780
Enantia melite (Linnaeus, 1763)
Enantia lina (Herbst, 1792)
Eurema daira (Godart, 1819)
Eurema sp.
Eurema albula (Cramer, 1776)
Eurema xanthochlora (Kollar, 1850)
Itaballia pisonis (Hewitson, 1861)
Itaballia demophile (Linnaeus, 1763)
Leptophobia aripa (Boisduval, 1836)
Leucidia brephos (Hübner, 1809)
Moschoneura pinthaeus (Linnaeus, 1758)
Patia oresis (Boisduval, 1836)
Perrhybis pyrrha (Cramer, 1782)
Perrhybis lorena (Hewitson, 1852)
Phoebis rurina (Felder & Felder, 1861)
Phoebis philea (Linnaeus, 1763)
Phoebis argante (Fabricius, 1775)
Phoebis trite (Linnaeus, 1758)
Pieriballia mandella (Felder & Felder, 1861)
Pyrisitia venusta (Boisduval, 1836)
Pyrisitia nise (Cramer, 1776)

Nymphalidae 307

Heliconiinae 22
Actinote sp.
Actinote pellenea Hübner, 1821
Agraulis vanillae (Linnaeus, 1763)
Dione juno (Cramer, 1780)
Dryadula phaetusa (Linnaeus, 1758)
Dryas iulia (Fabricius, 1775)
Eueides tales (Cramer, 1776)
Eueides aliphera (Godart, 1819)
Eueides isabella isabella (Cramer, 1782)
Eueides lampeto acacetes Hewitson, 1869
Eueides lybia (Fabricius, 1775)

Eueides vibilia (Godart, 1819)
Heliconius erato lativitta Butler, 1877
Heliconius hecale quitalena Hewitson, 1853
Heliconius elevatus elevatus Nöldner, 1901
Heliconius wallacei Reakirt, 1866
Heliconius sara (Fabricius, 1793)
Heliconius melpomene aglaope Felder & Felder, 1862
Heliconius numata euphone Felder & Felder, 1862
Laparus doris (Linnaeus, 1771)
Neruda aoede bartletti Druce, 1876
Philaethria dido (Linnaeus, 1763)

Nymphalinae 20
Anartia amathea (Linnaeus, 1758)
Anartia jatrophae (Linnaeus, 1763)
Anthanassa drusilla (Felder & Felder, 1861)
Castilia perilla (Hewitson, 1852)
Castilia angusta (Hewitson, 1868)
Castilia ofella (Hewitson, 1864)
Eresia clara clara Bates, 1864
Eresia eunice eunice (Hübner, 1807)
Eresia nauplius (Linnaeus, 1758)
Eresia sp.
Eresia perna Hewitson, 1852
Eresia pelonia pelonia Hewitson, 1852
Hypanartia lethe (Fabricius, 1793)
Junonia evarete (Cramer, 1870)
Metamorpha elissa Hübner, 1819
Phyciodes sp.
Phyciodes aveyrana (Bates, 1864)
Siproeta stelenes Linnaeus, 1758
Tegosa claudina (Eschscholtz, 1821)
Telenassa burchelli (Moulton, 1909)

Limenitidinae 78
Adelpha boeotia (Felder & Felder, 1867)
Adelpha delinita (Fruhstorfer, 1913)
Adelpha iphiclus (Linnaeus, 1758)
Adelpha erotia (Hewitson, 1847)
Adelpha cytherea (Linnaeus, 1758)
Adelpha celerio (Bates, 1864)
Adelpha boreas (Butler, 1866)
Adelpha sp. 3
Adelpha sp. 2
Adelpha lerna (Hewitson, 1847)
Adelpha melanthe (Bates, 1864)
Adelpha sp. 1
Asterope degandii (Hewitson, 1850)
Baeotus japetus (Staudinger, 1885)
Baeotus deucalion (Felder & Felder, 1860)
Baeotus amazonicus (Riley, 1919)
Batesia hypochlora (Felder & Felder, 1862)
Biblis hyperia (Cramer, 1780)
Callicore cynosura (Doubleday, 1847)
Callicore lyca (Doubleday, 1847)
Callicore hystaspes (Fabricius, 1782)
Callicore hesperis (Guérin, 1844)
Callicore eunomia (Hewitson, 1853)
Callicore cyllene (Doubleday, 1847)
Catacore kolyma (Hewitson, 1852)
Catonephele acontius acontius (Linnaeus, 1758)
Catonephele numilia numilia (Cramer, 1776)
Colobura dirce (Linnaeus, 1758)
Diaethria clymena (Cramer, 1776)
Dynamine geta (Godman & Salvin, 1878)
Dynamine racidula (Hewitson, 1852)
Dynamine zenobia (Bates, 1865)
Dynamine glauce (Bates, 1865)
Dynamine gisella (Hewitson, 1852)
Dynamine athemon (Linnaeus, 1758)
Dynamine artemisia (Fabricius, 1793)
Dynamine anubis (Hewitson, 1859)
Ectima iona (Doubleday, 1848)
Ectima lirides (Staudinger, 1885)
Eunica eurota eurota (Cramer, 1776)
Eunica sophonisba agele Seitz, 1915
Eunica norica occia Fruhstorfer, 1909
Eunica alpais alpais (Godart, 1824)
Eunica mygdonia mygdonia (Godart, 1824)
Eunica marsolia fasula Fruhstorfer, 1909
Eunica amelia erroneata Oberthür, 1916
Eunica clytia (Hewitson, 1852)
Haematera pyramus (Fabricius, 1782)
Hamadryas laodamia laodamia (Cramer, 1777)
Hamadryas arinome arinome (Lucas, 1853)
Hamadryas amphinome amphinome (Linnaeus, 1767)
Hamadryas feronia feronia (Linnaeus, 1758)
Hamadryas chloe chloe (Stoll, 1791)
Historis acheronta (Fabricius, 1775)
Historis odius (Fabricius, 1775)
Marpesia furcula (Fabricius, 1793)
Marpesia iole (Drury, 1782)
Marpesia chiron (Fabricius, 1775)
Marpesia berania (Hewitson, 1852)
Marpesia crethon (Fabricius, 1776)
Marpesia petreus (Cramer, 1776)
Marpesia themistocles (Fabricius, 1793)

Nessaea obrina lesoudieri Le Moult, 1933
Nessaea hewitsonii hewitsonii (Felder & Felder, 1859)
Nica flavilla (Godart, 1824)
Panacea prola (Doubleday, 1848)
Panacea procilla (Hewitson, 1854)
Panacea regina (Bates, 1864)
Paulogramma pyracmon (Godart, 1824)
Peria lamis (Cramer, 1780)
Pyrrhogyra neaerea (Linnaeus, 1758)
Pyrrhogyra otolais (Bates, 1864)
Pyrrhogyra crameri (Aurivillius, 1882)
Smyrna blomfildia (Fabricius, 1782)
Temenis pulchra (Hewitson, 1861)
Temenis laothoe (Cramer, 1777)
Tigridia acesta (Linnaeus, 1758)
Vila azeca (Doubleday, 1848)

Charaxinae 26
Agrias claudina (Godart, 1824)
Agrias hewitsonius Bates, 1860
Agrias amydon Hewitson, 1854
Archaeoprepona licomedes (Cramer, 1777)
Archaeoprepona demophoon (Hübner, 1814)
Archaeoprepona demophon (Linnaeus, 1758)
Archaeoprepona amphimachus (Fabricius, 1775)
Coenophlebia archidona Felder & Felder, 1862
Consul fabius aequatorialis (Butler, 1875)
Fountainea ryphea ryphea (Cramer, 1776)
Fountainea eurypyle (Felder & Felder, 1862)
Hypna clytemnestra (Cramer, 1777)
Memphis morvus (Fabricius, 1775)
Memphis florita (Druce, 1877)
Memphis sp.
Memphis philumena philumena (Doubleday, 1849)
Memphis arachne (Cramer, 1776)
Memphis xenocles (Westwood, 1850)
Memphis offa (Druce, 1877)
Memphis oenomais (Boisduval, 1870)
Memphis polycarmes (Fabricius, 1775)
Prepona pheridamas (Cramer, 1777)
Prepona laertes (Hübner, 1814)
Prepona pylene Hewitson, 1854
Siderone marthesia (Cramer, 1777)
Zaretis itys (Cramer, 1777)

Apaturinae 8
Doxocopa cherubina (Felder & Felder, 1867)
Doxocopa clothilda (Felder & Felder, 1867)
Doxocopa cyane (Latreille, 1813)
Doxocopa felderi (Godman & Salvin, 1884)
Doxocopa laure (Drury, 1773)
Doxocopa pavon (Latreille, 1809)
Doxocopa sp.
Doxocopa agathina (Cramer, 1777)

Morphinae 8
Antirrhea avernus (Hopffer, 1874)
Antirrhea sp.
Morpho achilles (Linnaeus, 1758)
Morhpo adonis (Cramer, 1776)
Morpho deidamia (Hübner, 1819)
Morpho hecuba (Linnaeus, 1771)
Morpho menelaus (Linnaeus, 1758)
Morpho rhetenor (Cramer, 1776)

Brassolinae 15
Brassolis sophorae (Linnaeus, 1758)
Caligo illioneus (Cramer, 1776)
Caligo idomeneus (Linnaeus, 1758)
Caligo eurilochus (Cramer, 1776)
Caligo placidianus (Staudinger, 1887)
Caligo euphorbus (Felder & Felder, 1862)
Catoblepia xanthicles (Godman & Salvin, 1881)
Catoblepia berecynthia (Cramer, 1777)
Catoblepia xanthus (Linnaeus, 1758)
Eryphanis polyxena (Meerburgh, 1780)
Opoptera aorsa (Godart, 1824)
Opsiphanes quiteria (Cramer, 1782)
Opsiphanes invirae (Hübner, 1808)
Opsiphanes cassiae (Linnaeus, 1758)
Selenophanes cassiope (Cramer, 1776)

Satyrinae 68
Amphidecta calliomma (Felder & Felder, 1862)
Amphidecta pignerator (Butler, 1867)
Bia actorion (Linnaeus, 1763)
Caeruleuptychia coelica (Hewitson, 1869)
Caeruleuptychia nr. pencillata
Caeruleuptychia sp. 2
Caeruleuptychia aegrota (Butler 1867)
Caeruleuptychia pilata (Butler, 1867)
Caeruleuptychia sp. 1
Cepheuptychia cephus (Fabricius, 1775)
Chloreuptychia herseis (Godart, 1824)
Chloreuptychia chloris (Cramer, 1782)

Chloreuptychia tolumnia (Cramer, 1777)
Chloreuptychia arnaca (Fabricius, 1776)
Chloreutychia agatha (Butler, 1867)
Cissia proba (Weymer, 1911)
Cissia terrestris (Butler, 1867)
Cissia penelope (Fabricius, 1775)
Cissia sp. 2
Cissia myncea (Cramer, 1782)
Cissia sp. 1
Cithaerias aurora (Felder & Felder, 1862)
Erichthodes erichtho (Butler, 1867)
Euptychia sp. 3
Euptychia sp. 4
Euptychia sp. 1
Euptychia picea (Butler, 1867)
Euptychia sp. 2
Haetera piera (Linnaeus, 1758)
Hermeuptychia hermes (Fabricius, 1775)
Magneuptychia analis (Godman, 1905)
Magneuptychia tricolor (Hewitson, 1850)
Magneuptychia modesta (Butler, 1867)
Magneuptychia alcinoe (Felder & Felder, 1867)
Magneuptychia ocypete (Fabricius, 1776)
Magneuptychia ayaya (Butler, 1867)
Magneuptychia nr. helle 1
Magneuptychia nr. helle 2
Magneuptychia nr. inani
Magneuptychia libye (Linnaeus, 1767)
Magneuptychia sp.
Manataria hyrnethia (Fruhstorfer, 1912)
Megeuptychia antonoe (Cramer, 1776)
Pareuptychia hesionides (Forster, 1964)
Pareuptychia ocirrhoe (Fabricius, 1776)
Pareuptychia sp.
Pierella lena (Linnaeus, 1767)
Pierella lamia (Sulzer, 1776)
Pierella hortona (Hewitson, 1854)
Pierella astyoche (Erichson, 1848)
Posttaygetis penelea (Cramer, 1777)
Pseudodebis sp.
Pseudodebis valentina (Cramer, 1780)
Pseudodebis marpessa (Hewitson, 1862)
Splendeuptychia nr. itonis
Splendeuptychia itonis (Hewitson, 1862)
Splendeuptychia sp. 1
Taygetis celia (Cramer, 1780)
Taygetis armillata (Butler, 1868)
Taygetis sosis (Hopffer, 1874)
Taygetis cleopatra (Felder & Felder, 1867)
Taygetis virgilia (Cramer, 1776)
Taygetis rufomarginata (Staudinger, 1888)
Taygetis thamyra (Cramer, 1779)
Taygetis laches (Fabricius, 1793)
Taygetis mermeria (Cramer, 1776)
Yphthimoides erigone (Butler, 1867)
Yphthimoides renata (Cramer, 1782)

Danainae 4
Danaus plexippus (Linnaeus, 1758)
Lycorea ilione (Cramer, 1776)
Lycorea pasinuntia brunnea Riley, 1919
Lycorea cleobaea atergatis Doubleday, 1847

Ithomiinae 58
"Hypoleria" orolina orolina (Hewitson, 1861)
"Hypoleria" seba oculata Haensch, 1903
"Pseudoscada" florula aureola (Hewitson, 1855)
Aeria eurimedea negricola (Felder & Felder, 1865)
Callithomia lenea zelie Guérin, 1844
Callithomia alexirrhoe butes Godman & Salvin, 1898
Ceratinia tutia poecila (Bates, 1862)
Ceratiscada hymen (Haensch, 1905)
Dircenna loreta loreta Haensch, 1903
Forbestra equicola equicoloides (Godman & Salvin, 1898)
Forbestra olivencia juntana (Haensch, 1903)
Godyris zavaleta matronalis (Weymer, 1883)
Godyris dircenna dircenna (Felder & Felder, 1862)
Heterosais nephele nephele (Bates, 1862)
Hyalyris coeno norellana (Haensch, 1903)
Hypoleria lavinia chrysodonia (Bates, 1862)
Hypoleria sarepta aureliana (Bates, 1862)
Hyposcada anchiala ecuadorina Bryk, 1953
Hyposcada illinissa ida Haensch, 1903
Hyposcada kena kena (Hewitson, 1872)
Hypothyris moebiusi unicolora (Tessmann, 1928)
Hypothyris mamercus mamercus (Hewitson, 1869)
Hypothyris euclea intermedia (Butler, 1873)
Hypothyris anastasia honesta (Weymer,

1883)
Hypothyris moebiusi moebiusi (Haensch, 1903)
Hypothyris semifluva satura (Haensch, 1903)
Hypothyris anastasia bicolor (Haensch, 1903)
Hypothyris fluonia berna (Haensch, 1903)
Ithomia salapia salapia Hewitson, 1853
Ithomia salapia travella Haensch, 1903
Ithomia amarilla amarilla Haensch, 1903
Ithomia agnosia agonsia Hewitson, 1855
Mechanitis mazaeus mazaeus Hewitson, 1860
Mechanitis mazaeus fallax Butler, 1873
Mechanitis mazaeus visenda Butler, 1877
Mechanitis messenoides messenoides Felder & Felder, 1865
Mechanitis polymnia dorissides Staudinger, 1844
Mechanitis lysimnia elisa (Guérin, 1844)
Melinaea mnasias abtigua Brown, 1977
Melinaea menophilus cocana Haensch, 1903
Melinaea marsaus monthone Hewitson, 1860
Melinaea maelus maenois Hewitson, 1869
Methona curvifascia curvifascia Weymer, 1883
Methona confusa psamathe Godman & Salvin, 1898
Napeogenes achaea achaea (Hewitson, 1869)
Napeogenes aethra aethra (Hewitson, 1869)
Napeogenes inachia avila Haensch, 1903
Napeogenes stella (Hewitson, 1855)
Napeogenes sylphis caucayaensis Fox & Real, 1971
Napeogenes pharo pharo (Felder & Felder, 1862)
Oleria gunilla lota (Hewitson, 1872)
Oleria tigilla tigilla (Weymer, 1899)
Oleria sexmaculata sexmaculata (Haensch, 1903)
Oleria lerda lerda (Haensch, 1909)
Oleria agarista agarista (Felder & Felder, 1862)
Oleria assimilis assimilis (Haensch, 1903)
Pseudoscada timna timna (Hewitson, 1855)
Pteronymia vestilla sparsa Haensch, 1903
Scada reckia ethica (Hewitson, 1861)
Thyridia psidii ino Felder & Felder, 1862
Tithorea harmonia hermias Godman & Salvin, 1898

Riodinidae 194
Adelotypa amasis (Hewitson, 1870)
Adelotypa alector Butler, 1867
Adelotypa senta (Hewitson, 1853)
Adelotypa sp. 1
Adelotypa sp. 2
Adelotypa sp. 3
Adelotypa sp. 4
Alesa amesis (Cramer, 1777)
Alesa sp.
Alesa telephae (Boisduval, 1836)
Amarynthis meneria (Cramer, 1776)
Ancyluris aulestes (Cramer, 1777)
Ancyluris meliboeus (Fabricius, 1777)
Anteros acheus (Stoll, 1781)
Anteros allectus Westwood, 1851
Argyrogrammana sp. 3
Argyrogrammana sp. 1
Argyrogrammana sp. 2
Argyrogrammana trochilia Westwood, 1851
Calospila trinitatis (Lathy, 1932)
Calospila parthaon (Dalman, 1823)
Calospila sp.
Calospila maeonides ?
Calospila rhodope (Hewitson, 1853)
Calospila emylius (Cramer, 1775)
Calydna punctata Felder & Felder, 1861
Caria trochilus Erichson, 1818
Caria sponsa Staudinger, 1888
Caria mantinea (Felder & Felder, 1861)
Caria nr. mantinea
Chalodeta theodora (Felder & Felder, 1862)
Chalodeta chaonitis (Hewitson, 1866)
Chalodeta lypera (Bates, 1868)
Chamaelimnas briola Bates, 1868
Charis nr. anius
Charis cleonus (Stoll, 1782)
Charis anius (Cramer, 1776)
Charis sp.
Cremna actoris (Cramer, 1776)
Crocozona caecias (Hewitson, 1866)
Cyrenia martia Westwood, 1851
Emesis ocypore (Geyer, 1837)
Emesis nr. lucinda 1
Emesis nr.lucinda 2
Emesis sp.
Emesis temesa (Hewitson, 1877)
Emesis fatima (Cramer, 1780)
Emesis lucinda (Cramer, 1775)
Eshtemopsis celina Bates, 1868
Eunogyra satyrus Westwood, 1851
Eurybia silaceana Stichel, 1924
Eurybia latifasciata Hewitson, 1869
Eurybia lamia (Cramer, 1777)
Eurybia nicaeas Fabricius, 1775
Eurybia sp.
Eurybia jemima Hewitson, 1869
Eurybia dardus Fabricius, 1787
Eurybia cyclopia Stichel, 1910
Euselasia uria (Hewitson, 1855)
Euselasia urites gr.
Euselasia mirania (Bates, 1868)
Euselasia sp. 1
Euselasia sp. 4

Euselasia sp. 2
Euselasia sp. 3
Euselasia pellonia Stichel, 1919
Euselasia orfita (Cramer, 1777)
Euselasia opalescens (Hewitson, 1855)
Euselasia sp. 8
Euselasia lysias gr.
Euselasia melaphaea (Hübner, 1823)
Euselasia lysimachus (Staudinger, 1888)
Euselasia sp. 5
Euselasia sp. 6
Euselasia euriteus (Cramer, 1777)
Euselasia issoria Hewitson, 1869
Euselasia hygenius gr.
Euselasia hahneli Butler, 1874
Euselasia gelanor (Stoll, 1780)
Euselasia sp. 7
Euselasia fabia?
Euselasia everitus (Hewitson, 1855)
Euselasia euryone (Hewitson, 1856)
Euselasia nr. euriteus
Euselasia crotopus gr. 2
Euselasia euoras (Hewitson, 1856)
Euselasia eumenes (Hewitson, 1855)
Euselasia eumedia (Hewitson, 1855)
Euselasia eulione (Hewitson, 1856)
Euselasia crotopus gr. 1
Euselasia crinon Stizhel, 1919
Euselasia arbas (Stoll, 1782)
Euselasia anica gr.
Hyphilaria parthenis (Westwood, 1851)
Hyphilaria nicia (Hübner, 1819)
Ithomiola cascella (Hewitson, 1870)
Juditha molpe (Hübner, 1808)
Lasaia agesilas (Latreille, 1813)
Lasaia sp.
Lasaia pseudomeris Clench, 1972
Leucochimona nr. philemon
Leucochimona hyphea (Cramer, 1776)
Lyropteryx apollonia Westwood, 1851
Melanis xarifa (Hewitson, 1853)
Mesene nola Herrich-Schäffer, 1893
Mesene hya Westwood, 1851
Mesophthalma idotea (Westwood, 1851)
Mesosemia sp. 3
Mesosemia steli Hewitson, 1858
Mesosemia philocles Linnaeus, 1758
Mesosemia sp. 2
Mesosemia judicialis Butler, 1874
Mesosemia sp. 1
Mesosemia eumene (Cramer, 1776)
Mesosemia nr. judicialis
Mesosemia loruhama Hewitson, 1869
Mesosemia cippus (Hewitson, 1859)
Mesosemia nr. cyanira
Mesosemia nr. ephyne
Mesosemia sp. 5
Mesosemia sp. 4
Mesosemia melpia (Hewitson, 1869)
Mesosemia gertraudis Stichel, 1910
Mesosemia ulrica (Cramer, 1777)
Mesosemia nr. thetys
Mesosemia nr. tenebricosa
Mesosemia magate?
Mesosemia nina (Herbst, 1793)
Metacharis lucius (Fabricius, 1793)
Metacharis nr. regalis
Metacharis regalis Butler, 1867
Methone cecilia (Cramer, 1777)
Monethe albertus Felder & Felder, 1862
Mycastor nealces (Hewitson, 1871)
Napaea melampia (Bates, 1867)
Notheme eumeus (Fabricius, 1781)
Nymphidium baoetia (Hewitson, 1853)
Nymphidium cachrus (Fabricius, 1787)
Nymphidium caricae (Linnaeus, 1758)
Nymphidium leucosia (Hübner, 1806)
Nymphidium nr. derufata
Nymphidium nr. lisimon
Nymphidium sp.
Nymphidium mantus (Cramer, 1775)
Nymphidium minuta gr.
Nymphidium omois Hewitson, 1865
Pandemos pasiphae (Cramer, 1775)
Parcella amarynthina (Felder & Felder, 1865)
Parnes philotes Westwood, 1851
Parnes nycteis Westwood, 1851
Perophthalma tullius Fabricius, 1787
Rhetus periander (Cramer, 1777)
Riodina lysippus (Linnaeus, 1798)
Sarota sp. 2
Sarota acantus (Stoll, 1782)
Sarota chrysus (Stoll, 1782)
Sarota sp. 3
Sarota sp. 1
Semomesia sp.
Setabis sp.
Setabis epitus (Cramer, 1780)
Setabis salvini?
Setabis buckleyi (Grose-Smith, 1898)
Stalachtis euterpe (Linnaeus, 1758)
Stalachtis calliope (Linnaeus, 1758)
Symmachia probetor (Stoll, 1782)
Symmachia sp.
Symmachia calligraphia (Hewitson, 1867)
Symmachia accusatrix Westwood, 1851
Symmachia asclepia Hewitson, 1870
Synargis gela (Hewitson, 1853)
Synargis sp.
Synargis abaris (Cramer, 1776)
Synargis chaonia (Hewitson, 1853)
Synargis orestesa (Cramer, 1780)

Syngaris ochra (Bates, 1868)
Syrmatia aethiops Staudinger, 1888
Teratophthalma phelina (Felder & Felder, 1862)
Themone pais (Hübner, 1820)
Theope sp.
Theope eudocia Westwood, 1851
Theope lycaenina Bates, 1868
Theope nr. thootes
Theope virgilius (Fabricius, 1793)
Thisbe fenestrella Lathy, 1932
Xynias christalla Grose-Smith, 1902
unknown (8)

Lycaenidae 59
"Thecla" hemon (Cramer, 1775)
"Thecla" bosora Hewitson, 1870
"Thecla" orobia (Hewitson, 1867)
"Thecla" gigantea Hewitson, 1867
"Thecla" maculata (Lathy, 1936)
"Thecla" cupentus (Stoll, 1781)
"Thecla" gibberosa (Hewitson, 1867)
"Thecla" tephraeus gr.
"Thecla" ophia Hewitson, 1868
"Thecla" tephraeus (Geyer, 1837)
"Thecla" phegeus (Hewitson, 1865)
"Thecla" nr. gadira
"Thecla" nr. augustinula
"Thecla" carteia Hewitson, 1870
"Thecla" ergina or ligurina
"Thecla" aruma (Hewitson, 1877)
"Thecla" nr. mycon
"Thecla" nr. empusa
"Thecla" hesperitis (Butler and Druce, 1877)
Arawacus dolylas (Cramer, 1776)
Arawacus aetolus (Sulzer, 1776)
Arcas imperialis (Cramer, 1775)
Calycopis anapa Field, 1967
Calycopis indigo (Druce, 1907)
Calycopis isobeon complex
Calycopis cerata (Hewitson, 1877)
Calycopis xenata (Hewitson, 1877)
Calycopis pisis complex 3
Calycopis pisis complex 2
Calycopis atnius complex
Calycopis calus (Godart, 1824)
Calycopis centoripa Hewitson, 1868
Calycopis pisis complex 1
Celmia celmus (Cramer, 1775)
Chalybs janias (Cramer, 1779)
Contrafacia imma Prittwitz, 1865
Cyanophrys amyntor ?
Electrostrymon ecbatana Hewitson, 1868
Eumaeus minijas (Hübner, 1809)
Evenus gabriela (Cramer, 1775)
Hypostrymon asa Hewitson, 1873
Janthecla leea Venables & Robbins, 1991
Janthecla sista Hewitson, 1867
Lamprospilus orcidia (Hewitson, 1874)
Mithras nautes (Cramer, 1779)
Ocaria ocrisia (Hewitson, 1869)
Ocaria thales (Fabricius, 1793)
Panthiades bitias (Cramer, 1777)
Panthiades aeolus (=pelion) (Fabricius, 1775)
Pseudolycaena marsyas (Linnaeus, 1758)
Rekoa palegon (Cramer, 1780)
Siderus leucophaeus (Hübner, 1818)
Strymon ziba (Hewitson, 1868)
Theclopsis lydus (Hübner, 1819)
Theclopsis gargara Hewitson, 1868
Theritas mavors (Hübner, 1818)
Thestius pholeus (Cramer, 1777)
Tmolus echion (Linnaeus, 1767)
Zizula cyna (Edwards, 1881)

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Flexural stiffness patterns of butterfly wings (Papilionoidea)

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Abstract. A flying insect generates aerodynamic forces through the active manipulation of the wing and the "passive" properties of deformability and wing shape. To investigate these "passive" properties, the flexural stiffness of dried forewings belonging to 10 butterfly species was compared to the butterflies' gross morphological parameters to determine allometric relationships. The results show that flexural stiffness scales with wing loading to nearly the fourth power ($p_w^{3.9}$) and is highly correlated with wing area cubed ($S^{3.1}$).

The generalized map of flexural stiffness along the wing span for *Vanessa cardui* has a reduction in stiffness near the distal tip and a large reduction near the base. The distal regions of the wings are stiffer against forces applied to the ventral side, while the basal region is much stiffer against forces applied dorsally. The null hypothesis of structural isometry as the explanation for flexural stiffness scaling is rejected. Instead, selection for a consistent dynamic wing geometry (angular deflection) in flight may be a major factor controlling general wing stiffness and deformability. Possible relationships to aerodynamic and flight habit factors are discussed. This study proposes a new approach to addressing the mechanics of insect flight and these preliminary results need to be tested using fresh wings and more thorough sampling.

Key Words: biomechanics, butterfly wings, flight, allometry, flexural stiffness, aerodynamics

INTRODUCTION

A flying insect generates aerodynamic forces primarily through the active manipulation of wing movements and the "passive" morphological properties of deformability and wing shape. The morphological parameters of insect flight have been the subject of various investigations (Weis-Fogh 1977, Wootton 1981, Ellington 1984, Betts 1986, Dudley 1990, Srygley 1994), complimenting an extensive body of work on the aerodynamics of insect and hovering flight (e.g., Jensen 1956, Weis-Fogh 1973, Nachtigall 1974, Ellington 1980, 1984b). However, empirical measures of aerodynamically relevant mechanical properties of wings are absent from the literature.

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Various measures of wing geometry have been used as surrogates for the biomechanical properties of wings, but these can be only crude approximations given the complex structure and construction of wings. Here, I measure the deformability of butterfly wings to determine its interspecific scaling relationships with various wing and body size parameters. This investigation complements qualitative analyses of structure and allometry, theoretical predictions of wing properties, and observations of flight performance and behavior.

Previous studies of insect flight have investigated the aerodynamics of flight through theoretical calculations (Weis-Fogh 1977, Ellington 1980), allometric patterns of wing shape and wing beat (Greenewalt 1962, Ellington 1984), wing movements and deformations during flight (Wootton 1981, Betts 1986), flight habit and behavior (Betts & Wootton 1988, Dudley 1990, Srygley 1994), the aerodynamic effects of angle of attack or presence of scales (Jensen 1956, Nachtigall 1974, Martin & Carpenter 1977), and common structural features of butterfly wings (Wootton 1981). To date, no study has measured deformability of wings. This study will demonstrate the potential of biomechanical approaches to understanding insect flight.

Flexural stiffness (*EI*) is a measure of deformability, which by controlling wing shape under aerodynamic load modifies aerodynamic forces. The flexural stiffness of a structure is a function of two properties: the elastic modulus (*E*, stress per unit strain) of the material that composes it; and the second moment of inertia (*I*), a function of the cross-sectional geometry. This study will 1) determine flexural stiffness patterns within butterfly wings, and 2) define allometric relationships among flexural stiffness and morphological parameters. Analysis of allometric patterns can provide insights into the importance of developmental or structural constraints relative to presumptive adaptations (Strauss 1990).

Some expectations for flexural stiffness patterns can be drawn from previous studies. Betts (1986) found that in a small sample of Heteroptera, angular deformation of the wing tip was weakly correlated with angular momentum of the wing. A principal conclusion derived from Betts (1986) and Wootton (1981) is that dorsal transverse flexion (producing a dorsally concave surface) is more strongly resisted by wing structure (i.e., ventrally stiffer) than is ventral transverse flexion. Wootton hypothesized that ventral flexion may reduce drag on the upstroke of wings exhibiting minimal wing-twisting, as in Lepidoptera. These studies would predict 1) that stiffness will decrease in the distal region, possibly associated with a flexion line (see Wootton, 1981 for detailed explanation), and 2) ventral stiffness (e.g., resistance to ventrally directed forces which would produce dorsal transverse flexion) will be significantly greater than dorsal stiffness.

Two alternative hypotheses regarding interspecific scaling of flexural stiffness are tested. H_0: the measured index of flexural stiffness is entirely a mechanical consequence of structural and geometric isometry. H_1: the index of flexural stiffness scales so that angular deflection under proportionate loading regimes remains consistent (cf. elastic similarity; McMahon, 1973). The predictions based on these hypotheses are presented in the Discussion.

MATERIALS AND METHODS

Species selected and morphometric measures

Three individuals for each of ten species were included among a mixed dry butterfly set obtained from Carolina Biologic Supply Company. The 10 species were *Battus polydamas* Linnaeus 1758 (Papilionidae) *Parides montezuma* Westwood 1842 (Papilionidae), *Danaus lotis* Cramer 1779 (Nymphalidae), *Phoebis statira* Cramer 1777 (Pieridae), *Eurema hecabe* Linnaeus 1758 (Pieridae), *Pereute charops* Boisduval 1836 (Pieridae), *Ascia monuste* Linnaeus 1758 (Pieridae), *Pyrrhogyra neaerea* Linnaeus 1758 (Nymphalidae), the heliconiine *Dione juno* Cramer 1782 (Nymphalidae), and the pierid *Catopsillia scylla* Linnaeus 1764. Two living *Vanessa cardui* Linnaeus 1758 (Nymphalidae) were included, and their wings measured both immediately after death and after three weeks of desiccation. Species were identified according to Lewis (1974). For each specimen, total body mass and mass of the right fore- and hindwing separately, were weighed with a Mettler H80 electro-balance (0.1 mg precision). Fore- and hindwings were drawn to scale using a camera lucida attached to a Wild microscope at magnification x6. These outlines were then digitized to determine wing area.

Flexural stiffness measures

The principal set of measurements consisted of force/deformation curves from forewings under cantilever loading to produce transverse bending (Fig. 1). These curves were generated for all 11 species. Cantilever loading was chosen over alternatives such as three- and four-point bending because, in natural flight, the base of the wing is fixed relative to the body while the remainder of the wing is aerodynamically loaded along its length as nearly perpendicular to the plane of the wing as possible. The 10 dried species were compared for allometric patterns in wing area (S), wing loading (dry body mass/wing area; r_w), and flexural stiffness (EI) as a function of dry body mass (m). Calculated wing loading will underestimate actual wing loading because dried specimens were used. All wings were loaded both dorsally and ventrally. As described in this paper, loading from the dorsal direction (dorsal loading) results in a dorsally convex surface, which is equivalent to ventral transverse flexion in other studies.

Two *Vanessa cardui* adults were tested two to three days after emergence from chrysalides. They were killed by pinching their thorax and then placed in a freezer for five minutes, immediately after which they were weighed. After the *V. cardui* were loaded in the tensiometer, they were allowed to dry for two to three weeks, then weighed and loaded again to provide an estimate of the effects that drying had produced upon the properties of the wings. A detailed map was made of stiffness along the span of a single *Vanessa cardui* wing. Use of dried wings hinders accurate estimation of flexural stiffness under natural conditions. For allometric studies though, the effects of drying need only be consistent across taxa. If drying does vary in its effects along the wing, this could bias interpretation of the wing maps

Basal attachment regions of individual forewings were glued using cyanoacrylate

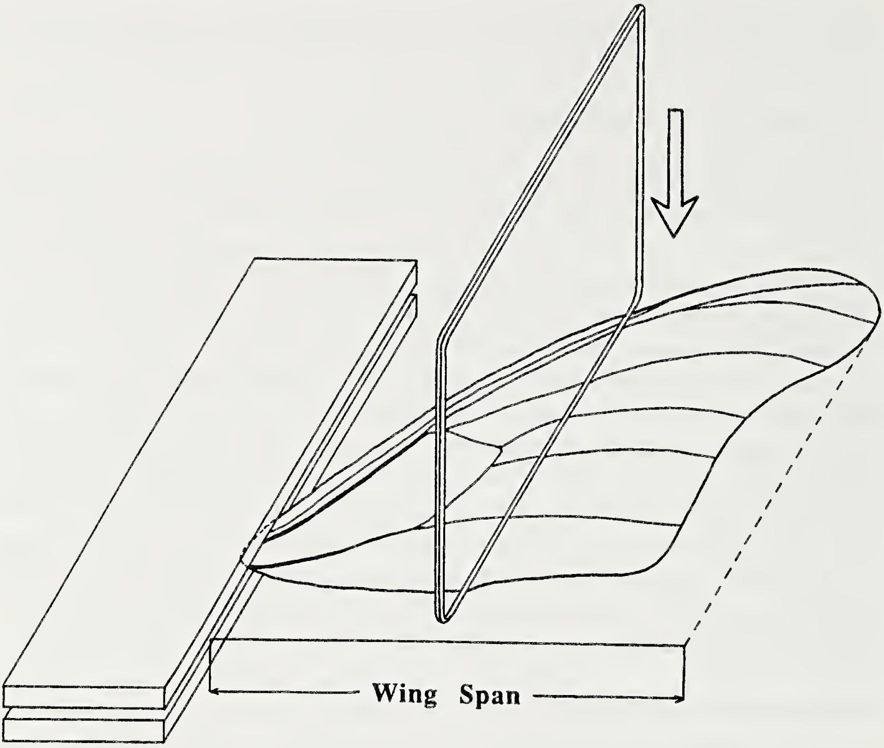

Figure 1. Diagrammatic representation of the method by which the wings were loaded for the stiffness measures. The rectilinear loading bar was displaced horizontally into the wing as indicated by the arrow. Measurements were taken at specified distances perpendicular to the line between wing base and tip. Remainder of the tensiometer apparatus not shown.

between two glass microscope slides. Spacers were placed between the glass slides to prevent crushing of the wing. Only one to two millimeters were grasped in this way, allowing the remainder of the wing to flex freely. Any discrepancy in the estimate of the actual place of attachment will affect stiffness calculations near the base much more than near the tip, because flexural stiffness varies with "beam" length to the third power. For example, an underestimate of 0.4 mm at 10% of wing length in the finely sampled *Vanessa cardui* (27 mm total length) would underestimate stiffness by 30%, while the same error at 90% of wing length would only underestimate stiffness by 5%. Wings were positioned with the span oriented perpendicular to the loading bar (Fig. 1).

The other principal wing deformations of camber and torsion are very important in wing aerodynamics, but are more difficult to measure accurately. Transverse flexion is observed widely in lepidopteran wings (Wootton 1981) and is amenable to experimental control. The loading bar was positioned using a millimeter scale at predetermined distances from the secured wing base (20%, 40%, 60%, and 80% of wing span) perpendicular to wing span. Another measurement was made at approximately 0.5 mm less than 100% wing span because loading at 100% wing span would result in the bar slipping off the wing. The wings were loaded in cantilever bending by fixing the glass slide grips to the carriage of a tensiometer. The loading bar, whose position could be adjusted with an accuracy estimated at ±0.4 mm, was displaced horizontally into the wing from either the dorsal or ventral directions. The diameter of the loading bar used in most measurements (including the detailed mapping) was 1.0 mm. Some of the wings wore loaded with a 2.5 mm diameter bar.

Fore wings were loaded in a tensiometer designed and assembled by M. LaBarbera. Displacement of the wing at the loading bar was measured by an LVDT, linear variable differential transformer (7307, Pickering, New York, USA), with a linear range of 2.5 mm attached to the carriage of the tensiometer. Force was measured by a force transducer (FTD-6-10 10 g, Schaevitz, New Jersey, USA), accurate to $\pm 7 \times 10^{-6}$ N at the most sensitive setting. The LVDT was calibrated by inserting the core rod a distance measured using an attached scale (±0.05 mm). The force transducer was calibrated by hanging known weights from the transducer when aligned vertically. Force and displacement were recorded on a chart recorder (2200, Gould, Ohio, USA). In regions of linear response of force to displacement, the slope was used to estimate the force (F) and displacement (D). These variables were then used to calculate flexural stiffness by the formula:

$$EI=(F*L^3/(3*D) \quad (1)$$

where EI is flexural stiffness in N m^2, F is force in Newtons, D is displacement at the loading bar in meters, and L is the length of the wing segment under bending (Wainwright et al. 1982) . This formula applies to a cantilever beam of uniform EI. The region between 60% and 80% of the wing span showed relatively constant stiffness. An index of flexural stiffness, $EI(W)$, was derived for each wing by averaging the dorsal and ventral stiffnesses at 60% and 80% wing spans. Averaging these four measures also reduced the expected error in EI that were due to errors in positioning the loading bar.

It must be emphasized that each position's EI is calculated assuming uniform material properties throughout the section under load. Therefore, the maps of EI do not plot *local* stiffness, but rather the integral of stiffness of the wing up to that position. Although this should not significantly affect the overall pattern, dorsal versus ventral differences basally could obscure discrimination of differences distally. For example, ventral stiffness in the tip region may actually be greater than that calculated for mean EI, but deflections for a given load may be similar because of greater deformation in the basal region under ventral loading.

Allometric patterns were determined by regressing morphological parameters and the index of flexural stiffness. Species means were used rather than individual measurements to avoid inflating the degrees of freedom in statistical tests, because within species values are naturally correlated due to phylogenetic relatedness. Reduced major axes (RMA) were calculated rather than least squares regressions because RMA is more appropriate for allometric investigation (Rayner 1985).

Degree of distastefullness for each species to avian predators was provided by R.

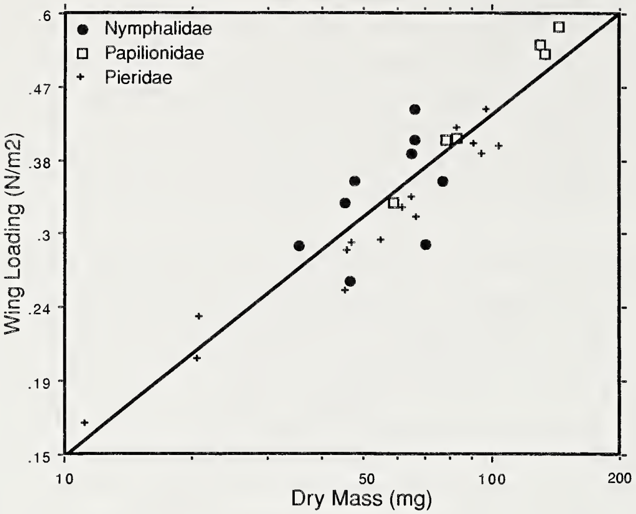

Figure 2. Log wing loading versus log dry body mass for 30 individuals representing 10 species. The RMA equation for the log-transformed data is l_{pw}=0.516 mm$^{-0.811}$ (r^2=0.810).

Srygley (Chai 1986, 1988).

RESULTS

Morphometric scaling

The slope of a regression line on a log-log plot defines the exponent in a power function relationship of the form $y=ax^b$. Log-transformed measures of wing area (S) were regressed against log-transformed total mass for the 10 dry species means. Isometric scaling would produce a regression line with slope of 2/3 ($S=am^{2/3}$). The reduced major axis (RMA) slope obtained for the 10 dry species means, 0.582, is not significantly less than 2/3 (r^2=0.846). Wing loading shows weak positive allometry; wing loading scales with the square root of mass (RMA=0.516, r^2=0.81), almost significantly different (P=0.06) from the null hypothesis of isometric scaling ($m^{1/3}$) (all 30 individuals shown in Figure 2). Additionally, wing area scaled isometrically with dry wing mass ($m_w^{0.70}$, n=10), therefore, wings are not becoming proportionately thicker (ignoring wing architecture like pleating). No strong conclusions regarding any taxonomic pattern can be drawn, given the small sample size, although nymphalids appear to have relatively higher wing loadings than pierids.

Flexural stiffness maps

The effect of drying on wing stiffness was estimated by measuring two *Vanessa cardui* wings immediately after killing the butterflies and then again after two to three weeks of drying. Drying appears to significantly increase stiffness, but the overall pattern of stiffness across the wing remains roughly

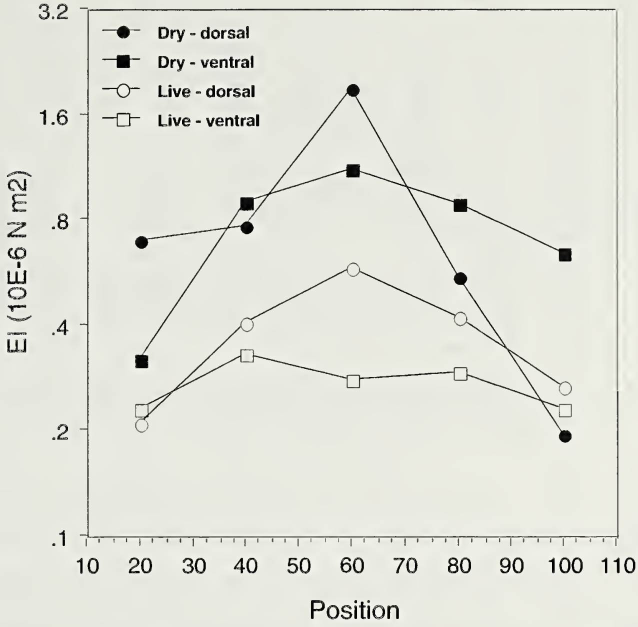

Figure 3. Effect of drying on wing stiffness averaged for the two *Vanessa cardui*. *EI* (10^{-6} kg m^2) plotted on log scale. *EI* values represent stiffness of entire wing up to measurement point.

similar with peak stiffness in the middle region (Fig. 3). Differences do exist between the patterns in the two conditions, primarily in the distal and proximal measurements (e.g., low dorsal stiffness at the tip for dry wings), and these may be due small errors in positioning the bar. Stiffness decreases rapidly in the distal 1.0 mm, and positioning errors are magnified in the basal region because of the cubic relationship between length and stiffness. Flexural stiffness (*EI*) for 10 species was determined for five positions along the wing both dorsally and ventrally. *EI* values ranged over two orders of magnitude from 2.3×10^{-8} N m^2 to 1.49×10^{-6} N m^2 (Table 1). Because wings varied so greatly in stiffness, values were normalized by dividing each wing's set of measurements by the maximum stiffness measured for that wing. The 10 wing maps so derived could then be compared as a proportion of maximum stiffness for each wing position. The normalized stiffness maps are displayed in Figure 4a. A single factor ANOVA showed that for the pooled data set (dorsal plus ventral), all adjacent positions (e.g. 40% with 20% and 60%) were significantly different in *EI* except for the 60% and 80% pair. The relative constancy in this region is one of the reasons that *EI* at 60% and 80% were averaged to give *EI*(*W*). An average wing is clearly stiffer under dorsal loading along the basal 40% of wing span. More pronounced than at 40%, the dorsally loaded wing is 55% stiffer at 20% of wing span ($P<0.001$). The distal 40% is less stiff under dorsal loading than ventral loading, but the difference is less pronounced and not statistically significant.

Table 1. Mean morphometric and flexural stiffness measures for the 10 species of butterflies acquired as dry specimens; wing loading in mg cm^2, flexural stiffness measures (*EI*) in 10^{-6} Kg m^2. Upper row for each species represent dorsal measures, lower row the ventral measures. Blank entries represent missing data for stiffness measures or not applicable to dorsal/ventral distinction. (p) = palatable, (u) = unpalatable, (–) = palatability unknown.

Direction	Species	dry mass (mg)	wing area (cm^2)	wing loading (N/m^2)	*EI*(20)	*EI*(40)	*EI*(60)	*EI*(80)	*EI*(100)	*EI*(*W*)
dorsal	*Parides montezuma* (u)	78.1	19.02	0.400	0.534	0.633	0.934	0.543	0.209	0.894
ventral	(Papilionidae)				0.373	0.422	1.367	0.734	0.333	
dorsal	*Battus polydamus* (u)	143.6	24.49	0.574	1.149	1.486	1.037	0.939	0.568	1.106
ventral	(Papilionidae)				0.428	0.672	1.226	1.220	0.375	
dorsal	*Pyrrhogyra neaerea* (p)	65.0	16.50	0.386	0.172	0.422	0.249	0.142	0.081	0.217
ventral	(Nymphalidae)				0.083	0.199	0.272	0.204	0.285	
dorsal	*Danaus lotis* (u)	70.2	23.74	0.290	0.715	0.971	0.758	0.528	0.227	0.716
ventral	(Nymphalidae)				0.304	1.002	0.896	0.683	0.240	
dorsal	*Dione juno* (u)	35.4	12.03	0.288	0.037	0.059	0.081	0.073		0.088
ventral	(Nymphalidae)				0.023	0.053	0.094	0.105		
dorsal	*Catopsilla scylla* (–)	45.7	17.96	0.250	0.276	0.324	0.461	0.299	0.154	0.431
ventral	(Pieridae)				0.211	0.379	0.474	0.450	0.198	
dorsal	*Eurema hecabe* (p)	20.8	8.86	0.230	0.053	0.062	0.044	0.074		0.063
ventral	(Pieridae)				0.044	0.071	0.074	0.062		
dorsal	*Phoebis statira* (p)	91.2	22.50	0.397	0.450	0.640	0.745	0.763	0.523	0.744
ventral	(Pieridae)				0.286	0.466	0.721	0.746	0.543	
dorsal	*Pereute charops* (–)	97.7	21.72	0.441	1.041	1.170	0.990	0.855	0.414	0.802
ventral	(Pieridae)				0.396	0.729	0.722	0.640	0.435	
dorsal	*Ascia monuste* (u)	55.3	18.52	0.294	0.129	0.438	0.461	0.393	0.201	0.416
ventral	(Pieridae)				0.250	0.318	0.502	0.309	0.309	

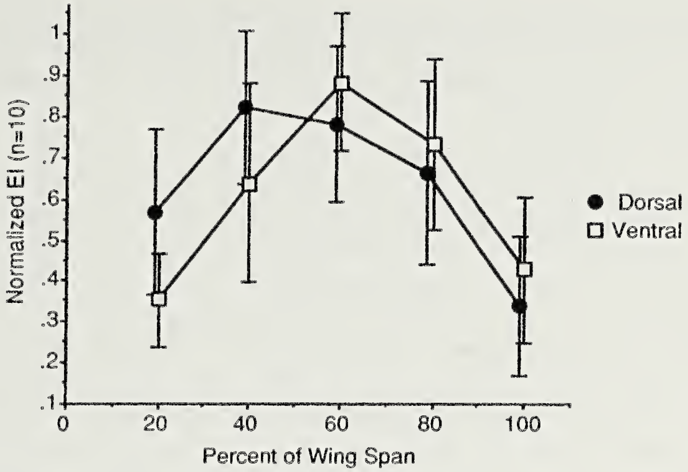

Figure 4a. Map of normalized stiffnesses for the mean values for 10 butterfly species under dorsal and ventral loading. Original measurements were normalized as a proportion of the maximum stiffness measured for each wing. Standard deviation bars shown. All positions are significantly different from each other except 60% and 80% (P<0.05). *EI* values represent stiffness of entire wing up to measurement point.

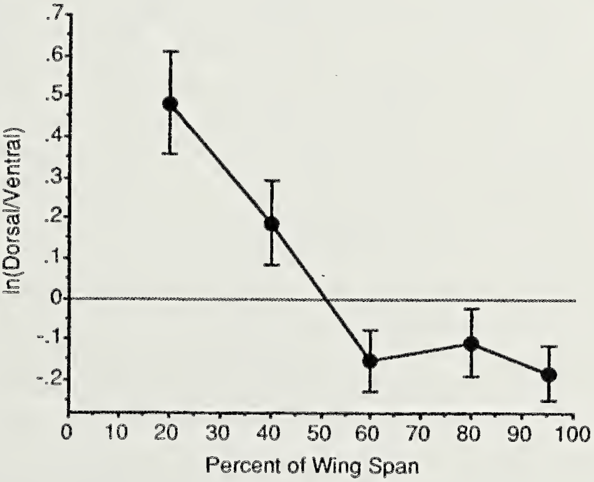

Figure 4b. Mean ratios of dorsal versus ventral stiffnesses by wing position. Standard error bars shown. Only at 20% of wing span are dorsal and ventral differences significantly different (P<0.001).

The 60% position shows a significant difference only at the 90% confidence level while the 40%, 80%, and 100% positions do not show significant differences (P>0.2). The relative stiffnesses of dorsal versus ventral are summarized in Figure 4b.

Figure 4a illustrates a possible common pattern across species but is a rather crude map of dorsal and ventral flexural stiffness along wing span. It also blends together slightly different stiffness patterns among species. To complement this data set, a dried forewing of *V. cardui* was mapped with much finer resolution, at approximately 1.4 mm intervals (Figure 5a). The general pattern is in agreement with the averaged wing map. The wing is dorsally stiffer (i.e., against ventral flexion) in the basal 60%, particularly in the basal 40%. The distal 20% to 30% seems to be slightly stiffer ventrally. When *EI* is plotted on a log-scale, two features stand out (Figure 5b). First, stiffness from 40% to 85% of wing span is relatively constant compared to the rest of the wing. Second, within the basal 25%, the wing is dorsally much stiffer than ventrally; on average about three times stiffer. The accuracy of *EI* estimates is lowest very near the base (e.g. <3 mm), due to small errors in distance measures from the actual base of the wing.

Flexural stiffness and morphological parameters

The index of flexural stiffness, *EI*(*W*), was regressed against several common wing parameters, using mean values for each species. It was hypothesized that by structural necessity, *EI*(*W*) would be correlated with wing loading, and indeed, *EI(W)* scales with wing loading to nearly the fourth power (3.9) with a moderate correlation coefficient of 0.598. Longer, more heavily loaded wings would need to be stiffer to prevent excessive deformation. However, *EI*(*W*) is more strongly correlated with dry body mass (r^2=0.814, RMA slope=1.80). The correlation of *EI(W)* with relative wing thickness (total dry wing mass/total wing area) drops to 0.417 (RMA slope=0.928). The strongest correlation is with wing area; r^2=0.911 (Figure 6). *EI(W)* scales with wing area cubed ($S^{3.1}$; 90% confidence interval, 2.46-3.73).

Figure 6 is slightly curvilinear. The power function provides a much better fit to the data than a simple linear model (r^2=0.785) which predicts zero stiffness at 10 cm^2. The remaining apparent curvilinearity is likely taxon specific. The two nymphalid species are approximately 40% less stiff than predicted by the regression, whereas the smaller of the papilionids is 64% stiffer than predicted. These would result in deflections 60% more or less than expected respectively.

The residuals from a polynomial regression constrained to pass through the origin were compared for two groups: those palatable to birds and unpalatable. The mean residuals were not significantly different between the two groups (P>0.5), indicating that palatable butterflies do not have relatively stiff wings.

