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New and revised descriptions of the immature stages of some butterflies in Sri Lanka and their larval food plants (Lepidoptera: Nymphalidae). Part 1: Sub-family Danainae

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Abstract. The immature stages of the 12 species of butterflies of the subfamily Danainae and their larval food plants in Sri Lanka are presented. The immature stages of six species and their larval food plants are documented for the first time. The immature stages of the remaining six species that have been previously described from Sri Lankan material are compared to findings of the current study and additional observations are presented. For these six species, new larval food plants are reported for the first time. For two of these species, larval food plants previously reported in Sri Lanka are confirmed. This study provides the basic information for further studies on the biology of these species. It also provides information for conservation management programs for butterflies in Sri Lanka.

Keywords: Immature stages, larval food plants, Sri Lanka, Ceylon, Danainae, Lepidoptera, butterflies, conservation.

Introduction

The first butterfly described from Sri Lanka (then known as Ceylon) was *Papilio hector* (now *Pachliopta hector*) by Linnaeus in 1758 (d'Abrera, 1998). In 1861, Sir J. Emerson Tennent listed a few butterflies known from the island in his book Sketches of the Natural History of Ceylon. Several major works followed, most notably Moore (1880, 1881) and Woodhouse in several editions (1942, 1949, 1950) (Appendix A) but the immature stages and larval food plants of many species were undescribed or described only briefly.

Woodhouse (1950) published descriptions of the immature stages of 191 species of butterflies in the island out of a total of 242. Of these descriptions, 80 were based on work done in Sri Lanka (mostly based on Moore (1880) and published and unpublished accounts of E. E. Green, Tunnard, Manders and Wiley) and 111 were based on work done in peninsular India by Bell, Marshall, de Nicéville and others. The immature stages of 51 species (including endemics and non-endemics) still remained unknown and undescribed in Woodhouse.

Little work has been published since Woodhouse though several individuals have reared many of the undescribed species of butterflies. Unfortunately, several recent books have repeated information from Woodhouse uncritically and so have propagated errors and misinformation. Many of the larval food plants used in India either do not occur in Sri Lanka or are not used by the same species in Sri Lanka or if it is used, it is not the preferred plant.

Sri Lanka is an island off the tip of India and is considered geographically and zoogeographically as part of the Indian subcontinent. Sri Lanka and the Western Ghats in India are considered one of the 25 biodiversity hotspots in the world by Conservation International. The island is broadly divided into 7 climatic zones (Fig. 1) (Sri Lanka, Ministry of Foresty and Environment, 1999). The arid zone (altitude 0-100 m) occurs as a small strip of land on the north-west coast and on the south-east coast. Rainfall is less than 1250 mm per year, occuring mainly from October to January with more than 5 dry months (less than 50 mm rainfall per month). The dry zone (altitude 0-500 m) covers most of the north and south-east of the island. Rainfall is 1250-1900 mm per year,

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occuring mainly from October to January with 4-5 dry months per year (less than 50 mm rainfall per month). The intermediate zone (altitude 0-1000 m) is found between the dry and wet zones. Rainfall is 1900-2500 mm per year with fewer than 3 dry months (less than 50 mm rainfall per month). The lowland wet zone (altitude 0-1000 m) covers the south-west coast and the central regions. Rainfall is 2500-5000 mm per year and there are no dry months. The submontane wetlands (altitude 1000-1500 m) receive 2500-5000 mm of rain per year with no dry months. The wet highlands (altitude 1500-2500 m) receive 2500-5000 mm of rain per year with no dry months. The intermediate highlands (altitude 1000-1500 m) receive 1900-2500 mm of rain per year with fewer than 3 dry months (less than 50 mm rainfall per month).

In the current study (conducted from 2004 to the present and ongoing), we have documented the immature stages and larval food plants of 162 of the 245 known species of butterflies in Sri Lanka.

In Part 1, we present the immature stages and larval food plants of the 12 species of the family Nymphalidae, subfamily Danainae, tribe Danaini. The immature stages of 6 species and their larval food plants in Sri Lanka are documented for the first time. The immature stages of the remaining 6 species have been previously described from Sri Lankan material. These descriptions are compared to the findings of the current study and additional observations are presented. For these six species, new larval food plants are reported for the first time. For two of these species, larval food plants previously reported in Sri Lanka are confirmed.

Adapted from: Sri Lanka, Ministry of Forestry & Environment, 1999.

Figure 1. Climatic zones of Sri Lanka

Materials and methods

Eggs, larvae and/or pupae were collected in the field and raised to eclosion in suitable containers with the larval food plant. Wherever possible, a potted plant covered with netting was used to rear the larvae in order to provide as natural a setting as possible to observe behavior and to provide a more natural place for the larva to pupate. If potted plants were not available, stems or branches of the plant were kept in a bottle of water and placed under netting. When the stem or branch was consumed or no longer suitable, new ones were introduced into the bottle alongside the old ones so that the larva could transfer to the fresh plant material on its own. Otherwise, pieces of the larval food plant were placed into a container with the larva and replenished as necessary, as in the case of flowers, fruits and mealy bugs. Twigs, leaves, branches, or soil were provided as necessary for the mature larva to pupate. All adults that eclosed normally were released to their place of origin. A plant was determined to be a true larval food plant if the larva successfully emerged as an adult.

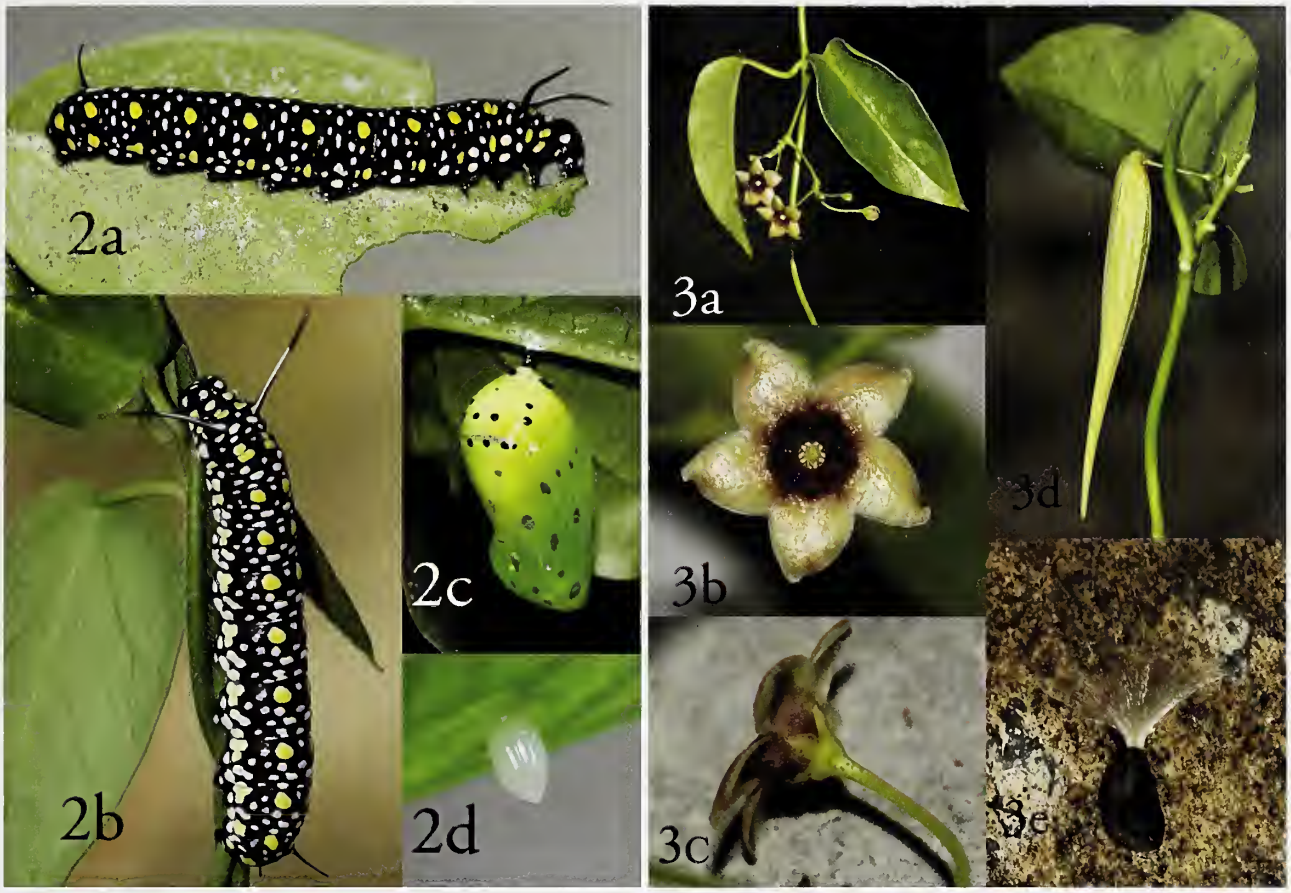
Conventions used: Segments are numbered S1 to S14 (S1 is the head; S2–4 are the 3 segments of the thorax and S5–14 are the 10 segments of the abdomen). These are applied to both the larva and the pupa.