DISCUSSION

Various selective forces and phylogenetic constraints have been proposed to account for insect wing morphology. The functional constraint of ther-

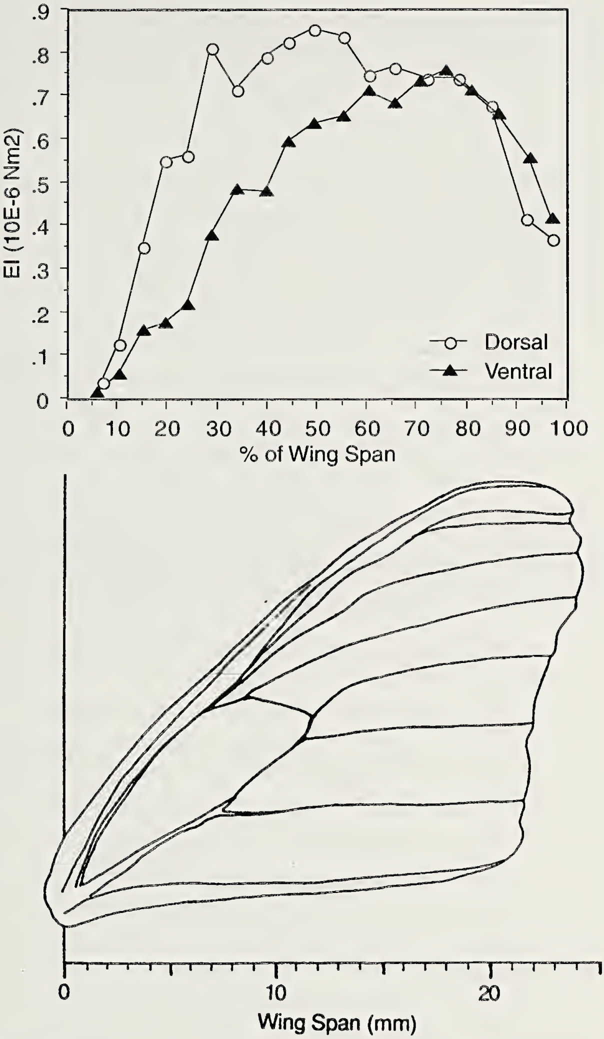

Figure 5a. Wing stiffness map for a dry *Vanessa cardui* individual. Below is a diagram of the wing, drawn to the same scale as the X-axis of the stiffness map. The loading bar was oriented parallel to the Y-axis. *EI* values represent stiffness of entire wing up to measurement point.

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moregulation may well have been significant during the early evolution of insect wings (Kingsolver and Koehl 1985). However, thermoregulation is probably of little importance to major scaling and structural patterns in butterflies because only the proximal 15% of the wing surface plays a significant role in conductive heat transfer to the body (Wasserthal 1975) and the combination of pigmentation and behavior significantly effect thermoregulation in species that utilize the entire wing (Kingsolver 1985). Strauss' (1990) study of shape allometry in nymphalids suggests that aerodynamic (i.e., functional) constraints may be less important than sexual (i.e.,

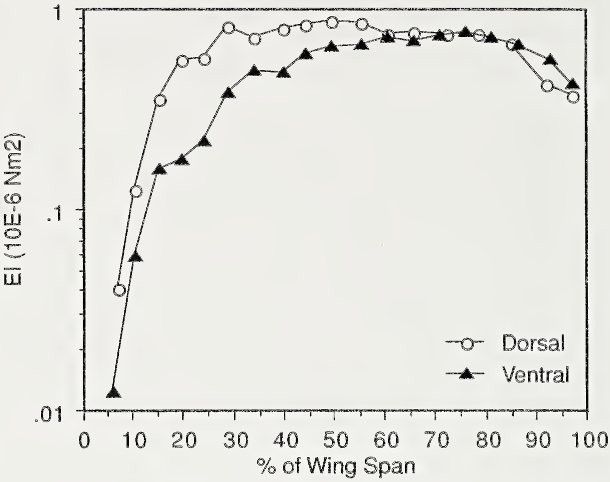

Figure 5b. Log-scaled wing stiffness map for a dry *Vanessa cardui* individual, illustrating the relatively constant stiffness from 40% to 85% of wing span and the large differences between dorsal and ventral stiffness basally.

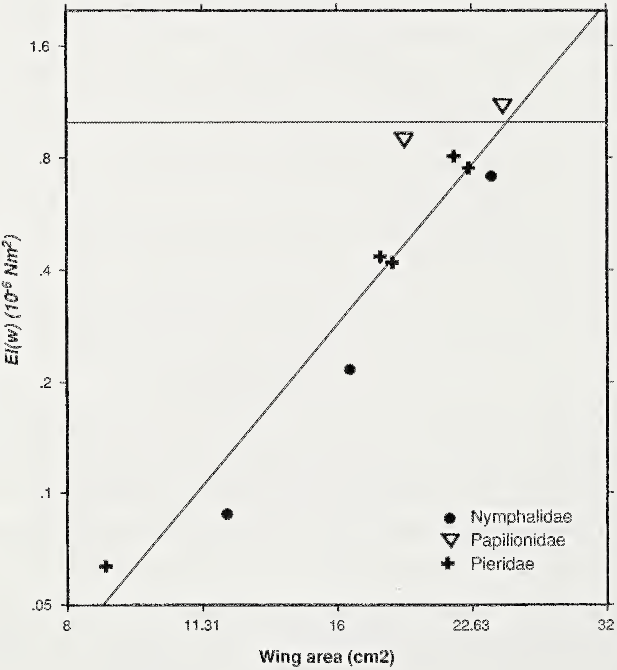

Figure 6 . Index of flexural stiffness, *EI(W)*, versus wing area, *S*. Log-log scale. RMA equation is $\ln EI(W) = 3.1S - 9.78$ ($r^2 = 0.911$).

display related) selection. Butterflies have unusually large wings used to attract mates, to confuse or warn predators, for camouflage, and for other display-related functions.

Scaling

The wing and body morphology measured in this study do not scale isometrically among the butterfly species sampled. Although wing thickness seems to scale isometrically, wing area shows a slight negative allometry with dry body mass. As a consequence, wing loading shows positive allometry. In addition, *EI*(*W*) increases more rapidly than any of the other parameters, and is most highly correlated with wing area. These results do not indicate strong selection for an optimal wing loading that is size-independent.

The impact of allometrically induced variation in propulsion related forces has been examined in other organisms. Because flying squirrel patagium did not scale so as to minimize allometric variation in wing loading, Thorington and Heaney (1980) concluded that other selective factors must be involved, resulting in size related differences in gliding habit and maneuverability. In response to isometric scaling, changes in the geometric alignment and utilization of propulsive limbs in mammals can compensate for size-dependent increases in mechanical stresses (Biewener 1989). These compensations can significantly limit maneuverability and accelerative ability. Possible examples of compensation in butterflies include flight habit and wing-stroke frequency. Indeed, Betts and Wootton (1988) found tendencies in flight mode among a small sample of butterflies to be associated with size and shape parameters of wings, including wing loading.

The results in this study can be compared to those reported elsewhere (Greenewalt 1962, Kokshaysky 1977, Dudley 1990). Greenewalt's analysis is generally in accord with the wing area/body mass result, but in disagreement with wing thickness. Greenewalt found that wing area increased with the 0.60 power of wing mass, and thus wing thickness increased with the 1.34 power of wing span. The result from this study is almost significantly different from Greenewalt's figure ($P<0.10$). It should be noted at this point that reanalyses of the original data (Magnan 1934, Sotavalta 1947) show a slightly weaker relationship but a similar slope than he reported ($r^2=0.702$ versus 0.772; RMA=0.652 versus his mean regression line 0.634). The reanalysis standardized sample sizes at one individual per species ($n=20$). As Kokshaysky (1977) also noted, the number of data points graphed (35) exceeded those listed in the regression table (33) and the number with complete data (23).

Two hypotheses of flexural stiffness allometry were tested; structural isometry and consistent dynamic wing geometry. For a beam with rectangular cross-section, I, the second moment of area, is a product of width*thickness^3. Assuming isometry, width and thickness will be proportional to L, yielding by substitution, $I \alpha L^4$. Area is proportional to L^2, and thus, EI should scale with area S^2. The hypothesis that EI scales isometrically with wing area is rejected because the allometric coefficient of 3.1 is significantly different from 2.0 ($P<0.02$).

Alternatively, aerodynamic constraints could result in angular deflection remaining constant; i.e., *EI* compensates for scaling in mass and wing area so as to maintain a size independent dynamic wing geometry. This concept is congruent with the elastic similarity which McMahon (1973, 1975) developed and applied to a variety of issues including tree shape and quadraped locomotion. Deformation may be the most important structurally controlled property of lepidopteran wings affecting aerodynamics. Greenewalt (1975) argued that if wing thickness scales isometrically, angular deflection should remain constant (since his results did not indicate isometry, he concluded that angular deflection must show negative correlation with size). However, under the assumption that deflection of the wing scales isometrically (D/L=constant c), rearrangement of eq. 1 yields a prediction for *EI.*

$$EI = F^*L^2/3c \qquad (2)$$

If, instead of inputting the experimental force that was used to calculate *EI,* we assume that the principal forces acting on the wing are proportional to body weight, and replace *EI* with *EI*(*W*), then eq. 2 predicts that *EI* is proportional to weight x wing area (L^2, assuming on average, wing shape scales isometrically). Multiplying wing loading by the area yields the total force acting on the wing; total body weight. (In addition, the virtual mass of the accelerated air can range from 0.3 [Diptera] to 1.3 [Odonata] times the wing mass [Ellington, 1984]. Virtual mass has not been taken into account in this analysis.) The results are close to the prediction; *EI* scales with $(m^*S)^{1.16}$ ($r^2=0.882$). The hypothesis of constant angular deflection cannot be rejected.

Wing stiffness patterns

The reduction in distal stiffness matches the expectation of previous workers. In Heteroptera, significant reduction in inertial stresses may be achieved by lightening the fore wing distally (Betts 1986), thereby reducing stiffness. Betts views transverse [ventral] flexion as improving aerodynamics by "optimizing camber and angle of attack ..., minimizing adverse aerodynamic forces at stroke reversal, ... creating favourable unsteady forces at stroke reversal" (1986, p. 298). Wootton (1981) felt that ventral flexion would preferentially reduce drag on the upstroke. The hypothesis of a structural basis for the limited dorsal flexion seen in previous studies is not strongly supported by the results of this study. The differences in the magnitude of *EI* appear to be less than the difference between dorsal and ventral deflections described by Betts and Wootton. Distal deflection will be affected by loading distribution in addition to structural properties. Differences in distal load may be due to differences in angular velocity, or related to the effects of angle of attack stemming from camber and torsion elsewhere on the wing. For example, *Pieris brassicae* supinates its wings on the upstroke to an angle of attack near zero, thus significantly reducing the force generated during the upstroke (Ellington 1980).

Perhaps the most striking result of the present work is the very low stiffness near the wing base. The thickening of the veins and wing structure observed near the base would be expected to increase the second moment of area, *I*, and therefore flexural stiffness. Although the smaller chord width near the base will reduce *I*, this reduction in width alone would seem insufficient to account for the magnitude of change documented here given that thickness increases near the base would increase stiffness. Some functional advantages may be suggested. Low ventral stiffness basally may permit wing geometries that facilitate the "clap and fling" mechanism for generating lift (see Weis-Fogh [1973] for description). This stiffness pattern would seem to be disadvantageous during normal flapping flight, where a stiff wing would transmit muscle power to the surrounding air more efficiently. If greater ventral flexibility is found to be aerodynamically disadvantageous, then these results imply that the requirements for initial take off using clap and fling impose the greater functional constraints and stronger selective forces on wing design.

Alternatively, the low stiffness at the base relative to the center of wing span may act to increase wing accelerations at stroke reversal in much the same manner as a whip. This flexibility may also reduce inertial stress, especially at stroke reversal. Basal curvature appears greatest near stroke reversal in high speed photos of butterflies in flight (Dalton 1975). These possibilities need to be tested further as well as testing whether the biomechanical properties of the glue and apparatus used to grasp the wing base account for some of the reduced stiffness measured near the wing base.

No association was found between relative stiffness and palatability to avian predators. A relationship might be expected if palatable species must be stronger fliers to escape predators (Srygley 1994) and if stronger fliers have stiffer wings. The findings here can be compared with those of Srygley (1994) who found that palatability was most strongly associated with positions of centers of body and wing mass, which related to flight speed and turning performance, but was less strongly associated with measures of wing shape.

At present, improved understanding of the phylogenetic and ecological contexts of butterfly flight are most needed in order to synthesize the biomechanical and performance studies. There appears to be a strong phylogenetic component to relative wing stiffness, with the nymphalids having relatively flexible wings and the papilionids having stiff wings. Future studies with greater taxonomic sampling should incorporate explicitly the phylogenetic relationships in order to avoid inflating significance levels, using, for example, independent contrasts rather than raw species values in the regression (Felsenstein 1985). Particularly important is the need to incorporate flight performance and flight habit parameters in studies such as Betts and Wootton (1988) and Dudley (1990), along with structural biomechanics and ecological correlates on comparable species.

The results of this study should be viewed as preliminary and subjected to further testing and refinement. Fresh rather than dried wings must be measured to avoid the assumptions of proportional effects of drying, both among species and across wings. Applying the load to the wing along a chord of constant rotational radius may be preferable to the transverse orientation used here. Local rather than integrated stiffnesses should be measured. The wing orientation chosen by Betts and Wootton (1988; fig. 2), which is rotated approximately 20° posteriorly relative to this study, may be more representative of loadings experienced during natural flight. The orientation used in this study is sometimes observed at stroke reversal (Betts & Wootton 1988). Furthermore, neither camber nor torsion were examined, and deformations and wing movements usually involve all three. However, this study introduces an approach based on direct measurement of the biomechanical properties of wings that has heretofore not been addressed. Biomechanical studies are currently the missing link between studies of allometry, flight performance, ecology, wing geometry, and theoretical aerodynamics.

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The number of copulations of territorial males of the butterfly *Callophrys xami* (Lycaenidae)

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Abstract. The number of copulations by different males and in different territories was evaluated in the field in the butterfly *Callophrys xami* (Lycaenidae). The total number of copulations per male and per hour was very low (.0027 and .0029 copulations / male / h in 1989 and 1990, respectively). There was high variance among males in the number of copulations. Data from the few males observed copulating more than once suggests a mating advantage for big, long lived males. Variation among territories in the number of resident males, frequency of occupation and number of copulations suggests variation in territory quality. Frequency of occupation was not correlated with the territory variables measured, and there were no differences in any territory variable between territories in which copulations were observed and those in which no copulation was observed. Furthermore, there were no between-years correlations in frequency of occupation and number of copulations in the territories studied in two different years. The location of territories may be important in determining territory quality.

KEY WORDS: *Callophrys xami*, Lycaenidae, copulation, mating success, territoriality

INTRODUCTION

The fitness of male insects is difficult to determine in the field (Thornhill and Alcock, 1983). Although the number of observed copulations has been used frequently as a measure of male fitness (Thornhill and Alcock, 1983), it is not possible to be confident about such a measure without knowledge of male mating costs, female copulation frequency, sperm competition pat-

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terns (Smith, 1984) and postcopulatory female choice criteria (Eberhard, 1996). However, some studies suggest that the number of copulations achieved by a male is an important fitness component at least in some species. One line of evidence supporting this suggestion is the fact that several aspects of the male phenotype seem to be specific adaptations to increase the number of copulations (reviews in Darwin, 1871; Thornhill and Alcock, 1983; Choe and Crespi, 1997).

In the butterfly *Callophrys xami* Reakirt (Lycaenidae) the number of copulations seems to be an important fitness component for males since they spend all their active adult lifetime defending territories that lack concentrations of larval and adult food resources (Cordero and Soberón, 1990) and that are used only as mating stations (Cordero and Soberón, 1990; Cordero, 1993). Laboratory observations suggest that copulation inhibits female sexual receptivity for a number of days (if it is the first mating of the female, these days correspond to the days in which oviposition rates are higher), and dissection of field collected females indicates a relatively low degree of polyandry (Cordero and Jiménez, unpublished data).

In this paper we report field observations of copulations by territorial males of the butterfly *C. xami*. Differences in the number of copulations performed by different males, and ocurring in different territories, are described and some factors possibly affecting such differences are discussed.

METHODS

The study was conducted in the Pedregal de San Angel ecological reserve, maintained by the Universidad Nacional Autónoma de México in the south of Mexico City. This zone is characterized by volcanic soil, rough topography, markedly seasonal rainfall regime, and xerophytic shrubby vegetation. *C. xami* is a multivoltine butterfly that can be found throughout the year at relatively low numbers, reaching its highest density from October to January (Soberón *et al.*, 1988). The main larval food plant in the study area is the perennial *Echeveria gibbiflora* (Crassulaceae), an abundant species (Soberón *et al.*, 1988; Larson *et al.*, 1994).

Study periods were chosen to coincide with population density "peaks" (Soberón *et al.*, 1988; personal observation); observations were made between November 1 and December 20, 1989 and between November 10 and December 6, 1990. Most territorial males observed were captured and individually marked on the wings with felt-tip pens and their right forewing length was measured through the mesh of the net with a calliper (in the laboratory, male wing length is correlated with adult body weight at emergence: $r = 0.91$, $p < 0.001$, $n = 28$; Cordero, unpublished data). Individuals were assigned to one of three wing wear categories: (1) similar to a recently emerged adult (wings mostly green with intact margins), (3) very worn male (wings mostly brown with worn margins), and (2) all individuals intermediate between (1) and (3). Longevity was defined as the number of days elapsed between the first and the last observation of the male. Territory limits were determined as explained in Cordero and Soberón (1990). We measured the (i) maximum length and the (ii) "cross" length (length of the perpendicular axis crossing through the middle point of (i)); territory area was approximated as (i) x (ii); the ratio (i) / (ii) was used as a measure of territory "shape".

The study period of each year was divided in two parts. During the first part we measured the frequency of occupation of each territory (= number of days the territory was occupied by a territorial male / number of days the territory was censused), determined the identity of each male defending the territory, and recorded all copulations observed. In this part of the study we made observations in 25 territories in 1989 and in 19 in 1990. One observer walked along transects joining several territories two times per day between 1000 and 1500 h, the daily territorial defense period (DTDP; Cordero and Soberón, 1990), during 31 days in 1989 and during 11 days in 1990, and observed each territorial male (if present) for at least two minutes. The observation period was longer if, for example, the male was interacting with a conspecific male or courting a female. The average number of days (±SD) each territory was censused was 26.2 ± 1.8 (median = 26; range: 22–30) in 1989, and 10.2 ± 0.6 (median = 10; range: 9–11) in 1990.

During the second part of each study period we estimated the probability of copulating twice in a day (previous work indicated that the maximum number of successful copulations per day that a male can achieve is two, since a male's first copulation of the day lasts 32 min on average, while the second copulation of the day lasts several hours; Cordero, 1993). We made focal observations of territorial males throughout the DTDP and recorded all copulations observed, during nine days in 1989 and 12 days in 1990. The number of males with focal observations was 15 in 1989 and 16 in 1990; the total number of hours of focal obsevations was 200 hours in 1989 (40 five hours periods of focal observations) and 130 hours in 1990 (26 five hours periods of focal observations). The number of days of focal observations per male varied from 1 to 6 in 1989 (mean ± SD = 2.7 ± 1.7, median = 2), and from 1 to 3 in 1990 (1.6 ± 0.8, median = 1). Focal observations were made in 14 territories in 1989 and in 11 territories in 1990. The number of days of focal observations per territory varied from 1 to 6 in 1989 (2.9 ± 1.6, median = 2), and from 1 to 3 in 1990 (2.4 ± 0.7, median = 3). All observations were made on sunny days since *C. xami* is not active under cloudy conditions. All summary statistics are given as mean ± standard deviation and/or median and range (minimum–maximum).

RESULTS

Throughout the study periods of 1989 and 1990, we observed territorial males (Cordero, 1997) and sexually receptive females. All successful courtships observed (n = 15) began inside territories and involved territorial males. Copulations were observed between 1100 and 1500 h in 1989 and between 1230 and 1500 h in 1990.

Number of copulations by different males

We observed a total of 27 copulations (Table 1). Although we marked and observed 159 territorial males (99 in 1989 and 60 in 1990), only 21 males (three of them unmarked) were observed copulating (12 in 1989 and 9 in 1990). Three males were observed copulating more than once (two, three and four times). Only one male was observed copulating two times in a day (this was the male that mated four times in 1989). We suspect that another male mated twice in one day (this was the male that mated three times in 1989), since this male was observed arriving at the territory at 1111 h and copulating at 1137 h for more than 268 min (observation was interrupted at 1605 h); therefore, it is possible that this male copulated before the begin-

Table 1. Distribution of copulations observed in different territories in each part of the study periods of 1989 and 1990. T: territory.

1989			1990		
	Number of copulations:			Number of copulations:	
T	First part	Second part	T	First part	Second part
3-4N	1	3[a]	3-4N	0	1
IV	0	2	IV	1	1[b]
Pnm	1	—[c]	Pnm	1	0
d	2	3[d]	a	1	1
Id	3	0	8-9	1	1
V	1	0	A	0	1
‡	1	—[c]	ICh2	0	1

[a] Territory in which a male copulated twice in a day.

[b] Although in this territory no focal observations were made, we casually observed one copulation during the second part of the study.

[c] Territory in which no focal observations were made.

[d] Territory in which a male probably copulated twice in a day.

ning of observations (focal observations began at 1004 and sometimes males began territory defense before 1000 h) and that the long copulation observed was the second of the day (remember that a male's second copulation of the day last several hours, while his first copulation of the day lasts on average 32 min). Therefore, only in one (possibly two) of the 40 five h periods of focal observations in 1989 we observed two copulations; no male copulating twice in a day was observed in any of the 26 five h periods of focal observations in 1990.

As expected from the different sampling methods employed during the first and second part of each study period, the proportion of marked males observed copulating in the first part of the study (10 / 144 = 6.9%; 8 / 92 in 1989 and 2 / 52 in 1990) was lower than the proportion observed copulating during the second part (10 / 31 = 32.3%; 4 / 15 in 1989 and 6 /16 in 1990). Seven of the nine copulations performed by the three males observed copulating more than once were observed during the second part of the study (including the two copulations performed in the same day by a male).

The number of copulations per hour calculated from the pooled focal observations was similar in both years of study: 0.04 copulations / h (= 8 copulations / 200 h of focal sampling) in 1989 and 0.046 copulations / h (= 6 copulations / 130 h of focal sampling) in 1990. The number of copulations per male and per hour calculated from the pooled focal observations was almost identical in both years of study: 0.0027 copulations / male / h (= 8 copulations / 15 males / 200 h) in 1989 and 0.0029 copulations / male / h (= 6 copulations / 16 males / 130 h) in 1990.

Characteristics of males

A total of 99 territorial males in 1989 and 60 in 1990 were individually marked. No significant differences between years were found in wing length (1989: 1.64 ± 0.1 cm, range: 1.36–1.89, n = 90; 1990: 1.65 ± 0.09 cm, range: 1.4–1.83, n = 55; t = -0.29, p = 0.77), longevity (1989: 4.8 ± 5.1 days, median = 2, range: 1–20, n = 99; 1990: 4.9 ± 5.9, median = 2, range: 1–28, n = 57; Mann-Whitney U = 2819, p = 0.99) and wing wear at the moment of being marked (1989: median = 1, range: 1–3, n = 90; 1990: median = 1, range: 1–3, n = 57; U = 2419.5, p = 0.51). There was no correlation between wing length and longevity (1989: $r_s = 0.13$, $p = 0.22$, $n = 90$; 1990: $r_s = 0.11$, $p = 0.43$, $n = 52$).

Due to the sampling methods employed in this study, we cannot look for a relationship between male traits and number of copulations in the data. However, the characteristics of the three males observed copulating more than once suggest that male size and longevity could be positively correlated with copulation success. The male with the most copulations (four) was also the biggest male observed in both years (wing length = 1.89 cm); this male was also the only one observed copulating twice in a day. The longevity of this male was 14 days, longer than that of 89.9% of the males observed in 1989. The male that was observed copulating three times in 1989 was bigger (wing length = 1.72 cm) than 73.3% of the males observed that year. The longevity of this male was 11 days, longer than that of 85.9% of the males observed in 1989. This male probably copulated twice in a day (see previous section). The male that was observed copulating two times in 1990 was bigger (wing length = 1.72 cm) than 74.5% of the males observed that year. The longevity of this male was 18 days, longer than that of 94.7% of the males observed in 1990. Therefore, the characteristics of the multiply mated males indicate that a study of the possible (positive) effect of wing length and longevity on male mating success would be particularly interesting in this butterfly (see Appendix).

Number of copulations in different territories

The 17 copulations of 1989 and the 10 copulations of 1990 were observed in seven territories each year, although only three of these were the same in both years (Table 1). To explore the relation between territory variables (maximum length, “cross” length, maximum length / “cross” length and area) and the frequency of occupation of the territory, and to compare the characteristics of territories in which copulations were observed with those in which no copulations occurred, only the data obtained during the first part of the study periods were analized. This decision was made considering that during the second part of both study periods the sampling effort was very heterogeneous (the number of days of focal observations per territory varied from 1 to 6 in 1989 [CV = 55.2%] and from 1 to 3 in 1990 [CV = 29.2%]), whereas during the first part of both study periods it was much more homogeneous, and, therefore, comparable, between territories (the number of days each territory was censused varied from 22 to 30 in 1989 [CV = 6.9%], and from 9 to 11 in 1990 [CV = 5.9%]).

Table 2. Comparison of characteristics of territories in which copulations were observed with those of territories in which no copulations were observed. Values are median (range). Statistics from Mann-Withney U test are given.

Territory variable	Year	Territories in which copulations were observed	Territories in which no copulations were observed	*U*	*p*
Maximum length (m)	1989	5.17 (2.69–6.2)	3.26 (2.32–7.1)	24.5	.2
	1990	3.81 (2.54–6.2)	3.88 (2.32–7.1)	19	.89
"Cross" length (m)	1989	3.27 (1.5–4.35)	2.5 (1.35–4.85)	24	.19
	1990	3.02 (2.14–4.35)	2.68 (2–3.86)	17	.67
Maximum length / "Cross" length	1989	1.49 (.87–3.21)	1.16 (1.01–2.49)	31	.48
	1990	1.23 (1.03–1.84)	1.36 (1.01–2.25)	17	.67
Area (m^2)	1989	16.93 (7.21–26.97)	7.78 (4.54–33.61)	22	.14
	1990	10.85 (6.22–26.97)	8.48 (4.56–27.41)	19	.54
Frequency of occupation	1989	.69 (.52–.92)	.33 (.04–1)	21.5	.024 [a]
	1990	.85 (.64–.91)	.4 (0–1)	18	.36

[a] This difference is not significant if we perform a sequential Bonferroni adjustment of significance levels using as a family of tests (Chandler, 1995) the five U tests of 1989, and using $\alpha = 0.1$, as suggested by Chandler (1995): $k = 5$, $\alpha/k = .02$.

Average frequency of occupation of territories during the first part of the study periods was 0.47 ± 0.29 (median = 0.5, range: 0.04–1) for 1989 and 0.6 ± 0.37 (median = 0.8, range: 0–1) for 1990. The frequency of occupation of territories was not correlated with any of the territory variables measured (Spearman correlations, all $p \geq 0.26$). Average number of copulations in territories during the first part of the study periods was 0.36 ± 0.76 (median = 0, range: 0–3) for 1989 and 0.24 ± 0.44 (median = 0, range: 0–1) for 1990. There were no significant differences between territories in which copulations were observed and territories in which no copulations were observed in maximum length, "cross" length, maximum length / "cross" length and area (Table 2). The frequency of occupation of territories in which copulations were observed was higher than that of territories in which no copulations were observed in 1989 (Table 2), but no difference was detected in 1990. However, even the 1989 difference is not significant if we perform a sequential Bonferroni adjustment of significance levels (see Table 2).

Twelve territories were observed in both years. Considering only the data collected during the first part of both study periods, there were no significant between-years correlations in the frequency of occupation of these territories ($r_S = 0.55$, $p = 0.078$, $n = 11$) or in the number of copulations (Gamma correlation, $\gamma = -0.09$, $p = 0.87$, $n = 11$) observed in these territories. Therefore, the "quality" of a territory in a given year was not a predictor of that in the next. In fact, the territory that in 1989 had the maximum number of observed copulations (five or, probably, six; Table 1) and the second highest frequency of occupation (0.94; maximum = 1), was not occupied by a territorial male in any of the more than 10 days in which it was censused in 1990.

Discussion

Male copulation frequency

As is common in insects exhibiting lek territoriality (*e.g.* Alcock, 1983, 1987; Alcock and O'Neill, 1986; Table 3), the overall rate of copulations observed in *C. xami* was low: 0.0027 and 0.0029 copulations / male / h in 1989 and 1990, respectively. Low copulation rates are expected since lek mating systems are favored when receptive females are scarce and widely dispersed (Thornhill and Alcock, 1983; Rutowski, 1991), and such conditions seem to apply to the population of *C. xami* in the Pedregal de San Angel (Cordero and Soberón, 1990).

This study suggests that there was relatively high variance in copulation success between territorial males. First, although most males were not observed copulating, some males copulated up to four times, including one (probably two) male that was observed copulating two times in a day. Second, one third of the copulations observed (nine out of 27) were performed only by three males. Although we were not able to obtain estimates of male lifetime reproductive success, these results, together with information indicating that females exhibit a low level of polyandry (in a sample of 28 field collected females, 78.6 % had only one or no spermatophore in their *corpus bursae*, and the mean number of spermatophores found in non-virgin females was 1.37 ± 0.6 [Cordero and Jiménez, unpublished data]), suggests that there is high variance in male fitness and, therefore, that the opportunity for sexual selection in males is high. Sexual selection may be acting in favor of an increase in male wing length and longevity if the mating advantage suggested by the characteristics of the few males that mated more than once is real. However, the relationships between male phenotypic traits and copulation success still needs clarification.

Number of copulations and territory variables

The substantial variation observed between territories in frequency of occupation, numbers of males and number of copulations suggests that territories of *C. xami* vary in quality. However, none of the territory variables measured affected the frequency of occupation or the number of copulations (Table 2). In species with non-resource based territoriality, such as *C.*

Table 3. Mating behavior of butterflies in which male copulation success and/or phenotypic traits associated to male copulation success have been studied in the field[a]

Species	MS	♂ MF	♂ TSRMF	♀ MF[b]	♀ TSRMF	Reference
Papilionidae						
Papilio polyxenes	LT	.13 ± .49 (0-3) [c]	ST^{R}	1.3 ± .54 (0-3)	WW^{R}	Lederhouse (1981, 1982)
Atrophaneura alcinous	SC	.43 ± 1.31[d] (0-5)	ED^{R}, L^{R}, ME^{R}, WL^{NR}	1.0	—	Suzuki & Matsumoto (1992)
Luehdorfia japonica	SC	—[e]	FA^{R}, WW^{R}, WL^{NR}	~1.0[f]	—	Tsubaki & Matsumoto (1998)
Nymphalidae						
Coenonympha pamphilus	LT	.019[g] .083	TB^{R}, WL^{PR}	.97 ± .05 (0-3)	—	Wickman (1985)
Danaus plexippus	SC	2.98 ± 2.65 (0-11) [h, i]	FA^{NR}, PL^{NR}, WL^{NR},WW^{NR}	3.50 ± 1.22 (1-6) [j]	FA^{R}, PL^{NR}, WL^{NR}, WW^{NR}	Frey *et al.* (1998)
Euphydryas editha	SC	—[k]	ED^{NR}	1.27 ± .46 (1-2) [l]	—	Baughmann (1991)
Heliconius hewitsoni	PM	—	BL^{R}, WL^{R}, WW^{NR}	1.0	—	Deinert *et al.* (1994)
Pieridae						
C. philodice eriphyle	SC	—	G^{R}	1.21 (0-3) [m]	WW^{PR}	Watt *et al.* (1986)
Colias eurytheme	SC	—	G^{R}	(3) [n]	—	Watt *et al.* (1986)
Pieris napi[o]	SC	—	PW^{R}	2.03 ± .11 (1-5) [p]	—	Wiklund & Kaitala (1995)
Lycaenidae						
Jalmenus evagoras	PM	.97 ± 2.56 (0-7) [i]	L^{R}, ED^{R}, WL^{R}	1.0	—	Elgar & Pierce (1988)
Callophrys xami	LT	.0027 (0-4) .0029 (0-2)[q]	WL^{PR}, L^{PR}	1.37 ± .60 (0-3)	WL^{NR}, WW^{NR}	This study & Cordero (1998)

[a] MS: male mating system according to the classification of Thornhill and Alcock (1983). LT: lek polygyny. PM: pupal mating. SC: scramble competition polygyny. MF: mating frequency. TSRMF: traits statistically related (^{R}), possibly related (^{PR}) or not related (^{NR}) to MF. BL: body length. ED: adult emergence date. FA: fluctuating asymmetry in forewing and hindwing radius length. G: genotype. L: longevity. ME: mating experience. PL: parasitism level. PW: pupal weight. ST: MF depends on specific territory. TB: territorial behavior (species with territorial and non-territorial males). WL: wing length (in the case of *L. japonica* this was measured as the forewing and hindwing radius length). WW: wing wear.

[b] Mean ± SD (range) of spermatophore number of mated females.

[c] Mean ± SD (range) for the second brood of 1975.

[d] Mean lifetime number of copulations ± SD (range).

[e] Number of matings estimated by assessing degree of scale loss from claspers.

[f] Fifty out of 51 field collected females had one spermatophore and one had two (Matsumoto and Susuki,1995).

[g] Number of copulations/ male/ census. Upper figure: non-territorial males; lower figure: territorial males.

[h] Studied in a big outdoors mating cage.

[i] Mean lifetime number of copulations ± SE (range).

[j] Pliske (1973), cited in Drummond (in Smith, 1984), estimated a mean number of spermatophores (maximum) = 2.23 (8).

[k] Relative number of matings estimated by marking male genitalia with powdered fluorescent dye.

[l] Data from Ehrlich & Ehrlich (1978), cited in Drummond (in Smith, 1984).

[m] Mean (range) (Drummond in Smith, 1984).

[n] Maximum number of spermatophores (Gwynne in Smith, 1984).

[o] Butterflies were raised in captivity and released in the field.

[p] Mean ± SE (range).

[q] Number of copulations / focal male / hour of focal observation (minimum number of copulations per male - maximum number of copulations per male). Upper figure: 1989 study period; lower figure: 1990 study period.

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xami, it has been proposed that female "rules of movement" may be responsible for territory location and quality (Bradbury, 1985; Cordero and Soberón, 1990; Rutowski, 1991; Wickman *et al.*, 1995). Although female movement in *C. xami* has not been studied, casual observations suggest that territories are located in the confluence of natural or manmade trails, which are used by females for their displacement through the habitat (Cordero and Soberón, 1990). If this suggestion is true, differences in territory quality may result from the specific location of territories with respect to areas of high probability of female transit, which may vary with time (as suggested by the lack of between-years correlations in occupation frequency and number of copulations in territories).

Male copulation success in other butterflies

Field estimates of male copulation success are scant. In Table 3 we summarize the information on the mating behavior of butterflies in which male copulation success and/or phenotypic traits associated with male copulation success have been studied in the field. Unfortunately, a formal quantitative comparison is prevented by the different methods employed to estimate copulation success (Table 3).

The copulation success of males has been shown to be affected by a variety of factors, such as weather conditions (Davies, 1978), adult emergence date (Elgar and Pierce, 1988), body size (Deinert *et al.*, 1994; Elgar and Pierce, 1988), longevity (Elgar and Pierce, 1988), mating experience (Suzuki and Matsumoto, 1992), type of behaviour (territorial *vs.* non-territorial; Wickman, 1985), female mate choice (Rutowski, 1981-83) and fluctuating asymmetry (Tsubaki and Matsumoto, 1998). A positive effect of body size on male mating frequency has been found in two (four, if the possible cases of *C. pamphilus* and *C. xami* are true) species (Table 3): *Jalmenus evagoras* and *Pieris napi*; while in *Heliconius hewitsoni* body length is negatively correlated with mating success. The first species exhibits pupal mating, a mating system that involves direct male-male competition (the same as lek polygyny, the mating system of *C. pamphilus* and *C. xami*), the second species exhibit scramble competition polygyny, a mating system with indirect male-male competition, and the third species also exhibits pupal mating. These data suggest that big body size (or correlated traits) confer advantages in different male competition settings, although there may be situations in which small size may be advantageous, as in *H. hewitsoni.* However, in *Atrophaneura alcinous* (Susuki and Matsumoto, 1992) and *Danaus plexippus* (Frey *et al.*, 1998), species showing scramble competition polygyny, no relation between male size and mating success was found. These observations are in accord with other studies that indicate that male size and resource holding power are correlated in some butterfly species (Rosenberg and Enquist, 1991) but not in others (Alcock, 1994). In the three species in which it has been investigated, a correlation between male longevity and number of copulations achieved has been found (*Atrophaneura alcinous* and *J. evagoras*) or is suspected (*C. xami*). These species have different mating systems, pertain to different families, and have very different adult body sizes (*Atrophaneura alcinous* is much bigger than the two lycaenids).

APPENDIX

A prospective comparison of all marked males observed copulating (CM) during the first and second parts of both study periods, with all marked males not observed copulating (NCM) supports the suggestion that copulation success may be correlated with wing length and longevity. CM had longer wing length (CM: 1.71 ± 0.1 cm, median = 1.72, range: 1.51–1.89, n = 14; NCM: 1.64 ± 0.1, median = 1.65, range: 1.36–1.88, n = 131; Mann-Whitney U = 569, P = 0.0197) and lived longer (CM: 10.1 ± 5.6 days, median = 9, range: 2–20, n = 18; NCM: 4.1 ± 5, median = 2, range: 1–28, n = 138; U = 397, $P = 10^{-6}$) than NCM, but the degree of wing wear at the moment of being marked was not different (CM: 1.4 ± 0.7, median = 1, range: 1–3, n = 15; NCM: 1.6 ± .7, median = 1, range: 1–3, n = 132; U = 845.5, P = 0.29). The mean number of copulations of the CM was 1.3 ± 0.8 (median = 1, range: 1–4, n = 18). We stress that these comparisons are based in data obtained from a heterogeneus, non-random, and probably biased sampling of males.

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Egg size in butterflies (Lepidoptera: Papilionoidea and Hesperiidae): a summary of data

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Abstract. A table summarising the estimated egg volumes, and adult wing lengths, of 1184 species of butterflies is presented. The estimates were primarily derived from published sources. They are expected to be reasonable approximations, although some amount of measurement error cannot be discarded. They may constitute a useful preliminary data base for studies relating egg size to adult size.

INTRODUCTION

The allometry of egg, or neonate size, to adult body size has frequently prompted the interest of evolutionary biologists. This relationship is of special relevance, first, because of the many potential implications of body size (Calder, 1984). And, second, because the ratio between body size and egg size may have relatively direct effects on the number of eggs that can be produced (that is, potential fecundity), depending on the availability of resources and other anatomical, or physiological characteristics (e.g., Reiss 1989).

The allometry of egg to body size has been subject for study in several kinds of organisms (examples in Reiss 1989), but work on arthropods, including insect orders, is comparatively recent (Blueweiss et al. 1978, Berrigan 1991, Blackburn 1991, Reavey, 1992). The first attempts to determine the interspecific correlation between egg size and ecological variables, or between egg size and parent body size in butteflies were those of Nakasuji (1987) and Wiklund et al (1987), based in small sets of grass-feeding Hesperiinae and Satyrinae, and north-European Pieridae. This not very relevant number of comparative studies is in contrast with the potentially important amount of descriptive material that has been published on butterfly life histories. While it is true that detailed data such as egg weight are scarce, generalizations based on relatively rough estimates such as egg volume probably can make general patterns arise, and thus help subsequent workers to determine the kind of data needed, and the taxa where such patterns probably occur. After a first approach to the interspecific allometry of egg to body size based on a selection of Holarctic butterfly species (García-Barros & Munguira 1997) it was evident that a wider sample, including data from the tropical and subtropical areas, could be attempted without much aditional effort. Consequently, I collected data on butterfly egg descriptions to obtain approximate estimates of egg volume. These were used in a comparative study that will be presented elsewhere. Because of

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the volume of the data base (which includes more than 1200 species), I considered the possibility of presenting them as a separate publication rather than as a summary of, e.g., genus, tribe, or family means. This has disadvantages (essentially, the amount of paper required), but also some advantages, namely the accessibility of the data to other entomologists. This is the main purpose of the present work. While the data are far from complete, and probably not free of error, they will be available for further study in a compyled printed form, and may help others to fill the gaps or even serve as a basis for a more comprehensive, world-based data base on butterfly sizes. While this work might be used to compyle information on egg morphology or related details, it is important to note that much descriptive material that did not contain information on egg size is not quoted here.

METHODS

The data collected included an estimate of egg size, and another of adult size, for each butterfly species. The coverage of the sample was determined by the accessibility of the data (I do not intend it to be exhaustive). Data collection was terminated when the number of species covered was judged to suffice for a preliminary comparative approach. Although some unpublished material was included, the largest part of the estimates derives from the literature alone.

Egg volume. This was calculated using the formula for a regular ellipsoid using the egg maximum diameter (*ed*) and length or heigth (*el*): Egg volume= $1/6(\pi)(ed^2)(el)$. An empyrical approach demonstrated that egg volumes calculated this way may constitute reasonable estimate for eggs with a rounded profile. The fit was not so good for other egg shapes, and was specially rough for very 'square' profiled eggs. Because the descriptions available in the literature are frequently based in very small sample sizes, a potentially important measurement error must be presumed anyway. When two or more descriptions (that included egg width and length) were available, the average was calculated. Eggs described as spheroid, spheric, or nearly spheric were considered to be of spheric shape unless this was contradicted by existing figures, or by information form the most closely related species. When scale figures were available, these were used to estimate the egg dimensions. Estimated egg volumes in mm^3 are given in the table under the heading EV.

Adult wing length. The length of the forewing, measured from the base to the apex, was used to estimate adult size. Actually, the average between the male and female sexes was estimated. Any available source was employed but, since collection material was available for a small part of the species, the live-sized specimens photographed in the plates by D'Abrera (1977–1995) were used by default. When measurements from the adults used in the rearings, or from the same country or geographic area as the egg descriptions were available, these were incorporated. Estimated wing lengths in mm are given in the table under the heading WL.

RESULTS

The data collected cover 1184 species. The results are presented in a single table with five columns. The first of these is the species number (1 to 1184).

The second column corresponds to the species names (with a few exceptions, followed by the author and date of description). I am afraid that the taxonomy had to be eclectic. The specific rank has been mantained for some taxa that should probably be treated as subspecies (in case of duobt, this at least ensures identification). The third and fourth columns give the estimated egg volumes (EV) and wing lengths (WL). The last column (Sources) gives numbered references; the sources are given after the table (see 'Sources').

Some further details on the taxonomic arrangement are given below (see 'Taxonomic arrangement'). Numbers in small case ([1] to [23]) refer to notes on the taxonomy, sources for taxonomic arrangement, or other pertinent detail, given at the end of the text. Finally, I have added one Appendix that summarises the taxonomic (or, when phylogenetic approaches exist, cladistic) relations between the species included. This is in parenthetical notation, and the numbers correspond to those in the species list. This arrangement is used in the comparative interspecific study of the data, that will be presented separately. It may be of use to assess the effect of taxonomic relationships in association with this data set, and it (or parts of it) can be used as input for computer programs as a means to reconstruct the tree structure adopted.

#	**Species**	**EV**	**WL**	**Sources**
1	*Coeliades forestan* (Stoll, 1782)	0.17	28.0	122
2	*C. keithloa* (Wallengren, 1857)	0.39	27.5	122
3	*Allora dolleschallii* (Felder, 1860)	0.42	22.5	219
4	*Acleros mackenii* (Trimen, 1868)	0.31	15.0	122
5	*Kedestes barberae* (Trimen, 1873)	0.71	15.0	122
6	*K. macomo* (Trimen, 1862)	0.57	14.0	122
7	*K. niveostriga* (Trimen, 1864)	0.67	12.5	122
8	*Cymaenes tripunctus* (Herrich-Schäffer, 1865)	0.25	13.5	45
9	*Lerema cornelius* (Latreille, [1824])	0.95	18.0	46
10	*Aeromachus inachus* (Ménétriés, 1859) [13]	0.11	12.5	182
11	*Metisella malgacha* (Boisduval, 1833)	0.20	14.0	122
12	*M. metis* (Linnaeus, 1764)	0.15	13.3	122
13	*Thoressa varia* (Murray, 1864) [13]	0.45	15.5	182
14	*Tsitana uitenhaga* Evans, 1937	0.51	15.5	122
15	*Calpodes ethlius* (Stoll, [1782])	0.65	25.0	129
16	*Nyctelius nyctelius* (Latreille, [1824])	0.82	18.0	45;260
17	*Panoquina nero* (Fabricius, 1798)	1.87	22.0	129
18	*P. sylvicola* (Herrich-Schäffer, 1865)	0.15	18.0	41;45
19	*Parosmodes morantii* (Trimen, 1873)	0.82	14.5	122
20	*Borbo cinnara* (Wallace, 1866) [13]	0.06	14.0	182
21	*B. fallax* (Gaede, 1916)	0.38	16.0	122
22	*B. fatuellus* (Hopffer, 1855)	0.31	18.5	122
23	*B. impar* (Waterhouse, 1932)	0.31	17.0	297
24	*B. lugens* (Hopffer, 1855)	0.33	15.0	122
25	*Gegenes niso* (Linnaeus, 1764)	0.31	14.5	122
26	*Parnara guttatta* (Bremer & Grey, 1853) [13]	0.17	18.5	158;182
27	*P. monasi* (Trimen & Bowker, 1889)	0.21	13.0	122
28	*P. naso* (Fabricius, 1789) [13]	0.13	14.5	182
29	*Pelopidas agna* (Moore, [1866]) [13]	0.30	13.5	182

30	*P. jansonis* (Butler, 1868)[13]	0.35	18.0	182
31	*P. mathias* (Fabricius, 1798)[13]	0.32	17.5	182
32	*P. thrax* (Hübner, [1821])	1.06	22.0	122
33	*Polytremis pellucida* (Murray, 1874)[13]	0.50	18.5	182
34	*Isoteinon lamprospilus* Felder & Felder, 1862[13]	0.36	18.0	182
35	*Amblyscirtes aenus* Edwards, 1878	0.28	12.3	83
36	*Lerodea eufala* (Edwards, 1869)	0.30	13.0	20
37	*Hidari irava* (Moore, [1858])	1.56	27.8	295
38	*Lotongus calathus* (Hewitson, 1876)	3.66	24.5	295
39	*Unkana ambasa* (Moore, [1858])	3.32	31.3	295
40	*Artitropa erinnys* (Trimen, 1862)	2.51	24.0	122
41	*Moltena fiara* (Butler, 1870)	3.77	24.0	122
42	*Zophopetes dysmephila* (Trimen, 1868)	1.18	21.0	122
43	*Ocybadistes knightorum* Lambkin & Donaldson, 1994	0.15	10.7	280
44	*Potanthus flavum* (Murray, 1875)[13]	0.30	15.0	182
45	*Choranthus radians* (Lucas, 1857)	0.15	14.5	41
46	*Hesperia comma* (Linnaeus, 1758)	0.43	15.3	53;156;233
47	*H. nabokovi* (Bell & Comstock, 1948)	1.06	19.0	209
48	*Ochlodes ochracea* (Bremer, 1861)[13]	0.20	14.0	182
49	*O. venatus* (Bremer & Grey, 1862)[13]	0.25	15.1	53;182;233
50	*Poanes hobomok* (Harris, 1862)	0.34	15.0	35
51	*Polites baracoa* (Lucas, 1857)	0.13	11.5	41
52	*P. mystic* (Edwards, 1863)	0.27	15.5	35
53	*P. origenes* (Fabricius, 1793)	0.34	14.5	35
54	*P. sabuleti* (Boisduval, 1852)	0.15	11.8	48
55	*Pompeius verna* (Edwards, 1862)	0.24	13.3	40
56	*Wallengrenia egeremet* (Scudder, 1864)	0.18	14.5	35
57	*W. misera* (Schaus, 1902)	0.26	14.0	41
58	*Ancyloxypha numitor* (Fabricius, 1793)	0.14	11.5	129
59	*Oarisma powesheik* (Parker, 1870)	0.15	12.6	91
60	*Thymelicus acteon* (Rottemburg, 1775)	0.21	12.5	233
61	*T. leoninus* (Butler, 1868)[13]	0.12	15.5	182
62	*T. lineola* (Ochsenheimer, 1808)	0.24	13.0	60
63	*T. sylvaticus* (Bremer, 1861)[13]	0.13	13.5	182
64	*T. sylvestris* (Poda, 1761)	0.38	13.6	60;233
65	*Carterocephalus palaemon* (Pallas, 1771)[13]	0.16	13.8	53;182;233
66	*C. sylvicola* (Meigen, 1728)[13]	0.11	12.5	182
67	*Leptalina unicolor* (Bremer & Grey, [1852])[13]	0.22	15.5	182
68	*Anisynta tillyardi* Waterhouse & Lyell, 1912	0.15	14.0	108
69	*Hesperilla crypsigramma* (Meyrick & Lower, 1902)	0.69	13.7	121
70	*H. furva* Sands & Kerr, 1973	0.69	14.4	121
71	*H. malindeva* Lower, 1911	0.89	18.0	121
72	*H. sarnia* Atkins, 1978	0.68	15.9	121;149
73	*H. sexguttata* Herrich-Schäffer, 1869	0.55	14.7	121
74	*Mesodina cyanophracta* Lower, 1911	2.10	17.7	292
75	*Neohesperilla crocea* (Miskin, 1889)	0.20	14.9	251
76	*N. senta* (Miskin, 1891)	0.35	13.6	251
77	*N. xanthomera* (Meyrick & Lower, 1902)	0.28	13.3	251
78	*N. xiphiphora* (Lower, 1911)	0.40	10.5	251
79	*Pasma tasmanica* (Miskin, 1889)	0.39	19.2	186
80	*Toxidia rietmanni* (Semper, 1879)	0.27	17.2	186
81	*Trapezites genevievae* (Atkins, 1997)	1.27	18.0	293
82	*T. iacchoides* Waterhouse, 1903	1.15	18.6	178
83	*T. maheta* (Hewitson, 1877)	0.66	14.9	161
84	*T. phygalioides* Waterhouse, 1903	1.60	15.9	178
85	*T. praxedes* (Plötz, 1884)	0.59	16.9	161
86	*T. heteromacula* Meyrick & Lower, 1902	0.52	13.4	114

87	*T. sciron* Waterhouse & Lyell, 1914	0.37	15.0	231
88	*T. waterhousei* Mayo & Atkins, 1992	0.15	13.8	300
89	*T. taori* Atkins, 1997	0.81	21.0	293
90	*Antipodia atralba* (Tepper, 1882)	1.47	17.0	152
91	*A. chaostola* (Meyrick, 1888)	0.83	16.3	152
92	*Croitana arenaria* (Edwards, 1879)	0.45	12.1	180
93	*C. croites* (Hewitson, 1874)	0.88	12.5	188
94	*Herimosa albovenata* (Waterhouse, 1940)	0.56	13.5	244
95	*Proeidosa polysema* (Lower, 1908)	0.75	14.0	97
96	*Abantis paradisea* (Butler, 1870)	0.34	21.5	122
97	*Celaenorrhinus mokeezi* (Wallengren, 1857)	0.28	20.0	122
98	*Eagris nottoana* (Wallengren, 1857)	0.34	14.3	122
99	*Eretis djaelaelae* (Wallengren, 1857)	0.17	14.0	122
100	*Netrobalane canopus* (Trimen, 1864)	0.26	18.5	122
101	*Anastrus sempiternus* (Butler & Druce, 1872)	0.27	21.0	125
102	*Erynnis afranius* (Lintner, 1878)	0.25	16.0	29
103	*E. tages* (Linnaeus, 1758)	0.11	13.5	53;60;233
104	*E. tristis* (Boisduval, 1852)	0.30	18.9	28
105	*E. zarucco* Lucas, 1857	0.15	20.0	15
106	*Alenia sandaster* (Trimen, 1868)	0.09	11.5	122
107	*Carcharodus alceae* (Esper, 1790)	0.20	14.0	304
108	*Gomalia elma* (Trimen, 1862)	0.25	13.5	191
109	*Heliopetes ericetorum* (Boisduval, 1852)	0.21	17.5	12;24
110	*Hesperopsis libya* (Scudder, 1878)	0.51	13.0	29
111	*Pyrgus alveus* (Hübner, 1803)	0.33	13.5	233
112	*P. communis* (Grote, 1872)	0.05	13.5	49;24
113	*P. malvae* (Linnaeus, 1758)	0.11	11.5	53;60;233
114	*P. oileus* (Linnaeus, 1767)	0.04	15.0	43
115	*Spialia asterodia* (Trimen, 1864)	0.09	11.5	122
116	*S. depauperata* (Strand, 1911)	0.21	12.5	122
117	*S. dromus* (Plötz, 1864)	0.23	11.5	122
118	*S. mafa* (Trimen, 1870)	0.13	11.5	122
119	*S. nanus* (Trimen & Bowker, 1889)	0.13	11.0	122
120	*S. sataspes* (Trimen, 1864)	0.16	12.0	122
121	*S. spio* (Linnaeus, 1767)	0.21	12.5	122
122	*Syrichtus proto* (Oschsenheimer, 1808)	0.39	14.5	102
123	*Sarangesa motozi* (Wallengren, 1857)	0.20	17.0	122
124	*S. phidyle* (Walker, 1870)	0.17	16.0	122
125	*Tagiades flesus* (Fabricius, 1781)	0.25	23.5	122
126	*Aguna albistria* (Plötz, 1881)	0.30	16.0	135
127	*Cabares potrillo* (Lucas, 1857)	0.26	18.0	43
128	*Codatractus aminias* (Hewitson, 1867)	0.30	23.5	38
129	*Polygonus leo* (Gmelin, [1790])	0.34	23.0	3;47
130	*Typhedanus undulatus* (Hewitson, 1867)	0.27	21.0	26
131	*Urbanus dorantes* (Stoll, [1790])	0.28	22.0	47;66;260
132	*U. simplicius* (Stoll, [1790])	0.34	20.0	38
133	*Archon apollinus* (Herbst, 1798)	0.26	28.3	239
134	*Hypermnestra helios* (Nickerl, 1846)	0.24	26.9	239
135	*Parnassius szechenyii* Frivaldszky, 1886	0.45	33.0	239
136	*P. acdestis* Grum-Grshimailo, 1891	0.65	28.5	239
137	*P. delphius* (Eversmann, 1843)	0.47	31.0	239
138	*P. imperator* Oberthür, 1883	0.68	40.1	239
139	*P. autocrator* Avinoff, 1913	0.67	36.0	239
140	*P. loxias* Püngeler, 1901	0.64	33.5	239
141	*P. maximinus* Staudinger, 1891	0.71	36.0	239
142	*P. acco* Gray, 1853	0.59	27.9	239
143	*P. simo* Gray, 1853	0.72	24.5	239