Results and discussion

Tribe: Danaini
Sub-tribe: Danaina

Parantica aglea aglea (Stoll, 1782) (Glassy Tiger)

The final instar larva and pupa of *Parantica aglea aglea* were described by Moore (1880) from Sri Lankan material. The larva and pupa of *P. aglea* were described by Bell (1909) from Indian material and quoted in Woodhouse (1950). These descriptions agree with the findings of the current study except for the following points: in *P. a. aglea*, a) in the larva,



Figures 2-3. **2**. *Parantica aglea aglea*. **2a**. Larva, final instar feeding on *Tylophora indica*. **2b**. Larva, final instar feeding on "kiri anguna." **2c**. Pupa. **2d**. Egg. **3**. Kiri anguna. **3a**. Inflorescence and leaves. **3b**. Flower. **3c**. Flower (ventral view) and calyx. **3d**. Seed pod. **3e**. Seed.

the filaments on S3 are black with white on the inside for about half the length, and the filaments on S12 are all black (not claret red as in Bell) (Fig. 2a, b); and b) the pupa often has a transverse silver line on S7 connecting the black spots (Fig. 2c).

Additional notes on immature stages: Egg: white, elongate, tapered to the apex, flattened at base, 18 longitudinal ribs with numerous fine transverse ridges (Fig. 2d). Duration of immature stages: pupation to eclosion 9 days; hatching to eclosion 22 days.

Larval food plants: In Sri Lanka, "*Cryptolepis*, &c" was reported by Moore (1880) and "*Calotropis*" was reported by Thwaites (Moore, 1890-92). In addition, *Tylophora tenuissima* was recorded by Woodhouse (1950), based on Bell (1909) reporting from India.

The current study showed for the first time that the following are larval food plants in Sri Lanka: *Tylophora tenuissima*, *Tylophora indica*, *Heterostemma* cf *tanjorense* and two additional as yet unidentified plant species of the family Asclepiadaceae. The authors have successfully reared *P. a. aglea* on a plant called kiri anguna in Sinhalese (note that in Sri Lanka, many different species have the local common name of kiri anguna). This plant is extensively cultivated in Sri Lanka as a green vegetable and is probably an introduced plant, likely a species of *Tylophora* (Fig. 3a–e). The other unidentified plant is a vine found in Wellawaya (H. D. Jayasinghe, pers. comm.) but flowers and fruits have not yet been seen. In the current study, the larvae of *P. a. aglea* that were collected from many different locations refused to feed on *Cryptolepis buchananii* or *Calotropis gigantea*.

P. a. aglea is common over most of the island and is also seen in the higher elevations where these larval food plants are not found. *P. a. aglea* is a migratory species and it is possible that the butterflies that are seen in the higher elevations are simply passing through. If they are breeding residents, there must be another larval food plant.

Figures 4-5. **4**. *Parantica taprobana*. **4a**. Larva, final instar feeding on *Cynanchum alatum*, lateral view. **4b**. Larva, final instar, feeding on *Cynanchum alatum*, dorsal view. **4c**. Pupa. **4d**. Eggs. **5**. *Ideopsis similis exprompta*. **5a**. Egg. **5b**. Larva, first instar. **5c**. Larva, second instar, feeding on *Tylophora indica*. **5d**. Larva, third instar. **5e**. Larva, final instar. **5f**. Pupa, ventro-lateral view. **5g**. Pupa, dorso-lateral view.

Parantica taprobana (Felder & Felder, 1865) (Sri Lankan Tiger)

The final instar larva and pupa of *Parantica taprobana* (endemic to Sri Lanka) were described briefly by Tunnard (Woodhouse, 1950) from Sri Lankan material. This description of the larva agrees with the findings of the current study except for the following points: in *P. tabrobana*, a) the larvae are purplish-brown with white and yellow markings (not "black and white"), b) subspiracular line yellow, c) S2–S13 with a yellow subdorsal spot, d) S14 with a white subdorsal spot which sometimes coalesces to form a band, e) filaments on S3 slope forwards while those on S12 slope backwards or are held almost vertically, f) filaments black with white inside and outside along the entire length, and g) large, white triangular spot at the apex of the clypeus (Fig. 4a, b).

Tunnard's description of the pupa agrees with the findings of the current study except for the following points: in *P. tabrobana*, a) black spots on S7 embedded on a wide silver-colored transverse band, b) S8 with 6 black spots, c) S9 with no spots, d) S13 with 2 black spots, e) cremaster black, f) S5 with 2 silver spots, g) S6 with 5 silver spots, h) S4 with no markings, i) S3 with 8 large silver spots, j) eye with one silver spot and k) several silver spots on the wings. The pupa is very similar to that of *P. aglea aglea* but *P. taprobana* is more cone-shaped from the last abdominal segment to the widest segment of the abdomen (rounded in *P. aglea aglea*) and the silver spots are usually larger and more extensive (Fig. 4c). These observations indicate that the larva and pupa are much more variable than described by Tunnard.

Additional notes on immature stages: Egg: white, elongate, tapered to apex, broadly flattened at base, longitudinal ribs with numerous fine transverse ridges (Fig. 4d). 1st instar: Newly emerged larva—head

black, body grayish, tiny filaments on S3 and S12; ate most of eggshell, then rested for several hours. One day later—body uniformly brownish gray, white transverse lines, white subdorsal and sublateral spots; ate stem as well as leaves; never very active.

Duration of immature stages: oviposition to emergence 4–5 days; emergence to 1st molt 3–5 days; 2nd instar 6.5 mm length; 1st to 2nd molt 2–3 days; 3rd instar 9 mm length; 2nd to 3rd molt 3–4 days; 4th instar 19 mm length; 3rd to 4th molt not recorded; 5th instar 30 mm length; 4th molt to pupation not recorded; length at pupation 40 mm; emergence to pupation 18–26 days; pupation to eclosion not recorded.

Larval food plants: In Sri Lanka, Manders (1903) reported that *P. taprobana* had been "frequently bred by Mr. Green, myself and others...on *Tylophora asthmatica*" [now *T. indica*] (family Asclepiadaceae). Tunnard tentatively identified the larval food plant in his study as *Ceropegia thwaitesii* (family Asclepiadaceae). Mackwood (1919) published a second-hand report that the larva feeds on *Allaeophania decipiens* (family Rubiaceae) [now *Metabolus decipiens*].

The current study showed for the first time that one of the larval food plants in Sri Lanka is *Cynanchum alatum* (family Asclepiadaceae). *Cy. alatum* has been reported from only two locations in Sri Lanka—Maturata and Hakgala (Dassanayake, 1983). However, in the current study, *P. taprobana* was seen ovipositing on *Cy. alatum* near Ambawella (Nuwara Eliya) and the plant was quite abundant along the roadsides. It is possible that *Cy. alatum* is more widespread than previously believed.

Larvae have also been found on a plant that has not yet been unidentified—in Haputale, *P. taprobana* was reared on an asclepid which is likely a species of *Tylophora* (S. Sanjeewa, pers. comm.).

Another possible larval food plant is *Tylophora cordifolia*. The authors observed a ♀ ovipositing on this plant in the Knuckles area but were not able to confirm that the larvae actually fed on this plant. Eggs that were collected did not hatch and no larvae or pupae were seen on the plant at subsequent visits.

Neither *Ceropegia thwaitesii* nor *M. decipiens* have been confirmed as a larval food plant. *Ce. thwaitesii* is a rare plant of the moist hill country and has not been found by any recent collector (Dassanayake, 1983). However since it is found in the range of *P. taprobana*, it is possible that it, or another species of *Ceropegia*, is a larval food plant. *M. decipiens* is probably not a larval food plant since no members of the family Rubiaceae are known to be used by species of *Parantica*. In the current study, we have been unable to confirm whether or not *T. indica* is a larval food plant, though it is very likely.

P. taprobana is common above 1200 m asl though it is found as low as 800 m asl.

Ideopsis similis exprompta Butler, 1874 (Blue Glassy Tiger)

There are no records of the immature stages of *Ideopsis similis exprompta*. In the current study, the immature stages are described for the first time.

Notes on immature stages: On January 26, 2006, the authors observed a ♀ in a coconut land on the west coast near Pamunugama oviposit on a plant that was later identified as *Parsonsia alboflavescens* (family Apocynaceae). The eggs were laid singly on the underside of the leaves. The ♀ spent considerable time flying slowly near the plant before it oviposited. Three larvae emerged from these eggs but refused to feed on *P. alboflavescens* on which they were laid. They readily ate the leaves of *Tylophora indica* (family Asclepiadaceae) and emerged as normal adults after pupation. *I. s. exprompta* was subsequently observed ovipositing on *T. indica* in the Sinharaja Forest Reserve. The larvae fed on *T. indica* and adults emerged successfully and were released back into the forest.

Egg: white, elongate, tapering to the apex, flattened at base, 12 longitudinal ribs with numerous fine transverse ridges (Fig. 5a). 1st instar: Newly emerged larva—head black, abdomen translucent with many fine, light-pink transverse lines along its length, small pink stubby filaments on S3 and S12, feeds on the eggshell as its first meal (Fig. 5b). 2nd instar: body light brownish-red with whitish spots all over, filaments brownish-red and slightly longer (Fig. 5c). 3rd instar: body purplish-brown with small whitish indistinct spots, filaments purplish-brown and longer (Fig. 5d). 4th instar: Not recorded. 5th instar: head black, body dark purplish-brown with small well-defined white to cream-colored spots, filaments black with claret-red bases and longer (Fig. 5e). The larva remains on the underside of a leaf near the ground and is rarely seen in the open.

Pupa: Pupation on the underside of fresh leaves near the ground. Pupa green with black and silver markings. Very similar to that of the *Parantica aglea aglea* but on S2 of *I. similis exprompta* there is a pair of silver spots with large black centers; on S5 above the silver line, only a single pair of black spots laterally below the spiracles (Fig. 5f-g).

Duration of immature stages: oviposition to emergence 3–5 days; molt (4 molts) every 2–4 days; length before pupation 35 mm; hatching to pupation 12–20 days; pupation to eclosion 7 days; hatching to eclosion 19–27 days.

Larval food plants: There are no published records

of the larval food plant in Sri Lanka. The current study showed for the first time that one of the larval food plants in Sri Lanka is *Tylophora indica* (family Asclepiadaceae).

T. indica is widely distributed over the island in all climatic zones up to about 1000 m asl though it is less common at the higher elevations.

I. s. exprompta occurs in the wet zone below 500 m asl but is restricted to the south-west coast from Negombo to Galle. Within this range, it occurs most commonly within a few kilometers of the coast, especially in mangrove and marsh habitats. However, it also occurs further inland in forest reserves such as Sinharaja, Morapitiya and Kanneliya. The reason for the very restricted distribution of *I. s. exprompta* despite the very wide distribution and availability of its larval food plant is not clear. There are also some locations (e.g. Sri Jayawardenapura) where *I. s. exprompta* is common but *T. indica* appears to be absent. These facts suggest that there is another larval food plant. The refusal of the larvae to feed on *P. alboflavescens* in the current study does not necessarily indicate that the plant is not used. The ♀ oviposited on the plant after much deliberation; perhaps the plant material offered to the larvae in the current study was unsuitable in some respect.

Tirumala limniace exoticus Gmelin, 1790 (Blue Tiger)

The final instar larva and pupa of *Tirumala limniace exoticus* were described by Moore (1880) from Sri Lankan material. The larva and pupa of *T. limniace* were described by Bell (1909) from Indian material and quoted by Woodhouse (1950). The descriptions of the larva agree with the findings of the current study except for the following points: in *T. l. exoticus*, a) spiracular band yellow to yellowish-brown and b) planta white (Fig. 6a). The descriptions of the pupa agree with the findings of the current study except for the following points: in *T. l. exoticus*, a) all spots that Bell described as golden are silver, b) spiracles oval to slit-like, and c) knobby transverse band on S7 silvery, not gold with a black streak below the band at the lateral edges. These differences may be significant in the identification of *T. l. exoticus* (Fig. 6b).

Additional notes on immature stages: Egg: white, cylindrical, tapered to apex, longitudinal ribs with numerous transverse ridges. 1st instar: Newly emerged—head dark brown, abdomen bluish creamy-white; after one day—head black, abdomen light brown with white transverse stripes apically and basally, S2 and S14 mostly white, filament buds on S3 and S12 (Fig. 6c). 2nd instar: similar to 1st instar except abdomen darker brown, filaments dark brown and longer (Fig. 6d).

Duration of immature stages: emergence to first molt 5 days; subsequent molts every 2–3 days (4 molts in all); pupation to eclosion 4–8 days; emergence to eclosion 19 days.