144	*P. simonius* Staudinger, 1889	0.80	25.5	239
145	*P. hardwickii* Gray, 1831	0.43	29.1	239
146	*P. ariadne* (Lederer, 1853)	0.97	34.5	239
147	*P. glacialis* Butler, 1866	1.06	37.3	239
148	*P. mnemosyne* (Linnaeus, 1758)	0.97	30.8	239;249
149	*P. nordmanni* (Nordmann, 1851)	1.30	33.0	239
150	*P. stubbendorfii* Ménétries, 1849	0.66	32.5	239
151	*P. actius* (Eversmann, 1843)	1.01	31.0	239
152	*P. apollo* (Linnaeus, 1758)	1.12	39.5	239
153	*P. apollonius* (Eversmann, 1847)	2.54	39.5	239
154	*P. epaphus* Oberthür, 1879	0.76	27.0	239
155	*P. honrathi* Staudinger, 1882	1.85	39.0	239
156	*P. jacquemontii* Boisduval, 1836	0.87	33.5	239
157	*P. phoebus* (Fabricius, 1793)	0.89	36.0	239
158	*P. tianschanicus* Oberthür, 1879	0.97	39.5	239
159	*Sericinus montela* Gray, 1853	0.20	37.0	295
160	*Allancastria cerisyi* (Godart, 1822)	0.17	28.0	239
161	*Zerynthia polyxena* (D. & Schiff., 1775)	0.20	28.3	60
162	*Z. rumina* (Linnaeus, 1758)	0.24	25.3	304
163	*Bhutanitis linderallii* Atkinson, 1873	1.05	59.0	295
164	*Luehdorfia japonica* Leech, 1889	0.53	31.0	295
165	*L. longicaudata* Lee [2]	0.60	35.0	295
166	*L. puziloi* (Erschoff, 1872)	0.41	29.5	295
167	*Eurytides celadon* (Lucas, 1852)	0.42	38.2	43
168	*E. epidaus* (Doubleday, 1846)	0.52	43.0	66
169	*E. belesis* (Bates, 1864)	0.52	46.0	73
170	*Iphiclides feisthameli* (Duponchel, 1832)	1.59	41.2	234;304
171	*I. podalirius* (Linnaeus, 1758)	1.58	39.5	60;234
172	*Graphium eurypylus* (Linnaeus, 1758)	0.52	38.0	37
173	*G. sarpedon* (Linnaeus, 1758)	0.76	45.5	39
174	*G. aristeus* (Cramer, [1775])	0.29	39.6	200
175	*G. antipathes* (Cramer, [1775])	0.80	55.0	37
176	*G. angolanus* (Goeze, 1779)	0.38	41.1	259
177	*G. antheus* (Cramer, [1779])	0.50	48.0	259
178	*G. leonidas* (Fabricius, 1793)	0.64	47.5	259
179	*G. morania* (Angas, 1849)	0.50	37.2	259
180	*G. policenes* (Cramer, [1775])	0.50	40.0	259
181	*Pharmacophagus antenor* (Drury, 1773)	4.61	68.5	290
182	*Battus polydamas* (Linnaeus, 1758) [13]	0.66	48.0	43;66;94
183	*Troides aeacus* (Felder & Felder, 1860)	6.12	81.0	295
184	*T. amphrysus* (Cramer, 1782)	7.64	77.0	295
185	*T. andromache* (Staudinger, 1892)	6.85	70.0	295
186	*T. helena* (Linnaeus, 1758)	2.18	81.0	295
187	*T. hipolitus* (Cramer, [1775])	5.40	87.5	295
188	*T. miranda* (Butler, 1869)	6.69	91.0	295
189	*T. brookiana* (Wallace, 1855)	2.54	83.5	295
190	*T. alexandrae* (Rothschild, 1907)	20.5	100.0	87;295
191	*T. priamus* (Linnaeus, 1758)	9.36	91.5	295
192	*Parides arcas* (Cramer, [1777]) [13]	0.68	39.0	94;101
193	*P. childrenae* (Gray, 1832) [13]	0.71	48.5	94
194	*P. iphidamas* (Fabricius, 1793)	0.55	39.5	119
195	*P. photinus* (Doubleday, 1844)	6.79	47.5	75
196	*P. alcinous* (Klug, 1836)	1.55	54.0	239
197	*P. horishana* (Matsumura, 1910)	9.39	70.0	295
198	*P. polyeuctes* (Doubleday, 1842)	3.07	57.0	295
199	*P. semperi* (Felder & Felder, 1861)	5.93	73.5	295
200	*P. varuna* (White, 1868)	2.41	55.0	295

201	*Pachliopta aristolochiae* (Fabricius, 1775)	1.32	48.0	295
202	*Cressida cressida* (Fabricius, 1775)	1.10	50.5	295
203	*Papilio homerus* Fabricius, 1793	3.02	75.9	210;222;238
204	*P. hellanichus* Hewitson, 1868	1.24	45.0	21;81
205	*P. thoas* Linnaeus, 1771	0.83	48.5	22
206	*P. anchisiades* Esper, 1788 13	0.82	52.5	94
207	*P. agestor* (Gray, 1832)	1.83	56.5	295
208	*P. epycides* (Hewitson, 1862)	0.46	33.0	295
209	*P. laglaizei* Depuiset, 1877	0.38	51.0	109
210	*P. clytia* Linnaeus, 1758	0.73	52.0	295
211	*P. maraho* (Shiraki & Sonan, 1934)	1.42	64.5	295
212	*P. demolion* Cramer, 1779	0.99	51.0	295
213	*P. gigon* Felder & Felder, 1864	0.91	70.0	295
214	*P. euchenor* Guérin-Méneville, 1829	2.53	66.5	295
215	*P. nireus* Linnaeus, 1758	0.66	50.5	259
216	*P. alexanor* Esper, 1799	0.39	42.0	235
217	*P. indra* Reakirt, 1866	0.68	38.5	71;82;103
218	*P. hospiton* Genée, 1839	0.50	40.0	197;235
219	*P. machaon* Linnaeus, 1758	0.68	40.0	60;197;304
220	*P. hippocrates* Felder & Felder, 1864	0.73	53.0	235
221	*P. echerioides* Trimen, 1868	0.75	42.8	259
222	*P. ophidicephalus* Oberthür, 1878	2.14	61.0	259
223	*P. dardanus* Brown, 1776	1.59	46.9	259
224	*P. demodocus* Esper, 1798	0.96	46.0	259
225	*P. demoleus* (L.)	0.60	41.0	211
226	*P. euphranor* Trimen, 1868	0.97	54.3	259
227	*P. paris* Linnaeus, 1758	1.77	48.5	37
228	*Dismorphia amphiona* (Cramer, [1777])	0.28	33.0	132
229	*D. foedora* (Lucas) [1]	0.38	29.0	98
230	*D. spio* (Godart, 1819)	0.51	33.0	260
231	*Leptidea sinapis* (Linnaeus, 1758)	0.15	20.2	53;60;233
232	*Colotis antevippe* (Boisduval, 1836)	0.18	21.3	259
233	*C. auxo* (Lucas, 1852)	0.25	21.1	259
234	*C. danae* (Fabricius, 1775)	0.14	23.7	259
235	*C. evagore* (Klug, 1829)	0.08	18.3	259
236	*C. evippe* (Linnaeus, 1758)	0.11	20.5	259
237	*C. erone* (Angas, 1849)	0.17	26.0	80
238	*C. ione* (Godart, 1819)	0.08	25.5	80
239	*C. vesta* (Reiche, 1849)	0.08	21.5	80
240	*C. eris* (Klug, 1829)	0.28	23.6	259
241	*Eronia cleodora* (Hübner, 1823)	0.28	29.2	259
242	*Hebomia glaucippe* (Linnaeus, 1758)	1.04	50.0	295
243	*Nepheronia argia* (Fabricius, 1775)	1.52	39.4	259
244	*N. buquettii* (Boisduval, 1836)	0.67	29.4	259
245	*Pareronia boebera* (Eschscholtz, 1821)	1.43	36.0	139
246	*Anthocharis cardamines* (Linnaeus, 1758)	0.16	21.1	233;53;60;233
247	*A. cethura* Felder & Felder, 1865	0.11	17.0	28
248	*Euchloe ausonia* Hübner, 1803	0.24	23.0	53
249	*E. belemia* (Esper, [1800])	0.12	22.9	175;281
250	*E. crameri* Butler, 1869	0.13	23.3	175;281
251	*E. ogilvia* Back, 1990	0.11	20.0	201
252	*E. tagis* (Hübner, [1804])	0.06	19.0	175;281
253	*E. hyantis* (Edwards, 1871)	0.11	21.0	28
254	*Pinacopteryx eriphia* (Godart, 1819)	0.09	29.3	259
255	*Aporia crataegi* (Linnaeus, 1758)	0.11	32.3	53;60;204
256	*Appias epaphia* (Cramer, [1779])	0.13	28.7	259
257	*Belenois aurota* (Fabricius, 1793)	0.12	25.8	259

258	*B. creona* (Cramer, [1775])	0.12	27.0	259
259	*B. gidica* (Godart, 1819)	0.08	29.0	259
260	*B. thysa* (Hopffer, 1855)	0.30	33.4	259
261	*B. zochalia* (Boisduval, 1836)	0.13	28.7	259
262	*Cepora nerissa* (Fabricius, 1775)	0.08	29.5	295
263	*Delias descombesi* (Boisduval, 1836)	0.21	41.5	295
264	*Dixeia charina* (Boisduval, 1836)	0.08	22.2	259
265	*D. pigea* (Boisduval, 1836)	0.16	24.9	259
266	*Ixias pyrene* (Linnaeus, 1764)	0.19	33.5	295
267	*Leptophobia caesia* (Lucas, 1852)	0.41	27.0	96
268	*Mylothris agathina* (Cramer, [1779])	0.26	31.5	259
269	*M. rueppellii* (Koch, 1865)	0.28	31.5	259
270	*M. trimenia* Butler, 1869	0.24	27.8	259
271	*Perrhybris lypera* (Kollar, 1850) [13]	1.00	35.3	94
272	*Phulia nymphula* (Staudinger? Blanch.?) [1]	0.05	17.0	184
273	*P. rosea* [1]	0.07	15.0	184
274	*Pieris brassicae* (Linnaeus, 1758)	0.18	29.8	53;60;233
275	*P. rapae* (Linnaeus, 1758)	0.13	24.5	53;60;233
276	*P. virginiensis* Edwards, 1870	0.10	24.4	184;206
277	*P. napi* (Linnaeus, 1758)	0.14	22.5	53;60;233
278	*P. brionniae* (Hübner, 1805)	0.31	22.5	172;208
279	*P. callidice* Hübner, 1800	0.05	23.7	184
280	*P. occidentalis* (Reakirt) [2]	0.05	23.7	184
281	*P. protodice* (Boisduval & Le Conte, 1833)	0.05	23.4	184
282	*Pontia daplidice* (Linnaeus, 1758)	0.14	22.5	53;60
283	*P. helice* (Linnaeus, 1764)	0.12	23.0	259
284	*P. chlorodice* (Hübner, 1808)	0.13	22.0	13
285	*Prioneris thestylis* (Doubleday, 1842)	0.29	46.0	295
286	*Tatochila mercedis* (Eschscholtz, 1821)	0.04	27.0	184
287	*T. microdice* [1]	0.10	21.0	184
288	*T. sterodice* [1]	0.07	28.0	184
289	*T. vanvolxemii* (Capr.) [1]	0.14	30.0	184
290	*Leptosia alcesta* (Stoll, 1870)	0.13	22.0	80
291	*Anteos clorinde* Godart, 1823	0.16	44.0	43
292	*Catopsilia florella* (Fabricius, 1775)	0.21	35.0	259
293	*C. pomona* (Fabricius, 1775)	0.13	34.5	295
294	*C. pyranthe* (Linnaeus, 1758)	0.17	36.0	295
295	*Colias alfacariensis* Ribbe, 1905	0.13	24.5	53;62;181
296	*C. croceus* (Geoffroy, 1785)	0.13	25.5	53;207;233
297	*C. electo* (Linnaeus, 1763)	0.09	24.3	259
298	*C. hyale* (Linnaeus, 1758)	0.10	24.0	53;60;62
299	*C. myrmidone* (Esper, 1781)	0.10	23.0	207
300	*C. palaeno* (Linnaeus, 1761)	0.13	25.0	53;212
301	*Eurema brigitta* (Stoll, [1780])	0.06	20.4	259
302	*E. jucunda* [1]	0.03	24.0	66
303	*E. lisa* (Boisduval & Le Conte, 1829)	0.03	17.0	43
304	*E. albula* (Cramer, [1775])	0.41	18.5	31
305	*E. desjardinsii* (Boisduval, 1833)	0.10	20.0	76
306	*E. hecabe* (Linnaeus, 1758)	0.18	22.5	76
307	*Gonepteryx cleobule* (Hübner, 1825)	0.06	37.0	215
308	*G. rhamni* (Linnaeus, 1758)	0.21	28.1	53;60;205;233
309	*Nathalis iole* Boisduval, 1836	0.02	14.3	43
310	*Phoebis cipris* (Fabricius) [2]	0.08	32.5	20
311	*Gandaca harina* (Horsfield, [1829])	0.14	24.0	139
312	*Abisara neophron* (Hewitson, 1860)	0.06	23.8	294
313	*Hamearis lucina* (Linnaeus, 1758)	0.22	15.2	53;60;233
314	*Euselasia hieronymi* (Salvin & Godman, 1868)	0.05	15.0	136

315	*E. hygenius* (Stoll, 1790)	0.06	13.5	279
316	*Napaea beltiana* Bates, 1869	0.09	17.0	227
317	*N. orpheus* (Hewitson, 1847)	0.08	14.3	58
318	*Mesosemia acuta* Hewitson, 1873	0.07	20.0	58
319	*Calephelis borealis* (Grote & Robinson, 1866)	0.05	13.5	33
320	*C. nilus* (Felder, 1861)	0.05	10.5	136
321	*C. rawsoni* McAlpine, 1939	0.06	12.5	136
322	*C. perditalis* (Barnes & McDunnough, 1918)	0.06	13.3	111
323	*Caria ino* (Godman & Salvin, 1866)	0.05	11.0	136
324	*Lasaia sula* Staudinger, 1888	0.06	16.0	136
325	*Metacharis ptolomaeus* (Fabricius, 1783)	0.03	17.5	194;216
326	*Panara thisbe* (Fabricius, 1781)	0.03	19.0	58
327	*Apodemia mormo* (Felder & Felder, 1859)	0.27	15.5	24;136
328	*A. nais* Edwards, 1874 [1,2]	0.22	15.5	136
329	*A. palmeri* (Edwards, 1871)	0.22	11.5	28;136
330	*A. walkeri* (Godman & Salvin, 1886) [2]	0.10	13.6	136
331	*Emesis emesia* (Hewitson, 1867)	0.05	13.0	136
332	*E. mandana* (Cramer, [1780])	0.15	22.5	136
333	*E. tegula* Godman & Salvin, 1886	0.21	19.5	136
334	*E. tenedia* Felder & Felder, 1861	0.11	19.0	136
335	*E. zela* Butler, 1870 [2]	1.06	14.1	57
336	*Audre susanae* Orfila, 1935	0.18	15.5	56
337	*A. colchis* (Felder, 1865)	0.10	22.5	58
338	*Lemonias caliginea* (Clench, 1964)	1.00	17.9	74
339	*L. epone* (Godart, 1825)	0.16	18.5	58
340	*Stichelia sagaris* (Cramer, [1777])	0.13	12.0	194
341	*Xenandra agria* (Hewitson, 1847)	0.07	19.5	58
342	*Charis calicene?* (Hewitson, 1866)	0.08	13.0	58
343	*Synargis phillone* (Godart, [1824])	0.12	21.5	58
344	*Baliochila aslanga* (Trimen, 1873)	0.03	16.0	85
345	*Durbania amakosa* Trimen, 1862	0.15	14.9	85
346	*Durbaniopsis saga* Trimen, 1883	0.17	16.8	85
347	*Alaena amazoula* Boisduval, 1847	0.15	13.5	85
348	*A. margaritacea* Eltringam, 1929	0.17	12.8	85
349	*Pentila tropicalis* (Boisduval, 1847)	0.08	17.7	85
350	*Lachnocnema bibulus* (Fabricius, 1793)	0.03	13.5	85
351	*L. durbani* Trimen, 1887	0.04	12.8	85
352	*Thestor basutus* (Wallengren, 1857)	0.13	18.0	85
353	*T. brachycerus* (Trimen, 1883)	0.07	14.1	85
354	*T. dicksoni* Riley, 1954	0.07	21.1	85
355	*T. dukei* van Son, 1951	0.08	14.5	85
356	*T. holmesi* van Son, 1951	0.08	16.8	85
357	*T. protumnus* van Son, 1941	0.14	19.6	85
358	*T. rileyi* Pennington, 1956	0.09	17.2	85
359	*T. yildizae* van Son, 1941	0.07	16.0	85
360	*Taraka hamada* (Druce, 1875)	0.05	14.5	299
361	*Curetis acuta* Moore, 1877	0.29	22.8	299
362	*Aloeides aranda* (Wallengren, 1857)	0.21	14.8	85
363	*A. clarki* Tite & Dickson, 1968	0.21	14.5	85
364	*A. damarensis* (Trimen, 1891)	0.13	16.6	85
365	*A. dentatis* (Swierstra, 1909)	0.17	16.5	240
366	*A. depicta* Tite & Dickson, 1968	0.21	18.3	85
367	*A. gowani* Tite & Dickson, 1968	0.26	17.7	85
368	*A. pallida* (Riley, 1938)	0.34	17.1	85
369	*A. pierus* (Cramer, [1779])	0.20	15.1	85
370	*A.* sp indet. [3]	0.24	16.0	85
371	*Aphnaeus hutchinsonii* (Trimen, 1887)	0.38	18.3	85

372	*Argyrocupha malagrida* (Wallengren, 1857)	0.61	15.2	85
373	*Axiocerses tjoane* Grose-Smith, 1900	0.21	15.9	85
374	*Chrysoritis zeuxo* (Linnaeus, 1764)	0.17	13.4	85
375	*Crudaria leroma* (Wallengren, 1857)	0.15	15.6	85
376	*Oxychaeta dicksoni* Gabriel, 1947	0.17	16.3	85
377	*Phasis braueri* Dickson, 1968	0.74	19.8	85
378	*P. thero* (Linnaeus, 1764)	0.74	18.8	85
379	*Poecilmitis adonis* Pennington, 1962	0.23	14.4	85
380	*P. aridus* Pennington, 1953	0.17	12.8	85
381	*P. braueri* Pennington, 1967	0.17	12.8	85
382	*P. felthami* (Trimen, 1904)	0.28	12.5	85
383	*P. lycegenes* (Trimen, 1864)	0.23	12.4	85
384	*P. lysander* Pennington, 1962	0.19	13.5	85
385	*P. nigricans* (Aurivillius, 1925)	0.21	13.9	85
386	*P. palmus* (Cramer, 1781)	0.19	12.8	85
387	*P. pyroeis* (Trimen, 1864)	0.28	14.1	85
388	*P. thysbe* (Linnaeus, 1764)	0.19	12.8	85
389	*P. uranus* Pennington, 1962	0.24	13.8	85
390	*Spindasis ella* (Hewitson, 1865)	0.17	14.1	85
391	*S. natalensis* (Westwood, 1852)	0.18	17.0	85
392	*S. takanonis* Matsumura, 1906	0.11	14.7	299
393	*Trimenia wallengrenii* (Trimen, 1887)	0.89	19.5	85
394	*T. argyroplaga* Dickson, 1967	0.53	17.6	85
395	*Tylopaedia sardonyx* (Trimen, 1868)	0.42	22.0	85;141;153
396	*Lycaena alciphron* (Rottemburg, 1775)	0.11	18.6	60;302
397	*L. clarki* (Clark & Dickson, 1971)	0.05	14.3	85
398	*L. dispar* (Haworth, 1802)	0.08	19.8	53;60
399	*L. epixanthe* (Boisduval & Le Conte, [1835])	0.14	12.8	163
400	*L. helle* (D. & Schiff., 1775)	0.07	12.8	53
401	*L. helloides* (Boisduval, 1852)	0.08	15.0	18;24
402	*L. hippothoe* (Linnaeus, 1761)	0.08	17.3	60
403	*L. orus* (Cramer, 1782)	0.06	10.5	85
404	*L. phlaeas* (Linnaeus, 1761)	0.06	14.6	60
405	*L. tityrus* (Poda, 1761)	0.10	14.3	53;60
406	*L. virgaureae* (Linnaeus, 1758)	0.20	16.4	60
407	*Heliophorus epicles* (Godart, [1824])	0.06	16.0	295
408	*Arhopala muta* (Hewitson, 1862)	0.12	16.5	295
409	*A. bazalus* (Hewitson, 1862)	0.09	17.3	299
410	*A. ganesa* Moore, 1857	0.09	16.0	299
411	*A. japonica* Murray, 1857	0.14	19.0	299
412	*Acrodipsas illidgei* (Waterhouse & Lyell, 1914)	0.14	13.9	199
413	*Paralucia aurifera* (Blanchard, 1848)	0.14	11.8	202
414	*P. pyrodiscus* (Rosenstock, 1885)	0.23	12.5	202
415	*P. spinifera* Edwards & Common, 1978	0.10	9.3	202
416	*Thecla betulae* (Linnaeus, 1758)	0.28	19.3	53;60;233;261
417	*Thecla? phydela* Hewitson, 1869	0.03	16.5	38
418	*Cordelia comes* (Leech, 1890)	0.11	15.5	295
419	*Laeosopis roboris* (Esper, [1793])	0.27	22.5	304
420	*Ussuriana takarana* (Araki & Hirayama, 1941)	0.11	23.0	295
421	*U. stygiana* (Butler, 1881)	0.20	22.5	299
422	*Shirozua jonasi* (Janson, 1877)	0.43	22.0	105;264;299
423	*Artopoetes pryeri* (Murray, 1873)	0.26	23.0	105;299
424	*Coreana raphaelis* (Oberthür, 1880)	0.14	19.5	299
425	*Chrysozephyrus rarasanus* (Matsumura, 1939)	0.31	19.0	295
426	*C. hisamatsusanus* (Nagami & Ishiga, 1937)	0.11	19.0	295;299
427	*C. ataxus* (Doubleday & Hewitson, 1852)	0.14	22.5	295;299
428	*C. brillantinus* (Staudinger) [2]	0.40	20.0	261;299

429	*C. smaragdinus* Bremer, 1864	0.32	18.5	299
430	*Habrodais grunus* (Boisduval, 1852)	0.38	16.8	141;153
431	*Neozephyrus quercus* (Linnaeus, 1758)	0.18	16.3	233;261
432	*N. japonicus* Murray [2]	0.11	16.0	261;299
433	*Sibataniozephyrus fujisanus* (Matsumura, 1910)	0.25	16.8	250;299
434	*S. kuafui* Hsu & Lin, 1994	0.30	16.6	277
435	*Iratsume orsedice* (Butler, 1882)	0.13	18.8	105;299
436	*Japonica adusta* Riley [2]	0.19	19.5	299
437	*J. lutea* (Hewitson, 1865)	0.24	20.0	261;299
438	*J. saepestriata* (Hewitson, 1865)	0.16	21.0	299
439	*Favonius jezoensis* (Matsumura, 1915)	0.20	20.0	299
440	*F. latifasciatus* Shirozu & Hayashi, 1959	0.16	20.0	299
441	*F. orientalis* (Murray, 1875)	0.18	19.8	299
442	*F. saphirinus* (Staudinger, 1887)	0.16	17.8	261;299
443	*F. taxila* (Bremer, 1861)	0.15	18.3	299
444	*F. ultramarinus* (Fixsen, 1877)	0.21	19.5	261;299
445	*F. yuasai* Shirozu, 1948	0.13	19.5	299
446	*Araragi entheum* (Janson, 1877)	0.11	15.3	105;299
447	*Wagimo signatus* (Butler, 1882)	0.18	15.5	261;299
448	*Antigius attilia* (Bremer, 1861)	0.19	17.0	261;299
449	*A. butleri* (Fenton, 1881)	0.22	16.8	261;299
450	*Ogyris genoveva* Hewitson, 1853	0.13	18.0	92
451	*Myrina dermaptera* (Wallengren, 1857)	0.25	16.8	85
452	*M. silenus* (Trimen, 1879)	0.28	19.9	85
453	*Eooxylides tharis* (Geyer, 1837)	0.32	16.0	236
454	*Iolaus silas* (Westwood, 1852)	0.15	17.7	85
455	*I. aemulus* (Trimen, 1895)	0.09	12.8	85
456	*I. alienus* (Trimen, 1898)	0.17	18.1	85
457	*I. aphnaeoides* (Trimen, 1837)	0.13	15.0	259
458	*I. mimosae* (Trimen, 1874)	0.15	15.8	85
459	*I. sidus* (Trimen, 1895)	0.13	16.2	85
460	*I. bowkeri* (Trimen, 1864)	0.21	18.1	85
461	*Hypolycaena philippus* (Fabricius, 1793)	0.05	16.5	85
462	*Leptomyrina hirundo* (Wallengren, 1857)	0.06	13.4	85
463	*L. gorgias* (Stoll, 1790)	0.19	14.5	85
464	*L. lara* (Linnaeus, 1764)	1.00	12.4	85
465	*Capys alphaeus* (Cramer, [1777])	1.34	20.0	85
466	*C. dijunctus* Trimen, 1885	0.31	18.5	85
467	*Deudorix antalus* (Hopffer, 1855)	0.17	16.6	85
468	*D. dinochares* Grose-Smith, 1887	0.28	18.0	85
469	*D. diocles* Hewitson, 1869	0.37	19.5	85
470	*D. epijarbas* (Moore, 157)	0.19	21.0	36
471	*Artipe eryx* (Linnaeus, 1771)	0.35	17.5	299
472	*Rapala aurata* (Bremer, 1864)	0.10	15.8	299
473	*Callophrys rubi* (Linnaeus, 1758)	0.13	13.8	60;233
474	*C. avis* (Chapman, 1909)	0.10	14.5	89
475	*C. loki* (Skinner) [2,4]	0.13	13.2	17
476	*C. nelsoni* (Boisduval) [2,4]	0.17	13.0	29
477	*C. ferrea* Butler, 1866	0.05	14.5	299
478	*Evenus regalis* (Cramer, [1775])	0.18	25.0	141;153
479	*Satyrium pruni* (Linnaeus, 1758)	0.17	16.4	233;299
480	*S. iyonis* Ota & Kusunoki, 1957	0.22	14.3	299
481	*S. mera* (Janson, 1873)	0.10	16.5	299
482	*S. esculi* (Hübner, [1806])	0.31	16.1	302
483	*S. spini* (D. & Schiff., 1775)	0.15	16.0	60
484	*S. w-album* (Knoch, 1782)	0.14	15.5	233;261;299
485	*Eumaeus debora* (Hewitson?) [1]	0.21	30.0	75

486	*E. toxea* Godart, 1824[5]	0.45	22.0	75
487	*E. minijas* (Hübner, 1809)	0.46	22.5	75;141;153
488	*Candalides* cyprotus (Olliff, 1886)	0.11	14.8	179
489	*C. gilberti* Waterhouse, 1903	0.13	14.5	274
490	*Anthene amarah* (Guérin, 1847)	0.04	12.8	85
491	*A. butleri* (Trimen, 1881)	0.10	14.3	85
492	*A. definita* (Butler, 1899)	0.03	14.3	85
493	*A. kersteni* (Cramer, [1780])	0.03	14.1	85
494	*A. lemnos* (Hewitson, 1878)	0.04	15.6	85
495	*A. otacilia* (Trimen, 1868)	0.12	12.2	85
496	*A.* sp indet.[6]	0.17	12.5	85
497	*A. talboti* Stempfer, 1936	0.06	12.5	85
498	*Cupidopsis cissus* (Godart, 1819)	0.08	17.6	85
499	*C. jobates* (Hopffer, 1885)	0.07	15.8	85
500	*Pseudonacaduba sichela* (Wallengren, 1857)	0.02	13.8	85
501	*Nacaduba kurava* (Moore, 1857)	0.04	12.0	288;299
502	*Actizera lucida* (Trimen, 1883)	0.03	10.5	85
503	*A. stellata* (Trimen, 1883)	0.03	9.0	85
504	*Cacyreus dicksoni* Pennington, 1962	0.06	11.8	85
505	*C. lyngeus* (Cramer, 1872)	0.04	14.7	85
506	*C. marshalli* Butler, 1897	0.04	13.5	85;221
507	*C. palemon* (Cramer, 1782)	0.04	10.5	85
508	*C. virilis* (Aurivillius, 1924)	0.03	15.2	85
509	*Harpendyreus notobia* (Trimen, 1868)	0.15	14.7	85
510	*Lampides boeticus* (Linnaeus, 1767)	0.04	16.5	85;112
511	*Jamides alecto* (Felder & Felder, 1860)	0.13	20.5	299
512	*J. bochus* (Stoll, 1782)	0.03	16.5	299
513	*Leptotes brevidentatus* Tite, 1958	0.04	13.8	85
514	*L. cassius* (Cramer, [1775])	0.03	12.0	127
515	*L. pirithous* (Linnaeus, 1767)	0.04	13.5	85;112
516	*Tarucus bowkeri* (Trimen, 1883)	0.08	13.5	85
517	*T. sybaris* (Hopffer, 1885)	0.06	12.9	85
518	*Tuxentius calice* (Hopffer, 1855)	0.03	11.5	85
519	*T. melaena* (Trimen, 1887)	0.06	12.2	85
520	*Zintha hintza* (Trimen, 1864)	0.08	13.0	85
521	*Zizeeria knysna* (Trimen, 1862)	0.03	11.5	85
522	*Z. maha* Kollar, 1848	0.04	12.8	299
523	*Zizina antanossa* (Mabille, 1877)	0.06	13.0	85
524	*Z. otis* (Fabricius, 1787)	0.04	10.5	299
525	*Zizula hylax* (Fabricius, 1775)	0.01	9.9	85;246
526	*Brephidium exilis* (Boisduval, 1852)	0.02	8.5	16;141;153
527	*B. metophis* (Wallengren, 1860)	0.02	9.0	85
528	*Cupido lorquinii* (Herrich-Schäffer, 1847)	0.04	10.2	189;302
529	*C. minimus* (Fuessly, 1775)	0.02	10.6	60;233
530	*Everes argiades* (Pallas, 1771)	0.03	13.0	60;299
531	*E. comyntas* (Godart, 1828)	0.06	14.5	78
532	*E. lacturnus* (Godart, [1824])	0.03	12.0	220;299
533	*E. fischeri* (Eversmann, 1843)	0.02	12.3	299
534	*Pithecops corvus* Fruhstorfer, [1919]	0.05	13.5	299
535	*P. fulgens* Doherty, 1889	0.05	12.5	299
536	*Azanus jesous* (Guérin, 1847)	0.03	12.3	85
537	*A. mirza* (Plötz, 1880)	0.02	12.5	85
538	*A. moriqua* (Wallengren, 1857)	0.02	11.9	85
539	*A. natalensis* (Trimen, 1887)	0.02	13.2	85
540	*Eiochrysops hippocrates* (Fabricius, 1793)	0.03	10.8	85
541	*E. messappus* (Godart, 1819)	0.04	10.5	85
542	*Celastrina argiolus* (Linnaeus, 1758)	0.06	14.5	60

543	*C. sugitanii* Matsumura [2]	0.04	13.8	299
544	*Actyolepis puspa* (Horsfield, [1828])	0.04	15.0	299
545	*Megisba malaya* (Horsfield, 1828)	0.03	12.5	299
546	*Udara albocaerulea* (Moore, 1879)	0.05	16.0	299
547	*Glaucopsyche alexis* (Poda, 1761)	0.09	15.0	60
548	*G. melanops* (Boisduval, [1828])	0.07	14.3	302
549	*G. piasus* (Boisduval, 1852)	0.05	17.0	14;24;141;153
550	*G. lygdamus* (Doubleday, 1841)	0.06	14.5	9;141;153
551	*G. lycormas* (Butler, 1868)	0.07	17.5	299
552	*Maculinea iolas* (Oschenheimer, [1816])	0.06	18.9	189;302
553	*M. alcon* (D. & Schiff., 1775)	0.05	17.9	53;60;189
554	*M. arion* (Linnaeus, 1758)	0.05	19.9	4;53;60;189
555	*M. nausithous* (Bergsträsser, [1779])	0.06	16.7	189;302
556	*M. rebeli* (Hirschke, 1904)	0.05	16.9	53;189;302
557	*M. teleius* (Bergsträsser, [1779])	0.05	17.0	53;299
558	*M. arionides* Staudinger [2]	0.10	19.5	299
559	*Pseudophilotes abencerragus* (Pierret, 1837)	0.02	10.1	302
560	*P. panoptes* (Hübner, [1813])	0.03	10.8	302
561	*P. bavius* (Eversmann, 1832)	0.04	14.0	263
562	*P. barbagiae* Prins & Porten, 1982	0.08	11.5	301
563	*Euphilotes rita* (Barnes & McDunnough, 1917) [7]	0.12	10.9	57
564	*E. enoptes* (Boisduval, 1852)	0.35	11.8	57
565	*Philotiella speciosa* (Edwards, 1877)	0.04	8.5	29
566	*Sinia divina* (Fixsen, 1887)	0.08	20.0	299
567	*Scolitantides orion* (Pallas, 1771)	0.08	12.5	299
568	*Euchrysops barkeri* (Trimen, 1893)	0.11	17.0	85
569	*E. dolorosa* (Trimen, 1877)	0.08	15.0	85
570	*E. malathana* Boisduval, 1833	0.04	17.8	85
571	*E. osiris* (Hopffer, 1885)	0.07	18.8	85
572	*E. cnejus* (Fabricius, 1798)	0.05	14.8	299
573	*Lepidochrysops asteris* (Godart, 1819)	0.06	19.7	85
574	*L. bacchus* Riley, 1938	0.06	14.2	77;85
575	*L. dukei* Cottrell, 1965	0.06	13.9	77
576	*L. ketsi* Cottrell, 1965	0.06	16.6	77;85
577	*L. methymna* (Trimen, 1862)	0.09	19.4	77;85
578	*L. oreas* Tite, 1964	0.09	14.5	85
579	*L. patricia* (Trimen, 1877)	0.06	21.5	85
580	*L. puncticilia* (Trimen, 1883)	0.05	14.0	77;85
581	*L. trimeni* (Bethune-Baker, 1823)	0.10	20.8	85
582	*L. variabilis* Cottrell, 1965	0.06	17.1	77;85
583	*Orachrysops lacrimosa* (Bethune-Baker, 1923)	0.06	17.9	85
584	*Oboronia ornata* (Mabille, 1890)	0.04	17.0	298
585	*O. liberiana* Stempffer, 1950	0.04	15.0	298
586	*Polyommatus damon* (D. & Schiff., 1775)	0.07	15.0	60
587	*P. thersites* (Cantener, 1834)	0.09	14.0	53
588	*P. semiargus* (Rottemburg, 1775)	0.05	15.0	53
589	*P. albicans* (Gerhard, 1851)	0.06	17.2	117;304
590	*P. bellargus* (Rottemburg, 1775)	0.05	15.8	60;233
591	*P. coridon* (Poda, 1761)	0.06	16.5	60;117;233
592	*P. eros* (Oschenheimer, 1807)	0.05	12.9	189;302
593	*P. golgus* (Hübner, [1813])	0.06	13.4	189;302
594	*P. icarus* (Rottemburg, 1775)	0.05	15.2	53;60;112;233;304
595	*P. nivescens* (Keferstein, 1851)	0.06	15.0	189;302
596	*Chilades trochilus* (Freyer, 1844)	0.03	9.5	85
597	*Plebeius pylaon* (Waldheim, 1832)	0.05	14.7	189;302
598	*P. argus* (Linnaeus, 1758)	0.10	14.0	53;233;299
599	*P. argyrognomon* (Bergsträsser, [1779])	0.10	15.0	60;299

600	*P. idas* (Linnaeus, 1761)	0.07	13.8	53;60
601	*P. subsolanus* Eversmann, 1851	0.11	16.5	299
602	*P. agestis* (D. & Schiff., 1775)	0.04	13.0	233
603	*P. artaxerxes* (Fabricius, 1793)	0.04	12.0	233
604	*P. morronensis* Ribbe, 1910	0.03	11.9	189;302
605	*P. nicias* (Meigen, 1829)	0.11	13.2	189;302
606	*P. anteros* (Freyer, [1838])	0.07	14.0	263
607	*P. emigdionis* (Grinell, 1905)	0.12	11.4	29
608	*Hemiargus hanno* Stoll[2]	0.01	11.5	43
609	*Niphanda fusca* (Bremer & Grey, 1853)	0.07	20.5	299
610	*Libythea geoffroy* Godart, 1820	0.05	37.5	196
611	*L. labdaca* Westwood & Hewitson, 1851	0.13	25.3	259
612	*Libytheana carinenta* (Cramer, [1777])	0.06	22.8	2;24
613	*Philaetria dido* (Linnaeus, 1763)	1.00	50.0	64;140
614	*P. wernickei* (Röber, 1905)	0.95	48.5	140
615	*P. pygmalion* Frühstorfer[1,2]	0.95	48.5	140
616	*Podotricha telesiphe* (Hewitson, 1867)	0.39	38.0	140;273
617	*Dryadula phaetusa* (Linnaeus, 1758)	1.06	40.5	64;140
618	*Agraulis vanillae* (Linnaeus, 1758)	0.41	37.6	64;140
619	*Dione juno* (Cramer, [1779])	0.30	38.4	64;140
620	*D. moneta* (Hübner, [1821])	0.37	38.0	140
621	*D. glycera* Felder, 1861[2]	0.51	35.0	140
622	*Dryas julia* (Fabricius, 1775)	0.66	43.5	64;66;75;140
623	*Eueides vibilia* Stichel, 1903	0.34	32.0	140
624	*E. pavana* (Ménétriés, 1857)	0.34	32.5	140
625	*E. lineata* Salvin, 1868	0.30	34.5	140
626	*E. procula* Doubleday, 1847[2]	0.27	34.5	140
627	*E. lampeto* Bates, 1862[2]	0.37	37.0	140
628	*E. isabella* (Cramer, 1781)	0.43	33.7	64;140
629	*E. lybia* (Fabricius, 1775)	0.26	31.5	140
630	*E. tales* (Cramer, [1780])	0.37	35.5	140
631	*E. aliphera* (Godart, 1819)	0.11	30.0	64;140
632	*Neruda godmani* (Staudinger, 1882)	0.37	37.0	140
633	*N. metharme* (Erichson, 1848)	0.26	41.5	140
634	*N. aoede* (Hübner, 1816)	0.23	36.5	140
635	*Laparus doris* (Linnaeus, 1771)	0.36	40.0	64;140
636	*Heliconius xanthocles* (Bates, 1862)	0.47	38.5	140
637	*H. wallacei* Reakirt, 1866	0.49	40.0	64;140
638	*H. burneyi* (Hübner, 1816)	0.47	46.0	140
639	*H. egeria* (Cramer, [1775])	0.51	46.0	140
640	*H. astraea* Staudinger, 1896	0.51	45.0	140
641	*H. nattereri* Felder, 1865[2]	0.37	41.0	140
642	*H. numata* (Cramer, [1780])	0.66	40.0	64;140
643	*H. ismenius* (Latreille, 1817)	0.44	43.5	140
644	*H. pardalinus* (Bates, 1862)	0.59	42.0	140
645	*H. hecale* (Fabricius, 1777)[13]	0.70	44.0	128;140;182
646	*H. ethilla* Godart, 1819[2]	0.70	42.0	38;140
647	*H. atthis* (Doubleday & Hewitson, 1847)	0.44	40.5	140
648	*H. cydno* (Doubleday & Hewitson, 1847)	1.10	42.0	102;140
649	*H. pachinus* Salvin, 1871	0.84	42.0	140
650	*H. heurippa* (Hewitson, 1854)	0.84	44.0	140
651	*H. timareta* Hewitson, 1867[2]	1.08	42.0	140
652	*H. elevatus* Nöldner, 1901	0.89	42.0	140
653	*H. luciana*[1,2]	0.95	42.0	140
654	*H. besckei* Ménétriés, 1857	0.51	34.5	140
655	*H. melpomene* (Linnaeus, 1758)	0.76	38.0	64;140
656	*H. charitonius* (Linnaeus, 1767)[13]	0.49	40.0	128;140

657	*H. hermathena* (Hewitson, 1853)	0.33	41.0	140
658	*H. erato* (Linnaeus, 1758) [13]	0.59	40.5	51;64;75;128;140
659	*H. clysonymus* Latreille, 1817 [2]	0.79	39.5	140
660	*H. telesiphe* (Doubleday, 1847)	0.54	42.0	140
661	*H. ricini* (Linnaeus, 1758)	0.31	34.4	64;140
662	*H. demeter* Staudinger, 1896	0.33	34.5	140
663	*H. leucadia* Bates, 1862	0.34	38.0	140
664	*H. sara* (Fabricius, 1793)	0.28	33.0	64;140
665	*H. antiochus* (Linnaeus, 1767)	0.37	42.0	140
666	*H. hewitsoni* Staudinger, 1875	0.40	37.5	140
667	*H. congener* Weymer [2,8]	0.26	38.0	140
668	*H. eleuchia* Hewitson [2,8]	0.34	39.0	140
669	*H. sapho* (Drury, 1782)	0.26	37.0	140
670	*H. hecalesia* Hewitson, 1853 [2,13]	0.42	46.5	128;140
671	*Argynnis paphia* (Linnaeus, 1758)	0.38	33.0	53;60;233
672	*Argyreus hyperbius* (Linnaeus, 1763)	0.23	39.0	116
673	*Brenthis daphne* (D. & Schiff., 1775)	0.55	23.0	53
674	*B. hecate* (D. & Schiff., 1775)	0.28	23.7	69;304
675	*B. ino* (Rottemburg, 1775)	0.27	20.0	53
676	*B. mofidii* Wyatt, 1969	0.35	26.1	241
677	*Fabriciana adippe* (Linnaeus, 1767)	0.28	27.5	53;60;233;304
678	*F. niobe* (Linnaeus, 1758)	0.30	28.0	53;304
679	*F. auresiana* (Fruhstorfer, 1908)	0.32	25.5	102
680	*Issoria lathonia* (Linnaeus, 1758)	0.12	21.0	53;60
681	*Mesoacidalia aglaja* (Linnaeus, 1758)	0.37	29.0	53;60;233
682	*Pandoriana pandora* (D. & Schiff., 1775)	0.08	34.0	304
683	*Speyeria aphrodite* (Fabricius, 1787)	0.15	33.0	2
684	*S. atlantis* (Edwards, 1872)	0.18	28.8	2
685	*S. cybele* (Fabricius, 1775)	0.27	39.8	2
686	*S. idalia* (Drury, 1773)	0.26	41.5	2
687	*S. hydaspe* (Boisduval, 1869)	0.22	27.9	42
688	*S. nokomis* (Edwards, 1862)	0.68	38.2	42
689	*S. callippe* (Boisduval, 1852)	0.22	29.3	42
690	*Boloria aquilonaris* (Stichel, 1908)	0.18	19.0	53
691	*B. bellona* (Fabricius, 1775)	0.21	20.0	2
692	*B. dia* (Linnaeus, 1767)	0.17	17.0	53;60
693	*B. euphrosyne* (Linnaeus, 1758)	0.19	21.3	53;233
694	*B. selene* (D. & Schiff., 1775)	0.15	20.8	53;60;233
695	*B. eunomia* (Esper, 1799)	0.14	19.5	53
696	*Euptoieta hegesia* (Cramer, [1779])	0.19	30.5	75
697	*Phalanta phalantha* (Drury, 1770)	0.21	27.6	131
698	*P. eurytis* (Doubleday, 1847)	0.17	26.2	131
699	*Acraea petraea* Boisduval, 1847	0.15	25.4	70
700	*A. violarum* Boisduval, 1847	0.23	20.5	70
701	*A. nohara* Boisduval, 1847	0.18	22.7	70
702	*A. caldarena* Hewitson, 1877	0.28	25.0	70
703	*A. oncaea* Hopffer, 1855	0.17	24.3	70
704	*A. natalica* Boisduval, 1847	0.23	31.5	70
705	*A. zetes* (Linnaeus, 1758)	0.32	34.0	70
706	*A. neobule* (Doubleday, 1848)	0.19	27.5	70
707	*A. horta* (Linnaeus, 1764)	0.22	30.3	70
708	*A. aganice* (Hewitson, 1852)	0.19	35.8	70
709	*A. igola* Trimen, 1889	0.08	24.0	70
710	*A. encedon* (Linnaeus, 1758)	0.98	29.5	70
711	*A. esebria* Hewitson, 1861	0.12	29.3	70
712	*A. eponina* (Cramer, [1780])	0.12	21.9	70
713	*A. cabira* Hopffer, 1855	0.12	23.8	70

714	*A. obeira* Hewitson, 1863	0.10	25.0	70
715	*A. anacreon* Trimen, 1868	0.19	25.5	70
716	*A. rahira* Boisduval, 1833	0.98	22.0	70
717	*Pardopsis punctatissima* (Boisduval, 1833)	0.21	16.8	70
718	*Aglais urticae* (Linnaeus, 1758)	0.20	23.8	60;233
719	*Araschnia levana* (Linnaeus, 1758)	0.99	18.0	60
720	*Cynthia cardui* (Linnaeus, 1758)	0.15	29.4	2;60;233;304
721	*Inachis io* (Linnaeus, 1758)	0.11	28.6	53;60;233
722	*Nymphalis antiopa* (Linnaeus, 1758)	0.24	33.8	2;53;60
723	*N. milberti* (Godart, [1824])	0.05	23.8	2
724	*N. polychloros* (Linnaeus, 1758)	0.23	30.5	60;233
725	*Polygonia comma* Harris, 1862	0.16	28.5	2
726	*P. c-album* (Linnaeus, 1758)	0.20	23.3	60;233;304
727	*P. faunus* (Edwards, 1862)	0.25	27.5	2
728	*P. interrogationis* (Fabricius, 1793)	0.45	29.0	2
729	*P. progne* (Cramer, [1775])	0.21	25.5	2
730	*Vanessa atalanta* (Linnaeus, 1758)	0.12	30.0	2;60;233
731	*Antanartia schaeneia* (Trimen, 1879)	0.47	26.2	131
732	*A. hippomene* (Hübner, 1806)	0.17	24.4	131
733	*Amnosia decora* Doubleday, 1849	1.05	43.5	295
734	*Anartia amathea* (Linnaeus, 1758)	0.15	26.0	130
735	*A. fatima* Godart, 1820 13	0.08	28.5	94;130
736	*A. jatrophae* (Linnaeus, 1763)	0.10	20.0	44;66
737	*A. lytrea* (Godart, 1819)	0.18	30.5	44
738	*Junonia coenia* Hübner, 1822	0.07	25.5	2
739	*J. evarete* (Cramer, 1782)	0.17	27.5	44
740	*J. oenone* (Linnaeus, 1758)	0.15	25.6	131
741	*J. hierta* (Fabricius, 1798)	0.11	25.0	131
742	*J. terea* (Drury, 1773)	0.13	27.2	131
743	*J. natalica* Felder & Felder, 1860	0.18	27.2	131
744	*Precis iphita* (Cramer, [1779])	0.17	38.0	295
745	*P. octavia* (Cramer, [1777])	0.21	29.0	63
746	*P. orithya* (Linnaeus, 1758)	0.14	26.5	131;295
747	*P. ceryne* (Boisduval, 1847)	0.18	24.2	131
748	*P. archesia* (Cramer, [1779])	0.20	30.3	131
749	*P. tugela* Trimen, 1879	0.27	29.5	131
750	*Siproeta epaphus* (Latreille, 1811) [13]	0.53	44.6	93;94
751	*S. stelenes* (Linnaeus, 1758) [13]	0.59	46.5	43;94
752	*Catacroptera cloanthe* (Stoll, [1781])	0.52	29.7	131
753	*Protogoniomorpha parhassus* (Drury, 1782)	0.63	43.8	131
754	*Hypolimnas misippus* (Linnaeus, 1764)	0.15	45.0	131
755	*H. deceptor* (Trimen, 1873)	0.15	39.5	131
756	*H. anthedon* (Doubleday, 1845)	0.15	44.5	131
757	*Euphydryas aurinia* (Rottemburg, 1775)	0.21	21.5	53;60
758	*E. beckeri* (Herrich-Schäffer, 1851)	0.16	23.4	304
759	*E. maturna* (Linnaeus, 1758)	0.14	21.0	53;60
760	*E. phaeton* (Drury, 1773)	0.21	28.0	2
761	*Thessalia leanira* (Felder & Felder, 1860)	0.34	19.7	27
762	*Chlosyne harrisii* (Scudder, 1862)	0.08	20.2	2
763	*C. nycteis* (Doubleday, 1847)	0.08	20.5	2
764	*Melitaea britomartis* (Assmann, 1847)	0.11	17.0	55
765	*M. cinxia* (Linnaeus, 1758)	0.09	19.8	53;60;233
766	*M. diamina* (Lang, 1789)	0.07	18.0	53;60
767	*M. didyma* (Esper, [1779])	0.19	22.0	53;60
768	*M. phoebe* (D. & Schiff., 1775)	0.08	23.2	157
769	*Mellicta athalia* (Rottemburg, 1775)	0.14	19.5	53;60;233
770	*M. aurelia* (Nickerl, 1850)	0.05	16.5	60

771	*M. deione* Duponchel, [1832]	0.18	20.9	79;304
772	*Eresia eutropia* Hewitson, 1874	0.17	25.0	100
773	*Phyciodes campestris* (Behr, 1863)	0.14	17.6	2;34
774	*P. tharos* (Drury, 1773)	0.05	17.5	2
775	*Atlantea tulita* (Dewitz, 1877)	0.26	31.0	260
776	*Colobura dirce* (Linnaeus, 1764)	0.36	36.0	31;54
777	*Historis acheronta* (Fabricius, 1775)	1.53	47.5	260
778	*H. odius* (Fabricius, 1775)	0.91	57.5	303
779	*Smyrna blomfildia* (Fabricius, 1782)	0.32	40.0	38
780	*Sea sophronia* (Godart, [1824])	0.26	32.0	258
781	*Eunica bechina* (Hewitson, 1852)	0.21	30.2	229
782	*Sallya natalensis* (Boisduval, 1847)	0.09	26.2	131
783	*S. boisduvali* (Wallengren, 1857)	0.11	23.3	131
784	*S. trimeni* (Aurivillius, 1889)	0.09	23.8	131
785	*Ariadne merione* (Cramer, [1777])	0.12	32.9	295
786	*Eurytela dryope* (Cramer, [1775])	0.27	28.5	131
787	*E. hiarbas* (Drury, 1782)	0.27	25.9	131
788	*Byblia acheloia* (Wallengren, 1857)	0.13	25.0	131
789	*B. ilithyia* (Drury, 1773)	0.13	25.0	131
790	*Hamadryas februa* (Hübner, 1823)	0.65	36.0	72
791	*Adelpha celerio* Bates, 1864	0.35	30.5	66
792	*A. iphiclus* (Linnaeus, 1758)	0.28	28.0	66
793	*A. syma* (Godart, [1824])	0.34	22.5	38
794	*Cymothoe alcimeda* (Godart, [1824])	0.30	27.0	131
795	*Limenitis archippus* (Cramer, [1775])	0.34	44.0	2
796	*L. arthemis* (Drury, 1773)	0.69	39.0	2
797	*L. camilla* (Linnaeus, 1764)	0.39	28.0	60;193
798	*L. populi* (Linnaeus, 1758)	1.03	40.0	181
799	*L. reducta* (Staudinger, 1901)	0.26	25.3	170;304
800	*Pseudacraea lucretia* (Cramer, [1775])	1.41	35.8	131
801	*P. boisduvalii* (Doubleday, 1845)	4.61	43.0	131
802	*Pantoporia hordonia* (Stoll, 1790)	0.73	24.5	295
803	*P. perius* (Linnaeus, 1758)	0.70	30.0	37
804	*Neptis praslini* Boisduval, 1832	0.48	29.0	185
805	*N. saclava* (Boisduval, 1833)	0.27	23.8	131
806	*N. laeta* Overlaet, 1955	0.58	27.5	131
807	*Bebearia orientis* (Karsch, 1895)	0.82	32.7	259
808	*Dophla evelina* (Stoll, 1790)	11.5	54.0	295
809	*Euthalia amanda* (Hewitson, 1862)	2.71	40.5	295
810	*Lexias dirtea* (Fabricius, 1793)	2.71	46.5	295
811	*Mahaldia formosana* (Frühstorfer, 1899)	2.87	45.0	295
812	*Tanaecia iapis* (Godart, [1824])	2.59	33.0	295
813	*Hamanumida daedalus* (Fabricius, 1775)	1.54	31.6	131
814	*Marpesia petreus* (Cramer, 1778)	0.13	40.0	66
815	*Cyrestis pantheus* (Lathi, 1901)	0.38	28.5	259
816	*Charaxes bernardus* (Fabricius, 1793)	2.74	46.5	295
817	*C. varanes* (Cramer, 1764)	1.58	40.5	23;86;131;195
818	*C. fulvescens* (Aurivillius, 1891)	1.86	47.9	23
819	*C. paphianus* Ward, 1871	0.90	29.4	195
820	*C. zoolina* (Westwood, 1850)	0.50	27.8	131;195
821	*C. nichetes* Grose-Smith, 1883	1.77	37.8	195
822	*C. candiope* (Godart, [1824])	1.65	44.6	23;131;195
823	*C. jasius* (Linnaeus, 1767)	2.74	42.9	304
824	*C. epijasius* Reiche, 1850	0.98	47.3	23;195
825	*C. saturnus* Butler, 1865	3.00	45.4	131;195
826	*C. pelias* (Cramer, [1776])	2.14	41.1	52;131;195
827	*C. castor* (Cramer, [1775])	2.14	52.5	23;131;195