Larval food plants: In Sri Lanka, "*Asclepias*" was reported by Moore (1880). "*Dregia volubilis, Asclepias* and sometimes ...*Calotropis* or *Hoya*" were reported as larval food plants by Woodhouse (1950), based on Bell (1909) reporting from India. It should be noted that the generic names *Asclepias* and *Hoya* have been previously applied to other genera, for example, *Tylophora*, so it is impossible to determine to which species Bell or Moore referred.

The current study showed for the first time that one of the larval food plants in Sri Lanka is *Wattakaka volubilis* (syn. *Dregea volubilis*) (family Asclepiadaceae). It also showed that *Calotropis* is unlikely to be a larval food plant in Sri Lanka as all larvae tested refused to feed on *Calotropis gigantea.*

T. l. exoticus is very common in the dry and intermediate zones and can be seen at higher elevations while flighting. *W. volubilis* is common in the dry and intermediate zones (Dassanayake, 1983) up to about 1000 m asl. If *T. l. exoticus* is breeding in the higher elevations, there must be another larval food plant.

Tirumala septentrionis musikanos Fruhstorfer, 1910 (Dark Blue Tiger)

There are no records of the immature stages of *Tirumala septentrionis musikanos.* In the current study, the immature stages are described for the first time.

Notes on immature stages: On October 10, 2010, a ♀ was observed in Moneragala ovipositing on a plant and the eggs were raised successfully to eclosion but on *Wattakaka volubilis* leaves (H. D. Jayasinghe, pers. comm.). On December 4, 2010, the authors also observed a ♀ ovipositing in the same location on the same plant. This plant has been tentatively identified as *Heterostemma* cf *tanjorense* (family Asclepiadaceae). Larvae of various sizes were also found on several other plants nearby. The eggs and larvae were successfully raised to eclosion on the leaves of this plant as well as on leaves of *Wattakaka volubilis.*

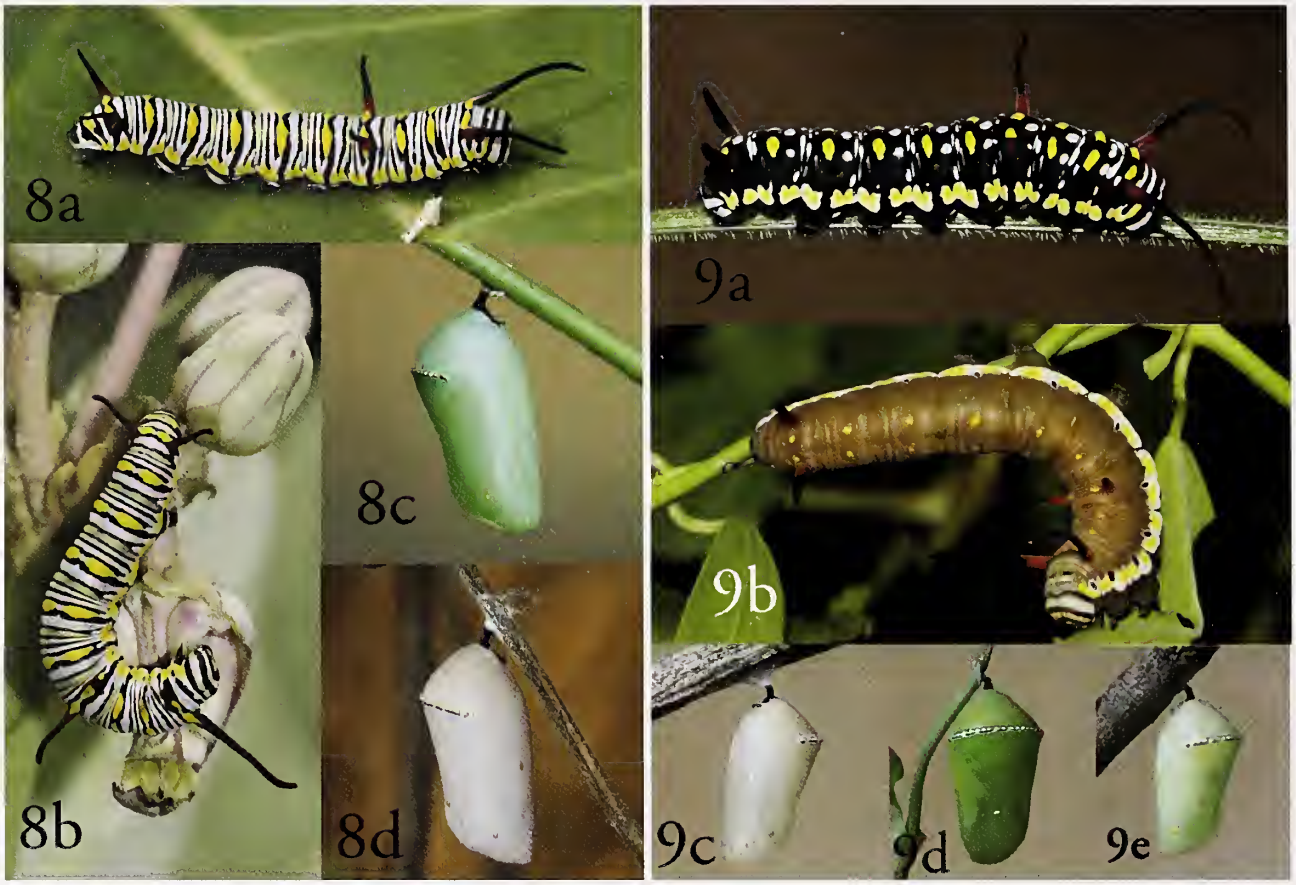
Egg: white, elongate, tapered to apex, flattened at base; 18 longitudinal ribs and numerous transverse ridges (Fig. 7a). 1st instar: newly emerged larva consumed its eggshell, then fed on the underside of the leaf; head black and abdomen white with black spot on S2 immediately after hatching; within a few hours abdomen green; one day later: abdomen yellowish-green with 2-3 light gray transverse bands

Figure 6-7. 6. *Tirumala limniace exoticus.* **6a.** Larva, final instar. **6b.** Pupa. **6c.** Larva, first instar showing method of feeding. **6d.** Larva, second instar, head capsule still adhering. **7.** *Tirumala septentrionis musikanos.* **7a.** Egg. **7b.** Larva, second instar, close-up of head. **7c.** Larva, second instar. **7d.** Larva, third instar, close up of head. **7e.** Larva, third instar. **7f.** Final instar, close up of head. **7g.** Larva, final instar. **7h.** Pupa, dorso-lateral view. **7i.** Pupa, dorso-lateral view. **7j.** Pupa, ventral view.

on each segment, S2 with black subdorsal spots, S3 dorsum flat with 2 very slight protuberances, S12 with 2 very slight protuberances, prolegs black. 2nd instar: head black with two light bluish-gray transverse stripes on the side, clypeus and base of antenna bluish-gray (Fig. 7b); abdomen light bluish-gray with dark maroon to brownish transverse stripes above the spiracular band, S2 with black subdorsal spot; stubby dark maroon filaments with white base on S3 and S12, obscure yellowish spiracular band, prolegs with white transverse band and black line below (Fig. 7c). 3rd instar: very similar to 2nd instar but filaments longer, and blue transverse bands on head longer and closer to dorsal line (Fig. 7d, e). 4th instar: filaments longer, white markings along filaments dorsally and ventrally extended towards the tip. 5th instar: blue bands on the head converge at the dorsum, much variation in the width of the dark transverse stripes which are closer to black, spiracular band more pronounced in some individuals while in others it is reduced to a series of disjointed dark yellow spots (Fig. 7f, g). Pupa: light green, cremaster black, silver spots variable but often seen on eye, wing bases and sub-dorsally on S2-S4; on S5, three silver spots (one dorsal, two subdorsal); S7 with knobby silver transverse band with short black band below at center and laterally (Fig. 7h, i, j).

Duration of immature stages: oviposition to emergence 2–4 days; emergence to 1st molt 2–3 days; 2nd instar 5 mm length; 1st to 2nd molt 1–2 days; 2nd to 3rd molt 2 days; 4th instar 20 mm length; 3rd to 4th molt 1–3 days; 5th instar 38 mm length immediately after molt; 4th molt to pupation 4–5 days; length at pupation 45 mm; emergence to pupation 21 days; pupation to eclosion 10 days.

Larval food plants: In Sri Lanka, "of the family Asclepiadaceae" was reported by Ormiston (1924). However, this record seems to have been based on MacKinnon & de Nicéville (1897) who recorded the



Figures 8-9. 8. *Danaus chrysippus chrysippus.* **8a.** Larva, final instar. **8b.** Final instar, feeding on flower buds of *Calotropis gigantea.* **8c.** Pupa, green form. **8d.** Pupa, whitish form. **9.** *Danaus genutia genutia.* **9a.** Larva, final instar, purplish maroon form. **9b.** Final instar, brown form. **9c.** Pupa, straw-colored. **9d.** Pupa, green. **9e.** Pupa, light green.

larval food plant for *T. septentrionis* in the Dun, India as *Vallaris dichotoma* (family Asclepiadaceae). The current study showed for the first time that one of the larval food plants in Sri Lanka is *Heterostemma* cf *tanjorense* (family Asclepiadaceae). A ♀ was observed in the Nitre Cave area in the Knuckles ovipositing on another plant (a large vine) that is yet unidentified (H. D. Jayasinghe, pers. comm.). *H. tanjorense* has not been recorded from this area.

Heterostemma tanjorense is reported as being rare in the wet zone but "not uncommon in the dry country along the east coast (Trincomalee to Amparai Districts)" (Dassanayake, 1983). It has not previously been recorded from Moneragala.

Although *T. s. musikanos* was earlier reported to be very common and widely distributed in the island (Woodhouse, 1950), it now appears to be common only in the plains of the east and southeast. It is uncommon in the northwest, scarce in the west and southwest, and seen in the hills only during migrations.

The distribution of *Heterostemma tanjorense* fits with most, but not all, of the distribution of *T. s. musikanos,* though it is possible that the distribution of *H. tanjorense* has not been fully documented. *Vallaris solanacea* is the species found in Sri Lanka though it is rare and not found where the butterfly is. There are no records of either species being used as larval food plants in Sri Lanka. Though the larvae were raised successfully on *Wattakaka volubilis* in the lab, there is no evidence that it feeds on this plant in the field.

Danaus chrysippus chrysippus (Linnaeus, 1758) (Plain Tiger)

The final instar larva and pupa of *Danaus chrysippus chrysippus* were described from Sri Lankan material by Moore (1880) and by Tunnard (Woodhouse, 1950). The larva and pupa of *D. chrysippus* were described

by Bell (1909) from Indian material and quoted by Woodhouse (1950). In general, these descriptions of the larva agree with the findings of the current study except for the following point: in *D. c. chrysippus*, only S14 has yellow spots wanting (S2 & S13 also wanting in Bell 1909) (Fig. 8a, b). These descriptions of the pupa also agree with the findings of the current study except for the following points: in *D. c. chrysippus*, on S7, a) there is only a single row of beads (double row reported by Bell); and b) the transverse band is golden above, then silver, then black below (Bell records only gold and black) (Fig. 8c, d).

Additional notes on immature stages: Egg: white, cylindrical, domed at apex, broadly flattened at base.

Larval food plants: In Sri Lanka, *Calotropis gigantea* and *Asclepias curassavica* were reported by Moore (1880), and *Gomphocarpus physocarpus* was reported by Tunnard (Woodhouse, 1950). The current study confirmed these three species as larval food plants in Sri Lanka and showed for the first time another new larval food plant: *Pentatropis capensis* (family Asclepiadaceae). The larva feed on leaves, flowers and flower buds of *Calotropis gigantea*, and on the leaves of *Pentatropis capensis*.

D. c. chrysippus is common over most of the island. *C. gigantea* is the most widely used larval food plant in the arid, dry and intermediate zones though the butterfly seems to have its highest preference for *A. curassavica*, a cultivated plant. *P. capensis* and *C. gigantea* are used in the dry coastal areas. When *P. capensis* was grown further inland (45 km) from the coast in the intermediate zone where it is not naturally found, adults of *D. c. chrysippus* did not use it for oviposition—perhaps the populations in this zone are sufficiently differentiated to feed on other plants. *A. curassavica* and *G. physocarpus* (a naturalized introduction) are used in the mid- and high elevations. It is possible that there is another larval food plant that is a native plant at the higher elevations.

Danaus genutia genutia (Cramer, 1779) (Common Tiger)

The final instar larva and pupa of *Danaus genutia genutia* were described briefly by Moore (1880) from Sri Lankan material. The larva and pupa of *D. genutia* were described by Bell (1909) from Indian material and were quoted by Woodhouse (1950). In general, these descriptions of the larva agree with the findings of the current study except for the following point: in *D. g. genutia*, the ground color of the larva is seldom black (as recorded by Bell) but is usually dark purplish-maroon to light brown (Fig. 9a, b). These descriptions of the pupa agree with the findings of the current study except that in *D. g. genutia*, the color of the pupa varies from pale straw-colored to green (Fig. 9c, d, e).

Additional notes on immature stages: Egg: white, elongate, tapered to apex, flattened at base.

Larval food plants: There are no published records of the larval food plant in Sri Lanka. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Oxystelma esculentum*, *Cynanchum tunicatum* and *Tylophora tenuissima*.

Although Woodhouse (1950) reported *Stephanotis* spp., *Raphis pullchellum* [*sic*], *R. lemma*, *Passularia*, *Ceropegai* [*sic*] *intermedia*, this was based on Indian records quoted in Bell (1909) and Moore (1890-92). Moore (1890-92) quoted *Raphis pulchellum* after Chaumette, *Raphis lemma* and *Passularia* after Grote and *Ceropegia intermedia* after Elliot. None of these plants is found in Sri Lanka except for *C. intermedia* (now *Ceropegia candelabrum*). *Raphis pulchellum* and *R. lemma* seem to be written in error. The genus *Raphis* is of the family Poaceae (Grasses) and is unlikely to be a larval food plant for this butterfly. *R. pulchellum* and *R. lemma* are likely to be *Raphistemma pulchellum* (family Asclepiadaceae) though this genus is not found in Sri Lanka. *Passularia* also appears to be written in error as there is no such genus and perhaps what was meant was *Passerina* (Thymelaeaceae family), which is a genus that is also not found in Sri Lanka. *Ceropegia candelabrum* is widely distributed in the dry zone and extends into the wet zone (Dassanayke, 1983), but its use as a larval food plant has so far not been recorded.