828	*C. brutus* (Cramer, [1779])	3.23	42.2	23;131;195
829	*C. pollux* (Cramer, [1775])	1.54	39.1	131;171;195
830	*C. dowsetti* Henning, 1988	4.15	50.8	195
831	*C. druceanus* Butler, 1869	3.61	41.4	131;171;195
832	*C. numenes* (Hewitson, 1865)	1.77	47.7	23;195
833	*C. tiridates* (Cramer, [1777])	4.19	56.1	23;195
834	*C. bohemani* Felder, 1859	5.24	44.7	195
835	*C. xiphares* (Cramer, 1781)	3.02	51.2	131;195
836	*C. nandina* Rothschild & Jordan, 1901	4.19	51.8	195
837	*C. cithaeron* Felder, 1859	3.59	45.5	23;86;131;195
838	*C. achaemenes* Felder & Felder, 1867	2.14	38.5	131;195
839	*C. etesipe* (Godart, [1824])	4.19	41.8	23;195
840	*C. jahlusa* Trimen, 1862	1.13	26.6	131;195
841	*C. eupale* (Drury, 1782)	0.52	31.2	23;195
842	*C. dilutus* Rothschild, 1898	0.52	28.3	23;195
843	*C. anticlea* (Drury, 1782)	0.29	27.5	23;195
844	*C. baumanni* Rogenhofer, 1851	0.28	27.6	23;195
845	*C. catachorus* Staudinger, 1896	0.52	36.8	195
846	*C. etheocles* (Cramer, [1777])	0.52	37.3	23;195
847	*C. marieps* Van Someren & Jackson, 1957	3.05	39.3	195
848	*C. karkloof* Van Someren & Jackson, 1957	1.77	35.7	195
849	*C. pondoensis* Van Someren, 1967	2.14	33.2	195
850	*C. nyikensis* Van Someren, 1975	3.05	38.7	195
851	*C. ethalion* Boisduval, 1847	1.61	35.4	131;195
852	*C. cedreatis* Hewitson, 1874	0.52	38.0	195
853	*C. chintechi* Van Someren, 1975	1.77	36.8	195
854	*C. chittyi* Rydon, 1980	1.15	34.3	195
855	*C. howarthi* Minig, 1976	1.15	34.3	195
856	*C. fulgurata* Aurivillius, 1889	0.52	33.3	195
857	*C. phaeus* Hewitson, 1877	1.77	34.6	195
858	*C. fionae* Henning, 1977	1.77	27.3	115;195
859	*C. viola* Butler, 1865	0.90	31.9	195
860	*C. kirki* Butler, 1881	0.90	39.1	195
861	*C. vansoni* Van Someren, 1975	0.90	31.6	23;129;195
862	*C. berkeleyi* Van Someren & Jackson, 1957	1.77	34.7	195
863	*C. martini* Van Someren, 1966	1.44	33.0	143;195
864	*C. gallagheri* Van Son, 1962	1.44	35.2	195
865	*C. guderiana* (Dewitz, 1879)	1.77	32.8	195
866	*Prothoe calydina* (Hewitson, 1855)	2.02	50.5	295
867	*Agrias amydon* (Hewitson, [1854])	3.56	44.0	155
868	*A. claudina* (Godart, [1824])	14.9	45.5	166
869	*Archaeoprepona demophoon* (Linnaeus, 1758)	7.92	52.4	113
870	*Noreppa chromus* (Guérin, 1844)	3.22	51.5	86
871	*Prepona omphale* (Hübner, 1819)	5.04	48.4	30;32;98
872	*Fountainea ryphea* (Cramer, [1775])	0.52	29.5	248
873	*Consul fabius* (Cramer, [1776])	0.52	36.9	104
874	*Euxanthe eurinome* (Cramer, [1775])	4.19	45.5	23;195
875	*E. wakefieldi* (Ward, 1873)	1.19	45.0	131;195
876	*E. tiberius* Grose-Smith, 1889	4.19	52.0	195
877	*Palla usheri* Butler, 1870	0.63	42.8	23;195
878	*Apatura iris* (Linnaeus, 1758)	0.70	37.5	60;233
879	*Asterocampa celtis* (Boisduval & Le Conte, [1835])	0.45	25.6	57;187
880	*A. leilia* (Edwards, 1874)	0.42	24.1	57
881	*A. clyton* (Boisduval & Le Conte, [1835]	0.20	27.6	2;187
882	*A. texana* (Skinner, 1911) [9]	0.37	28.3	65;187
883	*A. idyja* (Geyer, [1828])	0.29	31.2	174;187
884	*Sephisa princeps* (Fixsen, 1887)	0.99	39.0	282

885	*Morpho anaxibia* (Esper, 1777)	7.00	73.0	38
886	*M. catenarius* (Perry, 1811)	1.52	63.0	50
887	*M. hercules* (Dalman, 1861?) [1]	2.15	71.5	38
888	*M. menelaus* (Linnaeus, 1758)	7.78	88.0	38
889	*M. peleides* Kollar, 1850	2.09	68.0	223
890	*Antirrhaea philoctetes* (Linnaeus, 1764)	4.09	47.0	214
891	*Amathusia phidippus* (Linnaeus, 1763)	1.68	55.0	295
892	*Faunis canens* (Hübner, [1819])	1.38	37.0	295
893	*F. phaon* (Erichson, 1834)	1.30	38.5	295
894	*Taenaris artemis* (Snellen, 1860)	1.65	47.5	287
895	*T. catops* ? [1]	1.65	47.0	287
896	*T. onolaus* ? [1]	1.77	47.0	159
897	*Thauria aliris* (Westwood, [1858])	5.05	58.0	295
898	*Zeuxidia amethystus* Butler, 1865	2.66	56.0	295
899	*Z. aurelius* (Cramer, [1777])	6.41	70.5	295
900	*Z. doubledayi* Westwood, 1851	3.57	59.0	295
901	*Pierella hyalinus* (Gmelin, 1788)	0.52	44.0	213
902	*Melanitis constantia* (Cramer, [1777])	1.77	42.0	265
903	*M. leda* (Linnaeus, 1763)	0.66	39.0	61;182
904	*Gnophodes parmeno* (Butler, 1880)	0.82	36.5	61
905	*Kirinia roxelana* (Cramer, [1777])	0.18	31.3	263
906	*Lasiommata maera* (Linnaeus, 1758)	0.56	24.9	53;60;262
907	*L. megera* (Linnaeus, 1767)	0.38	22.4	53;60;233;262
908	*L. petropolitana* (Fabricius, 1787)	0.40	21.4	262
909	*Lethe diana* Butler, 1866 [13]	0.52	27.0	182
910	*L. dura* (Marshall, 1882)	0.86	38.5	295
911	*L. europa* (Fabricius, 1775) [13]	1.38	34.0	295;182
912	*L. gemina* Fruhstorfer, 1914	0.24	33.3	278
913	*L. rohria* (Fabricius, 1787)	0.85	33.5	295
914	*L. sicelis* (Hewitson, 1866)	0.70	33.0	218
915	*L. verma* (Kollar, 1884)	0.58	27.0	295
916	*Lopinga achine* (Scopoli, 1763)	0.72	26.5	262
917	*Neorina lowii* (Doubleday, [1849])	3.55	57.0	295
918	*Pararge aegeria* (Linnaeus, 1758)	0.36	21.9	53;60;233;262
919	*P. xiphia* (Fabricius, 1775)	0.92	26.1	262
920	*P. xiphioides* (Staudinger, 1871)	0.49	25.3	262
921	*Satyrodes eurydice* (Johannsen, 1763)	0.60	23.8	2
922	*S. portlandia* (Fabricius, 1781)	0.45	30.0	2
923	*Aeropetes tulbaghia* (Linnaeus, 1764)	0.76	46.0	61
924	*Paralethe dendrophilus* (Trimen, 1862)	0.52	38.0	61
925	*Zethera pimplea* (Erichson, 1834)	1.79	42.5	295
926	*Elymnias agondas* ? [1]	1.54	42.5	162;243
927	*E. casiphone* Geyer, [1827]	2.22	46.0	295
928	*E. melias* (Felder, 1863)	1.77	43.0	295
929	*E. nesaea* (Linnaeus, 1764)	1.95	37.0	295
930	*Bicyclus anynana* (Butler, 1879)	0.52	21.2	259
931	*B. safitza* Hewitson, 1851	0.57	25.5	61
932	*Mycalesis anaxioides* (Marshall, 1883)	1.97	32.0	295
933	*M. gothama* Moore, 1857	0.55	25.5	182
934	*M. maiaenas* Hewitson, 1864	0.96	25.5	295
935	*M. perseus* (Fabricius, 1775)	0.49	23.7	245
936	*M. sirius* (Fabricius, 1775)	0.58	24.8	245
937	*M. terminus* (Fabricius, 1775)	0.56	24.8	245
938	*Orsotriaena medus* (Fabricius, 1775)	0.52	23.0	265
939	*Henotesia perspicua* (Trimenn 1873)	0.47	21.5	61
940	*Ragadia luzonia* Felder & Felder, 1863	0.28	23.3	147
941	*Acrophtalmia artemis* Felder & Felder, 1861	0.07	18.8	147

942	*Hypocista angustata* Waterhouse & Lyell, 1914	0.11	18.0	190
943	*H. irius* (Fabricius, 1775)	0.27	19.0	190
944	*Tisiphone helena* (Olliff, 1888)	1.41	36.0	232
945	*Ypthima asterope* (Moore, 1857)	0.39	24.0	176
946	*Y. impura* Elwes & Edwards, 1873	0.47	19.0	259
947	*Y. loryma* Hewitson, 1865	0.27	20.5	295
948	*Y. praenubila* Leech, 1891	0.70	30.4	295
949	*Coenyra aurantiaca* Aurivillius, 1910	0.37	20.0	61
950	*C. hebe* (Trimen, 1862)	0.47	17.0	259
951	*Melampias steniptera* Van Son, 1955	0.42	19.3	259
952	*M. huebneri* van Son, 1955	0.47	20.0	61
953	*Strabena tamatavae* (Boisd., 1833)	0.70	19.0	183
954	*Physcaeneura panda* (Boisduval, 1847)	0.72	19.0	61
955	*Cassionympha cassius* (Godart, 1823)	0.55	19.0	61
956	*Neita durbani* (Trimen, 1887)	0.63	21.0	61
957	*N. extensa* (Butler, 1898)	0.73	23.5	61
958	*Pseudonynpha hippia* (Cramer, 1782)	0.69	19.5	61
959	*P. trimenii* (Butler, 1868)	0.65	21.0	61
960	*P. magus* (Fab., 1793)	0.34	19.5	61
961	*P. magoides* van Son, 1955	0.47	21.0	61
962	*P. detecta* Trimen, 1914	0.44	19.5	61
963	*Stygionympha vigilans* (Trimen, 1887)	1.38	24.5	61
964	*S. wichgrafi* van Son, 1955	0.58	22.5	61
965	*S. irrorata* (Trimen, 1873)	0.47	17.5	61
966	*Megisto cymela* [1]	0.31	20.2	2
967	*Neonympha areolata* (Abbot & Smith, 1779)	0.69	18.1	2
968	*Taygetis andromeda* (Cramer, [1779])	1.15	35.0	164
969	*Coenonympha oedippus* (Fabricius, 1787)	0.13	21.0	182
970	*C. arcania* (Linaeus, 1761)	0.49	18.1	53;60;233;262
971	*C. glycerion* (Borkhausen, 1788)	0.29	17.0	60
972	*C. hero* (Linnaeus, 1761)	0.23	16.8	145
973	*C. iphioides* Staudinger, 1870	0.42	19.1	262;304
974	*C. leander* (Esper, [1784])	0.29	16.7	304
975	*C. tullia* (Müller, 1764)	0.23	18.9	53;233
976	*C. austauti* Oberthür, 1881	0.40	14.7	192
977	*C. corinna* (Hübner, 1804)	0.30	15.0	284;304
978	*C. dorus* (Esper, [1782])	0.53	16.7	262;304
979	*C. elbana* Staudinger, 1901	0.17	13.3	285
980	*C. pamphilus* (Linnaeus, 1758)	0.20	16.6	53;60;123;233;262
981	*C. saadi* Kollar, 1848	0.07	17.0	148
982	*C. thyrsis* Freyer, 1845	0.24	14.1	169
983	*Aphantopus hyperantus* (Linnaeus, 1758)	0.26	21.2	53;60;233;262
984	*Cercyonis oetus* (Boisduval, 1869)	0.36	21.8	275;24
985	*C. pegala* (Fabricius, 1793)	0.45	29.8	2;90;230;275
986	*Hyponephele lupinus* (Costa, [1836])	0.13	22.7	230;262
987	*H. lycaon* (Kühn, 1774)	0.22	22.3	60;262;230
988	*H. maroccana* (Blachier, 1908)	0.08	19.0	102
989	*Maniola jurtina* (Linnaeus, 1758)	0.08	25.8	53;60;230;262
990	*M. nurag* Ghiliani, 1852	0.08	22.8	230
91	*Pyronia bathseba* (Fabricius, 1793)	0.27	20.4	230;262
992	*P. cecilia* (Vallantin, 1894)	0.11	19.6	6;230;262
993	*P. tithonus* (Linnaeus, 1771)	0.13	18.9	53;233;262
994	*Proterebia afra* (Fabricius, 1787) [10]	1.04	22.8	160
995	*Erebia eriphyle* (Freyer, 1836)	0.26	17.5	25
996	*E. euryale* (Esper, [1805])	0.45	21.3	304
997	*E. ligea* (Linnaeus, 1758)	0.45	24.3	53;60
998	*E. manto* (D. & Schiff., 1775)	0.36	20.0	142

999	*E. meta* Staudinger, 1886	0.50	24.0	198
1000	*E. meolans* (Prunner, 1798)	0.58	22.9	5;60;165;169;262
1001	*E. palarica* Chapman, 1903	0.76	26.7	262
1002	*E. medusa* (D. & Schiff., 1775)	0.40	21.6	53;60;146;263
1003	*E. aethiopella* (Hoffmannsegg, 1806)	0.30	18.5	59
1004	*E. cassioides* (Hochenwartz, 1793)	0.42	18.4	262
1005	*E. epistygne* (Hübner, [1824])	0.47	25.0	252
1006	*E. gorge* (Esper, [1805])	0.39	19.1	304
1007	*E. hispania* Butler, 1868	0.42	19.5	59;262;266
1008	*E. ottomana* Herrich-Schäffer, [1847]	0.40	21.1	59;263
1009	*E. claudina* (Borkhausen, 1789)	0.30	17.0	138
1010	*E. epiphron* (Knoch, 1783)	0.26	17.5	233
1011	*E. lefebvrei* (Boisduval, 1828)	0.59	21.2	304
1012	*E. melancholica* Herrich-Schäffer, [1846]	1.05	21.3	263
1013	*E. melas* (Herbst, 1796)	0.87	21.0	253
1014	*E. neoridas* (Boisduval, 1828)	0.47	22.8	170;262
1015	*E. scipio* (Boisduval, 1832)	0.53	22.0	59
1016	*E. zapateri* Oberthür, 1875	0.47	24.5	88;262;267
1017	*E. triarius* (Prunner, 1798)	0.82	24.5	304
1018	*E. aethiops* (Esper, 1777)	0.72	23.2	60;263
1019	*E. niphonica* (Janson, 1877)	0.48	22.0	218
1020	*Calisto batesi* Michener, 1943	0.17	14.0	291
1021	*C. confusa* Lathy, 1899	0.30	15.0	291
1022	*C. grannus* Bates, 1939	0.34	16.5	291
1023	*C. herophile* Hübner, 1823	0.18	17.5	43
1024	*C. hysius* (Godart, 1819)	0.18	17.0	291
1025	*C. pulchella* Lathy, 1899	1.29	23.5	291
1026	*Oeneis glacialis* (Moll, 1783)	1.21	28.8	1
1027	*O. jutta* (Hübner, 1806)	0.59	28.8	2
1028	*O. polixenes* (Fabricius, 1775)	0.51	23.1	2
1029	*Arethusana arethusa* (D. & Schiff., 1775)	0.30	24.0	53;262;263
1030	*Kanetisa circe* (Fabricius, 1775)	0.33	37.1	53;262
1031	*Minois dryas* (Scopoli, 1763)	0.64	32.7	60;262
1032	*Berberia abdelkader* (Pierret, 1837)	2.68	35.0	10
1033	*B. lambessanus* (Staudinger, 1901)	2.78	66.5	10
1034	*Satyrus actaea* (Esper, 1780)	0.51	26.1	256;257;262
1035	*S. amasynus* Staudinger, 1861	0.61	26.4	263
1036	*S. favonius* Staudinger, 1892	2.55	28.8	263
1037	*S. ferula* (Fabricius, 1793)	1.03	28.9	53;262;283
1038	*Chazara briseis* (Linnaeus, 1764)	0.33	31.6	10;53;60;137;262
1039	*C. prieuri* (Pierret, 1837)	0.40	34.0	7;10;262
1040	*Pseudochazara cingovskii* Gross, 1973	0.90	26.0	134
1041	*P. graeca* (Staudinger, 1870)	0.63	26.3	133
1042	*P. hippolyte* (Esper, 1784)	0.61	25.0	262;266;304
1043	*P. lydia* (Staudinger, 1878)	0.71	28.6	263
1044	*P. mnizechii* (Herrich-Schäffer, [1851])	0.71	28.3	263
1045	*Hipparchia alcyone* (D. & Schiff., 1775)	0.59	30.2	8;60;217
1046	*H. fagi* (Scopoli, 1763)	0.71	32.2	53;304
1047	*H. neomiris* (Godart, [1824])	0.39	24.5	269
1048	*H. ellena* (Oberthür, 1894)	0.66	31.5	10
1049	*H. aristaeus* (Bonelli, 1826)	0.19	28.6	269
1050	*H. azorina* (Strecker, 1899)	0.56	24.1	150
1051	*H. pellucida* (Stauder, 1924)	0.23	29.8	263
1052	*H. semele* (Linnaeus, 1758)	0.25	26.8	53;60;217;233
1053	*H. leighebi* Kudrna, 1976	0.42	32.9	268;304
1054	*H. sbordoni* Kudrna, 1984	0.38	29.9	304
1055	*H. hansii* (Austaut, 1879)	0.34	24.0	10

1056	*H. statilinus* (Hufnagel, 1766)	0.29	26.9	217;262
1057	*H. powelli* (Oberthür, 1910)	0.27	24.0	102
1058	*H. fidia* (Linnaeus, 1767)	1.07	29.7	10;217;254;262
1059	*H. wyssii* (Christ, 1889)	0.91	30.5	226
1060	*Melanargia halimede* (Ménétriés, 1859)	0.51	31.0	151;262
1061	*M. russiae* (Esper, 1783)	0.44	29.0	151;262;271
1062	*M. larissa* (Geyer, [1828])	0.38	25.9	151;263
1063	*M. hylata* (Ménétriés, 1832)	0.67	30.0	151
1064	*M. grumi* Standfuss, 1892	0.55	26.0	151
1065	*M. titea* (Klug, 1832)	0.41	28.5	151;263
1066	*M. galathea* (Linnaeus, 1758)	0.55	25.9	60;64;151;233
1067	*M. lachesis* (Hübner, 1790)	0.69	28.5	151;257;262
1068	*M. arge* (Sulzer, 1776)	0.26	28.0	154;255
1069	*M. ines* (Hoffmannsegg, 1804)	0.65	25.1	173;262;304
1070	*M. occitanica* (Esper, 1793)	0.66	26.5	262;270
1071	*M. pherusa* (Boisduval, 1833)	0.70	27.0	286;304
1072	*Dira clytus* (Linnaeus, 1764)	0.38	29.0	61
1073	*D. oxylus* (Trimen, 1881)	0.52	34.5	61
1074	*D. swanepolei* (van Son, 1939)	0.70	35.0	61
1075	*D. jansei* (Swiestra, 1911)	0.58	31.3	61
1076	*Dingana dingana* (Trimen, 1873)	0.70	29.0	61
1077	*D. bowkeri* (Trimen, 1870)	0.35	23.5	61
1078	*Torynesis mintha* (Geyer, 1837)	0.90	26.5	61
1079	*Tarsocera cassus* (Linnaeus, 1764)	0.47	26.0	61
1080	*Anetia thirza* Geyer, [1833]	1.28	46.5	242
1081	*A. briarea* (Godart, [1819])	0.44	45.0	228
1082	*Idea hypermnestra* (Westwood, 1848)	2.05	73.7	144
1083	*I. leuconoe* Erichson, 1834	1.94	61.0	168;295
1084	*Euploea sylvester* (Fabricius, 1793)	0.20	39.5	296
1085	*E. mulciber* (Cramer, [1777])	0.92	51.5	168;295
1086	*E. darchia* (Macleay, 1827)	0.13	34.0	289
1087	*E. crameri* Lucas, 1853	1.36	45.0	144
1088	*Amauris crawshayi* Butler, 1897	1.16	40.0	168
1089	*A. echeria* (Stoll, [1790])	1.36	39.5	61;168
1090	*A. albimaculata* (Butler, 1875)	0.79	34.6	61
1091	*A. ochlea* (Boisduval, 1847)	1.36	40.1	61
1092	*Ideopsis juvenata* (Cramer, [1777])	1.22	41.0	168
1093	*Parantica luzonensis* (Felder & Felder, 1863)	0.57	38.0	295
1094	*P. aspasia* (Fabricius, 1787)	0.99	41.5	168;295
1095	*P. vitrina* (Felder & Felder, 1861)	0.76	35.0	168;295
1096	*Tirumala petiverana* (Doubleday, [1847])	0.52	46.8	168
1097	*T. limniace* (Cramer, [1775])	0.63	48.0	168
1098	*T. hamata* (Macleay, 1827)	0.54	41.0	168
1099	*T. ishmoides* Moore, 1883	0.42	44.0	168
1100	*Danaus chrysippus* (Linnaeus, 1758)	0.48	40.0	61;168
1101	*D. gilippus* (Cramer, [1775])	0.53	33.5	168
1102	*D. erippus* (Cramer, [1775])	0.72	48.8	31;168
1103	*D. plexippus* (Linnaeus, 1758)	0.50	45.8	168
1104	*D. genutia* (Cramer, [1779])	0.51	43.0	168;272
1105	*D. melanippus* (Cramer, [1777])	0.55	41.5	168
1106	*D. philene* (Stoll, [1782])	0.39	39.8	168
1107	*Athesis clearista* Doubleday, 1847	0.79	38.0	247
1108	*Patricia dercyllidas* (Hewitson, 1864)	0.53	35.0	247
1109	*Tithorea harmonia* (Cramer, [1777])	0.19	39.0	247
1110	*T. tarricina* Hewitson, 1853	0.80	41.0	247
1111	*Aeria eurimedea* (Cramer, [1779])	0.51	24.0	124
1112	*A. olena* Weymer, 1875	0.18	23.5	247

1113	*Melinaea ethra* (Godart, [1819])	0.52	45.5	247
1114	*M. ludovica* (Stoll, [1780])	0.83	41.8	247
1115	*Athyrtis mechanitis* Felder, 1862	0.50	44.5	247
1116	*Eutresis hypereia* Doubleday & Hewitson, 1847	0.65	44.0	247
1117	*Paititia neglecta* (Müller, 1886)	1.07	34.5	247
1118	*Placidula eurynassa* (Felder, 1860)	0.25	38.5	237
1119	*Methona themisto* (Hübner, [1818])	0.86	47.5	247
1120	*Thyridia psidii* (Linnaeus, 1758)	0.18	41.5	247
1121	*Scada karschina* (Herbst, 1792)	0.30	24.5	247
1122	*Sais rosalia* (Cramer, [1779])	0.23	29.5	247
1123	*Mechanitis lysimnia* (Fabricius, 1793)	0.35	37.5	31;247
1124	*Callithomia lenea* (Cramer, 1782)	0.26	32.0	247
1125	*Talamancana lonera* (Butler & Druce, 1872)	0.36	35.0	247
1126	*Velamysta pupilla* (Hewitson, 1874)	0.37	32.0	247
1127	*Ithomia ellara* (Hewitson, 1874)	0.31	33.0	247
1128	*I. drymo* Hübner, 1816	0.15	24.5	247
1129	*Miraleria cymothoe* (Hewitson, 1854)	0.24	28.5	247
1130	*Napeogenes harbona* (Hewitson, 1869)	0.48	29.5	247
1131	*Hyaliris frater* (Salvin, 1869)	0.47	29.5	247
1132	*H. oulita* (Hewitson, 1858)	0.55	31.5	247
1133	*Rhodussa cantobrica* (Hewitson, 1875)	0.18	26.5	247
1134	*Hypothyris euclea* (Godart, [1819])	0.23	30.8	247
1135	*H. leprieuri* Feisthamel, 1835 [2]	0.23	27.0	247
1136	*H. ninonia* (Hübner, 1806)	0.27	28.5	247
1137	*H. semifulva* Salvin, 1869 [2]	0.21	29.5	247
1138	*Epityches eupompe* (Geyer, 1832)	0.16	28.5	247
1139	*Oleria aquata* (Weymer, 1875)	0.22	23.0	247
1140	*O. astraea* (Cramer, [1775])	0.35	25.0	247
1141	*O. zelica* (Hewitson, 1856)	0.76	26.5	107
1142	*Hyposcada cyrene* (Latreille, 1811)	0.81	31.0	247
1143	*H. virginiana* (Hewitson, 1856)	0.77	31.5	247
1144	*Ollantaya canilla* (Hewitson, 1874)	0.82	32.5	247
1145	(?) *susiana* (Felder, 1862) [11]	0.78	37.0	247
1146	*Hyalenna pascua* (Schaus, 1902)	0.22	28.0	247
1147	*Dircenna dero* (Hübner, 1823)	0.15	36.5	247
1148	*D. relata* Butler & Druce, 1862	0.13	35.0	99
1149	*Pteronymia carlia* Schaus, 1902	0.12	22.5	247
1150	*P. pronuba* (Hewitson, 1870)	0.45	25.5	247
1151	*P. thabena* (Hewitson, 1869)	0.25	24.0	247
1152	*P. notilla* Butler & Druce, 1872	0.63	27.0	106
1153	*Episcada clausina* (Hewitson, 1876)	0.15	23.5	247
1154	*E. philoclea* (Hewitson, 1854)	0.14	23.5	247
1155	*Prittwitzia hymenaea* (Prittwitz, 1865)	0.11	23.5	247
1156	*Ceratiscada canaria* Brown & D'Almeida, 1970	0.18	23.5	84;247
1157	*Dygoris dircenna* (Felder, 1867)	0.16	35.5	247
1158	*Godyris duilia* (Hewitson, 1852)	0.40	41.0	247
1159	*G. hewitsonii* (Haensch, 1903)	0.27	34.5	247
1160	*Hypoleria adasa* (Hewitson, 1854)	0.26	23.0	247
1161	*H. cassotis* (Bates, 1864)	0.13	25.5	118
1162	*Hypomenitis dercetis* (Doubleday & Hewitson, 1847)	0.28	28.0	247
1163	*Greta andromica* (Hewitson, 1854)	0.35	27.0	247
1164	*G. cyrcilla* (Hewitson, 1854)	0.34	31.5	247
1165	*G. diaphanus* (Drury, 1773)	0.15	26.0	276
1166	*G. nero* (Hewitson, 1854)	0.19	25.5	95
1167	*Pseudoscada erruca* (Hewitson, 1855)	0.21	24.0	247
1168	*P. quadrifasciata* Talbot, 1928	0.25	25.0	247
1169	*Mcclungia salonina* (Hewitson, 1855)	0.22	24.5	247

1170	*Heterosais edessa* (Hewitson, 1854)	0.19	30.0	247
1171	(?) *derama* (Haensch, 1905) [12]	0.30	25.0	247
1172	*Brassolis isthmia* Bates, 1864	1.60	49.0	11;177
1173	*Caligo eurilochus* (Cramer, [1775])	3.88	89.5	67
1174	*C. mnemon* (Felder & Felder, 1866)	4.31	86.0	68
1175	*C. illioneus* (Cramer, [1775])	3.98	69.5	19
1176	*Dynastor darius* (Fabricius, 1775)	5.07	53.5	120;225
1177	*D. macrosiris* Doubleday, 1849	11.5	52.5	224
1178	*Eryphanis aesacus* (Herrich-Schäffer, 1850)	5.54	67.3	167
1179	*E. polyxena* (Meerburgh, 1775)	5.28	59.0	126
1180	*E. reevesi* (Doubleday & Westwood,1849)	4.19	50.5	31
1181	*Opoptera sulcius* (Staudinger, 1887)	1.39	38.0	38
1182	*Opsiphanes cassina* Felder, 1862	4.04	39.0	66;110
1183	*O. quiteria* (Stoll, [1780])	1.65	54.9	167
1184	*O. tamarindi* (Felder, 1861)	4.00	47.9	68;110

Taxonomic arrangement. The high level taxa were arranged after De Jong et al. (1996). Other relevant references are given in the notes 14 to 23 below. A detailed arrangement of the species is given in the Appendix. This was constructed after varied sources, phylogenetic approaches having being given priority. The families and subfamilies included in the Table are as follows (for each taxon, the first and last species numbers are given):

Hesperiidae[14]	1–132
Coeliadinae	1–3
Hesperiinae	4–67
Trapezitinae	68–95
Pyrginae	96–132
Papilionidae[15]	133–227
Parnassiinae	133–166
Papilioninae	167–227
Pieridae	228–311
Dismorphiinae	228–231
Pierinae	232–290
Coliadinae	291–311
Lycaenidae[16]	312–609
Riodininae[17]	312–343
Poritinae	344–349
Miletinae	350–360
Curetinae	361
Lycaeninae	362–609
Nymphalidae[18]	610–1184
Libytheinae	610–612
Heliconiinae[19]	613–717
Nymphalinae	718–775
Limenitinae	776–815
Charaxinae	816–877
Apaturinae	878–884
Morphinae	885–900

Satyrinae[20]	901–1079
Danainae[21]	1080–1106
Ithomiinae[22]	1107–1171
Brassolinae[23]	1172–1184

NOTES 1–23 to the Table and the taxonomic arrangement.

[1] No reference was found to reliably quote the author of the species name.

[2] No reliable information was found on the date of description of the species or the genus where the species was originally described.

[3] According to Clark & Dickson (1971), a species formerly confused with *A. taikosama* (Wallengren), of which I have been unable to stablish the correct identity.

[4] After some authors, a subspecies of *Callophrys (Mitoura) gryneus* (Hübner, 1819).

[5] As *E. minyas* in the original reference (see Fiedler 1991).

[6] Clark & Disckson (1971) refer to *Anthene sp*, close to *A. talboti* Stempffer, but I have been unable to secure the correct identity of the species.

[7] According to Emmel & Emmel (1989) this record might be adscribed to *Euphilotes mojave* (Watson & Comstock).

[8] As 'forms' of *H. sapho* (Drury) in D'Abrera (1984).

[9] Following Friedlander (1988), probably better as a subspecies of *A. clyton* (Boisduval & Le Conte).

[10] *P. afra*, sin.: *P. phegea* (e.g., Hesselbarth et al. 1995).

[11] Proposed for a new genus by Brown et al. (1994), I have not traced further references.

[12] Proposed for a new genus by Brown et al. (1994), formerly in *Pteronymia*.

[13] References 94, 128, and 182, give estimates of the egg volumes based in their own estimates or former references.

[14] =*Hesperioidea auct.*, arrangement following Bridges (1994)

[15] Arrangement after Miller (1988), other references in Collins & Morris (1985).

[16] Following De Jong et al. (1996) for the relationships among subfamilies, and Fiedler (1991) for other details.

[17] Based in the provisional consensus provided by De Vries (1997).

[18] After De Jong et al. (1996) up to subfamilies, and other details after Harvey (1991) unless otherwise stated.

[19] Arrangement based in a strict consensus of the results of Brown (1981) and Brower (1997).

[20] Taxonomy simplified from Miller (1968) (see Harvey 1991).

[21] Relationships between species are a consensus based on Acery & Vane-Wright (1984), Kitching (1985), Vane-Wright et al. (1992), and Sourakov & Emmel (1996).

[22] Relationships among species after Brown et al. (1994).

[23] Brassolinae was kept independent from Morphinae.

Sources. Numbers 1 to 304 correspond to those quoted in the data table: 1-Scudder 1873; 2-Scudder 1889; 3-Dyar 1897; 4-Gillmer 1904; 5-Chapman 1905; 6-Powell 1905a; 7-Powell 1905b; 8-Rebel 1910; 9-Bower 1911; 10-Oberthür 1914; 11-Dunn 1917; 12-Coolidge 1923a; 13-Coolidge 1923b; 14-Coolidge 1923c; 15-Coolidge 1923d; 16-Coolidge 1924a; 17-Coolidge 1924b; 18-Coolidge 1924c; 19-Cleare 1926; 20-Hayward 1926; 21-Hayward 1926; 22-Hayward 1926; 23-Van Someren & Van Someren 1926; 24-Comstock 1927; 25-Stubenrauch 1929; 26-Hayward 1931; 27-Comstock & Dammers 1932; 28-Comstock & Dammers 1932; 29-Comstock & Dammers 1932; 30-Le Moult 1932; 31-Hoffmann 1933; 32-Lichy 1933; 33-Dos Passos 1936; 34-Dos Passos 1936; 35-Dethier 1938; 36-Djou 1938; 37-Hoffman et al. 1938; 38-Hoffmann 1938; 39-Tsang 1938; 40-Dethier 1939; 41-Dethier 1939; 42-Comstock 1940; 43-Dethier 1940; 44-Dethier 1941; 45-Dethier 1942; 46-Dethier 1942; 47-Dethier 1942; 48-Dethier 1943; 49-Dethier 1944; 50-Bourquin 1948; 51-Bourquin 1949; 52-Dickson 1949; 53-Sarlet 1949-1957; 54-Beebe 1952; 55-Urbahn 1952; 56-Bourquin 1953; 57-Comstock 1953; 58-Zikan 1953; 59-De Lesse 1954; 60-Döring 1955; 61-Van Son 1955; 62-Jarvis 1956; 63-Clark & Dickson 1957; 64-Beebe et al. 1960; 65-Comstock 1961; 66-Comstock & Vazquez 1961; 67-Malo & Willis 1961; 68-Harrison 1963; 69-Niculescu 1963; 70-Van Son 1963; 71-Emmel & Emmel 1964; 72-Hayward 1964; 73-Ross 1964a; 74-Ross 1964b; 75-Ross 1964c; 76-Clark & Dickson 1965; 77-Cottrell 1965; 78-Lawrence & Downey 1966; 79-Templado 1966; 80-Clark & Dickson 1967; 81-Hayward 1967; 82-Emmel & Emmel 1968; 83-Heitzman & Heitzman 1969; 84-Brown & d'Almeida 1970; 85-Clark & Dickson 1971; 86-Rydon 1971; 87-Straatman 1971; 88-Bodi 1972; 89-Dujardin 1972; 90-Emmel & Mattoon 1972; 91-Mcalpine 1972; 92-Quick 1972; 93-Young 1972a; 94-Young 1972b; 95-Young 1972c; 96-Young 1972d; 97-Atkins 1973; 98-Muyshondt 1973; 99-Young 1973a; 100-Young 1973b; 101-Young 1973c; 102-Young 1973d; 103-Emmel & Emmel 1974; 104-Muyshondt 1974; 105-Shirozu & Hara 1974; 106-Young 1974a; 107-Young 1974b; 108-Atkins 1975; 109-Straatman 1975; 110-Young & Muyshondt 1975; 111-De la Maza & De la Maza 1976; 112-Martin 1976; 113-Muyshondt 1976; 114-Atkins & Miller 1977; 115-Henning 1977; 116-Lambkin & Lambkin 1977; 117-Schurian 1977; 118-Young 1977a; 119-Young 1977b; 120-Aiello & Silberglied 1978; 121-Atkins 1978; 122-Pennington 1978; 123-Roos 1978; 124-Young 1978; 125-Dias 1979; 126-Dias 1979; 127-Downey & Allyn 1979; 128-Dunlap-Pianka 1979; 129-Henning 1979; 130-Silberglied et al. 1979; 131-Van Son 1979; 132-Aiello 1980; 133-Aussem 1980; 134-Aussem & Hesselbarth 1980; 135-Dias 1980; 136-Downey & Allyn 1980; 137-Roos 1980; 138-Roos & Arnscheid 1980; 139-Yata & Fukuda 1980; 140-Brown 1981; 141-Downey & Allyn 1981; 142-Roos & Arnscheid 1981; 143-Henning 1982; 144-Kirton et al. 1982; 145-Roos et al. 1982; 146-Arnscheid & Roos 1983; 147-Fukuda 1983; 148-Hesselbarth 1983; 149-Johnson & Valentine 1983; 150-Oehmig 1983; 151-Wagener 1983; 152-Atkins 1984; 153-Downey & Allyn 1984; 154-Eitschberger & Racheli 1984; 155-Furtado 1984; 156-Heath et al. 1984; 157-Martín & Templado 1984; 158-Nakasuji & Kimura 1984; 159-Parsons 1984; 160-Roos et al. 1984; 161-Sands et al. 1984; 162-Wood 1984; 163-Wright 1984; 164-Young 1984; 165-Arnscheid & Roos 1985; 166-Casagrande & Mielke 1985; 167-Cubero 1985; 168-Kitching 1985; 169-Boillat 1986; 170-Boudinot 1986; 171-Callaghan 1986; 172-Eitschberger & Ströhle 1986; 173-Eitschberger et al. 1986; 174-Friedlander 1986; 175-Huertas 1986; 176-Roos 1986; 177-Young 1986; 178-Atkins 1987; 179-Atkins & Heinrich 1987; 180-Atkins & Miller 1987; 181-Benz et al. 1987; 182-Nakasuji 1987; 183-Roos 1987; 184-Shapiro 1987; 185-Wood 1987; 186-Atkins 1988; 187-Friedlander 1988; 188-Graham 1988; 189-Munguira 1988; 190-Wood 1988; 191-Benjamini 1989; 192-Boillat 1989; 193-Boudinot 1989; 194-Callaghan 1989; 195-Henning 1989; 196-Johnson & Valentine 1989; 197-Marini & Trentini 1989; 198-Roos & Arnscheid 1989; 199-Samson 1989; 200-Valentine & Johnson 1989; 201-Back 1990; 202-Braby 1990; 203-Eitschberger 1990; 204-Eitschberger 1990; 205-Eitschberger 1990; 206-Eitschberger 1990; 207-Eitschberger & Ströhle 1990; 208-Eitschberger & Ströhle 1990; 209-Emmel & Emmel 1990; 210-Emmel & Garraway 1990; 211-Goyle 1990; 212-Köppel 1990; 213-Urich & Emmel 1990; 214-Urich & Emmel 1990; 215-Ziegler & Jost 1990; 216-Callaghan 1991; 217-Garcia-Barros & Martín 1991; 218-Hara 1991; 219-Johnson & Doherty 1991; 220-Samson 1991; 221-Sarto & Masó 1991; 222-Turner 1991; 223-Urich & Emmel 1991; 224-Urich & Emmel 1991; 225-Urich & Emmel 1991; 226-Wiemers 1991; 227-Brevignon 1992; 228-Brower et al. 1992; 229-Freitas & Oliveira 1992; 230-Thomson 1992; 231-Williams et al. 1992; 232-Braby 1993; 233-Dennis 1993; 234-Eitschberger 1993; 235-Eitschberger 1993; 236-Fiedler 1993a; 237-Freitas 1993; 238-Garraway et al. 1993; 239-Häuser et al. 1993; 240-Henning et al. 1993; 241-Leestmans & Carbonell 1993; 242-Llorente-Bousquets et al. 1993; 243-Merrett 1993; 244-Atkins 1994; 245-Braby 1994; 246-Braby & Woodger 1994; 247-Brown & Freitas 1994; 248-Caldas 1994; 249-Freina 1994; 250-Hsu & Lin 1994; 251-Johnson et al. 1994; 252-Jutzeler 1994a; 253-Jutzeler 1994b; 254-Jutzeler 1994c; 255-Jutzeler 1994d; 256-Jutzeler & Leestmans 1994a; 257-Jutzeler & Leestmans 1994b; 258-Otero 1994; 259-Pringle et al. 1994; 260-Smith et al. 1994; 261-Dantchenko et al. 199; 262-García-Barros & Martín 1995; 263-Hesselbarth et al. 1995; 264-Hirukawa & Kobayashi 1995; 265-Johnson et al. 199; 266-Jutzeler 1995a; 267-Jutzeler 1995b; 268-Jutzeler, Grillo & De Bros 1995; 269-Jutzeler, Pitzalis & De Bros 1995; 270-Jutzeler et al. 1995a; 271-Jutzeler et al. 1995b; 272-Meyer 1995; 273-Penz 1995; 274-Samson & Wilson 1995; 275-Sourakov 1995; 276-Sourakov & Emmel 1995; 277-Yen & Jean 1995a; 278-Yen & Jean 1995b; 279-Zanuncio et al. 1995; 280-Atkins 1996; 281-Caballero 1996; 282-Dantchenko et al. 1996; 283-Jutzeler 1996; 284-Jutzeler & De Bros 1996; 285-Jutzeler, Biermann & De Bros 1996; 286-Jutzeler et al. 1996; 287-Merrett 1996; 288-Meyer 1996a; 289-Meyer 1996b; 290-Parsons 1996; 291-Sourakov 1996; 292-Williams & Atkins 1996; 293-Atkins 1997; 294-Callaghan 1997; 295-Igarashi & Fukuda 1997; 296-Meyer 1997a; 297-Meyer 1997b; 298-Sourakov & Emmel 1997; 299-Teshirogi 1997; 300-Williams & Atkins 1997; 301-Leigheb & Cameron-Curry 1998; 302-M.L. Munguira, unpublished data on Spanish Lycaenidae; 303-F. Urich, unpublished; 304-E. García-Barros, unpublished.

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Appendix. Relationships among the species included in the data set (see 'Sources' for the main references), in parenthetical notation.

((((1,2),3),(((4,(5,6,7),(8,9),(10,(11,12),13,14),(15,16,(17,18)),19,((20,21,22,23,24),25,(26,27,28),(29,30,31,32),33),34,(35,36),(37,38,39),(40,41,42),(43,44),((45,(46,47),(48,49),50,(51,52,53,54),55,(56,57)),(58,59,(60,61,62,63,64))),((65,66),67)),(68,(69,70,71,72,73),74,(75,76,77,78),79,80,((81,82,83,84,85),86,(87,88),89),((90,91),(92,93),94,95))),((96,97,98,99,100),(101,(102,103,104,105)),(106,107,108,109,110,(111,112,113,114),(115,116,117,118,119,120,121),122),((123,124),125),(126,127,128,129,130,(131,132)))))),((((133,134,(135,(136,137),138,(139,140),141,142,(143,144),145,(146,147,148,149,150),(151,152,153,154,155,156,157,158))),(159,160,(161,162),163,(164,165,166))),(((167,168,169),((170,171),((172,173),((174,175),(176,177,178,179,180))))),((181,(182,((((183,184,185,186,187,188),189),(190,191)),((192,193,194,195),(196,197,198,199,200)),(201,202)))),(((203,204),((205,206),((207,208),209,210,211))),((212,213,214),215,(216,(217,(218,(219,220)))),221,222,223,(224,225),226,227))))),(((228,229,230),231),(((((232,233,234,235,236,237,238,239),240),241,242,(243,244),245),((246,247),(248,249,250,251,252,253),254),(255,256,((257,258,259),(260,261)),262,263,(264,265),266,267,(268,269,270),271,(272,273),(((274,275),(276,277,278)),((279,280,281),(282,283),284)),285,(286,287,288,289),290)),(291,(292,293,294),(295,296,297,298,299,300),(301,302,303,304,305,306),(307,308),309,310,311))),((((312,313),(314,315),(((316,317),318),((319,320,321,322),323,324,325,326),((327,328,329,330),(331,332,333,334,335)),((336,337),(338,339)),(340,341),342,343)),(((((344,345,346),((347,348),349)),(((350,351),(352,353,354,355,356,357,358,359)),360)),361),(((362,363,364,365,366,367,368,369,370),371,372,373,374,375,376,(377,378),(379,380,381,382,383,384,385,386,387,388,389),(390,391,392),(393,394),395),((396,397,398,399,400,401,402,403,404,405,406),407),(((408,409,410,411),(412,(413,414,415))),((416,417,418,419,(420,421),422,423),(424,(425,426,427,428,429),430,(431,432),(433,434),435,(436,437,438),(439,440,441,442,443,444,445)),(446,447,(448,449))),450),((451,452),453,(454,(455,456,457,458,459),460),(461,(462,(463,464))),((465,466),((467,468,469),470),471,472),(((473,474),(475,476),477),478,((479,480,481),(482,483,484)),(485,486,487))),((488,489),(490,491,492,493,494,495,496,497),((498,499),500,501,(502,503),((504,505,506,507,508),509,510,(511,512)),(513,514,515),((516,517),(518,519)),520,((521,522),(523,524)),525,(526,527),((528,529),(530,531,532,533),(534,535)),(536,537,538,539),(540,541),((542,543),544,545,546),(((547,548,549,550,551),552,(553,554,555,556,557,558)),(559,560,561,562),(563,564),565,566,567),((568,569,570,571,572),(573,574,575,576,577,578,579,580,581,582),583,(584,585)),(((586,587),588,(589,590,591),(592,593,594,595)),596,(597,(598,599,600,601),((602,603,604),605,606),607),608)),609)))),(((610,611),612),(((((613,(614,615)),((616,(617,(618,(619,(620,621))))),(622,(((623,624,625),(626,627,628,629,630,631)),((632,633,634),(635,(636,(637,638),(639,640),(641,(642,643),644,645,646,647,(648,649,650,651),(652,653),654,655),(656,657,658,(659,660),(661,662),(663,664),665,666,(667,(668,669)),670)))))))),(671,672,(673,674,675,676),(677,678,679),680,681,682,(683,684,685,686,687,688,689)),((690,691),(692,693,694),695),696,(697,698)),((((699,700,701),(702,703,704)),((705,(706,707)),708)),(709,((710,711),((712,713),(714,(715,716)))))),717),((718,719,720,721,(722,723,724),(725,726,727,728,729),730,(731,732)),(733,(734,735,736,737),(738,739,740,741,742,743),(744,745,746,747,748,749),(750,751),752,753,(754,755,756)),(((757,758),759,760),(761,(762,763),(764,765,766,767,768),(769,770,771)),(772,(773,774)),775)),((776,(777,778),779),((780,781,(782,783,784)),(785,(786,787),(788,789)),790),(((791,792,793),794,(795,796,797,798,799),(800,801)),((802,803),(804,805,806)),(807,808,809,810,811,812,813),(814,815))),((816,(817,818),((819,820),(821,(822,((((823,824,825),826,827,828,829,830,831),(832,833,834,835,836,837)),((838,839),(840,((841,842),((843,844),(845,846,847,848,849,850,851,852,853,854,855,856,857,858,859,860,861,862,863,864,865)))))))))),866,((867,868),869,870,871),(872,873),((874, 875),876),877),(878,((879,880),((881,882),883)),884),(((885,886,887,888,889),890),(891,(892,893),(894,895,896),897,(898,899,900))),(901,((902,903),904),((905,(906,907,908),(909,910,911,912,913,914,915),916,917,(918,919,920),(921,922),923,924),925,(926,927,928,929),((930,931),(932,933,934,935,936,937),938,939),(940,941),(((942,943),944),((945,946,947,948),(949,950),(951,952),953,954,955,(956,957),(958,959,960,961,962),(963,964,965)),(966,967,968),(969,(970,971,972,973,974,975),(976,977,978,979,980,981,982)),(983,(984,985),(986,987,988),(989,990),(991,992,993)),(994,((995,996,997,998),999,(1000,1001),1002,(1003,1004,1005,1006,1007,1008),(1009,1010),(1011,1012,1013,1014,1015,1016),1017,(1018,1019))),(1020,1021,1022,1023,1024,1025),(1026,1027,1028),((1029,1030,1031),((1032,1033),(1034,1035,1036,1037))),((1038,1039),(1040,1041,1042,1043,1044),(((1045,1046,1047,1048),(1049,1050,1051,((1052,1053),1054))),((1055,1056,1057),(1058,1059)))),((1060,1061),(((1062,1063,1064,1065),(1066,1067)),1068,(1069,(1070,1071)))),((1072,1073,1074,1075),(1076,1077),1078,1079))),(((1080,1081),((1082,1083),((1084,(1085,1086)),1087)),((1088,(1089,(1090,1091))),(1092,(1093,(1094,1095))),((1096,1097,1098,1099),((1100,1101),(1102,1103),(1104,1105,1106))))),((1107,1108),((1109,1110),((1111,1112),((1113,1114),(1115,(1116,1117)),((1118,1119),(1120,(1121,(1122,1123)))),((1124,1125,1126,(((((1127,1128),1129),1130),((1131,1132),(1133,(1134,1135,1136,1137))),1138),((1139,1140,1141),(1142,1143),1144,1145))),(((1146,(1147,1148)),(1149,1150,1151,1152)),(((1153,1154,1155),1156),(1157,(1158,1159),(1160,1161),1162,(1163,1164,1165,1166),(1167,1168),1169,1170,1171))))))))),(1172,(1173,1174,1175),(1176,1177),(1178,1179,1180),1181,(1182,1183,1184)))))))

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Book Reviews

THE WILD SILK MOTHS OF NORTH AMERICA, by Paul M. Tuskes, James P. Tuttle and Michael M. Collins, 1996. Cornell University Press, Ithaca, NY, IX + 250 pages, including 30 color plates. ISBN 0-8014-3130-1. Price: $75 US.

The Saturniidae, or wild silk moths, have historically captured the attention of lepidopterists and others often attracted by the large size and rich colors of many of these moths, which number more than 1200–1300 species worldwide. This beautiful book covers about 70 species in 18 genera that occur within the limits of the continental United States and Canada. The authors' many years of experience with these remarkable insects have been condensed and translated into an easily readable tome replete with black and white photographs, maps and drawings. Thirty fine-quality color plates illustrate in life-size all adult moths treated, with smaller photographs of the last instar caterpillars of all but two species. That the authors were able to rear and photograph so many species of moths reveals just part of the dedication, enthusiasm and labor required to produce this outstanding work.

The authors are well-known in the United States for their contributions to saturniid research. Paul Tuskes has published numerous papers on the U.S. Saturniidae; James Tuttle, a police detective-lieutenant, has been an officer of the Lepidopterists' Society, and collects, rears and photographs wild silk moths; Michael Collins is a research associate with the Carnegie Museum of Natural History, and is especially interested in speciation and natural hybridization.

The text is divided into two main sections, both in small print, allowing ample information to be packed in: Part One, entitled Behavior and Ecology, discusses such topics as metamorphosis and development, parasitism, diseases, species concepts and taxonomy, collecting, rearing, and silk moth impact on human culture. Part Two, Species Accounts, contains the color plates, and presents a description of each subfamily (three in U.S. and Canada), genus and species. Each species receives about one or more pages of coverage, including general comments, adult diagnosis, variation and biology, immature stages and rearing notes. I was gratified to see that the striking photographs of caterpillars were presented in the natural "hanging down" position beneath the limb instead of the reverse, as is often the case. Two appendices list host-parasitoid records and saturniid hybrids. An extensive bibliography of cited literature is especially valuable for the student.

However, there is a tendency to overlook or disregard recent taxonomic opinions and conclusions by other U.S. and international saturniologists. An obvious example is the arbitrary decision to reinstate the genus *Sphingicampa* Walsh 1864, removing all species except *molina* from the genus *Syssphinx* Hübner [1819], on the basis that *molina*, which is the type species for *Syssphinx*, differs morphologically and in the genitalia from the others. The authors "feel that the North American species are phylogenetically closer to each other than to *Syssphinx molina*." This is followed by the statement that "The genus *Sphingicampa* is obviously related to *Anisota* and *Dryocampa* and to the tropical genus *Adelocephala*." *Adelocephala* Duponchel 1841 is not a valid generic name, because it is actually a junior objective synonym of *Anisota* Hübner [1820], which occurs mainly in North America. Such a provincial approach dismisses or ignores the landmark 1988 updated revision of Claude Lemaire (The Saturniidae of America: Ceratocampinae) who worked with the much greater number of species found throughout the new world, and the 1982 work of Fletcher and Nye of the British Museum (The Generic Names of Moths of the World, Vol. 4) and others. Thus, this otherwise excellent book is a bit weak in its taxonomic treatment, and will perpetuate some confusion among its readers.

The geographical area covered reflects the focus of many U.S. saturniolo-gists, an area limited to North America north of the Mexican border. This political boundary separates a faunistically extremely rich territory from the rest of North America, and hampers or discourages study of its insects by U.S. investigators. But because more than half of North American silk moth species reside there, I would like to see a book integrating the saturniid fauna of the entire North American continent. Also, a more complete introductory overview of worldwide Saturniidae and recognition of international saturniid researchers would have been welcome. Nevertheless, for areas north of the border this book represents an impressive reference work that belongs in the library of every serious lepidopterist.

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GARDEN BUTTERFLIES OF NORTH AMERICA: A GALLERY OF GARDEN BUTTERFLIES AND HOW TO ATTRACT THEM. Rick Mikula. 1997. 143 pp. Willow Creek Press, Minocqua, WI. $29.50.

Are butterflies “disappearing?” Butterfly gardening books certainly are not. This one has what might be called a charismatic, or at least media-friendly, author. Rick Mikula, son of a coal miner and a sales clerk, dropped out of college, did a stint in the Navy, work in his native Hazelton, Pennsylvainia as a machinist, and somehow got “into” butterflies. He started the Hole-in-Hand Butterfly Farm in Hazelton in 1980, selling monarchs and other species for weddings, garden parties, and the like. Nowadays he raisees 50 species and reportedly sells 25,000 a year — shipping FedEx in summer (because its trucks are cooler) and UPS in winter (because its brown trucks are warmer). He’s been profiled in *People* and the *Wall Street Journal* and on the Discovery Channel. He designed the Butterfly Emporium at Dollywood, Dolly Parton’s resort-theme park in Pigeon Forge, Tennessee. No academic stuffed shirt he!