D. g. genutia is common and found over most of the island and appears to use different larval food plants depending on the region. *Cynanchum tunicatum* is not uncommon in the drier areas of the island (Dassanayke, 1983). *Oxystelma esculentum* is more common in swampy areas of the dry coastal belt (Dassanayke, 1983). *Tylophora tenuissima* was used in the mid-elevations at Soragune (Haldumulla) and at Kurunegala in the intermediate zone.

Subtribe: Euploeina

Euploea core asela Moore, 1877 (Common Indian Crow)

The final instar larva and pupa of *Euploea core asela* were described from Sri Lankan material by Moore (1880) and by Tunnard (Woodhouse, 1950). The larva and pupa of *E. core* were described by Bell (1909) from Indian material and quoted by Woodhouse (1950). These descriptions of the larva and pupa agree with the findings of the current study except for the following point: in *E. c. asela*, in the pupa, the ground color is highly variable, ranging from yellow to lemon-

green to beige to brown (Fig. 10a, b, c, d, e, f).

Additional notes on immature stages: Egg: yellowish, cylindrical but wider sub-apically, tapered at apex, honey-comb-like depressions. 1st instar: newly emerged larva—head black, abdomen uniformly pale green, last segment green or with a black spot, legs black; 1 day later—abdomen brownish-yellow with tiny filament buds.

Duration of immature stages: oviposition to emergence 3 days; emergence to first molt 2 days; next 3 molts every 1–3 days; length of larva before pupation 55 mm; length of pupa 21 mm; pupation to eclosion 6 to 10 days; oviposition to eclosion 18 to 23 days.

Larval food plants: In Sri Lanka, "*Nerium oleander*, &c." was reported by Moore (1880), and *Nerium oleander* and *Ficus religiosa* were reported by Tunnard (Woodhouse 1950). Tunnard also reported that the larvae fed on *Gomphocarpus physocarpus* though the ♀ did not oviposit on that plant.

The current study confirmed *N. oleander*, *F. religiosa* and *G. physocarpus* as larval food plants in Sri Lanka. It also showed for the first time that the following plants are larval food plants in Sri Lanka: *Ficus pumila*, *Ficus benjamina* (family Moraceae); *Cryptolepis buchananii*, *Hemidesmus indicus* (family Periplocaceae); *Adenium obesum*, *Allamanda cathartica*, *Parsonsia alboflavescens*, *Ichnocarpus frutescens* (family Apocynaceae); and *Pentatropis capensis* (family Asclepiadaceae). Larvae have also been successfully reared on a plant near Soragune, Haldumulla called 'gon-na' in Sinhalese (S. Sanjeewa, pers. comm.). This plant has been tentatively identified as *Ochrosia oppositifolia* (family Apocynaceae).

E. c. asela is common over most of the island. The larva feeds on a variety of widely distributed common plants and appears to show regional differences in larval food plant preferences. For example, *E. c. asela* was found to feed on *Pentatropis capensis* in Arippu (Mannar) in the arid zone on the west coast but it feeds preferentially on *Cryptolepis buchananii* in the wetter areas of the island and on *Ichnocarpus frutescens* in the intermediate zone. There may be other larval food plants.

Euploea klugii sinhala Moore, 1877 (Brown King Crow)

The final instar larva and pupa of *Euploea klugii* were described by Bell (1909) from Indian material and quoted by Woodhouse (1950). This description of the larva and pupa agrees with the findings of the current study except for the following points: in the larva of *E. k. sinhala*, a) the spiracular band has variable amounts of orange, sometimes equal to the white; and b) the lower half of the filaments is claret-red while the upper half is black. In addition, Bell's statement that the front pair of filaments are generally held curled only in *E. klugii* does not agree with the observations of the current study; they are also curled in *E. sylvester montana* (Fig. 11a, b, c).

Additional notes on immature stages: Egg: pale yellow, cylindrical, domed at apex, honey-comb-like depressions (Fig. 11d). 1st instar (newly emerged larva): blackish-brown head, honey-colored body, tiny filament buds. 2nd instar: head black, abdomen with faint whitish transverse bands and short, light brown filaments (Fig. 11e).

Duration of immature stages: hatching to 1st molt 1 day; the next 3 molts every 1–2 days; pupation took 2 days to complete; pupation to eclosion 7 days; hatching to emergence 15 days.

Larval food plants: There are no published records of the larval food plants in Sri Lanka. The current study showed for the first time that one of the larval food plants in Sri Lanka is *Streblus asper* (family Moraceae). Although Woodhouse (1950) reported "*Ficus hispida*; doubtless other figs as well" as larval food plants, this was based on Bell (1909) reporting from India. In the current study, the larvae refused to feed on *Ficus hispida*.

E. k. sinhala is widely distributed over the island but is most common in dry semi-deciduous monsoon forests where *S. asper* is quite common (Dassanayake, 1981). Since both *E. k. sinhala* and *S. asper* occur sparingly elsewhere, *S. asper* may be the only larval food plant in Sri Lanka though it is possible that another one will be discovered.

Euploea phaenareta corus Fabricius, 1793 (The Great Crow)

The final instar larva and pupa of *Euploea phaenareta corus* were described by Moore (1880). The descriptions were based on a drawing in Horsfeld & Moore (1857) of a specimen from Sri Lanka. This description of the larva and pupa agrees with the findings of the current study except for the following points: in the larva of *E. p. corus*, a) the color of the abdomen, filaments and markings are variable; and b) the subspiracular line is orange or yellow. The current study describes all stages for the first time.

Additional notes on immature stages: On July 20, 2006, a ♀ was observed laying eggs on *Cerbera odollam* (family Apocynaceae). Eggs were laid singly on the underside of tender leaves. The eggs were successfully reared to eclosion.

Egg: whitish-yellow, cylindrical, domed at the apex, with honey-comb-like depressions (Fig 12a). 1st instar: Newly emerged larva ate part of the eggshell;