So how is the book? OK. The sections on butterfly biology and butterfly gardening are pretty standard. The lists of recommended garden plants are uneven. Those on pages 35, 43 and 46 have no scientific names for the plants, while that on page 44 does. The numerous color photos appear mostly from life, though several of them give hints of being posed, perhaps with chilled specimens. Only one is a blatant fake. It’s on page 116 and purports to be a *Colias philodice.* It’s a winter form of *C. eurytheme,* and is rather obviously dead. The male *Pieris rapae* on page 112 is suspect, too.

Mikula has inexplicable Pierid problems. On page 118 are two photographs of what are supposed to be Phoebis sennae but are in fact two rather different-looking male Colias eurytheme. On page 124 there is a real *Phoebis sennaes* identified as C. eurytheme. There are other slip-ups, too. On page 63 Mikula says “All swallowtails perform a ritual called hilltopping,” which might be a surprise to quite a few of them. On page 33 is a lovely photograph identified as “Eastern Tiger Swallowtails puddling in Guadalupe Mountains National Park” — they’re *P. multicaudatus.* On page 28 two photos share a caption: "Supply host plants for butterflies to lay eggs on as well as nectar plants for feeding." One picture is a male *Hylephila phyleus* feeding. The other is a very un-skippery clutch of eggs laid on a tendril of something. And so on.

In short: this is a fairly pretty book, neither the best nor worst of the lot of butterfly-gardening books in print. There is no compelling reason to buy it unless one collects butterfly gardening books or stuff peripherally related to Dolly Parton.

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BUTTERFLIES ON BRITISH AND IRISH OFFSHORE ISLANDS: ECOLOGY AND BIOGEOGRAPHY. Roger Dennis and Tim Shreeve. Gem Publishing Company, Wallingford. 131 pp. ISBN 0-906802-06-7. £16.00.

Although a slim volume of 131 pages, this book is a tour de force on the ecology and biogeography of butterflies on British and Irish offshore islands. No more, no less. It is actually two books in one, the first a checklist of butterflies species found on British and Irish islands, the second a rigorous analysis of those data. The checklist alone represents an enormous effort on the part of Dennis and Shreeve, with records gleaned from every conceivable source, as evidenced by the extensive list of personal communications and the 571 references in the bibliography.

Dennis and Shreeve present their analysis of the data in a series of short, dense chapters. They kindly provide a short explication of the their statistical methods, which include many multivariate ordination and clustering techniques, for those who may be rusty in that realm. The review is warranted, because the authors put the data through serious manipulation in their attempts to explain the variation in species incidence on islands. After starting by placing species number on islands in the obvious context of island biogeography, the authors proceed to explore all of the issues that confound the basic relationship described by MacArthur and Wilson. Their first analytical chapter explores the determinants of species richness. The following two chapters explore the affinities among island butterfly faunae (they are nested) and among incidence of butterfly species on islands (confirming the nested-species subsets across islands). Following a chapter predicting butterfly species number on islands, they present an interesting discussion of migration. Drawing from the extensive literature assembled for the book, they document instances of butterflies in hostile habitats that belie the conventional characterizations of butterfly populations as "closed" or "open." In the light of records of butterflies from supposedly closed population structures observed over open ocean, they call for increased attention to the spatial and temporal variation in mobility and its implications for metapopulation structure. The next chapter reapplies an ecological explanation for butterfly incidence on islands earlier developed by Dennis. The final two substantive chapters consider intraspecific variation on islands and historical (Holocene) influences on patterns of butterfly abundance on islands.

The writing is straightforward, almost terse, and packed on the page. The authors use an inordinate number of occasionally non-intuitive abbreviations for variables, forcing the reader to repeatedly check back to previous pages to decipher tables. Even more annoying is the use of numbers to designate points on graphs that in some instances refer to islands (listed elsewhere) and other times to butterfly species (listed in yet another location). In this age of computerized publishing and graphic design the layout could have been much kinder to the reader by at least using words instead of abbreviations in the tables and highlighting species or islands discussed in figures.

The minor annoyance caused by the typesetting does not diminish from the thorough treatment of the subject. The book makes an excellent case study of the issues in island biogeography, but the reader must relate it to the wider literature without the help of the authors. And although the cover claims that the author's findings have ramifications for butterfly conservation, the authors do not discuss them. The work does illustrate the importance of amateur observation of butterflies to scientific inquiry and even provides an appendix describing how to make effective observations of butterflies and moths on islands.

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Notes

A Million White Butterflies (Pieridae) At Ouray National Wildlife Refuge, Utah

Key Words: *Pontia protodice, Pieris rapae,* superabundance, *Glycyrrhiza,* censusing

On 8.VIII.1996 the authors visited Ouray National Wildlife Refuge, Uintah County in northeastern Utah. The 5000 hectare Refuge is located about 25 km west of Vernal. Part of the refuge is accessible by an 8 km loop road through marshes and fresh water impoundments along the Green River. Near the entrance to the loop road we noted large numbers of white butterflies (Pieridae), both Cabbage White, *Pieris rapae* Linnaeus, and Checkered White *Pontia protodice* Boisduval & LeConte, nectaring on Rabbitbrush (*Chrysothamnus nauseosus,* Pall., Asteraceae). As we continued on to the loop road the butterflies appeared extremely abundant. We estimated the numbers of white butterflies within 20 m of the road using order of magnitude categories. We classified stretches of road as having 5-50, 50-500, 500-5000, or 5000-50,000 butterflies per 100 m (column 1 in table 1). For example, we estimated between 50 and 500 individuals per 100 linear meters, along the first 1 km of road. Then after a short spell of low density, the number of butterflies increased and we began finding them nectaring on Tamarisk or Salt Cedar (*Tamarix gallica* French, Tamariaceae). A sample of 15 plants with between 10 and 40 butterflies nectaring, showed an average of 9% Checkered Whites among the more abundant Cabbage Butterflies.

As we proceeded through the marshes, we encountered many Tamarisk bushes on either side of the road, and as we turned to parallel the river, the roadside ditches were clogged with stands of American Wild Licorice (*Glycyrrhiza lepidota* Pursh, Fabaceae), in a band ranging from 10-20 m wide, occupying one or both sides of the road. At this point the butterflies were so numerous that we could only estimate them by the thousands. Some licorice plants had over 100 individuals nectaring at flower clusters partially hidden under foliage. In the densest area we used 4 spot counts (1 m radius circles) which yielded a mean of 48.3 individuals per 3.14 m^2, to validate our estimate. These yielded an estimate of 30,800 for a 100 m long segment (2000 m^2), comfortably close to the midpoint of our range (27,500). We noted whether the butterflies occurred on one or both sides of the road, and clocked distances with the odometer to estimate the length of each segment. We ended a segment at a point where the density seemed to change markedly. Table 1 shows the calculation for the 8 km route. Taking the midpoint of the estimated range for each segment (2nd column in table 1) as representative, and multiplying by the length of each road segment and the number of sides occupied by butterflies, yielded an estimate of over 1,000,000 butterflies within 20 m of the road along the 8 km route. (There were very few further away because of lack of nectar sources). We doubt that the number was less than 750,000 nor more than 1.5 million.

Although one occasionally reads about "millions" of butterflies, these usually refer to migratory movements occurring over periods of hours or days. This is by far the largest localized aggregation we have ever seen. Ironically, we were unable to identify the larval host plants that the Pierids might have been using. We observed

Table 1. Estimation of abundance of white butterflies at Ouray National Wildlife Refuge, Utah, 8 August 1996.

Range of estimate per 100 m of roadside	Midpoint value for 100 m segment[1]	Length of road segment (meters)[2]	Number of sides occupied[3]	Estimate for segment
50 – 500	275	960	1	2,640
5 – 50	27.5	320	1	88
50 – 500	275	480	1.5	1,980
500 – 5000	2750	1600	1.25	55,000
5000 – 50000	27500	2080	1.7	972,400
500 – 5000	2750	800	2	44,000
50 – 500	275	1280	2	7,040
5 – 50	27.5	960	1.5	396
			Total Estimate	1,083,544

[1] This value multiplied by length of segment (column 3) and number of sides occupied (column 4), divided by 100, yielded the segment estimate in the 6th column.

[2] Converted from mileage on odometer

[3] Either one or both sides of the road were occupied by butterflies, depending mainly on distribution of *Glycyrrihiza.* For example, a value of 1.7 indicates that both sides were occupied for most of the segment.

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that *P. protodice* occurred most commonly where *P. rapae* was also common. Such superabundant aggregations are probably not rare, but linear distribution along the roadside ditches afforded an unusually favorable opportunity for estimating numbers.

We thank our companions Guy Tudor and Michelle LeMarchant for their patience, and botanist Tamara Naumann for identifying *Glycyrrhiza.*

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A Study of the Riodinid Butterflies of the Genus *Dodona* in Nepal (Riodinidae)

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Abstract. I present and discuss the adult habits of five riodinid species from the Kathmandu valley, Nepal; *Dodona egeon* (Westwood, 1851), *Dodona eugenes* (Bates,1867), *Dodona ouida* (Hewitson, 1865), *Dodona dipoea* (Hewitson, 1865) and *Dodona adonira* (Hewitson, 1865) , including oviposition, feeding, perching and distribution, and describe the immature biology and larval habits of *D. egeon, D. eugenes* and *D. dipoea* for the first time. The food plant for *D. egeon* is *Myrsine capitellata* Wall. (1824) and for *D. eugenes* and *D. dipoea* is *Myrsine semiserrata* Wall. (1824), both family Myrsinaceae. Principal adult food resources were bacteria and algae found on wet earth and leaves and to a lesser extent pollen and faeces. All species had a proboscis modified with numerous small lateral projections to assist in absorbing nutrients. I conclude that sympatric *Dodona* species use perching in different micro- habitats as a mechanism to maintain species isolation.

Key Words: Nepal, Oriental Region, Riodinidae, immature biology, adult habits.

INTRODUCTION

Although the butterfly fauna of the Oriental region has arguably been studied more than any other tropical region, its riodinid fauna has been sadly neglected. Aside from short mentions in species lists and general faunal books starting with "Seitz", the only works dealing with riodinid biology are Sevastopoulo (1946) and Johnston & Johnston (1980). As a start in filling this void, this paper presents field and laboratory observations on the biology and habits of five *Dodona* species from Kathmandu valley, Nepal; *Dodona egeon* (Westwood, 1851), *Dodona eugenes* (Bates,1867), *Dodona ouida* (Hewitson, 1865), *Dodona dipoea* (Hewitson, 1865) and *Dodona adonira* (Hewitson, 1865). I describe the immature biologies of *D. egeon, D. eugenes* and *D. dipoea* for the first time and include field observations and discussions on ovipositing, feeding, perching and distribution.

MATERIALS AND METHODS

I made field observations in the hills surrounding Kathmandu Valley in southern Bahktapur District and Lalitpur District during December 1995 and February to September, 1996. The study area (fig. 27) extended from Suryebinayak ridge south to Godawari and Pulchok peak, all forming part of the Pulchok massive, a range of hills on the southeast side of Kathmandu valley, with altitudes from 1300 m to 2762 m. Between 1400 m and 2100 m is *Schima-Rhododendron*-oak forest, the dominant tree species being *Schima wallachii, Quercus glauca* and *Rhododendron arboreum.* Above 2000

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m *S. wallachii* is replaced by *Quercus lamellosa.* Parts of this formation not used for agricultural terraces have been altered into scrubland by the gathering of fuel wood and animal fodder (fig. 23); however, on the steeper slopes and partially protected areas like the Suryebinayak ridge and the headwaters of Nag creek (fig. 24), less disturbed forest remnants are found. Between 2100 m and 2400 m is a transition zone between *Rhododendron arboreum* and the *Quercus semicarpifolia* forest which continues to Pulchok peak (2762m) (Khadka *et al*,1984).

I discovered food plants and larvae through observing oviposition, and on one occasion hired local people to search for eggs and larvae. Five immature *D. egeon* were studied, 42 *D. eugenes* and 3 *D. dipoea.* All larvae and eggs were raised in petri dishes, each larva receiving a unique reference code for recording its development. I examined immature stages with a binocular lupa. Some larvae and parasites were preserved in formaldehyde, and adults in papers. Voucher specimens are in the collection of the author.

RESULTS

Dodona egeon (Westwood, 1851) (fig 2,3)

D. egeon ranges from Central Nepal east to western China and Burma. In Nepal, it has been recorded as far west as Baglung, Baglung District (fig. 28). It flies between 1000 m and 2235 m, with an average locality elevation of 1400m.

Dodona egeon, immature stages

EGG: Diameter 0.7 mm, height 0.6 mm. Color reddish-brown when first laid, changing to white before hatching. Surface smooth. Micropyle is a tiny depression on top of egg. Duration: 7 days. n=5.

FIRST INSTAR LARVA: Length 2.5 mm. Thorax and abdomen slightly dorsally compressed with segments T2 through A8 protruding laterally at base; larva initially transparent, turning light green upon feeding. Head dark yellow, face setose with black spot in center; headcapsule width 0.4 mm. T1 light yellow, transverse prothoracic shield high, bifurcated dorsally with 5 long setae projecting cephalad on each side and one long lateral setae. Segments T2 through A8 light green, each with four white dorsal tubercles and a "Y" shaped forked dorsal setae from each, and one long unforked setae and several small ones on each lateral protrusion; anal shield triangular with 6 setae around edge and 6 dorsad. Spiracles light green, lateral/ posterior on T1 and superior to lateral protrusions on A1 to A8. Duration: 5 days. n=4.

SECOND INSTAR LARVA: (fig. 4) Length 5.0 mm. Thorax and abdomen dorsally compressed, segments T2 through A8 with larger lateral protru-

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Fig. 1	*D. egeon* foodplant, *Myrsine capitellata*
Fig. 2	*D. egeon* female on leaf of foodplant.
Fig. 3	*D. egeon* perching male
Fig. 4	*D. egeon* second instar larva
Fig. 5	*D. egeon* third instar larva
Fig. 6	*D. egeon* fourth instar larva
Fig. 7	*D. egeon* fifth instar larva
Fig. 8	*D. egeon* pupa


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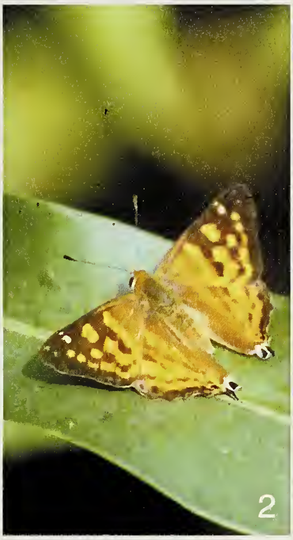
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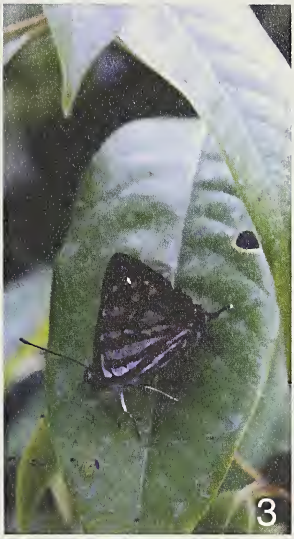
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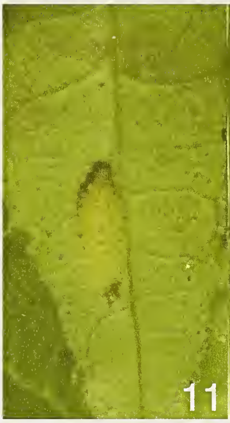


Fig. 9 *D. eugenes* male feeding
Fig. 10 *D. eugenes* foodplant, *Myrsine semiserrata*
Fig. 11 *D. eugenes* second instar larva
Fig. 12 *D. eugenes* third instar larva
Fig. 13 *D. eugenes* fourth instar larva
Fig. 14 *D. eugenes* fifth instar larva
Fig. 15 *D. eugenes* pupa

sions. Head yellow-brown, face setose with dark spot in center; headcapsule width 0.8 mm. T1 light yellow-brown, bifurcated ridge on prothoracic shield lower than first instar with 5 long setae projecting cephalad from each side and a cluster of long lateral setae. T2 through A8 greenish white dorsad with row of green dorsal spots flanked by a row of smaller elongated green spots and 4 white tubercles, each with two unitary setae; dorsal spots on T2, T3 and A3-A7 larger. Each segment protrudes laterally at base with a cluster of long setae at tip and numerous shorter setae dorsad; anal shield light brown with 6 setae around edge and 4 dorsad. Spiracles as on first instar. Duration: 6 days. n=3.

THIRD INSTAR LARVA: (fig. 5) Length 10.7 mm. Thorax and abdomen light green with darker green markings, dorsally compressed with segments T2 through A8 protruding laterally. Head light brown, setose; headcapsule width 1.5 mm. T1 light green with long setae on rim projecting cephalad, short line dorsad. T2 through A8 lighter green-yellow dorsad, darker green laterally, dark green spots on each segment forming triangular pattern with base cephalad and apex as a large dorsal spot on posterior segment margin. Lateral protrusions green-white, triangular with numerous long setae; anal shield rounded with four white spots dorsad with one setae each and more setae around edge. Spiracles as on first instar. Duration: 6 days. n=3.

FOURTH INSTAR LARVA: (fig. 6) Length 16.0 mm. Thorax and abdomen less dorsally compressed. Head light green, face setose with white spots forming circular pattern dorsad (fig. 7); headcapsule width 2.0 mm. T1 light green with short forward projecting setae and a short green line dorsad. T2 through T8 light green, dorsal pattern as in third instar but fainter with numerous short setae; triangular lateral protrusions on segments T2 through A8 less prominant, with long lateral setae; anal shield thick with four white spots dorsad and long setae around edge. Spiracles as on first instar. Duration: 3 days. n=3.

FIFTH INSTAR LARVA: (fig. 7) Length 22.5 mm to 28 mm. Head as in fourth instar, headcapsule width 2.7 mm. T1 light green mottled with white spots, short line dorsad. T2 through A8 light mottled green with light brown spiracles; otherwise as in fourth instar; anal shield mottled light green with long setae around edge and dorsad. Two days before pupating, larva turns uniform light green. Duration: 7 days. n=3.

PUPA: (fig. 8) Length 19.2 mm; width at widest point 12.0 mm. Color light green with light blue and yellow markings. Pupa attached by a cremaster and a girdle which crosses dorsum at A1. T1 crest indented with cerated, yellow edge; light blue dorsal line from T1 to A9 flanked on each side by a broken blue line on T1-T3 and blue spots A1 to A10; yellow spiracles on T1 and A2 through A8, wing cases white. Duration: 10 days. n= 2.

Dodona eugenes (Bates, 1867) (fig. 9)

D. eugenes is found from Nepal east to Burma and central China. In Nepal it ranges across the country between 1600 m to 2700 m, with an average locality elevation of 1870 m.

***Dodona eugenes*, immature stages**

EGG: Diameter 0.7 mm, height 0.6 mm. Color cream when first laid, changing to brown as the larva matures. Sides smooth. Duration: 6 days. n=4.

FIRST INSTAR LARVA: Length 3.0 mm. Thorax and abdomen tubular with segments T2 through A8 protruding slightly laterally; larva initially transparent, turning light green upon feeding. Head black with setae on face, headcapsul width 0.4 mm. T1 light green with prothoracic shield as bifurcated black transverse ridge, with 6 long setae from each side and a lateral/posterior white spiracle and one long lateral setae. T2, T3 light green, shorter setae dorsad and one long lateral setae from fleshy protrusion at segment base. Segments A1 through A8 each with 2 pairs of forked "Y" shaped dorsal setae, lateral protrusions with one long and 3 short black setae on each side and numerous shorter setae dorsad; anal shield with 8 long black setae around edge and 4 dorsad. Spiracles white, lateral on A1 to A8. Duration: 7 days. n=7.

SECOND INSTAR LARVA: (fig. 11) Length 4.2 mm. Thorax and abdomen dorsally compressed with segments T2 through A8 protruding laterally at base. Head light brown with setae and sometimes two spots or a faint bar on face, headcapsule width 0.7 mm. T1 light green with prothoracic shield as high, transverse bifurcated dorsal ridge with 6 long setae and a brown spot caudad on each side; several long lateral setae at base cephalad of spiracle. T1 covers neck initially, but before molting, neck is exposed. T2 through A8 gray-green dorsad, light brown/ green laterally, a row of faint gray-brown dorsal spots, each flanked by a short line and numerous shorter setae on each segment; lateral protrusions pronounced with long laterally projecting setae; anal shield fleshy with black setae around edge and dorsad. Spiracles as on first instar. Duration: 5 days. n=5.

THIRD INSTAR LARVA: (fig. 12) Length 7.0 mm. Head light green, rounded, setose, some individuals with a brown bar across face; headcapsule width 1.2 mm. T1 light green with dark green line dorsad flanked by a light brown spot with 6 long setae projecting cephalad and several long lateral setae; neck exposed on molting. Segments T2 through A8 gray-green dorsad with numerous short setae and a dorsal spot flanked by two smaller ones, and a short lateral line cephalad at segment division, largest spots on T2-3, A3-A6; laterally light green, lateral basal projections rounded, with long setae; anal shield rounded with setae around edge and dorsad. Spiracles white, lateral on T1 and A1 to A8. Duration: 6 days. n=17.

FOURTH INSTAR LARVA: (fig. 13) Length 12.0 mm. Thorax and abdomen dorsally compressed with segments T2 through A8 protruding laterally along base. Head light green, with circular pattern of white dots on face and numerous setae, headcapsule width 1.7 mm. T1 light green, neck covered initially by prothoracic shield, then exposed upon molting (fig. 11, 13); dorsad long setae projecting cephalad, a short dark green line dorsad, two brown spots fainter, or lacking. T2 through A8 light olive green dorsally, darker green laterally, with same pattern of dark green spots as third instar; anal shield with setae around edge and two white tubercles dorsad with one setae each. Spiracles light brown. Duration: 5 days. n=42.

FIFTH INSTAR LARVA: (fig. 14) Length 19 mm to 24/28.4 mm. Olive green dorsad, laterally mottled white/green. Head as in fourth instar, headcapsule width 2.7 mm. Prothoracic shield covers neck with short setae on cephalad rim. Segments T2-A8 dorsal pattern same as fourth instar, but becoming fainter as larva matures; dorsal spots on T2-3, A3-A6 black, connected by a line of tiny black setae, dorsad with tiny white setae with black heads. Anal shield mottled green with setae around edge and dorsad. Spiracles black. Prepupa uniform light green, black spiracles prominent. Duration: 12 days. n=26.

PUPA: (fig. 15) Length 13-20 mm, width at widest point 5- 6.4 mm. Color light green with light blue and yellow markings . Pupa attached by a cremaster and a girdle which crosses dorsum at A1. T1 with indented crest with ragged edge tinged with yellow. Dorsal blue line from T1 to T9, flanked on T1 by a shorter blue line, and from T2 to A9 with a broken light blue line; spiracles outlined in yellow at T1/T2 and A2-A8; wing cases darker green outlined dorsad by faint blue markings; A10 yellow, pointed. Duration: 10 days. n= 20.

Dodona dipoea (Hewitson, 1865) (fig. 16)

D. dipoea ranges from central Nepal to Assam and north Burma. In Nepal, it has been recorded as far west as Pokhara valley, and between 1500 m to 2870 m with an average locality elevation of 2200 m. Farther west it is replaced by *Dodona durga* (Kollar, 1844).

Dodona dipoea, immature stages

EGG: Unknown.

FIRST INSTAR LARVA: Unknown.

SECOND INSTAR LARVA: (fig. 18) Length 4.3 mm. Thorax and abdomen tubular with segments T2 through A8 protruding slightly basad. Head light green/ brown with face setose and two dark brown spots above sutures, headcapsule width 0.7 mm. T1 dark gray- green dorsad, laterally lighter green, prothoracic shield high, bifurcated, with 6 long brown setae extending over head on each side, and a black lateral/posterior spiracle. T2 through A8 brown-green dorsad, flanked by two rows of white spots, inner row elongated on T2-A1, narrower A2-A8; laterally light brown, with long, white setae from basal protrusions and black spiracles on A1-A8. Anal shield flat, triangular with setae around edge and dorsad. Duration: At least 5 days. n=1.

THIRD INSTAR LARVA: (fig. 19) Length 5.5 mm. Head light yellow-brown, pubescent, initially with dark bar across face; headcapsule width 1.2 mm. T1 light brown dorsad with transverse bifurcated ridge on prothoracic shield separated by short, red-brown dorsal line and with 6 long setae on each side, laterally with long setae and a black spiracle; before molting, neck is exposed as with *D. eugenes.*T2 through A8 dark green dorsad with two rows of elongated white marks flanked on each side by a white, irregular line and covered with short setae; laterally lighter green with some white mottling, lateral projections at base small with long setae. Anal shield larger, triangular with black setae. Spiracles as on second instar. Duration: 8 days. n=2.

FOURTH INSTAR LARVA: (fig. 20) Length 13 mm. Larva laterally compressed, from A3 tapering to point caudad. Head as in third instar, headcapsule width 1.7 mm. Prothoracic shield light green, low, with 9 long setae on each side, lateral spiracle black; T2-T3 olive green with reddish brown line dorsad, darker green laterally. T2-A8 with short, bristle- like setae dorsad, lateral projections reduced with long, white setae; A1-A8 darker mottled green, faint trace of reddish brown dorsal line, flanked on either side by a faint, irregular lighter green line. Anal shield elongated, pointed with black setae. Spiracles black. Duration: 7 days. n=2.

FIFTH INSTAR LARVA: (fig. 21) Length 14.5 mm to 20 mm. Head round, yellow/green, face setose, headcapsule width 2.4 mm. T1 uniform light green, bristle-like short brown setae on cephalad rim, black posterior/lateral spiracle, numerous brown, bristle-like setae dorsad. T2- A8 uniform, light mottled green, with red/ brown line from T2 to A8, widest on T2-T3; body covered with short, bristle- like setae, lateral setae at base shorter. Anal shield more elongated, pointed. Prepupa lighter green. Duration: 8 days. n=2.

PUPA: (fig. 22) Length 13 mm, width at widest point 6.0 mm. Color light green with light blue and yellow markings . Pupa attached by a cremaster and a girdle which crosses dorsum at A1. T1 with bifurcated dorsal crest reduced. Dorsal blue line from A1 to T9, spiracles outlined in dark green on T1-T2 and A2-A8; wing cases darker green. A10 pointed, yellow. Duration: 10 days. n= 2.

Dodona ouida **Hewitson, 1865 (fig. 25)**

D. ouida ranges from Nepal east to central China . In Nepal it is found across the country between 1450 m and 2900 m, with an average locality elevation of 2000 m.

Dodona adonira **(Hewitson, 1865) (fig. 26)**

D. adonira is found from Nepal east to Assam, Sikkim, Burma and northern Thailand. In Nepal, it is recorded as far west as the Pokhara valley, and between 1451 m and 2353 m with an average habitat elevation of 1854 m.

DISCUSSION

Food plant and species distribution

The food plant of *D. egeon, Myrsine capitellata* Wall. (1824) (Myrsinaceae) (fig.1), is distributed from Central and Eastern Nepal to Burma and Indo-China. *M. capitellata,* "Seti Kath" in Nepali, grows on exposed, degraded lower slopes of the *Schima-Rhododendron*-oak forest zone below 1600 m where it is very common, and to a lesser extent in secondary forests. It grows to a tree, 4 to 9 m tall, with large (6-20 cm long), elliptic- lanceolate leaves crowded near the branch tips, with small red glands on the ventral edge and small round pinkish fruit.

The food plant of *D. dipoea* and *D. eugenes, Myrsine semiserrata* Wall. (1824)

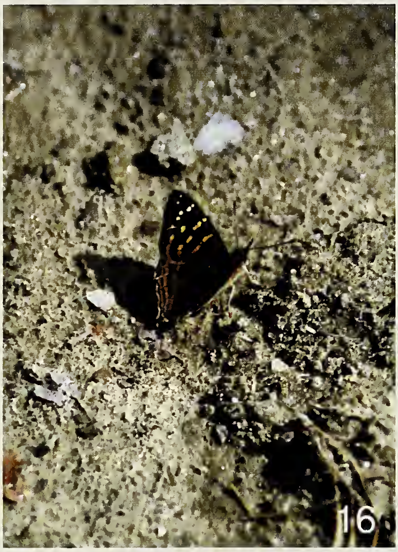


Fig. 16 *D. dipoea* male
Fig. 17 *D. dipoea* foodplant, *Myrsine semiserrata*
Fig. 18 *D. dipoea* second instar larva
Fig. 19 *D. dipoea* third instar larva
Fig. 20 *D. dipoea* fourth instar larva
Fig. 21 *D. dipoea* fifth instar larva
Fig. 22 *D. dipoea* pupa

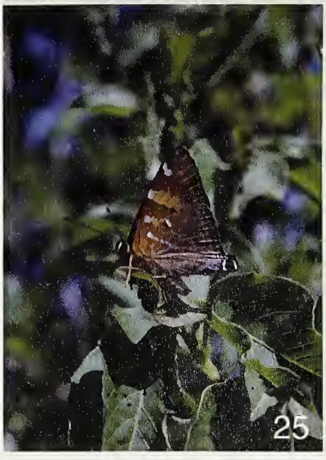


Fig. 23 Degraded scrub habitat, Bhamare creek, Godawari.
Fig. 24 Mature *Schima-Rhododendron* -oak forest, Nag creek, Godawari.
Fig. 25 *D. ouides* male perching.
Fig. 26 Male *D. adonira* feeding on stream bed.

(Myrsinaceae) (fig. 10, 17), "Kali Kath" in Nepali, ranges from Nepal through Burma to central China and is found most commonly on wooded slopes in the upper *Schima- Rhododendron* -oak zone from 1600 m to 2300 m. It grows into a small tree 6 m high with lanceolate, entire denticulate leaves with small, red dotted glands on the ventral margin.

The reported food plant of *D. ouida* and *D. adonira* , *Maesa chisia* Buch. (Myrsinaceae) (Sevastopoulo, 1946), is found from east Nepal to north Burma. It grows into a small shrub or tree with 5 to 17 cm long lanceolate , glabrous, crenate leaves with small clusters of white flowers or fruit. Known locally as "Bilauni", it is used as an insecticide and grows on the edges of disturbed forests and along streams below 1800 m. It is also the food plant of two other local riodinids, *Abisara fylla* (Doubleday,1847) and *Zemeros flegyas* (Cramer,1780) (Sevastopoulo, 1946; Callaghan, unpublished data).

The distribution of *Dodona* in the study area follows that of their food plants. The range of *D. egeon* is the same as *M. capitellata,* under 1700 m, while *D. dipoea* and *D. eugenes* share the same distribution as *M. semiserrata* (fig. 27), 1700 to 2300 m. There is a slight overlap of food plant and *Dodona* ranges near the 1700 m contour on Bhamare creek. As an experiment, I successfully raised two *D. eugenes* larvae on *M. capitellata.* However, I found no evidence in the field suggesting that the two species oviposit on each other's food plant.

D. ouida males perch on the highest summits, above the range of *M. chisia* , but return to the lower valleys for feeding. *D. adonira* has not been recorded from the study area above 1900 m, except for an old (1963) and dubious record from Phuchok peak.

Larval Habits

The development time for *D. eugenes* averaged 51 days and *D. egeon* 46 days from oviposition to eclosure. The fifth instar had the greatest duration and increase in body size . Early instar larvae spent all their time on the food plant, feeding on plant tissues between the veins, consuming all leaf tissues only from the third instar. Up to the fifth instar, the larvae fed at any time of the day, alternating with periods of inactivity when they rested against the center vein of the leaf. Fifth instar larvae fed mainly at night. During molting and pupation, the larvae moved off the food plant, resting on the sides of their container, which suggests a similar behaviour in the field. Larvae raised in the same container cohabited peacefully.

Besides crypsis, *Dodona* larvae defend themselves by raising the front half of the body and snapping vigorously with their mandibles. Young *D. dipoea* larvae raised both front and rear portions, and they may also regurgitate black stomach contents. Despite these tactics, parasitism accounted for 32 % of the field collected *D. eugenes* larvae, 19% by an unidentified dipterid and 13 % by an *Ichneumen* wasp. The fly larvae appeared in the fifth instar, causing the larva to enter the prepupal stage prematurely. A single fly larva emerged through the body wall of each infected larva and quickly pupated. The wasp larvae emerged through the body wall during the fourth instar, 5 to 7 per larva, and quickly pupated, forming white cocoons.

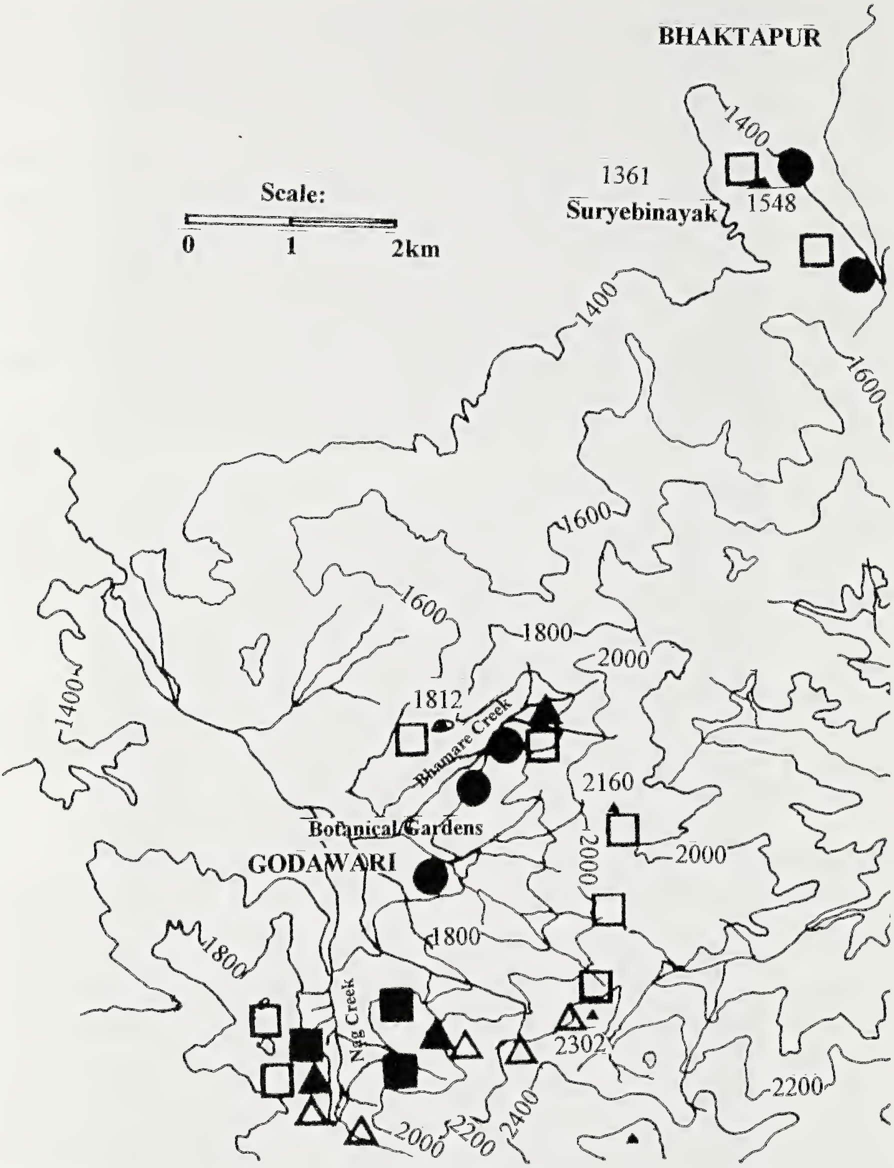


Fig. 27 Study area, showing *Dodona* species distribution. *D. egeon* □ *D. adonira* ■ *D. ouides* ● *D. eugenes* ▲ *D. dipoea* △

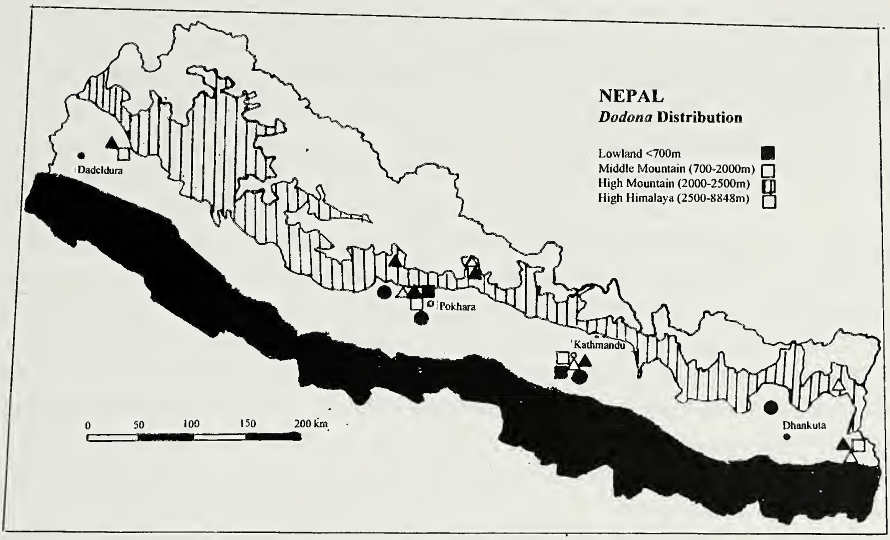
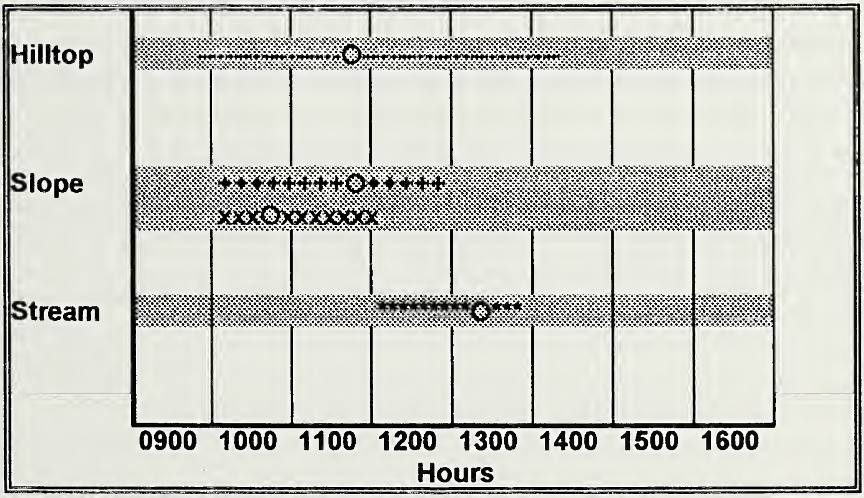


Fig. 28 Distribution of *Dodona* in Nepal. *D. egeon* □ *D. adonira* ■ *D. ouides* ● *D. eugenes* ▲ *D. dipoea* △



Species	Distribution of Observations. O = mean.
D. ouida	----------O--------
D. dipoea	+++++O++++++
D. eugenes	xxxxxxOxxxxx
D. egeon	********O******

Fig. 29 Spacing of male *Dodona* perching activity by locality and time of day.

Adult Habits

Capture records for the *Dodona* species in the Kathmandu valley (C. Smith, pers comm.) and my own observations suggest that most species fly throughout the year. *D. eugenes* and *D. dipoea* are recorded from February to December, *D. egeon* from February to November, and *D. ouida* from January to December. *D. adonira* flies from March to November. There are definite peaks in the populations of these butterflies. Adults are most common in April and May before the start of the rains. I observed a virtual population explosion of *D. egeon* at Suryebineyak on April 21,1996. At Godavari populations peaked the middle of May, then dropped precipitously at the beginning of the rains in June, increasing with the onset of dry weather in September.

The adults of both sexes fed mainly on algae, salts and bacteria growing on damp soil, leaves and rocks near streams. Other food resources were pollen, nectar and excrement. They were assisted by a modified proboscis with a wide, flat tip supporting numerous small black lateral projections, resembling a small brush when extended. When feeding, the proboscis was in constant motion over the substrate. Evidently the greater area of the proboscis created by the projections facilitates the absorption of nutrients. This modification is found in other Old World riodinid genera such as *Abisara* (Callaghan, unpublished data).

When feeding, wings may be raised or flat (fig. 9, 16). In either case, the lobes and tails at the anal angle of the hindwing bend outwards resembling two eyes when viewed from behind, or, in the case of *D. eugenes* and *D. egeon,* as eyes with antennae. The white scaling around the lobes of *D. ouides* mimic the butterfly's eyes (fig 25). These modifications suggest they serve to decoy predators, like the "false heads" of Theclinae.

Feeding times also differed between species and sexes. *D. egeon* males and females fed from 0845 to 1130, then from 1410 to 1540. *D. ouida* females fed between 1015 and 1120, then 1300 to 1530 and males from1330 to 1530. *D. eugenes* females fed from 0830 to 0930, then 1200 to 1530 and males from 1215 to 1530. Female *D. dipoea* fed throughout the day and males fed from noon to 1500. Three or four species may feed together. The feeding times, particularly for the males, reflected perching times discussed below.

I observed oviposition activity in *D. eugenes* and *D. egeon. D. eugenes* oviposited at 1130 and *D. egeon* at 0910, 0945, 1115 and 1215. Females of both species landed on the food plant leaf dorsal surface, walked to the edge, and placed a single egg on the ventral surface by reaching underneath with the abdomen. They then flew off in search of another plant.

Dodona species used perching behavior for locating mates, in which males await females in prominent locations and at certain times. The hypothesis that closely related, or congeneric riodinid species use different perching times and localities as an isolating mechanism has been advanced previously (Callaghan,1982), and is examined here with respect to *Dodona.*

The results of my observations on perching behaviour for four *Dodona* species are shown in figure 29. The micro-habitat type and the hours over which perching took place, and the mean of the observations are shown for each species.

D. ouida males (fig. 25) perched on ridges, especially on summits where up to 6 or 7 individuals vied for preferred spots. Perching was from 0945 to 1400, with maximum activity between 1100 and 1200. Males rested with wings together on dorsal leaf surfaces from 1 to 3 meters high, but never on the highest branches.

D. dipoea males perched on the hillsides along trails or on prominent bushes from 0934 to 1300 with peak activity at 1200. They defended their perches vigorously from other males, thus spacing themselves over the habitat. When a female appeared, the males would follow and when she landed, hover in the air above, beating their wings to spread pheromones, as suggested by the long scent hairs which cover both surfaces of the male hindwings.

D. eugenes males also perched on hillsides from 0945 to 1200 with peak activity at 0945, congregating around prominent vegetation, but without the aggressiveness of *D. ouida* or *D. dipoea*. Their resting position was the same.

D. egeon males perched along streams or gullies on the upper branches of prominent trees from noon until 1345, defending their perching spots vigorously against other males.

The foregoing observations suggest that sympatric *Dodona* species use perching in different micro habitats as a mechanism to maintain species isolation. Only *D. eugenes* and *D. dipoea* males perch in similar habitats, but never together, and the peak of *D. eugenes* perching activity is earlier..

Acknowledgements. I thank Mr. Colin Smith of the Annapurna Museum, Pokhara, for his orientation to the study area, advice and distribution records for *Dodona*; Drs T.C. Majupuria and Krishna K. Shrestha of Tribhuvan University for identification of the plant species, Mr. Mehendro S. Limbu of Godawari for his help in the field work, and two anonomous reviewers for their helpful comments.

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Journal of Research on the Lepidoptera 36:16–23, 1997 (2000)

On the correct placement of *Erebia epipsodea* Butler, 1868 within the genus *Erebia* Dalman, 1816 (Lepidoptera: Satyridae)

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Abstract. It is demonstrated that the Nearctic species *Erebia epipsodea* Butler, 1868 is the closest relative to the Palaearctic species *Erebia medusa* (Denis & Schiffermüller), [1775] and has no affinity with the species of the *Alberganus* group, in which it was placed previously. This conclusion is suggested by certain details of the male genitalic structure, but is confirmed by the structure of the female genitalia. Therefore *E. epipsodea* is removed from the *Alberganus* species group and placed into the *Medusa* group of species.

Since the time of the original description, the position of *Erebia epipsodea* Butler, 1868 within the system of the genus *Erebia* Dalman, 1816 was not stable. While describing it, Butler (1868) has clearly stated that the new species is very similar to *Erebia psodea* (Hübner, 1804): "*Alae supra forma et coloribus fere Psodeae* (Hbn.)... *Alae anticae subtus velut in Psodea sed magis rufescentibus...*". In contrast to the explanation in Bird et al. (1995), the specific epithet "epipsodea" is given exactly in this connection: "epi" in Greeks means "on", "towards" and "psodea" is [at present] the name of a Southeast European subspecies of *Erebia medusa* (Denis & Schiffermüller), [1775]. In the time of Butler the name *Erebia psodea* (Hübner, 1804) was in common usage for the species called at present *Erebia medusa* (Denis & Schiffermüller), [1775].

When the structure of the male genitalia of *E. epipsodea* and *E. medusa* was studied and compared, the first species was placed far from the second one on the basis that the male genitalia of both species look quite different (Chapman 1898). Chapman divided the genus *Erebia* into two sections and nine groups. *E. medusa* was placed in the section "A" group "VII"; *E. epipsodea* in section "B" group "VIII".

However, even knowing this, at the same time Elwes again placed *E. epipsodea* near *E. medusa* as its closest relative, basing this on the clear external similarity of both species (Elwes 1898).

Warren refuted this point of view in his monumental work on the genus *Erebia* (Warren 1936). He divided the genus into 15 specific groups, placing both discussed species in different groups, taxonomically distant from each other. *E. medusa* was placed into "IX. *Medusa* Group" while *E. epipsodea* was placed into "XI. *Alberganus* Group".

Warren (1936) had noticed very characteristic features in the genitalia of *E. epipsodea*: branches of juxta heavily chitinized and covered with teeth,

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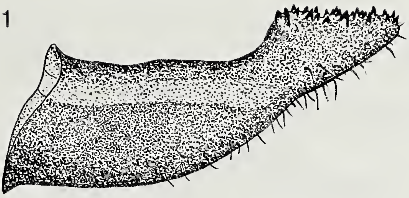

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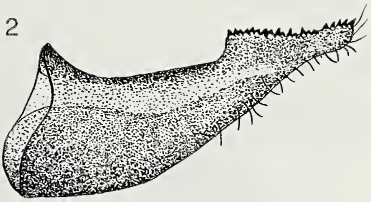

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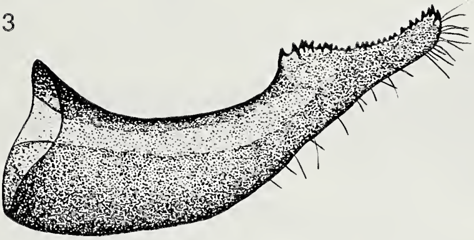

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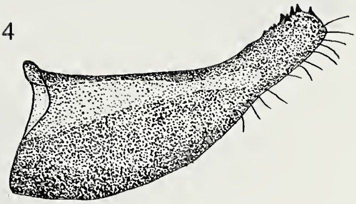

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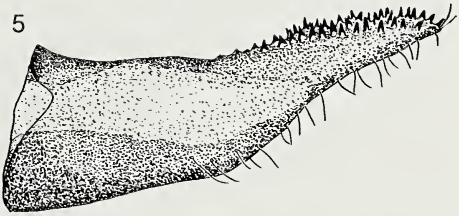

Fig. 1. *Erebia epipsodea*: left valva, lateral view. USA, Montana, Missoula Co., Miller Creek, 12.VI.1982, S. Kohler *leg.*

Fig. 2. *Erebia theano*: left valva, lateral view. Canada, Manitoba, Churchill, 20.VII.1981, P. Klassen *leg.*

Fig. 3. *Erebia alberganus*: left valva, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz - Alp Laden, 11.VII.1977, C. Häuser *leg.*

Fig. 4. *Erebia medusa*: left valva, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*

Fig. 5. *Erebia kozhantshikovi*: left valva, lateral view. Russia, Yakutia, Oymiakon distr., vic. Ust'-Nera, 25.VI.1993, S. Sazonov *leg.*

and coarse teeth on the aedoeagus (Fig. 6). He noted that the presence of these structures makes *E. epipsodea* a unique species within the whole genus. However he was certainly disoriented by two things. First is the general superficial similarity of the form of the valvae in *E. epipsodea* male genitalia (Fig. 1) to those of the species of the *Alberganus* group. Though not exactly resembling any species of the *Alberganus* group, the outline and comparative sizes of valvae elements in *E. epipsodea* are especially similar to those of some Nearctic representatives of *E. theano* (Tauscher, 1806) (Fig. 2). For the comparison, the shape of the valvae of *E. alberganus* is also shown here (Fig. 3). Second is the clearly considerable difference in the form of the valvae between the genitalia of *E. epipsodea* and of *E. medusa* (Fig. 4).

After the exhaustive work of Warren (1936) there were no further attempts

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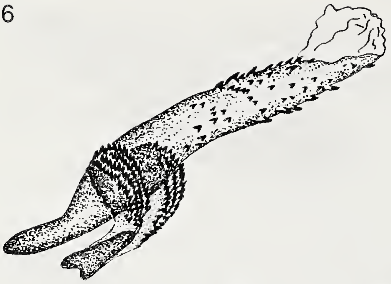

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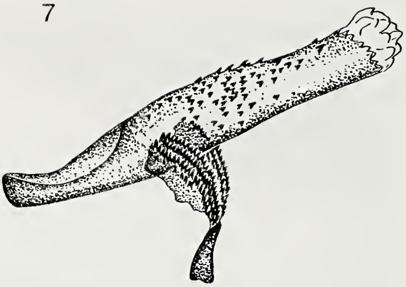

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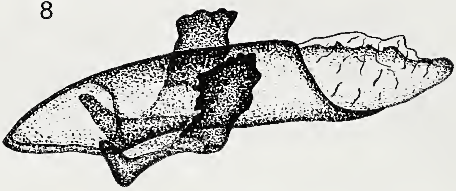

Fig. 6. *Erebia epipsodea*: aedoeagus and juxta, lateral view. Canada, Manitoba, Riding Mountains, 21.VI.1982, P. Klassen *leg.*

Fig. 7. *Erebia medusa*: aedoeagus and juxta, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*

Fig. 8. *Erebia alberganus*: aedoeagus and juxta, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz - Alp Laden, 11.VII.1977, C. Häuser *leg.*

at critical revision of the genus *Erebia.* Kurentzov (1970), reviewing systematics and distribution of the genus *Erebia* both in the Eastern Palaearctic and partly in the Nearctic region, mentioned *E. epipsodea* as a member of the *Alberganus* species group. Later there were two publications by Japanese authors. First of these publications was the paper of Murayama (1975), which was a brief illustrated abstract of Warren's "Monograph of the genus *Erebia*" rather than a new critical review of the genus. Published recently was the well illustrated work of Kogure & Iwamoto (1992; 1993). In both these papers *E. epipsodea* was also placed into the *Alberganus* species group, though the latter authors stated: "This species is placed in Group XI, *Alberganus* group because of structural characteristics of the male genitalia, but its morphological characteristics such as the size and the pattern of the wings are similar to those of *E. medusa*" (Kogure & Iwamoto 1993).

The question about a close relationship between *E. medusa* and *E. epipsodea* was raised again by Pringle (1992). It is demonstrated in that article that male genitalia of *E. medusa* have the same characteristic features that Warren (1936) considered as unique for *E. epipsodea.* The branches of the juxta are heavily chitinized and covered with teeth, and there are well developed teeth on the aedoeagus (Fig. 7). For the comparison, the aedoeagus and the juxta of *E. alberganus* are also illustrated here (Fig. 8) to show the shape of these structures in members of the *Alberganus* group. The author's study of specimens of *E. medusa* from various localities (from West Europe to Transbaikal Siberia) has confirmed the data reported by Pringle (1992) [**Note:** in all examined species the vesica is without cornuti]. Warren seems

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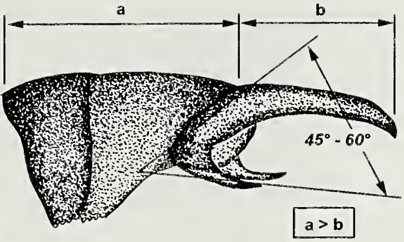

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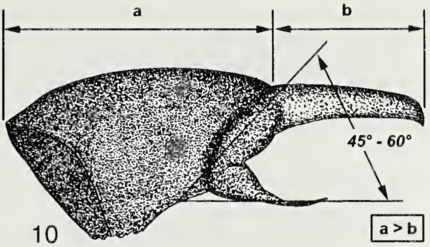

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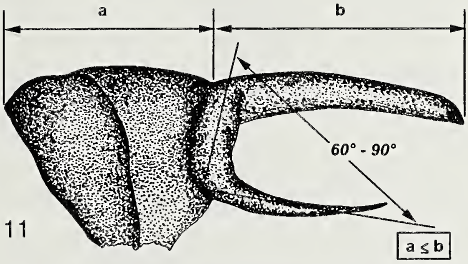

a — length of tegumen
b — length of uncus

Fig. 9. *Erebia epipsodea*: tegumen and uncus, lateral view. USA, Montana, Missoula Co., Miller Creek, 12.VI.1982, S. Kohler *leg.*

Fig. 10. *Erebia medusa*: tegumen and uncus, lateral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*

Fig. 11. *Erebia alberganus*: tegumen and uncus, lateral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz - Alp Laden, 11.VII.1977, C. Häuser *leg.*

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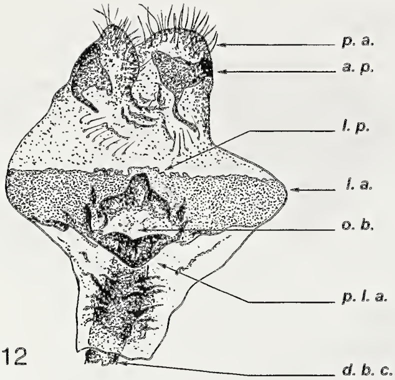
to have completely overlooked these important details in the male genitalia of *E. medusa.*

Studying the morphology of various species of *Erebia,* the author has noticed that the male genitalia of *E. epipsodea* and *E. medusa* have two other similar features, which at the same time distinguish *E. epipsodea* from all species of the *Alberganus* group. Sometimes these features are not clearly developed, but on material from series it is quite notable. The first feature is the comparative length of uncus and tegumen. In *E. epipsodea* and *E. medusa* the uncus is shorter than the tegumen (Figs. 9–10), in species of the *Alberganus* group the uncus is of equal length to the tegumen or even somewhat longer (Fig. 11). The second feature is that both in *E. epipsodea* and *E. medusa* the uncus with gnathos is connected to the tegumen with a rather acute angle, which varies from near 45° to 60° (Figs. 9–10). In members of the *Alberganus* group the uncus with gnathos is connected to the tegumen with a less acute angle, from 60° to 90° (Fig. 11). Numerous examples of these facts may be observed in the figures of Warren (1936: Figs. 334–338, 357–385); more examples of male genitalia of some North American species of the *Alberganus* group are shown by Troubridge & Philip (1983: Figs. 46–51).