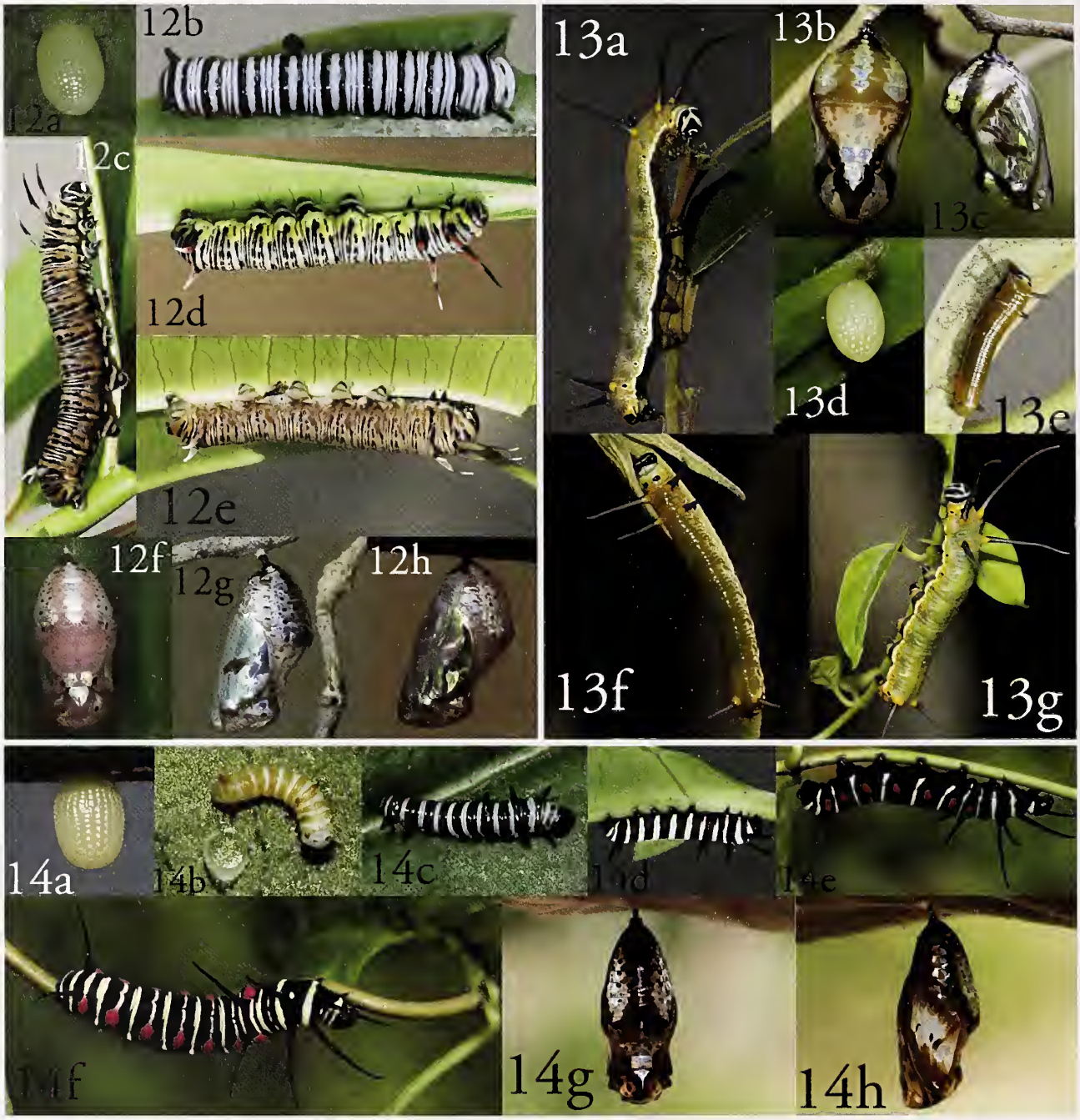
Figures 10-11. 10. *Euploea core asela*. **10a**. Larva, final instar, purple form. **10b**. Final instar, brown form. **10c**. Pupa. **10d**. Pupa. **10e**. Pupa. **10f**. Pupa. **11.** *Euploea klugii sinhala*. **11a**. Larva, final instar, white spiracular line with orange. **11b**. Larva, final instar, orange spiracular line with white. **11c**. Pupa, lateral view. **11d**. Egg. **11e**. Larva, second instar.

then fed both on tender leaves (where it remained on the upperside of the leaf) and on older leaves (where it remained on the underside); head black, body whitish with black transverse stripes, no filaments, 5 mm in length. 2nd instar: white with black transverse stripes, filaments on S3, S4 and S12 black, 9 mm in length (Fig. 12b). 3rd instar: ground color variable and filaments colored as in fifth instar, 12 mm in length. 4th instar: similar to 3rd instar, 22 mm in length (Fig. 12c). 5th instar: head black with white v-shaped band along the adfrontal area, laterally a white band that joins at the top, clypeus light blue; abdomen, smooth cylindrical, ground color variable from light brown to almost white with black transverse bands, of variable thickness; spiracular band irregular, much convoluted, light brown to cream-colored or yellow; filaments with colors variable (S3 & S4—larvae with a brown ground color have filaments that are light brown at the base, then black in the middle with white tips; those with a whitish ground color have filaments that are claret red at the base with black or white tips); filaments on S3 longest and point forward; those on S12 shortest and point backwards and without black (only brown and white or claret red and white or all white); base and crochets of prolegs white, planta black; 27 mm in length immediately after the molt, 50 mm in length just before pupation (Fig. 12 d, e).

Pupation occurred on same tree on which the larva fed and took 2 days to complete. The ground color of the pupa is silvery gray and beige or pinkish; abdominal segments convex; lateral margin of the abdomen with a band of dark brown to black spots above the spiracular line (Fig. 12 f, g, h).

Duration of immature stages: oviposition to emergence 5 days; 4 molts, every 2–3 days; pupation to eclosion 8–12 days; emergence to eclosion 19–24 days.

Larval food plants: There are no published records of the larval food plant in Sri Lanka. The current study showed for the first time that one of the larval



Figures 12-14. **12.** *Euploea phaenareta corus*. **12a**. Egg. **12b.** Larva, second instar. **12c**. Larva, fourth instar. **12d**. Larva, final instar. **12e**. Larva, final instar. **12f**. Pupa, pink ground color, dorsal view. **12g**. Pupa, beige ground color, lateral view. **12h**. Pupa, pink ground color, lateral view. **13**. *Euploea sylvester montana*. **13a**. Larva, final instar. **13b**. Pupa, dorsal view. **13c**. Pupa, lateral view. **13d**. Egg. **13e**. Larva, second instar. **13f**. Larva, third instar. **13g**. Larva, fourth instar. **14**. *Idea iasonia*. **14a**. Egg. **14b**. Larva, newly emerged with eaten eggshell. **14c**. Larva, second instar. **14d**. Larva, third instar. **14e**. Larva, final instar, lateral view. **14f**. Larva, final instar, dorsal view. **14g**. Pupa, dorsal view. **14h**. Pupa, lateral view.

food plants in Sri Lanka is *Cerbera odollam* (family Apocynaceae).

C. odollam is a medium-sized tree that is fairly widespread along the east and west coast in both the wet and dry zones. It is also frequently planted along roads and the edges of rice fields. Where it occurs naturally, it tends to grow in shady locations; when planted it survives quite well in open sunny areas.

E. p. corus is locally common along the south-west coast from Negombo to Galle and up to 15 km inland, preferring shady habitats such as mangroves and well-wooded marshy areas.

The distribution of *E. p. corus* maps well with the distribution of *C. odollam* along the west coast where the plant occurs naturally in shade. However, *E. p. corus* does not colonize trees that have been planted in open sunny areas. Nor has it been recorded from the mangroves on the east and north coast despite the presence of *C. odollam*. Manders (1904) suggested that *E. p. corus* may have been accidentally introduced into the port of Galle from China and spread from there. This would account for the distribution.

However, there is also one population of *E. p. corus* in the Sinharaja Forest Reserve, 45 km from the coast. It probably arrived and established itself there with the planting of *C. odollam* alongside the rice fields adjacent to the forest. The rice fields have long been abandoned and the land is now protected under the stewardship of the Ministry of the Environment. *E. p. corus* still thrives there, but only along the trail that borders the rice fields where *C. odollam* still grows. *C. odollam* is probably the only larval food plant for *E. p. corus*.

Euploea sylvester montana Felder & Felder, 1865 (Double Branded Black Crow)

The final instar larva and pupa of *Euploea sylvester* were described by Bell (1909) from Indian material and quoted by Woodhouse (1950). This description of the larva and pupa agrees with the findings of the current study except for the following points: in the larva of *E. s. montana*, a) filaments on S3 are curved and b) legs are brown (Fig 13a, b, c). The current study describes all stages for the first time.