However, all the mentioned features (phenetic similarity of *E. epipsodea* with *E. medusa* and notable external difference of *E. epipsodea* from all species of *Alberganus* group; the same features in male genitalic structures of



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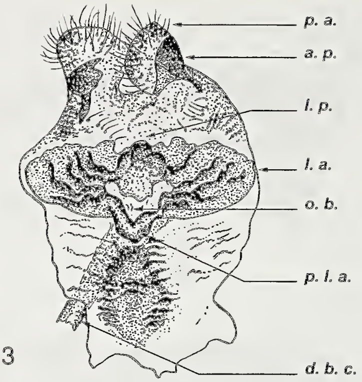

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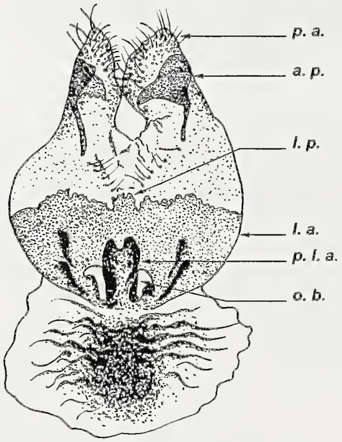

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p. a. — papillae anales
a. p. — apophyses posteriores
l. p. — lamella postvaginalis
l. a. — lamella antevaginalis
o. b. — ostium bursae
p. l. a. — processus lamellae antevaginalis
d. b. c. — ductus bursae copulatrix

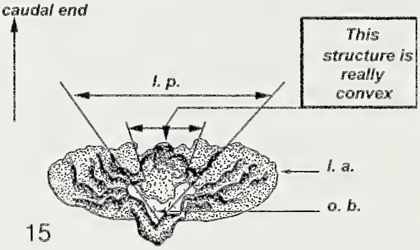

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Fig. 12. *Erebia epipsodea*: female genitalia, ventral view. Canada, Manitoba, Riding Mountains, 5.VI.1977, P. Klassen *leg.*

Fig. 13. *Erebia medusa*: female genitalia, ventral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*

Fig. 14. *Erebia alberganus*: female genitalia, ventral view. Switzerland, Wallis, NE Hohtenn/Lonza, Alp Tatz - Alp Laden, 11.VII.1977, C. Häuser *leg.*

Fig. 15. *Erebia medusa*: sterigma (female genital plate), ventral view. Russia, Chita region, Yablonovyy mountain range, vic. Yablonovo, 20.VI.1995, A. Belik *leg.*

E. epipsodea and *E. medusa*, which are lacking in the male genitalia of species of the *Alberganus* group) seem to be not quite enough to remove *E. epipsodea* from the Alberganus group and to place it into *Medusa* group. There is still the shape of the valvae in the male genitalia of *E. epipsodea*, which is not consistent with the idea of the affinity of *E. epipsodea* with *E. medusa*.

The author believes that the form of the valvae in male genitalia within the genus *Erebia* is a less stable trait, more subjected to adaptive radiation and specialization during the evolutionary process of speciation. For example, *E. kozhantshikovi* Sheljuzhko, 1925 undoubtedly belongs to the

Alberganus group, but the form of the valvae (Fig. 5) may be very different from the generalized shape of valvae in this group. At the same time the form and comparative sizes of the uncus and tegumen, and the form and chitinization of the juxta and aedoeagus seem to be much more conservative. So in certain cases the intrageneric arrangements of Warren, when based primarily on the form of the valvae, are not natural.

The author's study of the comparative morphology of female genitalia in the genus *Erebia* has revealed new and indisputable proof that *E. epipsodea* belongs to the *Medusa* group and has no relationship to the *Alberganus* group.

The female genitalia of *E. epipsodea* (Fig. 12) are very similar to those of *E. medusa* (Fig. 13). Both species have a structure in the female genitalia the shape of which is very uncommon for the genus *Erebia* as a whole: a very short flat triangular process associated with lamella antevaginalis (processus lamellae antevaginalis), which is directed anteriorly. Therefore, the ostium bursae opens freely to the ventral side. In females of most species of the genus *Erebia* that were studied by the author, and in members of the *Alberganus* group in particular, the processus lamellae antevaginalis (of varying form, usually bifurcated at the distal end) is well developed. It is directed caudally and therefore covers the ostium bursae from the ventral side. This is illustrated for the case of *E. alberganus* (de Prunner, 1798) (Fig. 14); other members of *Alberganus* group have female genitalia of similar shape. Furthermore, in the female genitalia of *E. epipsodea* and *E. medusa* the lamella postvaginalis has a characteristic convexity (Figs. 12–13, 15), while in species of the *Alberganus* group the lamella postvaginalis is quite flat (Fig. 14). [**Note:** the author believes that the structure of the bursa copulatrix has no significant taxonomic value for the intrageneric systematics of the genus *Erebia*. In all species examined, it has the same structure (with two signa, identical in all species). Therefore the bursa copulatrix is not illustrated on Figs. 10–13.]

CONCLUSION

Summarizing the preceding argument, it is clear that the Nearctic species *E. epipsodea* is the closest relative of the Palaearctic species *E. medusa*, having no affinity with members of the *Alberganus* group. So herein *E. epipsodea* is removed from the *Alberganus* species group and placed into the *Medusa* species group of the genus *Erebia*.

APPENDIX: MATERIAL EXAMINED AND THE RANGE OF VARIATIONS

The conclusions presented in this paper, to be meaningful, could not be based merely on the study of single specimens. During the preparation of the present paper, genitalia were examined of a representative series of specimens from each discussed species and, for completeness of comparison, from all species of the *Alberganus* group:

Erebia epipsodea: 10♂, 5♀; from Idaho, Wyoming, Montana and Manitoba.

Erebia medusa: 17♂, 7♀; from Norway, Austria, Italy, Bulgaria, Ukraina, Cisbaikal Siberia and Transbaikal Siberia.
Erebia alberganus: 10♂, 6♀; from France and Switzerland.
Erebia maurisius (Esper, 1803): 5♂, 1♀; from Altai and East Sayan Mtns.
Erebia theano (Tauscher, 1806): 37♂, 13♀; from Altai, East Sayan Mtns., Yakutia, Magadan region, Yukon, Manitoba, Montana, Wyoming, Colorado.
Erebia youngi Holland, 1900: 2♂ from Yukon;
Erebia dabanensis Erschoff, 1871: 20♂, 4♀; from Polar Ural Mtns, Putorana Plateau, East Sayan Mtns. and Magadan region.
Erebia anyuica Kurentzov, 1966: 13♂, 2♀; from East Sayan Mtns. and Yakutia.
Erebia occulta Roos & Kimmich, 1983: 4♂, 2♀ from Yukon.
Erebia kozhantshikovi Sheljuzhko, 1925: 5♂, 2♀ from Yakutia.
Erebia lafontainei Troubridge & Philip, 1983: 2♂ from Alaska.

A number of non-critical individual variations were seen in the genitalic structures of all above-mentioned species. In the male genitalia, these individual variations affect mainly the form of the valvae, while in the female genitalia they affect the general shape of the sterigma and the form of the processus lamellae antevaginalis.

Acknowledgements. Serious work in the field of lepidopteran systematics is impossible without study of numerous scientific publications, the majority of which are foreign ones and inaccessible here in the heart of Russia because of known reasons.

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Pontia occidentalis (Pieridae) Near Sea Level in California: a Recurrent Enigma

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Abstract. Two definite and one probable *Pontia occidentalis* have been taken near sea level in the Sacramento Valley of California in 27 years. This species normally breeds above 1500m at this latitude. All were taken in October, flying with the lowland sibling species *P. protodice.* The only explanation of these captures that is at all parsimonious entails long-range downslope dispersal, a seldom-documented event in montane non-migratory butterflies.

INTRODUCTION

Pontia occidentalis (Reakirt), the Western White, and *P. protodice* (Boisduval and LeConte), the Checkered White, are sibling species that largely replace each other altitudinally in California. They are, however, frequently sympatric in the western Great Basin, and intermittently so on the mid-west slope of the Sierra Nevada (Shapiro 1992). *P. occidentalis* is not known to be resident anywhere in north-central California below 1000m, and its breeding range at the latitude of Sacramento is upslope from 1500m. Most collections contain misidentified individuals of both species, leading to erroneous distributional reports, but Shapiro (1977) recorded a definite *P. occidentalis* near sea level in the Sacramento Valley. This was noteworthy for at least three reasons: it was the first record of this species in the California Central Valley, the first in Sacramento County, and one of surprisingly few records of apparent long-range downslope dispersal by a montane California butterfly. Low-altitude species, in contrast, are commonly recorded high in the mountains and most common Central Valley species have been recorded in most or all of the Sierran counties. It is not clear that this strong asymmetry is purely a function of either flight season or area, though both are likely to play roles in it (Sheehan, Richerson and Shapiro, in preparation).

I have tracked the dynamics of *P. protodice* in both space and time in the vicinity of Sacramento for 27 years, and the presence/absence of both species along a permanent 10-station transect across California parallel to Interstate Highway 80. *Pontia protodice* fluctuates tremendously in abundance and distribution in the Valley and indeed in most of its range, but in most years the largest populations occur on dredge tailings along the American River in northeastern Sacramento County; the capture of *P. occidentalis* reported by Shapiro (1977) was made there. Since the early 1970s the population density of *P. protodice* there has varied through four orders of magnitude, and with several apparent local extinctions. Among many thousands of individual *Pontia* examined here and elsewhere in the Sacramento

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Valley, the 1976 *P. occidentalis* remained unique until 1995, when a second (albeit problematic) individual was taken some 100m from the site of the earlier capture! A third was then taken in nearby Yolo County in 1998. The conditions of these captures are unusual enough as to require comment.

The first collection was a dark female of the "winter" phenotype "*calyce*," taken 17.X.1976 at Rossmoor Bar, Rancho Cordova, Sacramento County (19.7 m) amidst a dense flight of *P. protodice.* Both sexes were present, mostly fresh, and presenting variable but normal early- autumn phenotypes easily distinguished from *P. occidentalis* (fig. 1).

The second specimen, a male, was taken at Rossmoor Bar 19 years later, 13.X.1995 also in the company of numerous *P. protodice,* again of normal seasonal phenotypes (fig. 2). This individual is somewhat ambiguous. It is strikingly different from the others collected the same day, varying in the direction of *P. occidentalis* in most characters. Had it been taken in the western Great Basin in an area of sympatry it would have been relegated to the roughly 1% of wild specimens I cannot assign confidently to either species, and suspect to be hybrids. These are quite variable among themselves, but most - including the 1995 Rossmoor Bar male - have been rather closely duplicated among laboratory hybrids. Similar specimens also occur in areas of sympatry in Colorado. Such ambiguous individuals are occasionally taken within apparently pure *occidentalis* populations, but this is the first and only one I have gotten in an ostensibly pure *protodice* population. I revisited the site at two-week intervals for the remainder of the season, finding nothing unusual.

The third specimen, like the 1976 one, is a heavily-marked "*calyce,*" in this case a male. It was taken among normal *protodice* at Willow Slough, Yolo County (14.5 m), 10.X.1998 and is strikingly different-looking from them (fig. 3). Willow Slough is approximately 30 km due west of Rancho Cordova. The site is a weedy, overgrown floodplain; the butterflies were nectaring at *Aster.* I revisited Willow Slough three times from mid-October into early November but found no more *P. occidentalis.* This is the first record of *P. occidentalis* in Yolo County; it was not expected. *P. protodice* is often found at Willow Slough in autumn, but is not persistent. For example, it was found there in 6 of 22 Fourth of July counts since 1977, and was common only twice (1977 and 1992).

All three specimens are deposited in the Bohart Museum of Entomology, UCD.

DISCUSSION

These three *P. occidentalis* were captured within 7 calendar days (X.10-17), but in different years. This hints at a common process giving rise to all three records. The obvious candidate is downslope dispersal.

In all three cases the weather pattern during the preceding week was the same, with strong high pressure and a gentle NNE (i.e., downslope) wind at the surface and aloft, giving fair, warm conditions. This is a very common autumnal pattern. I have reviewed my long-term records and can find no

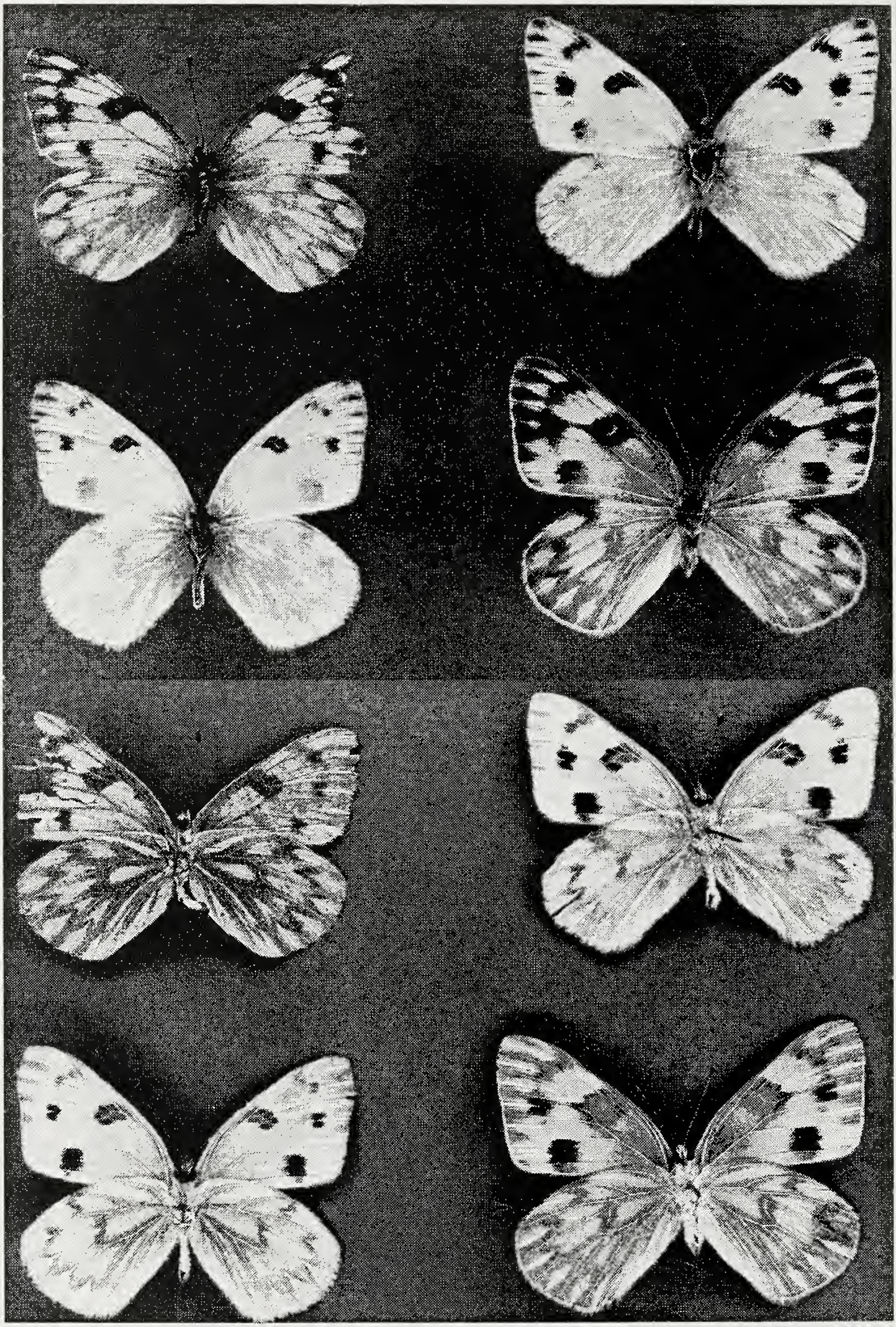

Fig. 1. Female *P. occidentalis* and several *P. protodice* collected with it, Rancho Cordova, Sacramento Co., CA, 17.X.1976, upper and lower surfaces.

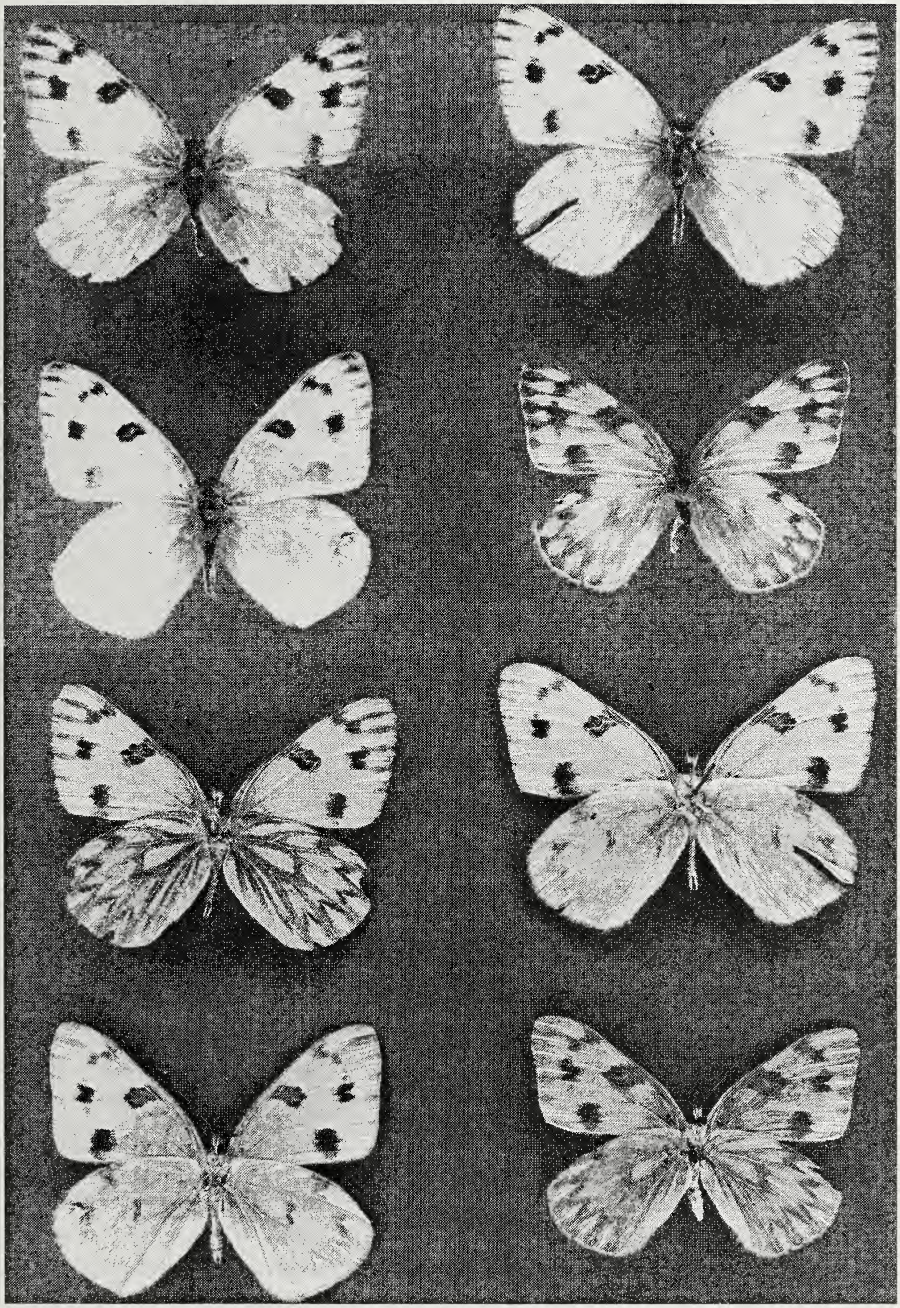

Fig. 2. Male *P. occidentalis*/hybrid (?) and *P. protodice* collected with it, Rancho Cordova, Sacramento Co., CA, 13.X.1995, upper and lower surfaces.

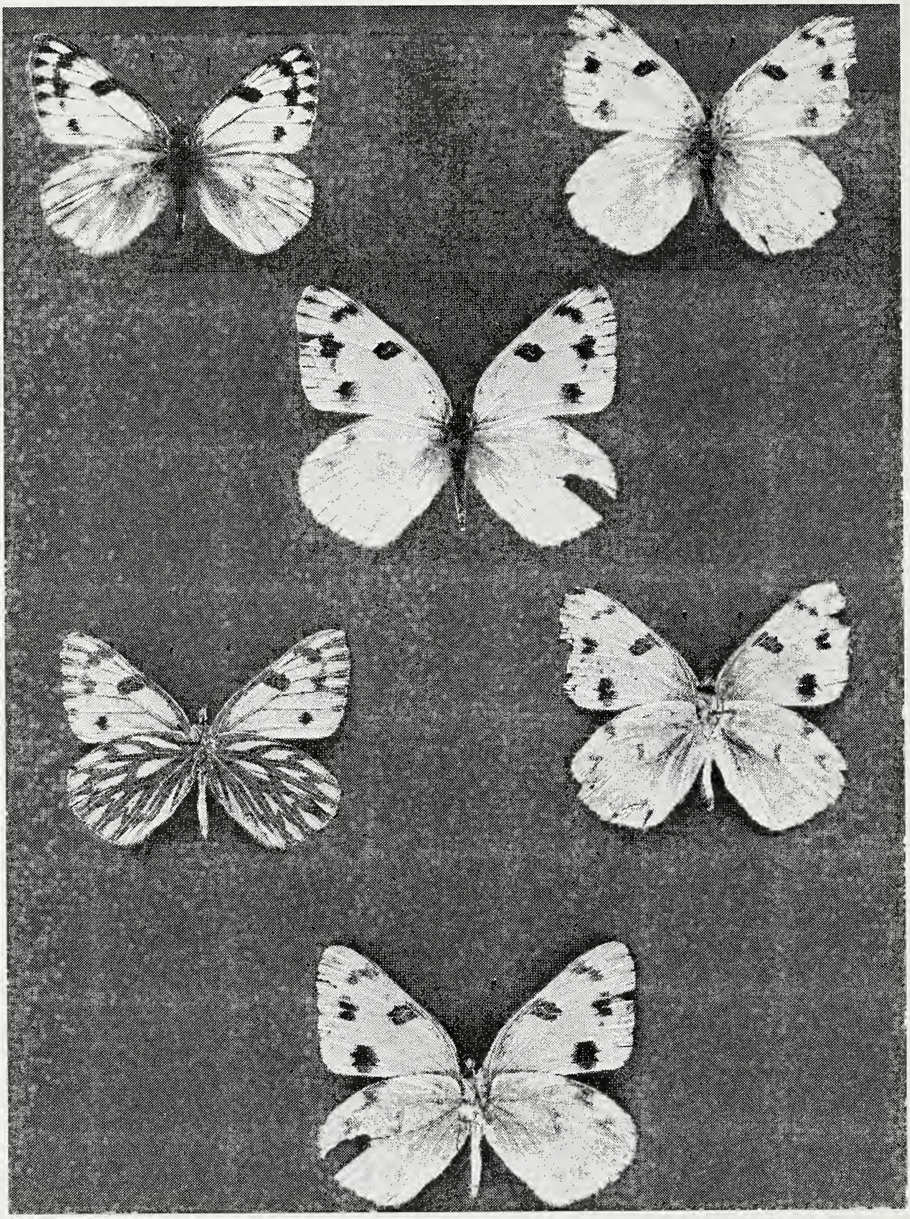

Fig. 3. Male *P. occidentalis* and *P. protodice* collected with it, Willow Slough, Yolo Co., CA, 10.X.1998, upper and lower surfaces.

pattern of downslope dispersal by other montane butterfly species under these conditions; however, such dispersal is very rarely seen at all in non-migratory montane species.

October is usually the month of maximum density and maximal areal occupation in the Valley for *P. protodice*, but it is difficult to see how this could account for the occurrence of *P. occidentalis.* Furthermore, October is not usually the month of greatest abundance for *P. occidentalis* in its normal montane range. Shapiro (1992) reviewed the dynamics of both species at 1500m on the Sierran west slope, where neither is a permanent resident. *P. occidentalis*, whose nearest permanent population (at 1900 m) is less than 15 km away, dispersed to my Lang Crossing site in 8 of 20 years, and bred in 4. This site is monitored biweekly from snowmelt through late October - early November. Of 17 dates when it was recorded there, 6 were in August and 4 each in July and September - only 1 in October. There is no evidence of a regular seasonal downslope movement, although we know *P. protodice* moves upslope from the Nevada desert in late spring (Shapiro 1992). In some years the densest populations of *P. occidentalis* at 1500m on the Sierran east slope do occur in October, where breeding occurs on Cruciferous weeds in irrigated alfalfa. The three Valley captures, however, do not coincide with known outbreaks of *P. occidentalis* on the east slope, and the dispersal distances required are on the order of 200 km, including the crossing of the Sierran crest. It is, however, noteworthy that both the 1976 and 1998 specimens correspond closely to the mean phenotypes flying at both 1500m on the east slope and 2100m on the crest (Donner Pass) at that time. The 1995 specimen is too idiosyncratic for such a comparison, but would not be "out of place" at either elevation as a putative hybrid; I have similar individuals taken in autumn at Sierra Valley, Sierra Co., an area of sympatry. See Shapiro (1976) for phenotypic exemplars.

Shapiro and Geiger (1986) demonstrated electrophoretically that under conditions of mutual abundance in sympatry, hybridization between these two species must be a rare event since no heterozygotes were found for a species-specific fixed allelic difference. It may occur more often when one species is much more abundant than the other. Hybridization appears to be more frequent in Colorado (J. Kingsolver, D. Wiernasz, personal communication).

When the species status of *P. protodice* and *P. occidentalis* was still unclear, the occurrence of *occidentalis* within what should be pure *protodice* populations could be ascribed to intrapopulational variation. This "explanation" is no longer tenable, at least for the 1976 and 1998 specimens, which are unambiguously *occidentalis* using Chang's (1963) and my own wing characters. Neither specimen would arouse any special comment if labeled as coming from 3000m in the High Sierra.

Shapiro (1977) observed that the similar habitat preferences and behaviors of the two species could account for a dispersing *P. occidentalis* lingering in a prime *protodice* habitat, such as Rossmoor Bar. That hypothesis remains tenable.

The idea that two and possibly three *P. occidentalis* would disperse in different years from the montane Sierra to the floor of the Sacramento Valley at exactly the same season - two to the exact same location! - and "join up" with resident populations of the sibling species *P. protodice*, where they were then accidentally discovered, strains credulity. Nonetheless, it is the only hypothesis that is at all parsimonious, and it suggests that there may indeed be an inconspicuous, low-density downslope movement by this species in autumn that we should be looking for.

Acknowledgments. I thank Michael Plotkin for acceding to my impulsive request to be dropped by the side of the road at Willow Slough on 10.X.1998, rather than at my house or lab. Without that bit of serendipity I would be much less perplexed.

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Effects of microclimate and oviposition timing on prediapause larval survival of the Bay checkerspot butterfly, *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae)

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Abstract. We tested empirically whether microclimate and relative timing of oviposition affected prediapause larval survival and development rates in the federally threatened Bay checkerspot butterfly, *Euphydryas editha bayensis* (Nymphalidae). Most mortality in Bay checkerspot butterflies occurs among prediapause larvae. Because phenology of the butterfly's larval hostplant, *Plantago erecta*, has been thought to drive prediapause larval survival patterns, we also tested whether *P. erecta* senescence and density over time varied among microclimatic zones. We found that microclimate had a significant effect on *P. erecta* phenology. Changes in density of edible *P. erecta* among microclimatic zones were out of phase temporally, but otherwise were similar. In the year of our study, neither microclimate nor oviposition date tended to affect prediapause larval survival, but both variables had significant effects on prediapause larval development rates. Because temperature and precipitation patterns in the butterfly's environment vary from year to year, whether microclimate and oviposition date significantly affect prediapause larval survival and development also may vary annually. At least in some years, however, senescence of *P. erecta* may not cause prediapause larval mortality. Our results support the hypothesis that topographic heterogeneity is critical to the long-term viability of the Bay checkerspot butterfly as well as other species that inhabit temporally variable environments.

Key Words: *Euphydryas editha bayensis*, invertebrates, conservation, microclimate, grasslands

INTRODUCTION

Spatial extent of suitable habitat is a fundamental consideration in conservation planning for viable populations of virtually all species. Certain landscape attributes that must be emphasized in conservation planning for invertebrates, however, differ from those that traditionally have received attention in conservation efforts targeting large vertebrates (Ehrlich and Murphy 1997). Habitat area is a primary concern for conservation of large vertebrates. These animals often require sizable protected zones in which population sizes can be maintained at or above a probabilistically safe

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baseline—for example, a 99% probability of remaining extant for 1000 years (Shaffer 1981, Boyce 1992). Not only geographic extent per se but also topographic heterogeneity of protected areas may be critical for the conservation of many invertebrates and small vertebrates, including the Bay checkerspot butterfly (*Euphydryas editha bayensis*) (Nymphalidae: Nymphalinae) (Ehrlich and Murphy 1987, Weiss *et al.* 1987, 1988, Launer and Murphy 1994). Spatial heterogeneity is important because invertebrate population dynamics frequently are density-independent and highly sensitive to climatic variability (Andrewartha and Birch 1954, Pollard and Yates 1993, DeVries *et al.* 1997, Crisp *et al.* 1998, Shaffer *et al.* 1998).

The Bay checkerspot butterfly, which inhabits patches of native serpentine soil-based grassland south of San Francisco, California, was listed in 1987 as threatened under the U.S. Endangered Species Act. Serpentine-based soils have a physical and chemical composition that limits the invasion of introduced Eurasian grasses, and thus can provide refugia for native vegetation (Kruckeberg 1954, 1984, Walker 1954, Thomas 1961, Turitzin 1981, Huenneke *et al.* 1990). The viability of these native grasslands and of the Bay checkerspot butterfly currently is jeopardized by suburban development (Murphy and Ehrlich 1980, Ehrlich and Murphy 1981, 1987). Conserving serpentine patches in the region is essential because the Bay checkerspot butterfly is structured as a "mainland-island" metapopulation in which local demographic units frequently go extinct and temporarily unoccupied habitat patches are recolonized (Ehrlich *et al.* 1975, 1980, Murphy and Ehrlich 1980, Ehrlich and Murphy 1981, 1987, Harrison *et al.* 1988).

Prediapause Bay checkerspot butterfly larvae suffer far greater mortality than any other life stage (Singer 1972, Ehrlich *et al.* 1975, 1980, Weiss *et al.* 1988, Cushman *et al.* 1994). Previous field studies estimated that survival of prediapause larvae rarely exceeds 10% annually (Singer 1972, Ehrlich *et al.* 1975, 1980, Singer and Ehrlich 1979, Dobkin *et al.* 1987, Weiss *et al.* 1988). Two interacting factors—microclimate and timing of oviposition during the growing season—are thought to affect rates of prediapause survival. Prediapause larval survival is believed to be highest among offspring of early-flying females that oviposit on cool north-facing slopes (Weiss *et al.* 1987, 1988, Murphy *et al.* 1990). On these slopes, the butterfly's larval hostplants [*Plantago erecta* (Plantaginaceae) and less commonly *Castilleja densiflora* or *C. exserta* (Scrophulariaceae)] remain edible until relatively late in the flight season (Weiss *et al.* 1987, 1988). Paradoxically, the females that fly earliest tend to be those that fed and pupated on warmer south-facing slopes, where hostplants senesce early and prediapause survival rates are thought to be lowest (Ehrlich *et al.* 1980, Weiss *et al.* 1988, Murphy *et al.* 1990). Eggs laid well into the flight season may be too late to produce larvae that survive on any slope (Weiss *et al.* 1988). For example, Cushman *et al.* (1994) estimated that just 1 week into the flight season, female reproductive success was less than 25% of that on the 1st day of the flight season. To date, estimates of prediapause larval survival over space and time have been based on measurements of hostplant senescence (Cushman *et al.* 1994) rather than measured directly. The purpose of this study was to test empirically the influence of microclimate and relative timing of oviposition on prediapause larval survival. In addition to quantifying hostplant senescence and density over time in different microclimatic zones, we monitored the survival and development rates of prediapause Bay checkerspot larvae that resulted from eggs laid in different microclimatic zones on different dates during the flight season.

Study system

Euphydryas editha bayensis is univoltine. Adults fly for 3-5 weeks between late February and early May (Weiss *et al.* 1988). Females lay masses of 20-200 eggs near the base of larval hostplants (Singer 1972, Weiss *et al.* 1988). Newly-hatched larvae feed until they reach the 3rd or 4th instar and then enter an obligatory diapause that lasts through the dry season (approximately May-November) (Ehrlich 1965, Singer 1972). If hostplants senesce before larvae reach the middle of the 3rd instar, the larvae starve prior to or die during diapause (Singer 1972, Singer and Ehrlich 1979). When the rainy season begins, surviving larvae break diapause and feed on newly germinated *Plantago erecta* until February or early March (Singer and Ehrlich 1979, Weiss *et al.* 1988). Adults emerge following 10-20 days of pupation and generally live for 1-2 weeks (Ehrlich 1965, Murphy *et al.* 1983, Cushman *et al.* 1994).

Extreme weather events can have markedly deleterious effects on Bay checkerspot butterfly metapopulations (Singer and Ehrlich 1979, Ehrlich *et al.* 1980, Murphy and Ehrlich 1980, Murphy *et al.* 1990). When seasonal precipitation is average or slightly above average, and the rainy season is not prolonged, the geographic distribution of the butterfly tends to expand and population sizes often increase. When precipitation patterns are extreme (drought or deluge), however, or when the start of the flight season is delayed by cool and cloudy weather, the geographic distribution of the butterfly tends to shrink and its abundance tends to decline (Singer and Ehrlich 1979, Ehrlich *et al.* 1980, Dobkin *et al.* 1987, Weiss *et al.* 1987, Murphy *et al.* 1990).

Because variation in aspect and tilt affects solar exposure and retention of soil moisture, local topography within habitat patches mediates hostplant senescence and therefore plays a key role in enabling Bay checkerspot butterfly metapopulations to survive extreme weather events (Ehrlich and Murphy 1987, Weiss *et al.* 1987, 1988). For example, south-facing slopes receive more solar radiation on clear days, thus are warmer and drier than north-facing slopes. *Plantago erecta* on south-facing slopes often senesce 3-4 weeks prior to those on cooler north-facing slopes (Weiss *et al.* 1988). Because hostplants on relatively cool slopes remain edible long into the spring, those slopes are believed to serve as "core" habitat for the Bay checkerspot butterfly. The availability of even a few cool slopes within a habitat patch can prevent its butterfly population from being extirpated during a short or mild drought. The importance of warmer slopes to the persistence of Bay checkerspot butterfly populations should not be underestimated, however (Harrison *et al.* 1988, Weiss *et al.* 1988). Even very warm slopes contribute to long-term viability of the Bay checkerspot butterfly by providing diverse early-season nectar, which can increase female fecundity and lifespan (Ehrlich and Murphy 1981, 1987, Murphy *et al.* 1983, Boggs 1997). Proximity of different microclimatic zones also is important because postdiapause larvae that disperse from cooler to warmer slopes may advance their adult emergence dates by a week or more, thus increasing their chances of reproductive success (Weiss *et al.* 1987, Cushman *et al.* 1994). In sum, survival and reproduction of the butterfly can occur under most macroclimatic conditions in a patch of habitat that includes a range of slope classes (Weiss *et al.* 1988).

METHODS

Our experiments were conducted at Kirby Canyon, Santa Clara County, California, USA (37°11′ N, 121°40′ W) in spring 1993. This site includes approximately 1350 ha of serpentine soil-based grassland and is the butterfly's largest remaining habitat patch. The site is believed to serve as an important source of emigrants that recolonize adjacent habitat patches from which the butterfly has been extirpated (Harrison *et al.* 1988).

We selected 5 slopes as representatives of their microclimatic zones (Weiss *et al.* 1988, Cushman *et al.* 1994). Each was classified as very warm (south- and west-facing slopes, tilt >17°), warm (south- and west-facing slopes, tilt >11°), moderate (all aspects, tilt <11°), cool (north- and northeast-facing slopes, tilt >11°), and very cool (north- and northeast-facing slopes, tilt >17°). Replication of microclimatic zones was not tractable in terms of time and personnel requirements.

Plantago erecta phenology and density

To test the null hypothesis that *Plantago erecta* phenology does not vary among microclimatic zones, we monitored the phenology of 200 individual *P. erecta* through the Bay checkerspot butterfly flight season. Prior to the flight season, when virtually all *P. erecta* appeared edible (no visible senescence) and displayed only vegetative growth, we randomly selected 40 *P. erecta* in each of the 5 microclimatic zones. We monitored the phenology of each plant every 3-4 d over a period of 63 d, until all plants had senesced. Phenology was ranked on a qualitative scale from 1 to 5 (1 = strictly vegetative growth, 2 = partial flower, 3 = full flower, 4 = partial senescence, 5 = full senescence).

For each plant, we calculated the number of days between the start of the flight season and each phenological stage (from partial flower through full senescence). We conducted experimentwise comparisons of phenology (days from the start of the flight season to each phenological stage) with a nested analysis of variance using the General Linear Models Procedure (SAS 1990). Because microclimatic zones were subsampled rather than replicated, we used the interaction term as the error sums of squares; i.e., we calculated the *F*-value for each of the 4 analyses by dividing the microclimatic zone mean square by the mean square for individual *P. erecta* within all microclimatic zones. *P*-values reported for this and later analyses are for Type III sums of squares. When there was a significant microclimatic zone effect, we compared zones with Duncan's Multiple Range Tests. The significance level for these and later Duncan's Multiple Range Tests was set at alpha = 0.05.

We tested 2 hypotheses concerning the density of edible *Plantago erecta* during the Bay checkerspot butterfly flight season. First, we tested whether the density of edible

P. erecta varied among microclimatic zones at any given point in the flight season. Approximately once a week through the flight season, in each microclimatic zone, we measured the distance between 50 randomly selected, edible *P. erecta* and the nearest neighboring edible *P. erecta.* Plants were selected each week; we did not monitor the same plants over time. Measurements were made on 7 d over a 45 d period in all microclimatic zones. On Day 56, we only measured plants in the cool and very cool zones because we were unable to find 50 edible *P. erecta* in the other 3 microclimatic zones. We tested the effect of microclimatic zone on *P. erecta* density for each day on which measurements were made with analysis of variance using the General Linear Models Procedure (SAS 1990). When there was a significant microclimatic zone effect, we used least-squared differences to compare zones. The significance level for the latter tests was set at alpha = 0.05.

Second, we tested whether density patterns of edible *Plantago erecta* across time (rather than on individual days) varied among microclimatic zones. This hypothesis was tested with a General Linear Model *F*-test for detecting differences among regression lines (Neter *et al.* 1990).

Larval survival and development

To test the hypothesis that prediapause larval survival and rates of prediapause larval development did not vary among microclimatic zones and oviposition dates, we carried out the following protocol on each of 3 consecutive weeks during the flight season. Weeks 1, 2, and 3 approximately corresponded to days 7, 14, and 21 of the flight season. On the 1st day of each week, we captured at least 100 adult female Bay checkerspot butterflies at Kirby Canyon. We fed them a sugar solution *ad libidum* to encourage oviposition and then returned them to the field. In each microclimatic zone, we placed 20 females in cylindrical cages over edible *Plantago erecta* (one butterfly per cage). After several hours, we checked each caged site for presence or absence of an egg mass. Butterflies were removed from the cages and released in the area of capture.

We monitored the life stage of each group of offspring in the field every 2-3 d for 47 d, until all animals had either entered diapause or disappeared. Development usually was synchronous within each group. We scored the life stage of each group on a scale from 1-6 (1 = egg mass, 2-5 = 1st through 4th instars, 6 = diapause). Mortality of egg masses or 1st or 2nd instar larvae often can be observed directly. Prior to 3rd instar, disappearance also implies mortality (D.A. Boughton, unpublished manuscript). Many 3rd instar larvae disperse from the hostplant where they were deposited as eggs. These larvae are cryptic and extremely difficult to track as they move through the habitat. Dispersing 3rd instar larvae can molt and enter diapause after feeding briefly (D.A. Boughton, unpublished manuscript). They also, however, may starve or be depredated. Therefore, our hypotheses addressed survival to 3rd instar rather than to diapause. Because we were not able to monitor individual larvae, our measurements of survival and development corresponded to survival or development of at least 1 individual animal from each group.

We conducted Goldstein's x^*-tests (Goldstein 1964), controlling first for oviposition date and then for microclimatic zone, to test the hypothesis that survival to 3rd instar did not vary among microclimatic zones and oviposition dates. When there was a significant effect of microclimatic zone or oviposition date, we used Goldstein's x^*-tests to compare survival at different life stages (i.e., survival between egg and 1st instar, 1st and 2nd instar, and 2nd and 3rd instar).

To test the hypothesis that larval development rates did not vary among microcli-

Table 1. Effect of microclimatic zone on phenology of *Plantago erecta*. Values are mean ± σ days from the start of the Bay checkerspot butterfly flight season to each phenological stage. Black lines indicate means that are not significantly different (alpha = 0.05).

	Microclimatic zone				
Phenological stage	very warm	warm	moderate	cool	very cool
partial flower	13.6 ± 8.7	11.0 ± 6.7	11.3 ± 6.0	24.7 ± 5.5	28.9 ± 6.0
full flower	17.9 ± 8.6	15.4 ± 6.3	15.3 ± 5.5	28.7 ± 7.0	34.3 ± 6.6
partial senescence	26.0 ± 6.0	23.4 ± 4.2	25.2 ± 3.8	38.2 ± 5.8	43.8 ± 3.8
full senescence	34.4 ± 6.3	31.0 ± 6.0	33.2 ± 6.1	45.8 ± 4.0	49.3 ± 4.4

matic zones and oviposition dates, we calculated the number of days between oviposition and each larval instar for each group of offspring. We conducted experimentwise comparisons of the days to 1st and 2nd instar with a two-way analysis of variance using the General Linear Models Procedure (SAS 1990). Small sample sizes precluded comparison of later life stages. When there was a significant effect of microclimatic zone or oviposition date, we carried out among-zone and among-week comparisons with Duncan's Multiple Range Tests.

RESULTS

Plantago erecta phenology and density

Numbers of days in each microclimatic zone from the start of the flight season to each *Plantago erecta* phenological stage are presented in Table 1. We rejected the hypothesis that *P. erecta* phenology does not vary among microclimatic zones. The experimentwise effect of microclimatic zone on *P. erecta* phenology was statistically significant ($P < 0.01$) for each phenological stage (partial flower: $F_{4,195} = 62.0$, full flower: $F_{4,195} = 63.5$, partial senescence: $F_{4,195} = 143.6$, full senescence: $F_{4,195} = 90.6$). *P. erecta* phenology was not distinct in each microclimatic zone, however (Table 1). Phenology of plants in the very warm, warm, and moderate microclimatic zones often was not significantly different (Table 1). Phenology of plants in the cool and very cool zones, by contrast, grouped neither with each other nor with plants in any of the warmer zones (Table 1).

Distances in each microclimatic zone from edible *P. erecta* to nearest neighboring edible individuals throughout the Bay checkerspot butterfly flight season are presented in Table 2. In each microclimatic zone, nearest neighbor distances across the flight season tended to decrease as new *P. erecta* germinated, then to increase as *P. erecta* senesced. The effect of microclimatic zone on nearest neighbor distances of edible *P. erecta* was statistically significant for each of the distinct points in time at which measurements were made, although the percentage of the variance in nearest neighbor distance

Table 2. Effect of microclimatic zone on density of apparently edible (no visible senescence) *Plantago erecta*. Values are mean ± σ nearest neighbor distances in mm. Degrees of freedom are 4,245 for days 1-45 and 2,98 for day 56. Black lines indicate means that are not significantly (alpha = 0.05) different. *** = $P \leq 0.0001$.

Day	Microclimatic zone						
	very warm	warm	moderate	cool	very cool	F	r^2
1	28.1±28.4	8.3±11.0	10.2±9.9	19.5±12.0	64.3±56.3	29.9***	0.328
8	17.6±20.5	8.1± 8.9	9.2±12.6	20.0±16.8	32.8±26.9	15.0***	0.196
14	16.9±55.6	3.4± 7.3	10.1±12.8	11.0±10.4	23.0±20.7	10.8***	0.150
21	22.2±34.4	7.2±10.5	19.6±26.9	16.1±20.2	29.9± 4.9	4.6***	0.070
28	62.9±84.0	41.4±32.6	40.7±45.5	25.2±20.4	28.5±33.5	4.7***	0.07
33	55.9±53.4	68.1±53.4	49.7±43.8	24.8±17.9	41.4±41.2	6.8***	0.100
45	129.4±94.2	114.9±87.2	135.2±82.7	38.3±36.1	43.1±42.9	21.4***	0.259
56				312.2±121.0	161.5±100.0	46.1***	0.320

explained by microclimatic zone often was small (Table 2). This result indicates that the relative timing of *P. erecta* germination and senescence varies among microclimatic zones. Significant differences ($P < 0.05$) in nearest neighbor distances among individual microclimatic zones are shown in Table 2. At the beginning of the flight season, edible *P. erecta* densities were greatest in the warm, moderate, and cool zones and lower in the very warm and very cool zones. From roughly the middle to the end of the flight season, the density of edible *P. erecta* was greatest in the cool and very cool zones.

Density patterns of edible *P. erecta* across the season as a whole (rather than on individual days) did not vary among microclimatic zones ($F_{12,22} = 0.69$, $F_{0.05,\,crit} = 2.23$, $P > 0.05$). In other words, density patterns among zones were out of phase temporally, but otherwise were similar.

Larval survival and development

Differences in *Plantago erecta* phenology are thought to be a key mechanism by which microclimate affects survival of prediapause Bay checkerspot butterfly larvae. We assumed *a priori* that the slopes on which we conducted our experiment had different microclimates (Weiss *et al.* 1988, Cushman *et al.* 1994). This led to the hypothesis that *P. erecta* senescence dates on each of the 5 experimental slopes would differ significantly. Our analysis of *P. erecta* phenology, however, rejected this hypothesis. Therefore, for analyses

Table 3. Number of groups of larvae with at least one representative surviving at each life stage.

	Microclimatic zone		
	warm group	cool	very cool
Week 1			
egg	34	16	5
1st instar	26	11	3
2nd instar	17	11	2
3rd instar	7	4	2
Week 2			
egg	24	16	4
1st instar	9	13	1
2nd instar	5	9	1
3rd instar	1	5	1
Week 3			
egg	28	8	8
1st instar	15	2	4
2nd instar	3	1	3
3rd instar	1	1	2

of larval survival and development, we grouped animals that had been deposited in the very warm, warm, and moderate microclimatic zones. We then tested whether (a) survival to 3rd instar and (b) development rates to 1st and 2nd instar differed significantly among 3 microclimatic zones (warm group, cool, and very cool) and among oviposition dates (weeks 1, 2, and 3). Sample sizes are presented in Table 3.

In most cases (8 of 9 tests), microclimatic zone did not have a statistically significant effect on survival to 3rd instar (Table 4). The single exception was that groups deposited in the middle of the flight season (week 2) had a greater probability of surviving to 3rd instar in the cool zone than in warm microclimatic zones. This largely was due to different probabilities of survival to 1st instar ($x^* = 2.725$, $P < 0.01$). Probabilities of survival from 1st to 2nd instar and from 2nd to 3rd instar were not significantly different between warm and cool zones on week 2 (1st-2nd: $x^* = 0.656$ ns, 2nd-3rd: $x^* = 1.288$ ns).

Likewise, only 1 of 9 tests showed a significant effect of oviposition date on survival to 3rd instar (Table 4). Groups deposited in warm zones on week 1 had a significantly higher probability of surviving to 3rd instar than did groups deposited in that zone on week 3. Survival from 1st to 2nd instar was higher in warm zones for those deposited on week 1 than on week 3 ($x^* = -2.800$, $P < 0.01$). Survival to 1st instar, and from 2nd to 3rd instar, however, was not significantly different between weeks 1 and 3 (egg-1st: $x^* = -1.896$ ns, 2nd-3rd: $x^* = -0.256$ ns).

Both microclimatic zone and oviposition date had a significant effect on rate of development from oviposition to 1st instar (microclimatic zone: $F_{2,79}$

Table 4. Goldstein's x^*-tests for survival to 3rd instar. * = $P \leq 0.05$ ($x^* \geq 1.960$), ** = $P \leq 0.01$ ($x^* \geq 2.576$), *** = $P \leq 0.001$ ($x^* \geq 3.291$).

Within week		Within microclimatic zone	
week 1	x^*	warm group	x^*
warm-cool	-0.351	weeks 1-2	1.786
warm-very cool	-0.962	weeks 1-3	1.989*
cool-very cool	-0.648	weeks 2-3	0.111
week 2		cool	
warm-cool	-2.350*	weeks 1-2	-0.393
warm-very cool	-1.498	weeks 1-3	0.711
cool-very cool	0.244	weeks 2-3	1.000
week 3		very cool	
warm-cool	-0.972	weeks 1-2	0.474
warm-very cool	-1.934	weeks 1-3	0.570
cool-very cool	-0.641	weeks 2-3	0.000

= 5.30, $P < 0.01$, oviposition date: $F_{2,79} = 44.80$, $P < 0.0001$) and from oviposition to 2nd instar (microclimatic zone: $F_{2,79} = 4.92$, $P = 0.01$, oviposition date: $F_{2,79} = 27.13$, $P < 0.0001$). The interaction of zone and date was not significant ($P = 0.19$) and therefore was removed from the model. Groups in warm zones developed more quickly than those in the cool zone (Table 5). Surprisingly, groups deposited in the very cool zone on week 1 also developed to 1st and 2nd instar more quickly than groups deposited in the cool zone on week 1 (Table 5). Relatively high densities of edible *P. erecta* (that is, limited senescence) may have accelerated the developmental rate of groups in the very cool zone. However, it is also possible that the accuracy of estimates of development rates in the very cool zone was affected by small sample sizes (Table 3). Within each microclimatic zone, mean rates of development were significantly different on weeks 1, 2, and 3. Groups that were deposited later in the flight season developed significantly more quickly (Table 5). As discussed below, the latter result was not independent of annual weather.

DISCUSSION

It long has been assumed that interactions among topographic heterogeneity, hostplant senescence, and timing of oviposition mediate survival of prediapause Bay checkerspot butterfly larvae and, by extension, population sizes and geographic distribution of the butterfly (e.g., Singer 1972, Ehrlich *et al.* 1975, 1980, Ehrlich and Murphy 1987, Weiss *et al.* 1987, 1988, Cushman *et al.* 1994). In our experiment, microclimate had statistically significant effects on *Plantago erecta* phenology and density of edible individuals. In terms of *P. erecta* phenology, we found that microclimatic zones tended to group into three classes: warm, cool, and very cool. Similarly, by the middle of the flight season, when members of the earliest experimental cohort of offspring began to reach 1st instar and thus to feed, nearest neighbor

Table 5. Development times (mean ± σ) in d from oviposition to 1st and 2nd instar. Black lines indicate means that are not significantly (alpha = 0.05) different.

	Microclimatic zone		
	warm group	cool	very cool
1st instar			
week 1	15.9 ± 2.0	17.0 ± 2.3	15.7 ± 0.6
week 2	12.0 ± 2.1	14.8 ± 1.7	16
week 3	11.2 ± 1.4	11.3 ± 0.4	11.9 ± 1.4
2nd instar			
week 1	18.1 ± 1.8	19.3 ± 2.1	16.8 ± 1.1
week 2	13.7 ± 0.8	16.6 ± 1.5	17
week 3	11.9 ± 2.6	14	14.7 ± 1.2

distances of edible *P. erecta* often grouped among the very warm, warm, and moderate zones.

We found that microclimate had significant effects on rate of development to 1st and 2nd instar of Bay checkerspot butterflies. Oviposition date also had a significant effect on larval development rates to 1st and 2nd instar, although daily weather patterns represent a potential confounding factor. Because differences in annual weather patterns have complex ramifications for plant senescence and invertebrate population dynamics, whether oviposition date significantly affects larval development may vary annually.

Surprisingly, in the year that our study was conducted, neither microclimate nor oviposition date tended to affect survival to 3rd instar of the Bay checkerspot butterfly. Again, the effects of oviposition date on prediapause larval survival may depend upon annual fluctuations in temperature and precipitation. Caveats about temporal variability admittedly are frustrating; scientists and managers naturally would prefer clear-cut rather than equivocal experimental results. Yet variability and uncertainty are integral aspects of natural systems that inevitably must be addressed in developing conservation plans for species or ecosystems. Recent advances in conceptual development and implementation of adaptive management, which seeks to apply scientific principles to decision-making in the face of uncertainty, reflect growing recognition of the need to study and respond to shifting ecological conditions (McLain and Lee 1998, Slocombe 1998). Similarly, Gaston *et al.* (1998) argue that inability to conclusively accept or reject an ecological hypothesis should be viewed as an opportunity to focus on drivers and ramifications of variation rather than a deficiency of theory or method.

The absence of an effect of microclimate or oviposition date on larval survival in this experiment also may be in part an artifact of our study design. There is no tractable way to monitor individual prediapause larvae over many days if the larvae are allowed to disperse freely. Therefore, we quantified survival at the group level rather than at the level of individual animals. If we had been able to track individuals, and most individuals deposited in the same egg mass starved before reaching 3rd instar or diapause, our survival estimates would be reduced dramatically. Conversely, our survival estimates might increase if many individuals that disappeared in fact survived to 3rd instar or to diapause. It is conceivable, although nearly impossible to quantify, that microclimatic zone and oviposition date have significant effects on the number of individuals per group that survive to diapause. We therefore agree with the inference of previous investigators that most reproductive females are likely to have some reproductive success, although the number of offspring per female that survive to diapause often decreases at later oviposition dates (Cushman *et al.* 1994).

Our results suggest that at least in some years, it is erroneous to assume that apparent senescence of *P. erecta* implies larval mortality (Ehrlich *et al.* 1975, 1980, Singer and Ehrlich 1979, Ehrlich and Murphy 1987, Cushman *et al.* 1994). For example, our data contradict the estimates of Cushman *et al.* (1994), which were based on hostplant senescence, that eggs laid after day 15 of the flight season (assuming a 28-day period of development from egg to diapause) or day 19 of the flight season (assuming a 24-day period of development) have no chance of reaching larval diapause. In our experiment, at least 1 individual from 4-31% of the egg masses laid on day 14 of the flight season (which developed to 4th instar in 25-28 days) survived to 3rd instar (the earliest stage at which larvae can enter diapause, Singer 1972). Similarly, at least 1 individual from 4-25% of the egg masses laid on day 21 of the flight season (which developed to 4th instar in 16-21 days) survived to 3rd instar. Again, our data cannot address the absolute number of individuals that survived, only the fraction of groups that had survivors. Moreover, the data of Cushman et al. were gathered in spring 1992, which was slightly warmer and drier than in 1993.

There are several possible explanations why we found that larvae survived after the majority of their hostplants had senesced. First, larvae may have developed on *P. erecta* that senesced later than most other *P. erecta* in the same microclimatic zone. Second, although *P. erecta* that have begun to senesce generally have been considered inedible (e.g., Cushman *et al.* 1994), prediapause Bay checkerspot butterfly larvae can eat *P. erecta* seeds that are green and developing even if the plant's flowers are dead (M.C. Singer, personal communication). Third, the mobility of 3rd instar larvae is considerable (mean = 17 mm in 10 min on warm sand; N. Mehdiabadi, Harrison, and C. Boggs, unpublished data), and these larvae may be able to seek out edible *P. erecta* even if those plants are few and far between. Fourth, it is probable that prediapause Bay checkerspot butterfly larvae are facultative cannibals (E. Fleishman, personal observation) that eat their siblings if edible hostplants are not available.

Previous work (e.g., Singer 1972, White 1974, Ehrlich *et al.* 1975, Weiss *et al.* 1988, Cushman *et al.* 1994) suggested that survival of prediapause Bay checkerspot butterflies occurs at the group level. In other words, if egg masses each contained 100 eggs, then 99% mortality could imply that all individuals in one group survived and all individuals in 99 other groups starved. Our experiment suggests that survival instead may be spread widely among groups. Whether the former or latter scenario is more accurate has important ramifications for population dynamics and viability of the threatened Bay checkerspot butterfly. As distribution of survival among groups increases, so should the effective size (N_e) of the butterfly population, as well as its ability to withstand stochastic genetic events that can reduce probabilities of long-term population viability (Allendorf 1986, Frankham 1996, Rabinowitz *et al.* 1986).

Although hostplants senesce earlier in warm microclimatic zones than in cooler zones, distribution of offspring in warm as well as in cool zones likely increases the long-term viability of populations of the Bay checkerspot butterfly. For example, larvae that survive to diapause on warm slopes may have relatively high reproductive fitness as adults because they eclose earlier than individuals on cooler slopes in the subsequent year, when they have a good chance of finding mates and can lay eggs while hostplants are still young and edible (Weiss *et al.* 1988). Also, macroclimate in coastal California is notoriously unpredictable. Timing of *P. erecta* senescence relative to the Bay checkerspot butterfly flight season, and the magnitude of the difference in senescence timing among microclimatic zones, varies among years. Postdiapause larval densities in warmer microclimatic zones tend to increase in years following a relatively cool and wet flight season (e.g., Weiss *et al.* 1988).

Topographic heterogeneity likely is key to the persistence of numerous residents of native grasslands and other temporally variable environments. The need for topographic refugia may be especially pronounced among native annual plants, invertebrates, and other species with relatively short generation times or habitat requirements that vary thoroughout their life cycle.

Research on checkerspot butterflies (*Euphydryas*) in the western United States has been conducted virtually uninterrupted for the past 35 years. Biological studies of such duration are notable both for their rarity and for their ability to provide vital information for single- or multiple-species conservation planning (Ehrlich and Murphy 1987, Stohlgren *et al.* 1995, Heikkinen 1998). Nonetheless, our study emphasizes that it is critical to examine empirically our assumptions about long-term study systems.

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The Lepidoptera of Marine Corps Air Station Miramar: Calculating Faunal Similarity among Sampling Sites and Estimating Total Species Richness

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Abstract. An intensive 3-year survey of the Lepidoptera of Marine Corps Air Station Miramar in southwestern San Diego County, California, was conducted from October 1995 through September 1998. Sampling methodology included blacklight trapping (364 nights), diurnal collecting (148 days), and pheromone "baiting." About 646 species of Lepidoptera were documented from the Station, including 20 (or more) undescribed moth species and one "sensitive" butterfly species - Hermes copper, *Lycaena hermes* (Edwards). Two species were newly recorded for the United States - *Dryadaula terpsichorella* (Busck) (Tineidae) and *Metapluera potosi* Busck (Gelechiidae). While the species accumulation curve reached a convincing asymptote, it is highly unlikely that all species of Lepidoptera present on the Station were sampled. Four methods extrapolated or estimated the fauna to be between 706 and 922 species. Based on the family Geometridae, faunal similarity among a subset of 10 permanent blacklight sites ranged from 0.29 to 0.69. We briefly discuss how Lepidoptera inventories may provide insight into identification of areas of high conservation value.

Key Words: Insecta, Lepidoptera, faunal survey, inventory, coastal sage scrub, conservation, species richness.

INTRODUCTION

Over the last decade the maintenance of biological diversity has become an issue of both local and global concern. The values of maintaining biodiversity have been discussed by numerous authors and were summarized best by Ehrlich (1990) as ethical, aesthetic, economic, and the provision of "ecosystem services." Before we can attempt to maintain biodiversity we must know its components; i.e., it is impossible to establish goals and/or methods for the long-term management and protection of biological resources without knowing what resources are present. Therefore, the process of inventory represents the first critical step in all efforts to effectively maintain biodiversity.

Because it is virtually impossible to inventory, monitor, and manage all aspects of a local or regional biota, specific taxa may be selected as "indicator" or "umbrella" species (or groups) based on their ability to reflect the diversity or health of an ecosystem and their ability (or inability) to respond to

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changing environmental conditions. New (1998) and others (e.g., Eyre & Rushton 1989, Sutton & Collins 1991, Kremen et al. 1993, Oliver & Beattie 1994) present convincing arguments that the use of insects for documenting biodiversity, assessing ecosystem health, monitoring environmental change, and identifying areas of high conservation value has many advantages over the use of vertebrates or vascular plants (but for differing points of view see Howarth & Ramsey 1991, Scott et al. 1993, Noss & Cooperrider 1994). Owing to insect abundance and diversity, the complex interrelationships between them and other organisms form the most prevalent and comprehensive elements of the fabric of all terrestrial and freshwater aquatic biological communities (Powell 1995). Insects frequently exhibit rapid and perceivable responses to habitat modification (e.g., local or regional changes in abundance, extinction and colonization of habitat patches, range expansions and contractions) (e.g., Kempton & Taylor 1974, Taylor et al. 1978, Pollard 1979, Razowski 1985, Murphy & Weiss 1991); non-biased, standardized techniques are available for sampling many types of insects (e.g., Merritt & Cummings 1978); large numbers of individuals can be sampled reliably over short periods of time (e.g., Murphy & Weiss 1988a, b); collections of insects can be stored easily and efficiently and maintained for verification of data and future use; and there are fewer societal and ecological constraints to collecting insects (e.g., Murphy & Weiss 1988b). The use of Lepidoptera as an exemplar taxon for estimating overall insect diversity has advantages that include the relative ease of identification at the species level (for many families), standardized sampling methodology (e.g., Thomas & Thomas 1994), and a high correlation with the spatial, architectural, and taxonomic diversity of vascular plants (e.g., Southwood et al. 1979, Brown & Opler 1990, Panzer & Schwartz 1998). In addition, Lepidoptera comprise the richest group of phytophagous insects in California.

A survey of the Lepidoptera of Marine Corps Air Station (MCAS) Miramar (= the Station), situated in southwestern San Diego County, California, was conducted from October 1995 through September 1998 by personnel associated with the San Diego Natural History Museum, under contract with the U.S. Navy. While the primary goal of the survey was to determine the presence/absence of one butterfly species (i.e., *Euphydryas editha quino* (Wright)) listed as endangered and two others (*Lycaena hermes* (Edwards) and *Euphyes vestris harbisoni* Brown & McGuire) formerly recognized as candidates for listing by the U.S. Fish and Wildlife Service, the fieldwork resulted in considerable information on local Lepidoptera diversity and phenology. This information may represent a baseline against which the effect of future environmental changes may be assessed.

Our purposes are to present an inventory of the Lepidoptera documented from MCAS Miramar; provide a cumulative or summary seasonal phenology for each species and the Lepidoptera community in general; estimate total species richness of the Station based on a number of different assumptions; discuss faunal similarity and site complementarity among a subset of 10 blacklight sampling sites; and identify features that may be useful in assessing the potential conservation value of any area based on its Lepidoptera fauna.

MATERIALS AND METHODS

Study Site

The study site, MCAS Miramar (formerly Naval Air Station Miramar), is an approximately 10,500-hectare (23,000-acre) property owned and managed by the U.S. Marine Corps, situated in the southwestern portion of San Diego County, California (Fig. 1), at about 33°N, 117°W. The Station extends nearly 16 km (10 miles) east-to-west, roughly from Santee Lakes to Interstate Highway 805, and about 5 km (3 miles) north-to-south, from Miramar Road to State Route 52. Elevations on the Station range from about 30 to 250 m above mean sea level.

While portions of the Station are highly disturbed/developed, with aircraft runways, warehouses, family housing, and an extensive road system, the vast majority supports native biotic communities, including coastal sage scrub, scrub oak chaparral, southern mixed chaparral, chamise chaparral, southern willow scrub, sycamore alluvial woodland, oak riparian woodland, and valley needlegrass grassland. The Station also supports extensive acreage of vernal pool habitat, a rare and highly depleted, ephemeral wetland community. This situation is not unusual in California or elsewhere in the United States, where military reservations often represent bastions of biodiversity in otherwise highly urbanized landscapes. Sampling was restricted to portions of the Station where native habitat occurs; we sampled about 50% of the entire site.

Several of the plant communities on the Station are highly depleted assemblages restricted to southern California. Among these are coastal sage scrub, the object of significant conservation efforts and the focus of the State of California's Natural Communities Conservation Plan. This community supports a large number of plant and animal species listed as rare, threatened, or endangered by the resource agencies, the most notable of which is the coastal California gnatcatcher (*Polioptila californica californica*), a small gray songbird. Coastal sage scrub occurs in a mosaic distribution with other native scrub and wetland communities, each of which contributes to the overall stability and long-term viability of the natural landscape.

Collecting Methods

Three general techniques were utilized to collect Lepidoptera: 1) blacklight trapping; 2) diurnal collecting; and 3) pheromone "baiting." Each of the methods is described below.

Blacklight Trapping. Through a trial-and-error approach, 10 permanent blacklight trapping sites were established during the first three months of the program; three additional sites were added during the second year (Fig. 1). The sites were located in all major habitat types on the Station as characterized by the base Geographic Information System vegetation mapping, including coastal sage scrub, chaparral, grassland, oak woodland, willow woodland, and sycamore/oak woodland. The thirteen sites are characterized in Table 1.

Regardless of season, ambient temperature, or phase of the moon, once a month each of the sites was sampled using two, three, or four blacklight traps, each equiped with a 15-watt ultra-violet light. The traps were deployed in the evening and retrieved the following morning. Blacklight trapping was conducted on 364 nights over the 3-year period. The frequency of trapping nights per month from October 1995 through September 1998 is illustrated in Fig. 2.

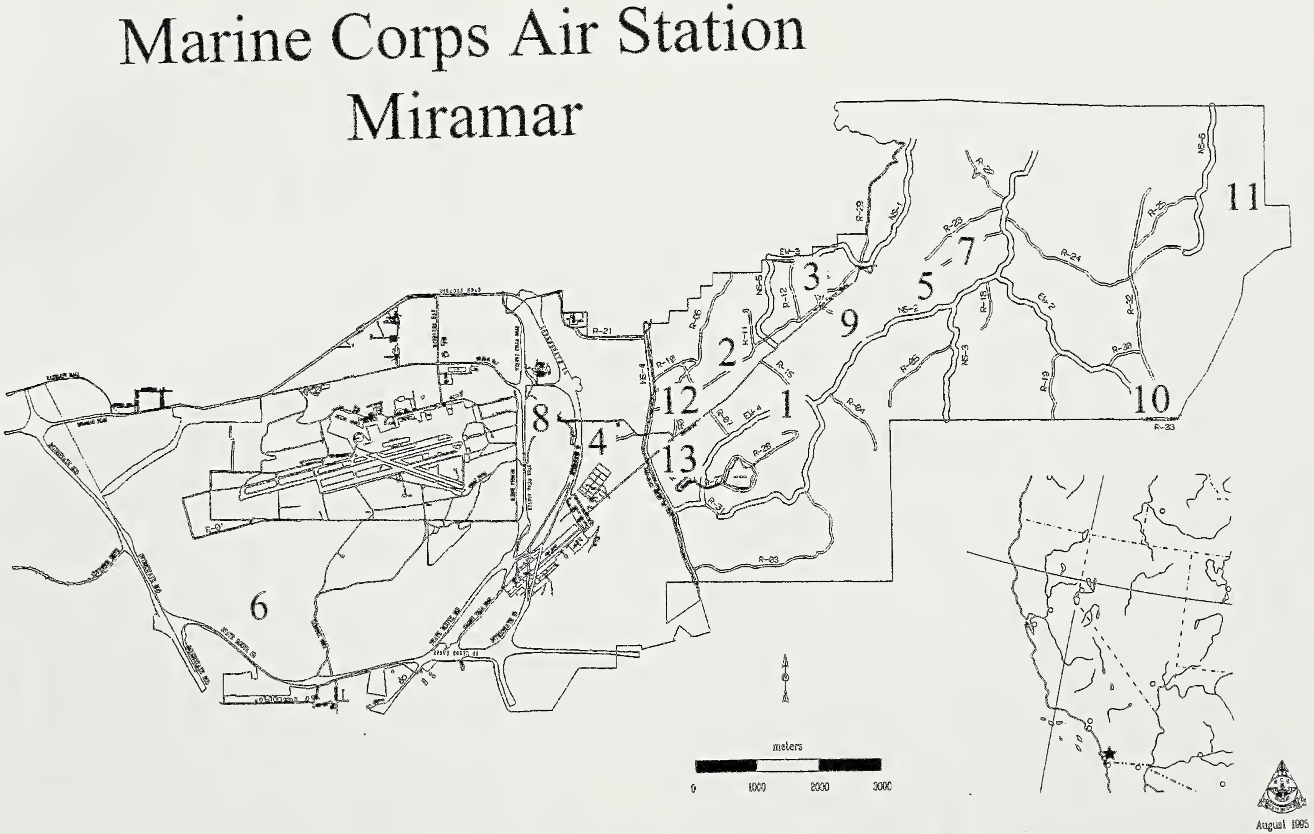

Fig. 1. Map of Marine Corps Air Station Miramar, with locations of sampling sites.

Table 1. Blacklight sampling sites.

Site	Habitat type	Location
1	Chaparral Ridge	1.5-2.2 km east of Interstate 15 (I-15), ca. 0.4 km south of Green Farm Road.
2	Coastal sage scrub/sparse sycamore woodland	ca. 1.5 km east of I-15, ca. 0.2 km north of Green Farm Road.
3	Southern willow scrub surrounded by chaparral	ca. 4.5 km east of 1-15, ca. 0.8 km north of Green Farm Road.
4	Coyotebrush scrub/scrub oak chaparral	immediately east of I-15, west end of Green Farm Road.
5	Area surrounding pond, including freshwater marsh, open water, and coastal sage scrub	just east of Green Farm.
6	Sycamore/oak riparian woodland	San Clemente Canyon near Miramar Landfill, west of Convoy Street.
7	Chaparral	ridge ca. 5.1 km east of I-15, ca. 0.4 km south of Green Farm Road.
8	Vernal pool and grassland	southwest of intersection of I-15 and Miramar Road.
9	North-facing chaparral slope	ca. 0.8 km east of Green Farm, ca. 0.2 km south of Green Farm Road.
10	Sycamore woodland/coastal sage scrub	West Sycamore Canyon, just northwest of Santee Lakes.
11	Oak riparian forest	Sycamore Canyon, ca. 2.2 km northwest of Santee Lakes.
12	Hilltop with coastal sage scrub and chaparral	just east of the pipeline scar, ca. 0.8 km north of Green Farm Road.
13	Coastal sage scrub and chaparral	adjacent to the pipeline scar, ca. 1.5 km south of Green Farm Road.

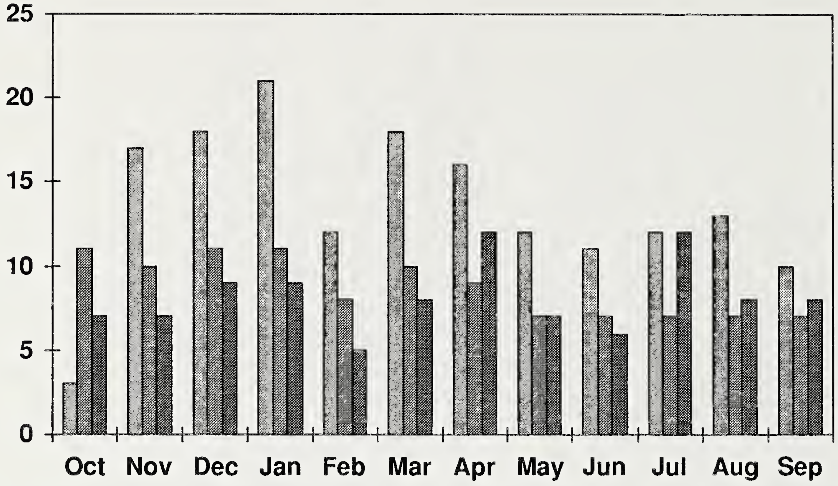

Fig. 2. Frequency of blacklight sampling by month; *x*-axis = month of the year, *y*-axis = number of sampling dates; first bar of each month = 1995-1996; second bar = 1996-1997; third bar = 1997-1998.

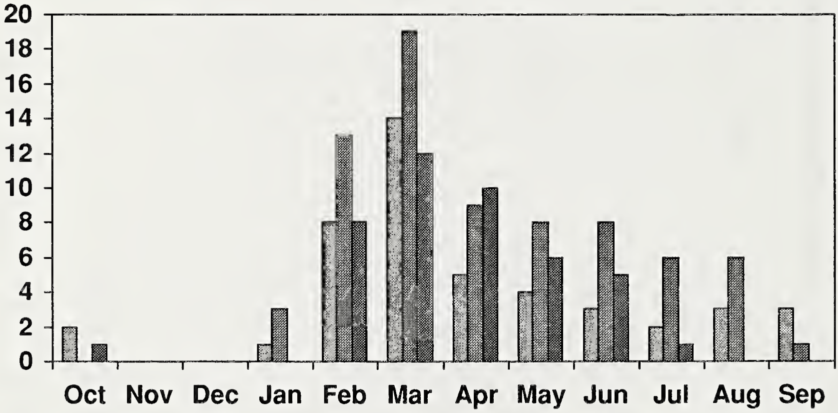

Fig. 3. Frequency of diurnal sampling by month; *x*-axis = month of the year, *y*-axis = number of sampling dates; first bar of each month = 1995-1996; second bar = 1996-1997; third bar = 1997-1998.

Diurnal collecting. Diurnal collecting was concentrated from the middle of February through the end of June to coincide with peak adult activity of the three target species of butterflies (i.e., *Euphydryas editha quino, Lycaena hermes, Euphyes vestris harbisoni*). Additional diurnal collecting was conducted sporadically throughout the remainder of the year. During the visits, meandering transects were walked while searching for adult Lepidoptera, primarily butterflies. Diurnal collecting was conducted on 148 days. The frequency of diurnal collecting per month from October 1995 through September 1998 is illustrated in Fig 3.

Because many species of butterflies are attracted to surface moisture, artificial

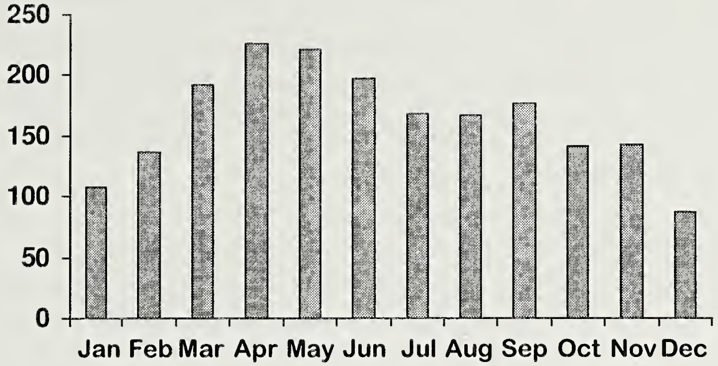

Fig. 4. Generalized annual pattern of adult Lepidoptera activity on the Station; *x*-axis = months of the year, *y*-axis = number of species collected/observed.

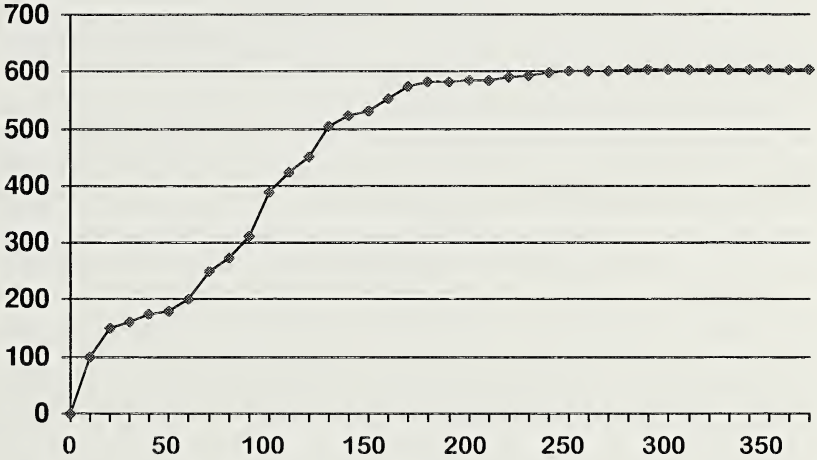

Fig. 5. Species accumulation curve; *x*-axis = cumulative number of sampling nights, *y*-axis = cumulative number of species collected/observed.

"puddles" were created during several diurnal surveys in May, June, and July 1996, by spraying water onto the surface of dirt roads. Also, because males of many butterfly species exhibit hilltopping behavior, brief visits frequently were made to the most prominent hill in the vicinity of the survey locality.

During the first full year of diurnal surveys (i.e., 1996), minimal time was spent examining vegetation for the presence of larval Lepidoptera; no time was invested in subsequent years. When larvae were discovered, they were taken to the laboratory and kept in half-gallon cardboard containers along with cuttings of the larval food plant.

Pheromone baiting. Aluminum pie plates filled with ethylene glycol (anti-freeze) (= pan traps) and baited with a synthetic sesiid moth pheromone were deployed at several of the permanent blacklight sites from about the middle of April through the middle of August 1996.

In October 1996 we used synthetic pheromone of *Hemileuca electra* (Wright) (Saturniidae) to determine the presence/absence of this species on the Station. In February 1997, we used a virgin female *Saturnia walterorum* Hogue & Johnson (Saturniidae) in an effort to attract males of this species to determine the presence of a resident population on the Station.

Data Analyses

The first date of capture was recorded for each of the identified species; for most unidentified species this date was not recorded because there was uncertainty regarding the taxonomic integrity of most of the "morphospecies." A species accumulation curve (Fig. 5) was derived by plotting the cumulative number of species documented from the Station against cumulative number of sampling nights; only identified species were included ($n \approx 600$).

For each identified species, all months of capture were recorded. The total number of species documented for each month (January through December) was tallied and used to generate a histogram illustrating the seasonal phenology or temporal distribution of the entire Lepidoptera community. Although flight periods of some species vary from year to year depending on environmental cues (e.g., timing of rainfall, winter/spring temperatures), such annual fluctuations probably contribute little to the overall pattern of community phenology.

Using the family Geometridae as an exemplar taxon, we constructed a matrix of species by blacklight sampling site (using sites 1-10 as a subsample). We used this matrix to evaluate faunal similarity and site complementarity. Faunal similarity (FS) was calculated by the following equation: $FS = C/(A+B)-C$, where "A" is the number of species recorded from site A, "B" is the number species recorded from site B, and "C" is the number of species shared by sites A and B. Complementarity (D) (dissimilarity), which is defined as the inverse of faunal similarity, was derived using the following equation: $D = 1-FS$, where FS equals faunal similarity.

Nomenclature, Arrangement of Taxa, and Disposition of Material

Scientific nomenclature and the sequence of families, genera, and species follow Hodges et al. (1983). Specimens from fieldwork conducted in 1995-1996 are deposited in the Entomology Department of the San Diego Natural History Museum; specimens from 1997 are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; specimens from 1998 are deposited in the Essig Museum of Entomology, University of California, Berkeley. The last material was used in development of the species accumulation curve and the overall species inventory, but not was included in the compilations of species' phenology or calculations of site complementarity because it was not examined by us.

RESULTS AND DISCUSSION

Fieldwork resulted in the collection of about 30,000 specimens representing about 646 species (Appendix A). Because numerous specimens of microlepidoptera are not yet identified (and are unlikely to be identified in the foreseeable future), it is likely that the actual total may exceed 700 species.

Nocturnal Lepidoptera

As would be expected, the Noctuidae (161 species; 25%) and Geometridae (90 species; 14%) comprise the largest portions of the Lepidoptera fauna. Other families that are well represented in the fauna of the Station include Pyralidae (including Crambidae) (75 species; 12%) and Tortricidae (60 species; 9%).

Among the material collected in blacklight traps were 20 (or more) undescribed species, including at least one species of *Amydria* (Acrolophidae) (D. Davis, pers. comm.), a species of *Lampronia* (Incurvariidae) (D. Davis, pers. comm.), two species of *Gnorimoschema* (Gelechiidae) (J. Powell, pers. comm., Povolny 1998), at least nine species of Blastobasidae (D. Adamski, pers. comm.), three species of Tortricidae, and four species of Noctuidae (T. Mustelin, pers. comm.). Also collected in blacklight traps were about 40 specimens of *Metapleura potosi* Busck (Gelechiidae), a Mexican species previously unrecorded from the United States, and a single specimen of *Dryadaula terpsichorella* (Busck) (Tineidae), also new to the U.S. fauna.

Among the Tortricidae are a new species of *Decodes* (Powell & Brown 1998), a new *Epinotia* (R. Brown, pers. comm.), and a new *Eucosma* (related to *E. hazelana* Klots). Among the Noctuidae are a new *Aseptis*, a new *Xylomoia*, a new *Lacinipolia*, and a new genus (and species) near *Miodera.* It is highly unlikely that any of the new species is restricted to the Station. For example, the new *Decodes* is known from two of the California Channel Islands, Silverwood Audubon Sanctuary (in central San Diego County), and northwestern Baja California, Mexico (Powell & Brown 1998). The new genus of Noctuidae is known from San Diego, Riverside, and San Bernardino counties, from sea level to about 1400 m (Mustelin, unpubl.).

Diurnal Lepidoptera

Species collected only during diurnal sampling represent about 11% of the Lepidoptera fauna of the Station. Four species of yucca moths (2 *Tegeticula* and 2 *Prodoxus*; Prodoxidae) were collected from the flowers of *Yucca whipplei* (Liliaceae). Five species of clearwing moths (Sesiidae) were collected in pan traps baited with pheromone. A single specimen of *Hemaris diffinis* (Boisduval) (Sphingidae) was collected and a second individual observed. The latter species previously was known in San Diego County only from the interior montane region.

Other diurnal Lepidoptera included one species of fairy moth (*Adela* sp.), one species of Plutellidae (*Pliniaca bakerella* Busck), and a small number of noctuids (e.g., *Schinia* spp.), geometrids (e.g., *Stamnodes* spp.) and pyralids, about half of which were not duplicated in blacklight samples.

Cnephasia longana (Haworth) (Tortricidae) was one of about 10-12 species collected both diurnally and in blacklight traps; it was abundant on the Station. Powell (1997) chronicled the spread of this Palaearctic moth southward and northward from the San Francisco Bay area, reporting it as far south as Santa Rosa Island. The presence of this species on MCAS Miramar represents a southern range extension of approximately 300 km from its previously documented range.

Using a synthetic pheromone for the diurnal buckmoth (*Hemileuca electra*), we attracted males of this rapid-flying species. It was abundant on the section of the Station known as Parcel G (Rubinoff 1998), but it is likely to be common wherever flat-top buckwheat (*Eriogonum fasciculatum* Benth.; Polygonaceae) is common. Using a virgin female *Saturnia walterorum*, we successfully attracted males of this species on the Station.

Fifty-one species of butterflies were recorded, approximately 40% of the butterfly fauna of San Diego County (i.e., about 125 resident species). Furthermore, it is likely that a few additional butterflies species are present and were not detected. For example, several common urban skippers (Hesperiidae) present in adjacent developed areas were not detected on the Station.

During 1996, single individuals of Hermes copper (*Lycaena hermes*) were observed at one location on the Station on two occasions. In 1997 this species was found at five different sites; it was common in both 1997 and 1998. Neither quino checkerspot (*Euphydyras editha quino*) nor Harbison's dun skipper (*Euphyes vestris harbisoni*) was observed.

Larval Lepidoptera

Larvae of only four species of Lepidoptera were collected in 1996: *Orgyia vetusta* on *Lotus scoparius* (Fabaceae); *Hemileuca electra* on *Eriogonum fasciculatum* (Polygonaceae); *Apantesis nevadensis* on *Lotus*, *Eriogonum*, and *Erodium* (Geraniaceae); and *Vanessa virginiensis* on *Gnaphalium californicum* (Asteraceae). All but the *Vanessa* were successfully reared to maturity.

Temporal Distribution

Appendix A presents a cumulative summary of the temporal distribution (for 1995-1997) of the identified Lepidoptera based on all survey methods; for most of the unidentified species, data are not presented. Based on the larger moths, butterflies, and identified small moths, the potential number of species per month ranged from a high of 226 in April to a low of 87 in December. A histogram of the overall annual pattern of adult Lepidoptera activity on the Station is presented in Fig. 4. In general, activity increases from January, peaking in April and May, stays relatively high through September, drops in October, and declines dramatically in December.

When we examine one family, such as the Geometridae, we find considerable deviation from the overall pattern described above. For example, geometrid adult activity was lowest in September (n = 14 species), increased through late winter and early spring (December through February), and peaked in March (n = 48 species). The Geometridae represented approximately 37% of the species sampled in January. This deviation from the overall pattern is not surprising: many geometrids fly in the winter and thus have been given the common name "winter moths."

Even during the period of lowest moth activity (i.e., December), at least 87 species (about 13.5% of the Lepidoptera fauna) were collected. Although the vast majority of species exhibited distinct seasonal patterns, a few species were present almost year-round: *Pseudochelaria scabrella* (Busck), *Holcocera gigantella* (Chambers), *Eucsoma pulverulenta* (Walsingham), *Amorbia cuneana* (Walsingham), *Pero radiosaria* (Hulst), *Aethaloidia packardaria* (Hulst), *Pherne subpunctata* (Hulst), *Apantesis proxima* (Guerin-Menetries), *Agrotis ypsilon* (Hufnagle), and *Spodoptera exigua* (Hübner). This pattern is most evident in Tortricidae, Geometridae, and Noctuidae - families that include many polyphagous, pest species that are opportunistic in their larval food plant selection.

Faunal Similarity and Site Complementarity

Using the family Geometridae (n = 90 species) as an exemplar taxon, we calculated faunal similarity and its inverse, complementarity (dissimilarity), among a subset of 10 permanent blacklight sampling sites. The number of species documented per site varied from 21 (23% of the geometrid fauna; site 8) to 56 (62%; site 3); one species was collected only diurnally on a meandering transect. This substantial variability suggests that although the native habitat on the Station has a rather homogeneous appearance, plant communities and the features that determine them (e.g., slope, exposure, soil type) strongly influence the fauna, resulting in localized assemblages of species. This finding corroborates the *a priori* (and highly logical) assumption that in order to maximize the number of species sampled, it is imperative to maximize the number of plant communities and microhabitats sampled. It also suggests that blacklights may attract only geometrid species that are in the immediate vicinity, suggesting localized or patchy distribution of many species. These data may be biased by the fact that blacklight traps are not as effective for geometrids as they are for noctuids (J. Powell, pers. comm.).

Faunal similarity (FS), as defined in the Materials and Methods section, is equivalent to Jacard's coefficient of similarity. This measure, emphasizing shared presence and disregarding shared absence, is useful in many biogeographic and conservation contexts. Tables 2 and 3 present the "unreduced" and "reduced" faunal similarity values, respectively, for a subset of 10 blacklight trapping sites (i.e., sites 1-10). As illustrated in Table 2, the highest combined species richness for any two sites was 73 (81% of all geometrids) (sites 6 and 7) and the lowest was 42 (47% of the geometrids) (sites 4 and 8). The highest number of shared species was 41 (by sites 2 and 7, and sites 3 and 7), the lowest was 13 (by sites 4 and 8). The low values for both combined species richness and shared species can be explained by the fact that sites 4 and 8 yielded the lowest numbers of species (i.e., 34 and 21, respectively) of the 10 sites. Faunal similarity (Table 3) was highest (0.69) between sites 2 and 7 and lowest (0.29) between sites 1 and 8 and 6 and 8. Mean faunal similarity was lowest for site 8 (0.32), a grassland area, and highest for site 2 (0.55), a site supporting coastal sage scrub and sparse sycamore woodland.

Complementarity (dissimilarity) (Table 4) varied from 0.31 (between sites 2 and 7) to 0.71 (between sites 1 and 8, and sites 6 and 8). While

Table 2. "Unreduced" values of faunal similarity (based on Jacard's coefficient of similarity) for a subset of 10 blacklight sampling sites. Highest and lowest values in **bold face**.

	1	2	3	4	5	6	7	8	9	10
Site 1	-									
Site 2	36/60	-								
Site 3	37/65	39/67	-							
Site 4	24/56	30/54	28/62	-						
Site 5	30/59	33/60	34/65	25/55	-					
Site 6	33/68	37/68	39/71	28/61	35/63	-				
Site 7	36/60	**41**/59	**41**/65	26/58	32/61	32/**73**	-			
Site 8	15/52	18/53	18/59	**13/42**	16/48	17/59	21/54	-		
Site 9	37/59	38/62	40/66	25/59	33/60	36/69	38/62	17/54	-	
Site 10	23/66	29/64	31/68	23/54	26/60	32/66	26/63	16/48	29/65	-

Table 3. Faunal similarity (based on Jacard's coefficient of similarity) for a subset of 10 blacklight sampling sites. Highest and lowest values in **bold face**.

	1	2	3	4	5	6	7	8	9	10
Site 1	-									
Site 2	0.60	-								
Site 3	0.57	0.58	-							
Site 4	0.43	0.56	0.45	-						
Site 5	0.51	0.55	0.52	0.45	-					
Site 6	0.49	0.54	0.55	0.46	0.56	-				
Site 7	0.60	**0.69**	0.63	0.45	0.52	0.44	-			
Site 8	**0.29**	0.34	0.31	0.31	0.33	**0.29**	0.39	-		
Site 9	0.63	0.61	0.61	0.42	0.55	0.52	0.61	0.31	-	
Site 10	0.35	0.45	0.46	0.43	0.43	0.48	0.41	0.33	0.45	-

Table 4. Complementarity (dissimilarity) for a subset of 10 blacklight sampling sites. Highest and lowest values in **bold face**.

	1	2	3	4	5	6	7	8	9	10
Site 1	-									
Site 2	0.40	-								
Site 3	0.43	0.42	-							
Site 4	0.57	0.44	0.55	-						
Site 5	0.49	0.45	0.48	0.55	-					
Site 6	0.51	0.46	0.45	0.54	0.44	-				
Site 7	0.40	**0.31**	0.37	0.55	0.48	0.56	-			
Site 8	**0.71**	0.66	0.69	0.69	0.67	**0.71**	0.61	-		
Site 9	0.36	0.39	0.39	0.58	0.45	0.48	0.39	0.69	-	
Site 10	0.65	0.55	0.54	0.57	0.57	0.52	0.59	0.67	0.55	-

complementarity is a relative indicator of dissimilarity, its value does not precisely reflect the presence of "different" species at the sites being compared. For example, site 8 had the highest complementarity values, but supported few species not present on other sites. Its overall high complementarity is the result of its low species number (i.e., the absence of shared species with other sites or "mismatches" based on absence) rather than its uniqueness (i.e., the presence of different species or species not present on other sites).

Species Richness Estimates

The species accumulation curve (Fig. 5) shows that the rate of encountering new species increased throughout the first year and began to reach an asymptote by October 1996. During the first year each successive month added an average of about 40 species to the inventory. In contrast, during the entire second year only 27 species total were added. This suggests that the first year of the survey successfully captured about 95% of the fauna. Only six additional species were added in the third year. Because sampling was conducted with greater frequency during the first year, these findings may be slightly biased; i.e., it is likely that uniform sampling during each of the three years would have produced slightly different results.

While we have documented about 646 species of Lepidoptera from Station (not all of which are identified and many of which are undescribed), and the species accumulation curve has reached a convincing asymptote, this number (646) may underestimate the fauna. The number of species potentially present can be estimated or extrapolated by at least four different methods: (1) comparison with plant species richness; (2) extrapolation from butterfly species richness; (3) evaluation of taxonomic components of the documented fauna; and (4) "Chao 1," a non-parametric statistical model.

Powell (1995) has found Lepidoptera species richness to be 1.5 – 3.0 times plant species richness at other sites in California (e.g., Big Creek in Monterey County). Because the flora of MCAS Miramar includes about 615 species of vascular plants (Wier & Brown, unpubl.), a conservative estimate of the Lepidoptera based on Powell's findings would be 922 species. Based on inventories of other sites in California, this estimate is too high; it may reflect the fact that the Station has been subject to numerous intensive botanical surveys that may be cumulatively more thorough than those of the sites used for Powell's calculations. Alternatively, Powell's values of 1.5-3.0 may not be applicable over a broad ecological range. The latter seems unlikely given that Powell has investigated habitats as diverse as redwood forest and coastal sand dunes. It is more likely that such extrapolations are not meaningful owing to the considerable difference in size of the study areas; i.e., the Station is nearly seven times the size of Powell's most thoroughly surveyed site, Big Creek.

Throughout the western United States, butterfly species typically represent about 7% of the Lepidoptera species richness at any particular site or geographic region (Powell 1995). Because butterflies are diurnal, easily observed, and comparatively easily identified, resident butterfly species richness can be documented fairly accurately in the western United States. If we extrapolate from the total number of butterfly species we observed (n = 51), we would expect the total Lepidoptera fauna to be about 729 species. This value seems a little high, but certainly is within a reasonable expected range based on other California inventories.

When we examine the relative components of the general "taxonomic" categories of Lepidoptera (i.e., Microlepidoptera, Pyraloidea, butterflies, Macrolepidoptera), we find that we are conspicuously low in the Microlepidoptera category. That is, Macrolepidoptera and Microlepidoptera typically each represent about 40% of the Lepidoptera fauna at most sites in California (Powell 1995). While we recorded about 287 species of Macrolepidoptera, we recorded only about 222 *identified* species of Microlepidoptera. Many species of Microlepidoptera are confined to highly localized areas that support their larval food plant, are not efficiently captured in blacklight traps, are exceedingly small and difficult to prepare, and are difficult to identify. If the Microlepidoptera richness of the Station is comparable to the sampled Macrolepidoptera richness (i.e., 287 species), the total Lepidoptera fauna would be about 65 species greater than we documented, or about 711 species. This value is fairly consistent with our estimates of the number of undetermined Microlepidoptera in our samples and the probability that this group has been under-sampled using our methodology.

Chao 1 (Chao 1984) is a non-parametric statistical model that can be used to estimate species richness from samples (e.g., Colwell & Coddington 1994). It is represented by an easily calculated mathematical equation: $S_t = S_{ob} + a^2/2b$, where S_t is the estimated species richness, S_{ob} is the observed species richness (n ≈ 646), "a" is the number of species represented by a single specimen (n ≈ 62), and "b" is the number of species represented by two specimens (n ≈ 32). The equation focuses on the number of species represented by one and two individuals because these are likely indicators of under-sampling. Using this equation we derive an estimate of about 706 species. This number is clearly a conservative estimate (or under-estimate) because with the exception S_{ob} it is based entirely on species that we have been able to identify at least to morphospecies.

If we disregard the conspicuous outlier (n = 922), based on the three other estimates described above, the total number of species on the Station may be between 706 and 729, with an average estimate of 715 species.

The most logical interpretation for the "false" asymptote of the species accumulation curve is that the pool of species that can be detected reliably using the methodologies we employed was nearly exhausted. This suggests that utilization of additional or different collecting techniques would add species to the inventory, in particular, the diverse leaf-mining fauna is poorly represented in our samples.

It is apparent that to sample thoroughly the entire Lepidoptera fauna of any site, one must employ a variety of techniques: diurnal sampling (i.e., approximately 11% of the fauna of MCAS Miramar was detected only by diurnal sampling), blacklighting (which yields the vast majority of moth species), pheromone "baiting" (which may be the best way to sample adequately Sesiidae and some Saturniidae), and larval collecting (particularly for leaf-mining and other Microlepidoptera). While our survey did not demonstrate that multiple years significantly increase the number of species detected (i.e., an increase of only about 5% was observed during the second year), it is likely that multiple years of effort are necessary to document some species. Our results are biased by the fact that nearly 45% of our entire sampling was conducted during the first year. According to Powell (1995), multiple-year surveys are less affected by fluctuations in year-to-year abundance and also have a higher likelihood of documenting vagrant and migrant species that may not be resident. The latter is not exclusive to multiple-year surveys; for example, it is highly likely that *Magusa orbifera* (Walker) and *Ascalapha odorata* (L.), each recorded once from the Station, are non-residents.

One of the greatest difficulties encountered while conducting Lepidoptera surveys that focus on the entire order is the paucity of taxonomic expertise to provide determinations of the samples, particularly for Microlepidoptera. While species names are not vital for compiling an inventory and estimating species richness, they are extremely useful. We found that the morphospecies concept of identification was inadequate for determining the number of species because of the similarity of many Microlepidoptera, especially Gelechioidea. Although we received considerable assistance from many taxonomists, because of the large number of specimens, it was impossible to obtain determinations of all the material. We suspect that our blacklight samples may include 5-10% more species that, when identified, will be "new" to the inventory.

Conservation Context

Although we cannot assume that any of the species documented on the Station are restricted to sensitive coastal sage scrub habitat, it is highly likely that most contribute to the functioning of the larger biotic landscape, which includes coastal sage scrub, through pollination, herbivory, or as prey. There is little doubt that Lepidoptera phenology (e.g., timing of larval availability as a food source for birds and small mammals) and density (e.g., amount of prey resources available for predators and the amount of herbivore pressure on plants) play a major role in determining the success or failure of many biotic functions of the community.

From a conservation perspective, what sort of information can be extracted from the Lepidoptera survey of MCAS Miramar? While there are numerous ways of examining biotic complexity or ecosystem health, we focus on three criteria that may be useful in assessing the potential conservation value of any site using Lepidoptera: (1) presence of endemics or rare taxa; (2) presence of "weedy" species; (3) and species richness and complementarity.

The presence of numerous "regional endemic" species (e.g., *Lycaena hermes*, *Decodes helix* Powell & Brown, *Eucosma williamsi* Powell, *Crambidia dusca* Barnes & McDunnough, and numerous undescribed species discussed above) indicates that there probably is considerable native habitat on the Station that is still intact, and that the general area supports biological resources of "regional" significance. Although none of these species is listed as threatened or endangered, and none is restricted to the Station, there may be few other places in southern California where as many co-occur. Hence the Station may support an "assemblage" of regional endemics that exceeds that found at other coastal southern California localities. The occurrence of assemblages of rare species is a common phenomenon wherever rare or depleted native habitats are present. For example, vernal pools throughout the Central Valley of California support numerous plant species listed (or as candidates for listing) as rare, threatened, or endangered, plus one or more species of "sensitive" fairy shrimp (Anostraca) and at least one "sensitive" amphibian.

The abundance of several widespread, weedy species, including *Spodoptera exigua*, *Pseudaletia unipuncta* (Haworth), *Agrotis ypsilon* (all Noctuidae), *Cnephasia longana* (Tortricidae), and others indicates the presence of disturbed or degraded habitat. While occurrence of these species can be explained in part by the adjacency of urbanization, there is little doubt that resident populations of these polyphagous "pests" are present in degraded habitat on the Station. It is likely that the native Lepidoptera fauna has suffered from the introduction of invasive weeds that serve as host plants for weedy moth species. On the other hand, numerous weedy species common in adjacent disturbed and/or urban areas are not present on the Station, or are present in exceedingly low density. For example, *Trichoplusia ni* (Hübner), *Spodoptera ornithogalli* (Guenée), *Peridroma saucia* (Hübner) (all Noctuidae), *Platynota stultana* (Walsingham), *Crocidosema plebejana* Zeller (both Tortricidae), and *Cadra cautella* (Walker) (Pyralidae) are common or abundant in adjacent urbanized and disturbed areas, but were uncommon or rare on the Station. Monitoring strategies capable of detecting changes in the abundance of these weedy species may provide insight into the affects of future environmental change and/or habitat perturbation on the Station.

While the preservation of maximum biodiversity may seem intimately linked with the preservation of areas of highest species richness, this may not always be the case. Areas of highest species richness may represent areas of greatest range overlap of common or widespread species. The number of common, weedy species in an urban area may exceed the number of native species in a depauperate, unique native habitat. Hence the total number of species alone may say little about the overall conservation value of a site or region. Other factors adding to the complexity of using species richness as a measure of conservation value are differences in sampling strategies leading to the richness numbers being compared, or the absence of comparative numbers altogether. For the Lepidoptera of MCAS Miramar, neither average species richness derived from the three methods of extrapolation ($n = 715$) nor the documented value ($n = 646$) provide useful conservation information because there are no other numbers to compare, i.e., no other sites in California of this size have been surveyed as thoroughly.

An alternative to focusing conservation efforts on areas of high biodiversity is to focus on landscape diversity and site complementarity. Maximizing conservation of the greatest variety of habitats, plant communities, slopes, exposures, etc. almost certainly will lead to the preservation of the greatest number of species. Evaluating site complementarity, likewise, may help identify scenarios that capture the greatest number of species. For example, areas of gabbro-derived or serpentine soils typically support exceedingly depauperate floras because the unusually high magnesium and iron content of the soil inhibits the growth of most plant species (Kruckeberg 1954, 1969). Consequently, these areas would receive little or no consideration in conservation efforts focused on areas of high diversity. However, these soils typically support an endemic flora (Raven & Axelrod 1978) that has exceedingly high conservation value. Under a strategy of conserving landscape diversity and areas with high complementarity, these unique areas would receive attention comparable to areas of high species richness. Just as high species richness may not always be an indication of high conservation value, high complementarity, likewise, may lead to conservation decisions that are not optimal for maximizing the preservation of biodiversity. For high complementarity to be an effective criterion, it must be the result of high cumulative species richness (the denominator of FS; see Table 2) as well as a low number of shared species. A site that supports only a subset of a more diverse site may have a high complementarity value with a diverse site, but make no contribution to the cumulative species richness.

In summary, Lepidoptera inventories may be used to focus conservation efforts towards areas of endemism (e.g., areas that support assemblages of regional endemics) and away from areas that support an abundance of weedy species. Species richness, per se, may be of little assistance in assessing conservation value, but a landscape approach that evaluates site complementarity may be highly useful in capturing the greatest species richness.

The growth of conservation biology and concern for the biological consequences of environmental change has stimulated a new and intense interest in ecological monitoring. However, before the results of monitoring programs can be interpreted, a baseline inventory is absolutely vital. We believe that the results of this inventory of MCAS Miramar represent a baseline against which changes in the Lepidoptera fauna of the Station can be measured.

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APPENDIX A. Adult flight period for Lepidoptera based on capture records and observations; months abbreviated by capital letters; + = observed or captured, - = not observed.

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Nepticulidae												
Stigmella (?) sp. 1	-	-	-	-	-	-	-	-	-	+	-	-
Stigmella (?) sp. 2	-	-	-	-	-	-	-	+	-	-	-	-
Stigmella (?) sp. 3	-	-	-	+	-	-	-	-	-	-	-	-
Opostegidae												
Opostega bistriguella Braun	+	-	+	+	-	-	-	-	-	-	-	-
Opostega sp.	-	-	-	-	-	-	-	-	-	-	+	-
Tischeriidae												
Tischeria sp.	-	-	-	-	-	-	-	-	-	-	+	-
Incurvariidae												
Lampronia sp.	+	-	-	-	-	-	-	-	-	-	-	-
Adela flammeusella Chambers	-	-	-	+	-	-	-	-	-	-	-	-
Prodoxidae												
Greya sp.	-	-	+	-	-	-	-	-	-	-	-	-
Tegeticula maculata (Riley)	-	-	-	+	-	-	-	-	-	-	-	-
Tegeticula yuccasella (Riley)	-	-	+	+	+	-	-	-	-	-	-	-
Prodoxus marginatus Riley	-	-	+	+	+	-	-	-	-	-	-	-
Prodoxus cinereus Riley	-	-	+	+	+	-	-	-	-	-	-	-
Prodoxus aenescens Riley	-	-	+	+	-	-	-	-	-	-	-	-
Acrolophidae												
Cephitinea obscurostrigella (Ch.)	-	-	+	+	-	+	+	+	+	-	+	-
Amydria arizonella Dietz	-	-	-	+	-	-	-	+	-	-	-	-
Amydria curvistrigella (Dietz)	-	+	+	+	+	+	+	-	-	-	+	+
Amydria confusella Dietz	+	+	+	+	-	-	+	+	-	+	+	-
Amydria obliquella Dietz	-	-	-	-	+	+	+	+	+	+	-	-
Amydria erecta (Braun)	-	-	-	-	+	+	+	+	+	+	-	-
Amydria n. sp.	-	-	-	-	+	-	-	-	-	-	-	-
Amydria sp (dark)	-	-	-	+	+	+	+	+	+	-	-	-
Acrolophus kearfotti (Dyar)	-	-	-	-	-	+	+	+	+	-	-	-
Acrolophus laticapitanus	-	-	-	+	+	+	+	+	+	-	-	-
Acrolophus pyramellus (B. & McD.)	-	-	-	+	+	+	+	+	+	+	-	-
Acrolophus variabilis (Wals.)	-	-	-	-	-	+	+	+	+	-	-	-
Tineidae												
Tinea occidentalis Chambers	+	-	+	+	+	+	+	+	+	+	+	-
Opogona sp. 1	-	-	+	-	-	+	-	+	+	+	+	-
Opogona sp. 2	-	-	-	-	-	+	-	-	-	-	-	-
Opogona omoscopa (Meyrick)	-	-	+	-	-	-	-	-	-	-	-	-
Dryadaula terpsichorella (Busck)	-	-	-	-	-	-	+	-	-	-	-	-
ca. 2 undetermined Tineidae												

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Bucculatricidae												
Paraleucoptera sp.	-	-	+	-	-	-	-	-	+	-	-	-
Bucculatrix sp.	+	-	+	-	+	-	-	+	+	-	+	-
Gracillariidae												
Caloptilia sp. 1	-	-	-	-	-	-	-	-	-	+	-	-
Caloptilia sp. 2	-	-	-	-	-	-	-	-	+	-	-	-
Caloptilia sp. 3	-	-	+	-	-	-	-	-	-	-	-	-
Caloptilia sp. 4	-	-	+	-	-	-	-	-	-	-	-	-
ca. 2 undetermined Gracillariidae												
Oecophoridae												
Ethmia arctostaphylella (Wals.)	-	+	+	+	-	+	-	-	-	-	-	-
Ethmia discostrigella (Chambers)	-	+	+	+	+	+	+	+	+	+	-	-
Inga concorella (Beutenmuller)	-	-	-	-	-	+	-	-	-	-	-	-
Pleurota albastrigulella (Kearf.)	-	-	+	+	+	-	-	-	-	-	-	-
ca. 2 undetermined Oecophoridae												
Elachistidae												
Coelopoeta glutinosi Walsingham	-	-	-	-	-	-	-	+	-	-	-	-
Elachista coniophora Braun	+	+	+	+	-	-	-	-	-	-	-	+
Elachista lurida Kaila	-	-	+	-	-	-	-	-	-	-	-	-
Blastobasidae												
Symmoca signatella (H.-S.)	-	-	-	-	+	-	-	-	-	-	-	-
Holcocera gigantella Chambers	+	+	+	-	+	+	+	+	+	+	+	+
Holcocera n. sp. 1	-	-	+	+	+	-	-	-	-	-	+	-
Holcocera n. sp. 2	-	-	-	-	-	+	+	-	-	-	-	-
Hypatopa interpunctella (Dietz)	-	-	+	+	+	-	-	-	+	-	+	-
Hypatopa n. sp. 1	-	-	-	-	+	+	-	-	-	-	-	-
Hypatopa n. sp. 2	-	-	-	-	-	+	-	-	-	-	-	-
Hypatopa n. sp. 3	-	-	-	+	-	-	-	-	-	-	-	-
Hypatopa n. sp. 4	-	-	+	+	+	-	+	-	+	-	+	-
Blastobasis n. sp. 1	-	-	-	-	-	-	+	-	-	-	-	-
Blastobasis n. sp. 2	-	-	-	-	-	-	-	+	-	-	-	-
Blastobasis n. sp. 3	-	-	-	+	-	+	+	+	-	-	-	-
Coleophoridae												
Coleophora accordella Wlsm.	-	-	-	+	-	+	-	-	-	-	+	-
Coleophora sp. 2	+	+	+	-	-	-	-	-	-	-	-	-
Coleophora sp. 3	+	+	+	-	-	-	-	-	-	-	-	-
Coleophora sp. 4	-	-	-	-	+	+	+	-	-	-	-	-
Coleophora sp. 5	-	+	+	-	-	-	-	-	-	-	-	-
Coleophora sp. 6	+	+	+	-	-	-	-	-	-	-	-	-
ca. 5 undetermined sp.												
Momphidae												
Mompha eloisella (Clemens)	-	-	-	-	-	+	+	+	-	-	-	-
Mompha sp.	-	-	-	-	-	-	-	-	+	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Cosmopterigidae												
Antequera acertella (Busck)	+	-	-	-	-	-	-	-	-	-	+	+
Cosmopterix sp.	-	-	-	-	-	-	+	-	-	-	-	-
Stagmatophora iridella Busck	-	-	-	-	-	+	+	+	-	-	-	-
Stagmatophora enchrysa (Hodg.)	-	-	-	-	-	+	+	+	-	-	-	-
Pyroderces sp.	-	-	-	-	-	-	-	-	-	-	+	-
Anoncia sp. 1	-	-	-	-	+	+	+	-	-	-	-	-
Anoncia sp. 2	-	-	-	-	-	-	+	-	-	-	-	-
Stilbosis sp.	-	-	-	-	-	-	+	+	+	-	-	-
Walshia miscecolorella	-	-	+	+	+	-	+	-	+	+	+	+
ca. 2 undetermined Cosmopterigidae												
Scythrididae												
Scythris sp. 1	-	-	-	+	+	+	+	+	+	+	+	-
Scythris sp. 2	-	-	-	+	+	+	+	+	+	+	+	-
Scythris sp. 3	-	-	-	-	-	-	-	-	-	+	-	-
Gelechiidae												
Isophrictis sp.	-	-	-	-	-	-	-	+	+	+	-	-
Aristotelia elegantella (Cham.)	-	-	-	+	+	+	+	+	+	+	+	-
Aristotelia sp. 1 (tan)	-	-	+	+	+	+	+	-	+	+	+	-
Aristotelia sp. 2 (rust)	+	+	+	-	+	-	+	+	+	-	+	-
Exotelia californica (Busck)	-	-	+	-	+	-	-	-	-	-	-	-
Exotelia graphicella (Busck)	-	-	-	-	+	-	+	-	-	-	-	-
Leucogoniella californica (Keifer)	-	-	-	+	+	+	+	+	-	-	-	-
Telphusa sedulitella (Busck)	-	-	-	-	+	-	+	-	+	-	-	-
Pseudochellaria scabrella (Busck)	+	+	+	+	+	+	+	+	+	+	+	+
Teleiopsis baldiana (Bar. & Bus.)	-	-	-	-	+	-	-	-	-	-	-	-
Gelechia sp. 1	-	-	-	+	-	-	-	-	-	-	-	-
Gnorimoschema powelli Povolny	-	-	-	+	-	-	-	-	-	-	-	-
Gnorimoschema sp. 1	-	-	-	-	+	-	-	-	-	-	-	-
Gnorimoschema saphirinella (Ch.)	-	-	-	-	-	-	-	+	-	-	-	-
Chionodes figurella (Busck)	-	-	-	-	+	-	-	-	-	-	-	-
Chionodes notandella (Busck)	+	+	-	-	-	-	-	-	-	-	-	+
Chionodes ochreostrigella (Cham.)	-	-	-	-	-	-	-	-	+	-	-	-
Chionodes sp. 1	-	-	-	+	-	-	-	-	-	-	-	-
Chionodes sp. 2	-	-	-	-	+	-	-	-	-	-	-	-
Chionodes sp. 3	+	-	-	-	-	-	-	-	-	-	-	-
Chionodes sp. 4	-	-	-	+	-	-	-	-	-	-	-	-
Chionodes sp. 5	-	+	-	-	-	-	-	-	-	-	-	-
Filatima sp. 1	+	-	-	-	-	-	-	-	-	-	-	-
Filatima sp. 2	-	+	-	-	-	-	-	-	-	-	-	-
Aroga morenella (Busck)	-	-	-	+	+	+	+	-	-	-	-	-
Anacampsis lacteusochrella (Ch.)	-	-	-	-	+	-	-	-	-	-	-	-
Dichomeris baxa Hodges	-	+	-	-	+	+	-	-	-	-	-	-
Metopleura potosi Busck	-	-	-	+	+	+	+	+	+	-	-	-
Gelechiidae sp. 1	-	-	-	-	-	-	-	-	-	+	-	-
Gelechiidae sp. 2	-	-	-	-	-	-	-	-	-	+	-	-
Gelechiidae sp. 3	+	-	-	-	+	-	-	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Gelechiidae sp. 4	+	-	-	-	+	-	-	-	-	-	-	-
ca. 22 undetermined Gelechiidae												
Alucitidae												
Alucita hexadactylon L.	-	-	-	+	-	-	-	-	-	-	-	-
Carposinidae												
Bondia comonana (Kearfott)	-	-	-	-	-	-	-	-	-	-	+	-
Plutellidae												
Euceratia securella Walsingham	-	-	+	+	-	-	-	-	-	-	-	-
Pliniaca bakerella Busck	-	-	+	+	-	-	-	-	-	-	-	-
Plutella albidorsella (Wals.)	-	-	-	-	+	-	-	-	-	-	-	-
Plutella xylostella (L.)	-	-	+	-	-	-	-	-	-	-	+	-
Plutella sp. (tan)	-	-	-	-	+	-	-	-	-	-	-	-
Ypsolopha cervella (Walsingham)	-	-	-	-	+	-	-	-	-	-	-	-
Yponomeutidae												
Zelleria sp.(?)	+	+	-	-	-	-	-	-	-	-	-	+
Sesiidae												
Paranthrene robinae (Edwards)	-	-	-	+	-	-	-	-	-	-	-	-
Synanthedon polygoni (Edwards)	-	-	-	+	+	-	-	-	-	-	-	-
Synanthedon resplendens (Edw.)	-	-	-	-	-	+	+	-	-	-	-	-
Synanthedon exitiosa (Say)	-	-	-	-	+	+	-	-	-	-	-	-
Penstemonia hennei Engelhard	-	-	-	-	-	+	+	+	-	-	-	-
Cossidae												
Prionoxystus robiniae (Peck)	-	-	-	-	+	-	-	-	-	-	-	-
Tortricidae												
Episimus argutanus (Clemens)	-	-	+	+	+	+	-	-	+	-	-	-
Bactra furfurana (Haworth)	-	-	-	+	-	+	-	-	-	-	-	-
Bactra verutana Zeller	-	+	+	+	+	+	+	+	+	+	+	+
Bactra priapeia Heinrich	-	-	-	-	-	-	+	-	-	-	-	-
Endothenia hebesana (Walker)	-	-	-	+	-	-	-	-	-	-	-	+
Endothenia nubilana (Clemens)	-	-	-	-	-	+	+	+	+	-	-	+
Rhyacionia frustrana (Comstock)	-	-	-	-	-	-	-	+	+	-	-	-
Phaneta apacheana (Wals.)	+	+	+	-	+	-	+	+	-	-	-	-
Phaneta misturana (Heinrich)	-	+	+	-	-	-	-	-	-	-	-	-
Phaneta pallidarcis (Heinrich)	-	-	-	-	+	+	+	+	+	-	-	-
Phaneta subminimana (Heinrich)	-	-	-	-	-	+	+	+	+	-	-	-
Phaneta sp. (brown)	+	-	-	-	-	-	-	-	-	-	-	-
Eucosma ridingsana (Robinson)	-	-	-	-	-	-	-	+	+	-	-	-
Eucosma sandiego Kearfott	-	-	-	-	-	-	-	+	+	+	-	-
Eucosma n. sp. (nr. *hazelana*)	-	-	-	-	-	-	+	+	-	-	-	-
Eucosma costastrigulana Kearfott	-	-	-	+	+	+	+	+	+	-	-	-
Eucosma williamsi Powell	-	-	-	-	-	+	+	+	+	+	-	-
Eucosma pulveratana (Wals.)	+	+	+	+	+	+	+	+	+	+	+	+

Months	J	F	M	A	M	J	J	A	S	O	N	D
Eucosma nr. *passerana* (Wals.)	-	-	-	-	-	-	+	-	+	-	-	-
Eucosma sp. 1	-	-	-	-	-	-	-	+	+	-	-	-
Eucosma sp. 2	-	-	-	-	-	-	-	-	-	+	-	-
Epiblema strenuana (Walker)	-	-	-	-	-	+	-	-	-	-	-	-
Suleima lagopana (Walsingham)	-	-	-	-	+	-	-	-	-	-	-	-
Sonia filiana (Busck)	-	-	-	-	-	-	-	-	+	+	+	-
Pseudexentra habrosana (Heinrich)	-	+	+	-	-	-	-	-	-	-	-	-
Chimoptesis chrysopyla Powell	-	+	-	-	-	-	-	-	-	-	-	-
Crocidosema plebejana Zeller	-	-	-	-	-	-	+	-	-	-	+	-
Epinotia siskiyouana Heinrich	-	-	-	-	-	+	-	+	-	-	-	-
Epinotia subplicana (Wals.)	-	-	+	-	-	-	-	-	-	-	-	-
Epinotia sagittana McDunnough	-	-	-	-	-	-	-	-	-	-	+	-
Epinotia columbia (Kearfott)	+	-	-	-	-	+	-	-	-	-	+	-
Epinotia bigemina Heinrich	+	-	-	-	-	-	-	-	-	-	+	+
Epinotia kasloana McDunnough	+	+	-	-	-	-	-	-	-	-	-	+
Epinotia signiferana Heinrich	+	-	-	-	-	-	-	-	-	-	+	+
Epinotia n. sp.	-	+	+	-	-	-	-	-	-	-	-	-
Ancylis nr. *simuloides* (McD.)	+	+	+	-	-	+	-	-	-	-	-	+
Ancylis mediofasciana (Clemens)	-	+	+	-	-	-	-	-	-	-	-	-
Cydia latiferreanus (Wals.)	-	-	-	-	-	-	+	+	+	+	-	-
undet. Olethreutinae sp. 3	-	-	-	+	-	-	-	+	-	-	-	-
undet. Olethreutinae sp. 4	-	-	-	+	-	-	-	-	-	-	-	-
Acleris senescens (Zeller)	-	+	-	-	-	-	-	-	-	-	-	-
Acleris foliana (Walsingham)	-	-	-	-	+	+	-	-	-	-	-	-
Cnephasia longana (Haworth)	-	-	-	+	+	+	-	-	-	-	+	-
Decodes fragarianus (Busck)	-	-	-	-	-	-	-	-	+	+	+	-
Decodes asapheus Powell	-	-	-	-	-	-	-	-	-	-	+	-
Decodes helix Powell & Brown	+	+	+	-	-	-	-	-	-	-	+	+
Anopina triangulana (Kearfott)	-	-	-	+	+	-	+	-	-	+	-	-
Argyrotaenia niscana (Kearfott)	-	-	+	+	+	+	-	-	-	-	-	-
Argyrotaenia franciscana (Wlsm.)	+	+	+	+	+	+	+	-	+	-	-	+
Archips argyrospila (Walker)	-	-	-	+	+	+	-	-	-	-	-	-
Clepsis peritana (Clemens)	-	-	+	+	-	-	+	+	+	-	+	-
Sparganothis senecionana (Wlsm.)	-	-	-	+	+	+	-	-	-	-	-	-
Platynota stultana (Walsingham)	-	-	-	-	-	-	+	+	+	-	-	-
Amorbia cuneana (Walsingham)	+	+	+	+	+	+	+	+	+	+	+	+
Henricus umbrabasanus (Kearfott)	-	-	-	-	+	+	+	+	+	-	-	-
Lorita scarificata Meyrick	+	-	+	-	-	-	-	-	+	+	-	-
Cochylis carmelana Kearfott	-	-	-	+	-	-	-	-	-	-	-	-
Saphenista (?) sp. 1	-	-	-	-	-	+	-	+	+	-	-	-
Saphenista (?) sp. 2	-	-	-	-	-	-	-	+	+	-	-	-
Saphenista (?) sp. 3	-	-	-	-	-	-	-	+	+	-	-	-
Hesperiidae												
Erynnis tristis (Boisduval)	-	-	-	-	-	+	+	+	-	-	-	-
Erynnis funeralis (Scud. & Burg.)	-	+	+	+	+	+	-	-	-	-	-	-
Pyrgus albescens Plotz	-	-	-	+	+	+	-	+	-	-	-	-
Heliopetes ericetorum (Boisduval)	-	-	-	-	-	+	-	-	-	-	-	-
Hylephila phyleus (Drury)	-	-	-	+	+	-	-	+	+	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Atalopedes campestris (Boisduval)	-	-	-	-	-	-	-	-	-	+	-	-
Ochlodes agricola (Boisduval)	-	-	-	+	+	+	-	-	-	-	-	-
Ochlodes sylvanoides (Boisduval)	-	-	-	-	-	-	-	+	+	-	-	-
Poanes melane (Edwards)	-	-	-	+	-	-	-	-	+	-	-	-
Lerodea eufala (Edwards)	-	-	-	-	-	-	-	-	+	-	-	-
Papilionidae												
Papilio zelicaon Lucas	-	+	+	+	+	-	-	-	-	-	-	-
Papilio cresphontes Cramer[1]	-	-	-	-	-	+	-	-	-	-	-	-
Papilio rutulus Lucas	-	-	+	+	+	+	+	+	-	-	-	-
Papilio eurymedon Lucas	-	-	-	+	+	+	-	-	-	-	-	-
Pieridae												
Pontia protodice (Bois. & LeCon.)	-	-	-	+	+	+	+	-	-	-	-	-
Pieris rapae (L.)	-	-	+	+	+	+	-	+	+	-	-	-
Anthocharis sara Lucas	-	-	+	+	+	-	-	-	-	-	-	-
Colias eurytheme Boisduval	-	+	-	-	-	-	-	-	-	+	-	-
Colias eurydice Boisduval[1]	-	-	-	-	-	+	-	-	-	-	-	-
Phoebis sennae (L.)	-	-	+	-	-	-	-	-	-	-	-	-
Nathalis iole Boisduval	-	-	-	-	+	-	-	-	-	-	-	-
Lycaenidae												
Lycaena hermes (Edwards)	-	-	-	-	+	+	-	-	-	-	-	-
Satyrium sylvinum (Boisduval)	-	-	-	-	-	+	-	-	-	-	-	-
Satyrium tetra (Edwards)	-	-	-	-	+	-	-	-	-	-	-	-
Satyrium saepium (Boisduval)	-	-	-	-	+	+	+	-	-	-	-	-
Callophrys dumetorum (Bois.)	-	+	+	+	-	-	-	-	-	-	-	-
Incisalia augustinus (Kirby)	-	-	+	+	-	-	-	-	-	-	-	-
Strymon melinus Hübner	-	+	+	-	+	-	-	-	+	-	-	-
Brephidium exile (Boisduval)	-	+	+	-	-	-	-	-	+	-	-	-
Leptotes marina (Reakirt)	-	-	+	-	-	+	-	-	-	-	-	-
Celastrina ladon (Cramer)	-	-	+	+	+	-	-	-	-	-	-	-
Philotes sonorensis (Feld. & Feld.)	-	-	+	-	-	-	-	-	-	-	-	-
Euphilotes bernardino (B. & McD.)	-	-	-	-	+	+	+	-	-	-	-	-
Glaucopsyche lygdamus (Doubl.)	-	+	+	+	-	-	-	-	-	-	-	-
Icaricia acmon (West. & Hew.)	-	-	+	+	+	-	-	-	+	-	-	-
Riodinidae												
Apodemia mormo (Feld. & Feld.)	-	+	+	+	+	+	+	+	+	+	-	-
Nymphalidae												
Agraulis vanillae (L.)	-	-	-	-	-	-	-	-	-	+	-	-
Nymphalis antiopa (L.)	-	-	-	-	+	-	-	-	-	-	-	-
Vanessa viginiensis (Drury)	-	+	-	-	-	-	-	-	-	-	-	-
Vanessa cardui (L.)	+	+	+	+	+	-	-	-	-	+	-	-
Vanessa annabella (L.)	-	-	+	-	-	-	-	-	-	-	-	-
Vanessa atalanta (L.)	-	-	-	+	-	-	-	-	-	-	-	-
Junonia coenia (Hübner)	-	-	+	+	+	+	+	-	+	+	-	-
Speyeria callippe (Boisduval)	-	-	-	+	+	+	-	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Chlosyne gabbii (Behr)	-	-	-	+	+	-	-	-	-	-	-	-
Euphydryas chalcedona (Doubl.)	-	-	-	+	+	-	-	-	-	-	-	-
Limenitis lorquini (Boisduval)	-	-	+	+	-	+	-	-	-	+	-	-
Adelpha bredowii (Geyer)	-	-	+	+	+	-	-	+	-	-	-	-
Coenonympha tullia Westwood	-	+	+	+	+	+	+	-	-	-	-	-
Danaus plexippus (L.)	-	+	+	+	-	+	-	+	+	-	-	-
Danaus gilippus (Cramer)[1]	-	-	-	-	-	+	-	-	-	-	-	-
Limacodiae												
Monoleuca occidentalis B. & McD.	-	-	-	-	-	+	+	+	+	+	-	-
Crambidae												
Scoparia palloralis Dyar	-	+	+	+	-	-	-	-	-	-	-	-
Eudonia rectilinea (Zeller)	-	-	+	+	+	+	-	-	-	-	-	-
Eudonia spenceri Munroe	-	-	-	-	+	-	-	-	-	-	-	-
Usingeriessa brunnidalis (Dyar)	-	-	-	-	-	-	-	+	-	-	-	-
Petrophila jaliscalis (Schaus)	-	-	-	-	-	-	-	-	-	+	-	-
Microtheoris ophionalis (Walker)	-	-	-	-	-	+	+	+	+	+	-	-
Nannobotys commortalis (Grote)	-	-	-	+	-	-	-	-	-	-	-	-
Mimoschinia rufofascialis (Steph.)	-	-	-	+	+	-	-	-	-	-	-	-
Hellula rogatalis (Hulst)	-	-	+	+	+	+	+	+	+	+	+	+
Stegea powelli Munroe	-	-	-	-	-	+	+	+	+	-	-	-
Abegesta reluctalis (Hulst)	-	-	-	-	-	-	+	+	+	-	-	-
Lipocosma albibasalis B. & McD.	-	-	-	+	+	+	+	+	+	+	+	-
Dicymolomia metalliferalis (Pack.)	-	-	-	+	+	+	+	+	+	-	-	-
Achyra occidentalis (Packard)	-	-	+	+	-	-	-	-	-	+	+	-
Pyrausta napaealis (Hulst)	-	-	+	+	-	-	-	-	-	-	-	-
Pyrausta nr. *roseivestalis* Mun.	-	-	+	-	-	-	-	-	-	-	-	-
Pyrausta pilatealis (B. & McD.)	-	-	-	+	-	-	-	-	-	-	-	-
Pyrausta volupialis (Grote)	-	-	-	+	+	+	-	+	+	+	-	+
Pyrausta morenalis (Dyar)	-	-	-	+	-	-	-	-	-	-	-	-
Pyrausta coccinea Warren	-	-	-	+	-	-	-	-	-	-	-	-
Pyrausta laticlavia (Gr. & Rob.)	-	+	-	+	+	+	+	+	+	+	+	+
Pyrausta fodinalis (Lederer)	-	-	-	-	+	-	-	-	-	-	-	-
Udea profundalis (Packard)	-	-	+	+	-	-	-	-	-	-	-	-
Udea octosignalis (Hulst)	-	-	-	-	+	+	+	-	-	-	-	-
Lamprosema sinaloanensis Dyar	-	-	-	-	+	-	-	-	-	-	-	-
Lineodes integra (Zeller)	-	-	-	-	-	-	-	-	+	+	-	-
Choristostigma elegantalis Warren	-	+	+	+	+	-	-	-	-	-	-	-
Mecyna mustelinalis (Packard)	-	-	+	+	+	+	+	-	-	-	-	-
Mimorista subcostalis Hamp.	-	-	-	-	-	+	-	-	+	-	-	-
Nomophila neartica Munroe	+	+	+	+	-	-	-	-	+	+	+	+
Spoladea recurvalis (Fabricius)	-	-	-	-	-	-	-	-	-	+	-	-
Lygropia octonalis (Zeller)	-	-	-	-	-	-	+	+	-	-	-	-
Diastictis fracturalis (Zeller)	+	-	+	+	+	+	+	+	+	+	+	-
Crambus occidentalis Grote	-	-	-	-	-	-	-	-	-	-	+	-
Crambus rickseckerellus Klots	-	-	-	-	-	-	-	-	-	+	+	-
Crambus cypridalis Hulst	-	-	-	-	+	-	+	-	+	+	-	-
Agriphila undata (Grote)	-	-	-	-	-	-	-	-	-	+	+	-

Months	J	F	M	A	M	J	J	A	S	O	N	D
Agriphila attenuata (Grote)	-	-	-	-	-	-	-	-	+	+	+	-
Agriphila angulata (B. & McD.)	-	-	-	-	+	+	+	+	+	+	+	-
Microcrambus sp. 1	-	-	-	-	-	-	-	-	+	-	-	-
Microcrambus sp. 2	-	-	-	-	-	-	-	-	+	-	-	-
Parapediasia teterrella Zincken	-	-	-	-	-	-	+	+	+	+	-	-
Euchromius californicalis (Pack.)	-	-	+	+	+	+	+	+	+	+	-	-
Hemiplatytes epia (Dyar)	-	-	-	-	-	+	+	+	+	-	-	-
Pyralidae												
Pyralis electalis Hulst	-	-	-	-	-	+	+	+	+	+	-	-
Pyralis cacamica Dyar	-	-	-	+	+	+	+	+	+	+	+	-
Herculia phoezalis Dyar	-	-	-	-	+	+	+	-	-	-	-	-
Acallis gripalis (Hulst)	-	-	-	+	+	+	+	+	+	+	+	+
Arta epicoenalis Ragonot	-	-	-	+	+	+	+	-	+	+	+	-
Jocara trabalis (Grote)	-	-	+	+	+	+	+	+	+	+	+	-
Tallula fieldi Barnes & McD.	-	-	-	-	+	+	-	-	-	-	-	-
Galleria mellonella (Linnaeus)	+	-	-	-	+	-	+	+	+	+	-	-
Achroia grisella (Fabricius)	-	-	-	-	+	-	-	-	-	-	-	-
Macrotheca angulalis B. & McD.	-	-	-	-	-	+	-	-	-	-	-	-
Macrotheca ponda (Dyar)	-	-	-	+	+	+	+	+	+	+	-	-
Rhodophaea caliginella (Hulst)	-	-	-	-	+	+	+	+	+	-	-	-
Myelopsis alatella (Hulst)	-	-	+	+	-	-	-	-	-	-	-	-
Ambesa walsinghami (Ragonot)	-	-	-	-	-	-	+	-	-	-	-	-
Nephopteryx bifasciella Hulst	-	-	-	+	-	+	-	+	+	+	-	-
Sarata pullatella (Ragonot)	+	+	+	-	-	-	-	-	-	-	-	-
Sarata dophnerella Ragonot	-	-	+	-	-	-	-	-	-	-	-	-
Lipographis fenestrella (Packard)	-	-	+	+	-	-	-	-	-	-	-	-
Adelphia ochripunctella (Dyar)	-	-	-	-	-	-	-	-	-	-	+	-
Elasmopalpus lignosellus (Zeller)	-	-	-	-	-	-	-	-	-	-	+	-
Eumysia fuscatella (Hulst)	-	-	-	-	-	-	+	+	+	+	+	-
Honora dotella Dyar	-	-	-	+	-	+	-	+	-	-	-	-
Homeosoma electellum (Hulst)	-	-	-	-	-	-	-	-	-	+	-	-
Homeosoma uncanale Hulst	-	-	-	+	-	-	-	-	-	-	-	-
Phycitodes mucidella (Ragonot)	-	-	-	+	-	+	+	+	+	-	-	-
Laetilia coccidivora (Comstock)	+	+	+	+	-	+	-	+	+	+	+	-
Laetilia zamacrella Dyar	-	-	-	-	-	-	-	+	-	-	-	-
Rhagea stigmella (Dyar)	-	-	+	+	+	+	+	+	+	+	+	+
Olycella subumbrella (Dyar)	-	-	-	-	-	-	-	-	+	-	-	-
Eremberga craebates (Dyar)	-	-	-	-	-	+	-	+	+	+	-	-
Ozamia fuscomaculelella (Wright)	-	-	-	-	-	+	+	+	+	+	-	-
Ephestiodes gilvescentella Ragonot	+	+	-	+	-	-	-	-	+	-	-	-
Ephestiodes erythrella Ragonot	-	-	+	-	-	-	-	-	-	-	+	-
Ephestiodes griseus Nuenzig	-	-	+	-	-	-	-	-	-	-	-	-
Manhatta setonella (McD.)	-	-	+	-	-	-	-	-	-	-	-	-
Sosipatra rileyella (Ragonot)	-	-	-	-	+	-	-	-	-	-	-	-
Anagasta kuehniella (Zeller)	-	-	-	+	-	-	-	-	-	-	+	+
Cadra cautella (Walker)	+	-	-	-	-	-	-	-	-	-	-	-
Arivaca albidella (Hulst)	-	-	-	+	+	+	+	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Pterophoridae												
Pterophorus ningoris (Wals.)	-	-	-	+	-	-	-	-	-	-	-	-
Platyptila carduidacyla (Riley)	+	-	-	-	-	-	-	-	-	-	-	-
Anstenoptila marmarodactyla (Dy.)	+	+	-	-	+	-	-	-	-	-	-	-
Stenoptilia zophodactyla (Dup.)	+	-	-	-	-	-	-	-	-	-	-	-
Emmelina monodactyla (L.)	-	+	-	-	-	-	-	-	-	-	-	-
ca. 3 undetermined Pterophoridae												
Geometridae												
Protitame subalbaria (Packard)	-	-	+	-	+	+	+	+	+	-	-	-
Itame quadrilinearia (Packard)	-	-	-	-	+	-	-	-	-	-	-	-
Itame semivolata (Dyar)	-	-	-	-	+	-	-	-	-	-	-	-
Itame extemporata B. & McD.	-	-	-	+	+	+	+	-	-	-	-	-
Itame guenearia (Packard)	-	-	-	+	+	+	+	-	-	-	-	-
Elpiste marcescaria (Guenée)	+	+	+	+	+	+	+	+	+	-	+	+
Elpiste metanemaria (Hulst)	+	+	+	+	+	+	+	+	+	+	+	+
Semiothisa pictipennata (Hulst)	+	-	+	+	+	+	-	+	-	-	+	+
Semiothisa californiaria (Hulst)	-	-	+	+	-	+	+	-	-	-	-	-
Semiothisa neptaria (Guenée)	+	+	-	+	+	+	+	+	+	+	+	-
Semiothisa s-signata (Packard)	-	-	-	-	-	-	-	-	-	-	+	-
Hesperumia sulphurararia Packard	-	-	-	+	+	+	-	-	-	-	-	-
Neoalcis californiaria (Packard)	-	-	-	-	-	-	+	+	+	+	+	+
Glaucina epiphysaria Dyar	+	+	+	+	+	-	-	-	-	-	+	+
Glaucina magnifica Grossbeck	-	-	-	-	-	-	-	-	-	+	+	-
Hulstina exhumata (Swett)	-	-	-	+	+	-	-	-	-	-	-	-
Hulstina wrightiaria (Hulst)	-	-	-	-	+	-	-	-	-	-	-	-
Pterotaea lamiaria (Strecker)	-	-	-	+	+	+	+	-	-	-	-	-
Anacamptodes fragilaria (Gross.)	+	-	-	-	-	-	+	+	+	+	-	-
Cochisea sinuaria B. & McD.	-	-	-	-	-	-	-	-	-	+	+	+
Phigalia plumogeraria (Hulst)	+	+	+	-	-	-	-	-	-	-	-	-
Paleacrita longiciliata Hulst	+	+	-	-	-	-	-	-	-	-	+	+
Lomographa elsinora (Hulst)	-	-	+	+	+	-	-	-	-	-	-	-
Sericosema juturnaria (Guenée)	-	-	-	-	+	+	-	-	-	-	-	-
Eudrepanulatrix rectifascia (Hulst)	+	-	-	-	-	-	-	-	-	-	-	+
Drepanulatrix unicalcaria (Guen.)	+	+	+	+	+	-	-	-	-	-	+	+
Drepanulatrix hulstii (Dyar)	-	-	-	-	-	-	-	-	+	-	-	-
Drepanulatrix bifilata (Hulst)	-	+	+	+	+	-	-	-	-	+	+	-
Drepanulatrix quadraria (Grote)	+	+	+	-	-	-	-	-	-	+	+	+
Drepanulatrix foeminaria (Guen.)	-	+	-	-	-	-	-	-	-	-	+	-
Drepanulatrix carnearia (Hulst)	-	+	-	-	-	-	-	-	-	+	-	-
Drepanulatrix falcataria (Pack.)	+	+	+	-	+	-	-	-	-	-	-	+
Drepanulatrix monicaria (Guen.)	+	+	+	-	-	-	-	-	-	+	+	+
Pero radiosaria (Hulst)	+	+	+	+	+	+	+	+	-	+	+	+
Pero mcdunnoughi (Cass. & Swett)	+	+	+	+	+	+	+	+	+	+	+	+
Aethaloidia packardaria (Hulst)	+	+	+	+	+	+	+	+	+	+	+	+
Parexcelsa ultraria Pearsall	-	-	-	-	-	-	-	+	+	+	+	+
Slossonia rubrotincta Hulst	-	-	-	-	+	+	+	-	-	-	-	-
Sicya laetula Barnes & McD.	-	-	-	+	+	+	-	-	-	-	-	-
Plataea personaria (Edwards)	+	+	+	+	+	+	+	+	+	+	+	+

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Eusarca falcata (Packard)	+	+	+	+	+	-	-	-	+	+	-	-
*Somatolopha simpliciana*B. & McD.	-	-	-	-	+	-	-	-	-	-	-	-
Pherne subpunctata (Hulst)	+	+	+	+	+	+	+	+	+	+	+	+
Synaxis hirsutaria Barnes & McD.	-	-	-	-	-	-	-	-	-	+	+	+
Synaxis mosesiani Sala	+	+	+	-	-	-	-	-	-	-	+	-
Prochoerodes truxaliata (Guenée)	+	+	+	+	+	-	-	-	-	+	+	+
Chlorosea banksaria Sperry	-	-	-	+	+	-	-	-	-	-	-	-
Nemoria pulcherrima (B. & McD.)	+	+	-	-	-	-	-	-	-	-	-	-
Nemoria pistaciaria (Packard)	-	-	+	+	+	+	+	-	-	-	-	-
Nemoria darwiniata (Dyar)	+	+	+	+	-	-	+	+	+	+	-	-
Nemoria leptalea Ferguson	-	+	+	+	+	-	+	+	+	+	+	+
Nemoria glaucomarginaria (Barnes & McDunnough)	-	+	+	+	-	+	-	+	-	-	-	-
Dichordia illustraria (Hulst)	+	-	-	-	+	+	-	+	+	+	+	+
Synchlora aerata (Fabricius)	-	-	-	-	-	-	+	+	+	+	-	-
Cheteoscelis faseolaria (Guenée)	+	-	+	+	+	+	+	+	+	+	+	+
Chlorochlamys triangularis Prout	-	-	-	+	+	-	-	-	-	-	-	-
Lobocleta ossularia (Geyer)	-	-	-	-	-	-	-	+	-	-	-	-
Lobocleta granitaria (Packard)	-	-	-	-	-	-	-	-	-	-	-	+
Lobocleta plemyraria (Packard)	-	-	-	-	-	-	-	-	+	-	-	-
Idaea bonifata (Hulst)	-	-	-	-	-	-	-	+	+	+	-	-
Idaea eremiata (Hulst)	-	-	-	-	-	+	+	+	+	-	-	-
Cyclophora dataria (Hulst)	-	+	-	-	+	-	-	-	-	-	-	-
Cyclophora nanaria (Walker)	-	-	-	+	-	-	-	-	+	-	+	+
Dysstroma mancipata (Guenée)	-	-	-	+	+	+	-	-	-	-	-	-
Hydriomena albifasciata (Pack.)	-	+	-	-	-	-	-	-	-	-	-	-
Hydriomena nubilofasciata (Pack.)	-	+	+	-	-	-	-	-	-	-	-	-
Triphosa californiata (Packard)	+	+	+	-	-	-	-	-	-	-	-	-
Archirhoe neomexicana (Hulst)	+	+	+	+	-	-	-	-	-	+	+	+
Perizoma custodiata (Guenée)	-	-	+	-	-	-	-	-	-	-	-	+
Anticlea switzeraria (Wright)	-	-	+	-	-	-	-	-	-	-	-	-
Stamnodes albiapicata Grossbeck	-	+	-	-	-	-	-	-	-	-	-	-
Stamnodes reckseckeri Pearsall	+	-	-	-	-	-	-	-	-	-	+	+
Stamnodes affiliata Pearsall	+	-	-	-	-	-	-	-	-	-	+	+
Stamnodes annellata (Hulst)	+	+	+	+	-	-	-	-	-	-	-	-
Stamnodes coenonymphata (Hulst)	+	+	+	+	-	-	-	-	-	+	-	-
Stamnodes cassinoi Swett	+	-	-	-	-	-	-	-	-	-	+	+
Epirrhoe plebeculata (Guenée)	-	+	-	-	-	-	-	-	-	-	-	-
Zenophleps lignicolorata (Packard)	+	+	+	+	-	-	-	-	+	+	+	+
Orthonama centrostrigaria (Woll.)	+	-	+	-	-	-	-	-	+	-	-	-
Venusia duodecelimeata (Packard)	-	-	+	+	-	-	-	-	-	-	-	-
Eupithecia maestoma (Hulst)	-	+	+	-	-	-	-	-	-	-	-	-
Eupithecia misturata (Hulst)	+	+	+	-	-	-	-	-	-	-	+	-
Eupithecia rotundopuncta Packard	-	+	-	-	-	-	-	-	-	-	-	-
Eupithecia zelmira Swett & Cass.	-	-	+	-	-	-	-	-	-	-	-	-
Eupithecia acutipennis (Hulst)	+	+	-	-	-	-	-	-	-	-	+	+
Eupithecia shirleyata Cass. & Sw.	-	+	+	-	-	-	-	-	-	-	-	-
Eupithecia nevadata Packard	+	+	+	+	-	-	-	-	-	-	-	-
Nasusina inferior (Hulst)	-	-	-	+	-	-	-	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Nasusina vaporata (Pearsall)	-	-	-	+	-	-	-	-	-	-	-	-
Trichopteryx veritata Pearsall	-	-	+	+	-	-	-	-	-	-	-	-
Lasiocampidae												
Tolype glenwoodi Barnes	-	-	-	-	+	+	+	+	-	-	-	-
Phyllodesma americana (Harris)	-	+	+	+	+	-	-	+	-	-	-	-
Gloveria medusa (Strecker)	-	-	-	-	-	+	+	-	+	+	+	-
Malacosoma constrictum (Edw.)	-	-	-	-	+	+	-	-	-	-	-	-
Saturniidae												
Hemileuca electra (Wright)	-	-	-	-	-	-	-	-	+	+	-	-
Saturnia walterorum Hog. & John.	-	-	+	-	-	-	-	-	-	-	-	-
Antheraea polyphemus (Cramer)	-	-	-	+	-	-	-	-	-	-	-	-
Hyalophora euryalus (Boisduval)	+	+	+	+	-	-	-	-	-	-	-	-
Sphingidae												
Manduca sexta (Linnaeus)	-	-	-	-	-	-	-	-	+	-	-	-
Sphinx perelegans Edwards	-	-	-	+	+	-	+	+	-	-	-	-
Smerinthus cerisyi Kirby	-	-	+	+	-	+	+	+	+	-	-	-
Pachysphinx occidentalis (Edw.)	-	-	-	-	-	-	-	+	-	-	-	-
Erinnyis ello (Linnaeus)	-	-	-	-	-	-	-	+	+	-	-	-
Hemaris diffinis (Boisduval)	-	-	-	-	-	-	+	-	-	-	-	-
Hyles lineata (Fabricius)	-	+	+	+	-	+	+	-	-	+	-	+
Notodontidae												
Clostera apicalis (Walker)	-	+	+	+	+	+	+	+	+	-	-	-
Datana perspicua Gr. & Rob.	-	-	-	-	-	-	-	+	-	-	-	-
Furcula cinerea (Walker)	-	-	-	+	+	-	+	+	+	-	-	-
Furcula scolopendrina (Bois.)	-	-	-	+	+	-	+	+	+	-	-	-
Dioptidae												
Phryganidia californica Packard	-	-	-	+	+	-	-	-	-	-	-	-
Arctiidae												
Crambidia dusca B. & McD.	-	-	-	+	+	+	-	+	+	+	+	-
Cisthene liberomacula (Dyar)	-	-	+	-	+	+	+	+	+	+	+	+
Cisthene deserta (Felder)	-	-	-	+	+	-	+	+	-	-	-	-
Cisthene dorsimacula (Dyar)	-	-	-	+	+	+	+	+	+	+	+	-
Cisthene perrosea (Dyar)	-	-	-	-	+	+	+	-	+	+	-	-
Cisthene faustinula (Boisduval)	-	-	-	-	-	-	-	-	+	-	-	-
Lycomorpha grotei (Packard)	-	-	-	-	-	-	-	-	+	-	-	-
Estigmene acrea (Drury)	-	-	+	-	-	-	-	-	-	-	-	-
Spilosoma vestalis Packard	-	-	+	+	-	-	-	-	-	-	-	-
Arachnis picta Packard	-	-	-	-	-	-	-	-	+	+	+	-
Apantesis hewletti B. & McD	-	-	+	+	+	-	-	-	-	-	-	-
Apantesis nevadensis (Gr. & Rob.)	-	-	-	-	-	-	-	+	+	+	-	-
Apantesis proxima (Guer.-Mene.)	+	+	+	+	+	+	+	+	+	+	+	+
Hemihyalia edwardsii (Packard)	-	-	-	-	-	-	-	-	-	+	-	-
Ctenucha brunnea Stretch	-	-	-	-	-	+	-	-	-	-	-	-

Months	J	F	M	A	M	J	J	A	S	O	N	D
Lymantriidae												
Orgyia vetusta (Boisduval)	-	-	-	+	+	+	-	-	-	-	-	-
Noctuidae												
Tetanolita palligera (Smith)	-	-	-	-	+	+	+	-	-	-	-	-
Mycterophora geometriformis Hill	-	-	-	-	-	-	-	+	+	-	-	-
Hemeroplanis finitima (Smith)	-	-	-	+	+	+	+	+	+	-	-	-
Hemeroplanis incusalis (Grote)	-	-	-	-	-	-	-	-	+	+	-	-
Melipotis indomita (Walker)	-	-	-	-	-	+	-	-	+	-	-	-
Melipotis jucunda Hübner	-	-	-	+	+	+	+	+	-	+	-	-
Bulia deducta (Morrison)	-	-	-	+	-	-	+	+	-	-	-	-
Synedoida ochracea (Behr)	-	-	-	-	+	+	+	-	+	-	-	-
Synedoida edwardsi (Behr)	-	-	+	+	-	+	+	+	+	-	-	-
Synedoida fumosa (Strecker)	-	-	-	+	+	+	+	+	+	+	-	-
Synedoida tejonica (Behr)	-	-	-	-	-	-	-	-	-	-	+	-
Ascalapha odorata (Linnaeus)	-	-	-	-	-	-	-	-	-	-	+	-
Zale insuda (Smith)	-	-	-	-	-	-	-	+	+	-	-	-
Zale termina (Grote)	-	-	-	-	-	+	-	-	-	-	-	-
Caenurgia togataria (Walker)	+	+	+	+	+	+	+	+	+	+	+	+
Catocala ilia (Cramer)	-	-	-	-	-	-	+	+	-	-	-	-
Catocala cleopatra Strecker	-	-	-	-	-	-	+	+	-	-	-	-
Catocala verrilliana Grote	-	-	-	-	-	+	+	+	-	-	-	-
Trichoplusia ni (Hübner)	-	-	-	+	+	-	-	+	+	+	+	-
Pseudeva palligera (Grote)	-	-	-	-	+	-	-	-	-	-	-	-
Autographa biloba (Stephens)	-	+	-	-	-	-	-	-	-	+	-	-
Autographa californica (Speyer)	+	-	+	+	+	-	-	-	-	+	+	+
Meganola fuscula (Grote)	-	+	+	+	-	-	-	-	-	-	-	-
Nola apera Druce	+	+	+	+	+	-	+	+	+	+	+	+
Tripudia balteata Smith	-	-	-	-	-	-	-	-	-	-	+	-
Cobubatha dividua (Grote)	-	-	-	-	-	-	-	-	-	+	-	-
Copibryophila angelica Smith	-	-	-	-	-	-	+	+	-	-	-	-
Eumicremma minima (Guenée)	-	-	-	-	+	+	+	+	+	-	-	-
Tarachidia candefacta (Hübner)	-	-	-	+	+	+	+	+	+	-	-	-
Conochares alter (Smith)	-	-	-	-	-	+	-	-	-	-	-	-
Conochares arizonae (Edwards)	-	-	-	-	-	-	-	-	-	+	-	-
Acontia cretata (Gr. & Rob.)	-	-	-	-	+	-	-	-	-	-	-	-
Acronicta othello Smith	-	+	+	+	+	+	+	+	+	+	-	-
Cryphia nanoides Franclemont	-	-	-	-	-	-	-	-	+	+	-	-
Cryphia viridata (Harvey)	-	-	+	+	+	+	+	+	+	-	-	+
Cryphia albipuncta (B. & McD.)	-	-	-	-	-	-	-	-	+	+	+	+
Apamea albina (Grote)	-	-	-	+	-	-	-	-	-	-	-	-
Apamea cinefacta (Grote)	-	-	+	+	-	-	-	-	-	-	-	-
Oligia marina (Grote)	-	-	-	+	+	+	-	-	-	-	-	-
Oligia tusa (Grote)	-	-	-	-	-	+	-	-	-	-	-	-
Oligia violacea (Grote)	-	-	-	+	+	+	-	-	-	-	-	-
Cobalos angelicus Smith	-	-	-	-	-	+	-	-	-	-	-	-
Xylomoia sp.	-	-	-	-	+	+	-	-	-	-	-	-
Benjaminiola colorada (Smith)	-	-	-	-	-	-	-	-	-	+	+	-
Mammifrontia riley Benjamin	-	-	-	-	-	+	+	-	-	+	+	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Archanara oblonga (Grote)	-	-	-	-	-	+	+	+	+	-	-	-
Helotropha reniformis (Grote)	-	-	-	-	-	+	-	-	-	-	-	-
Aseptis perfumosa (Hampson)	-	-	-	+	+	+	-	-	-	-	-	-
Aseptis n. sp.	-	-	-	-	-	-	+	-	-	-	-	-
Aseptis paviae (Strecker)	-	-	+	+	+	+	+	-	-	-	-	-
Aseptis pausis (Smith)	-	-	-	+	-	-	-	-	-	-	-	-
Aseptis genetrix (Grote)	-	-	-	-	+	+	-	-	-	-	-	-
Aseptis susquesa (Smith)	-	-	-	+	+	-	-	-	-	-	-	-
Chytonix divesta (Grote)	-	-	-	-	-	+	+	-	-	-	-	-
Properigea albimacula (B. & McD.)	-	-	-	-	+	+	+	+	-	-	-	-
Properigea suffusa (B. & McD.)	-	-	-	-	-	-	-	-	+	-	-	-
Pseudobryomima fallax (Hamp.)	+	+	+	-	-	-	-	-	-	+	+	+
Magusa orbifera (Walker)	-	-	-	-	-	-	+	-	-	-	-	-
Protoperigea posticata (Harvey)	-	-	-	-	-	-	-	-	-	-	+	-
Micranthetis triplex (Walker)	+	+	+	+	+	+	-	+	+	-	+	+
Platyperigea extima (Walker)	-	-	-	+	-	-	-	-	-	-	-	-
Platyperigea mona (B. & McD.)	-	-	-	-	-	-	-	+	+	+	-	-
Spodoptera exigua (Hübner)	+	+	-	+	+	+	+	+	+	+	-	-
Spodotera frugipera (Smith)	-	-	-	-	-	-	-	-	-	+	-	-
Spodotera ornithogalli (Guenée)	-	-	-	-	-	-	-	+	-	-	-	-
Galgula partita Guenée	-	-	-	-	-	-	-	-	-	+	-	-
Draudtia leucorena (Smith)	-	-	-	+	-	+	+	-	+	-	-	-
Draudtia funeralis (Hill)	+	+	+	+	+	+	-	-	+	-	+	+
Polenta tepperi (Morrison)	-	-	+	-	-	-	-	-	-	-	-	-
Lineostristiria olivalis (B. & McD.)	-	-	+	-	-	-	-	-	-	-	-	-
Nocloa rivulosa Smith	-	-	-	+	+	+	-	-	-	-	-	-
Cosmia calami (Harvey)	-	-	-	-	+	+	-	-	-	-	-	-
Homoglaea californica (Smith)	+	+	-	-	-	-	-	-	-	-	-	-
Homoglaea carbonaria (Harvey)	+	-	-	-	-	-	-	-	-	-	+	+
Pseudoglaea olivata (Harvey)	-	-	-	-	-	-	-	+	-	+	+	-
Agrochola purpurea (Grote)	-	-	-	-	-	-	-	-	-	-	-	+
Feralia februalis Grote	+	+	+	-	-	-	-	-	-	-	+	+
Pleromella opter Dyar	-	+	+	+	-	-	-	-	-	-	-	-
Pleromellodia cinerea (Smith)	+	-	-	-	-	-	-	-	-	-	-	+
Catabena lineolata Walker	-	-	-	+	-	-	-	-	-	-	-	-
Homoncocnemis fortis (Grote)	-	-	-	-	-	-	-	-	-	-	-	+
Oncocnemis nita Smith	-	-	-	-	-	-	-	-	-	+	+	-
Oncocnemis ragani Barnes	-	-	-	+	+	+	+	+	+	-	-	-
Lepipolys perscipta Guenée	+	+	+	+	+	-	-	-	-	-	-	-
Lepipolys behrensi (Grote)	-	-	-	+	-	-	-	-	-	-	-	-
Behrensia conchiliformis Grote	+	+	+	-	-	-	-	-	-	-	-	-
Cucullia serraticornis (Lintner)	+	+	+	-	+	-	-	-	-	-	-	-
Cucullia excissica Dyar	-	-	-	-	+	-	-	-	-	-	-	-
Cucullia eulepis (Grote)	-	-	-	-	-	-	-	+	-	-	-	-
Discestra chartaria (Grote)	-	-	-	-	-	-	-	-	+	-	-	-
Tripedia nova (Smith)	-	-	-	-	-	-	+	+	-	-	-	-
Admetovis similaris Barnes	-	-	-	+	+	+	-	-	-	-	-	-
Polia nipana (Smith)	-	-	-	+	+	+	-	-	-	-	-	-
Lacinipolia cuneata (Grote)	-	-	-	+	-	-	-	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Lacinipolia n. sp.	-	-	-	-	-	-	-	-	+	-	-	-
Lacinipolia stricta (Walker)	-	-	-	-	-	-	-	-	-	+	-	-
Lacinipolia strigicollis (Wallen.)	-	-	-	-	-	-	+	+	-	-	-	-
Lacinipolia quadrilineata (Grot.)	-	-	+	+	+	+	+	-	+	+	-	-
Lacinipolia patalis (Grote)	-	-	-	+	+	-	-	-	-	-	-	-
Dargida procincta (Grote)	-	-	-	-	-	-	-	-	-	+	-	-
Pseudaletia unipuncta (Haw.)	-	+	+	+	+	-	+	+	-	+	+	+
Leucania farcta (Grote)	-	-	+	-	-	-	-	-	-	-	-	-
Leucania februalis (Hill)	-	+	+	-	-	-	-	-	-	-	-	-
Leucania oaxacana Schaus	-	+	+	+	-	+	-	-	-	+	-	-
Perigonica tertia Dyar	+	+	+	+	-	-	-	-	-	-	-	-
Stretchia inferior Smith	-	+	+	-	-	-	-	-	-	-	-	-
Orthosia erythrolita (Grote)	+	+	+	+	+	-	-	-	-	-	+	+
Orthosia transparens (Grote)	+	+	+	+	+	-	-	-	-	-	-	-
Orthosia praeses (Grote)	+	+	-	-	-	-	-	-	-	-	+	+
Orthosia mys (Dyar)	+	-	-	-	-	-	-	-	-	-	+	+
Orthosia ferrigera (Smith)	-	+	+	-	-	-	-	-	-	-	-	-
Orthosia terminata (Smith)	+	+	+	-	-	-	-	-	-	-	-	+
Orthosia behrensiana (Grote)	-	+	-	-	-	-	-	-	-	-	-	-
Orthosia arthrolita (Harvey)	-	-	-	-	-	-	-	-	-	+	+	+
Orthosia pacifica (Harvey)	-	+	-	-	-	-	-	-	-	-	-	-
Orthosia hibisci (Guenée)	+	+	+	-	-	-	-	-	-	-	-	-
Egira hiemalis (Grote)	-	-	+	+	-	-	-	-	-	-	+	+
Egira crucialis (Harvey)	-	+	+	-	-	-	-	-	-	-	-	-
Egria cognata (Smith)	-	+	+	-	-	-	-	-	-	-	-	-
Egira curialis (Grote)	+	+	+	-	-	-	-	-	-	-	-	-
Egira rubrica (Harvey)	-	-	+	-	-	-	-	-	-	-	-	-
Anhimella contrahens (Walker)	-	-	-	-	-	-	+	-	-	-	-	-
Homorthodes communis (Dyar)	-	+	+	-	-	-	-	-	-	-	-	-
Protorthodes rufula (Grote)	+	+	+	-	-	-	-	-	-	+	+	-
Protorthodes alfkeni (Grote)	-	-	-	-	+	-	-	-	-	-	-	-
Protorthodes variablis (B. & McD.)	-	-	-	-	-	-	-	+	-	+	-	-
Protorthodes melanopis (Hamp.)	-	+	+	-	-	-	-	-	-	-	-	-
Ulolonche disticha (Morrison)	-	-	-	-	-	+	-	-	+	+	-	-
Zosteropoda hirtipes Grote	-	+	+	+	+	+	+	+	+	-	-	-
Miodera stigmata Smith	+	+	+	-	-	-	-	-	-	-	+	+
New gen., new sp.	+	+	+	-	-	-	-	-	-	-	-	-
Tricholita fistula Harvey	-	-	-	-	-	-	-	-	+	+	+	-
Agrotis vetusta Walker	-	-	-	-	-	-	-	-	-	+	+	-
Agrotis venerabilis Walker	-	-	-	-	-	-	-	-	-	+	+	-
Agrotis ipsilon (Hufnagel)	+	+	+	+	-	+	+	+	+	+	+	+
Agrotis subterranea (Fabricius)	-	-	-	-	-	-	-	-	-	-	+	+
Euxoa atomaris (Smith)	-	-	-	-	-	-	-	-	-	-	+	-
Euxoa auxiliaris (Grote)	-	-	-	-	-	-	-	-	-	-	+	-
Euxoa septentrionalis (Walker)	-	-	-	-	-	-	-	-	-	+	+	-
Euxoa olivia (Morrison)	-	-	-	-	-	-	-	-	-	-	+	-
Euxoa tocoyae (Smith)	-	-	-	+	-	-	-	-	-	-	-	-
Euxoa simulana McDunnough	-	-	-	-	+	-	-	-	-	-	+	-
Euxoa brunneigera (Grote)	-	-	-	+	-	-	-	-	-	-	-	-

Months	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Euxoa selenis (Smith)	-	-	-	-	-	-	-	-	-	+	+	-
Euxoa henrietta (Smith)	-	-	-	-	-	-	-	-	-	-	+	-
Euxoa perexcellens (Grote)	-	-	-	-	-	-	-	-	-	+	+	-
Euxoa difformis (Smith)	-	-	-	-	-	-	-	-	-	+	+	+
Pseudorthosia variabilis Grote)	-	-	-	-	-	-	-	+	+	+	+	-
Hemieuxoa rudens (Harvey)	-	-	+	+	-	+	+	-	+	-	+	+
Peridroma saucia (Hübner)	+	+	+	+	-	+	-	-	-	-	+	+
Anomogyna infimatis (Grote)	-	-	-	-	-	-	-	-	+	+	+	+
Adelphagrotis indeterminata (W.)	-	-	-	-	-	-	-	-	+	+	+	-
Abagrotis kirkwoodi Buckett	-	-	-	-	-	-	-	-	-	+	+	-
Abagrotis denticulata McD.	-	-	-	-	-	-	-	+	-	-	-	-
Parabagrotis formalis (Grote)	-	-	+	+	+	+	+	+	+	-	+	-
Heliothodes diminutivus (Grote)	-	-	-	+	+	+	-	+	-	-	-	-
Helicoverpa zea (Bodie)	-	-	-	+	+	-	-	+	+	-	-	-
Heliothis phloxiphagus G. & R.	-	-	-	-	-	+	-	+	-	-	-	-
Schinia pulchripennis (Grote)	-	-	+	+	-	-	-	-	-	-	-	-
Schinia buta Smith	-	-	-	-	-	-	+	+	-	-	-	-
Schinia oleagina Morrison	-	-	-	-	-	-	-	-	+	-	-	-
Schinia oculata Smith	-	-	-	-	-	-	-	+	+	-	-	-

[1] species observed only, not collected

INSTRUCTIONS TO AUTHORS

Manuscript format: Two copies *must* be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. Italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All **measurements** must be metric. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (e.g. 6.IV.1992). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

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