Additional notes on immature stages: Egg: white, cylindrical, domed at apex, flattened at base, honeycomb-like depressions (Fig. 13d). 1st instar (newly emerged larva): head black, body golden-brown, filaments on S3, S4 and S12 short and brown. 2nd instar: head black with white transverse stripes, body yellowish-brown, subspiracular line whitish, filaments light brown, S14 black, legs black (Fig. 13e). 3rd instar: head black with white transverse stripes, body brownish-green, subspiracular line white, S2 with 2 black dorsal spots surrounded by yellow and 2 smaller black spots laterally, filaments smoky gray and bright yellow or orange at base, longest filament on S3, legs brownish-green with black marking, S14 with black spot posteriorly (Fig. 13f). 4th instar: head black with white transverse stripes, body light grayish-green, white subspiracular line with pale orange above and gray below, filaments dark gray with orange base, spiracles black, S2 orange with 2 black dorsal spots and 2 smaller black spots laterally (Fig. 13g). 5th instar: head black with white stripes, body grayish-green, white subspiracular line, spiracle on S12 very prominent, filaments dark gray with yellow or orange base, anal flap black, all spiracles black and ringed with white, S2 with 2 black transverse dorsal markings and 2 lateral ones.

Duration of immature stages: hatching to first molt 4 days (length 12 mm); successive molts every 1–2 days (4 molts in all); last instar 52 mm in length before pupation; length of pupa 19 mm; pupation to eclosion 9 days; hatching to eclosion 20 days.

Larval food plants: There are no published records of the larval food plant in Sri Lanka. The current study showed for the first time that one of the larval food plants in Sri Lanka is *Gymnema sylvestre* (family Asclepiadaceae). Although Woodhouse (1950) reported *Ichnocarpus frutescens* (family Apocynaceae) as the larval food plant, this was based on Bell (1909) reporting from India. In the current study, the larvae refused to feed on *I. frutescens*.

G. sylvestre is not very common but is found in the dry and intermediate zones up to about 1000 m asl (Dassanayake, 1983).

E. s. montana is not common but is widely distributed over most of the island up to about 1000 m asl. Since the distribution of *G. sylvestre* does not fit that of *E. s. montana*, it is likely that there is another larval food plant.

Idea iasonia Westwood, 1848 (Sri Lankan Tree Nymph)

The final instar larva of *Idea iasonia* (which is endemic to Sri Lanka) was described by de Nicéville and Manders (1899) but the description was based on a colored drawing that was sent to de Nicéville by Mr. E. Ernest Green from Sri Lanka. This general description agrees with the findings of the current study which describes all stages for the first time.

Additional notes on immature stages: On March 16, 2007, the authors observed a ♀ *I. iasonia* in the Knuckles area ovipositing on the leaf of a plant that was later identified as *Parsonsia alboflavescens* (family Apocynaceae). Eggs were laid singly on the underside of leaves, low to the ground, on young plants that were in dense shade. The plants used were not more than a meter high even though *P. alboflavescens* is a vine that grows to several meters long and reaches the canopy. The eggs were collected and reared to eclosion. Larvae were also collected from the underside of a leaf, low to the ground, and were raised

to eclosion. Eggs and larvae were also collected from *P. alboflavescens* in the Knuckles area one month later, and also raised to eclosion. *I. iasonia* was also observed ovipositing on *P. alboflavescens* in the Sinharaja Forest Reserve as well and larvae were raised successfully to eclosion. All adults that eclosed were normal and were released to their places of origin.

Egg: white, cylindrical, domed at the apex, flattened at the base with honey-comb-like depressions (Fig. 14a). 1st instar (newly emerged larva): consumed most of the eggshell, then moved to the underside of the leaf and fed by gnawing away the lower epidermis and the cells beneath but leaving the upper epidermis intact; head black; body pale yellow-brown and somewhat transparent; S5, S6, S7 and S8 with a tinge of green; two white transverse bands on each of S3 to S13, broadest dorsally, one apical, one basal; S3, S4, S6 and S12 with paired fleshy filaments on either side of the dorsal line; filaments short and stubby, basally pale yellow-brown, distally dark brown; S2 white, with two dark gray spots dorsally, more or less lined up with the paired filaments behind; legs black (Fig. 14b).

2nd instar: Molt eaten as its first meal, except for the head shield. Ground color velvety black; skin smooth and glossy; spiracles black; pale yellow transverse bands extend ventrally to just above the base of the prolegs; anterior and posterior transverse bands on S2 usually coalesced on the lateral margins and dorsally, leaving two black patches dorsally; paired subdorsal filaments on S3, S4, S6, and S12, long and slightly curved; filaments on S3 often pointing forwards over the head; those on S12 held vertically, often with the tip pointing backwards; S6 to S12 with a lateral, oval dark reddish-pink spot which is sometimes indented irregularly. The larva fed from the margins of the plant but continued to remain on the underside of the leaf, quite sedentary and well concealed (Fig. 14c).

3rd instar: similar to 2nd instar. Molt eaten. In each pair of transverse bands, the anterior one is shorter than the posterior one and is of variable length. Sometimes a small lateral spot in S5 near the spiracle, similar in color to those on S6 through S12 (Fig. 14d).

4th instar: Molt eaten. Similar to 3rd instar but the transverse bands on adjacent segments merge to form a single pale yellow line in most larvae; pads on prolegs more or less transparent.

5th instar: Molt eaten. Similar in color and markings to 4th instar larva but in most larvae, the paired lateral spots on each segment are joined dorsally by a pale yellow irregular transverse band (Fig. 14e, f). *Idea malabarica*, the closely related Indian species, lacks the paired spots on S12 (Talbot, 1947).

Pupa: Silk pad glistening and coppery. 30 mm in length and 10 mm at its widest point. Ground color metallic orange-brown. Numerous black spots over much of the surface. Stalk black with two small protuberances beyond the end of the abdomen. Head light reddish-brown. Silver markings on eyes. Thin silver transverse line on S2. Triangular silver marking on dorsal line of S3. A square silver patch on S4. Wings with silver markings at the base. A broader rectangular silver patch on S5, usually with black spots. S6 reddish-brown with silver dorso-lateral patch posteriorly. S7 to S10 reddish-brown with silver dorso-lateral band with numerous black spots increasing in density towards S10. S11–S12 without silver. S13–14 dark reddish-brown with orange dorsal transverse band (Fig. 14g, h).

Most of the 4th and 5th instar larvae found in the field were amongst dense foliage within 1 m of the ground. Although no pupae were found in the field, it is very likely that pupation occurs within these dense stands of vegetation.

Duration of immature stages: oviposition to emergence 4–5 days; molting every 3–5 days (4 molts); fully grown larva about 50 mm long; pupation took 2 days to occur on average; pupation to eclosion 8–14 days; oviposition to eclosion 32–33 days (An exception was 2 eggs that were collected in October 2008 in which molting occurred every 2–3 days and the time from oviposition to eclosion was 25 days.)

Larval food plants: In Sri Lanka, "a climbing asclepidaceous plant allied to *Hoya*" was reported by de Nicéville and Manders (1899) based on a drawing. The current study showed for the first time that one of the larval food plants in Sri Lanka is *Parsonsia alboflavescens* (family Apocynaceae). Though several authors reference *Hoya* as a larval food plant, these citations seem to be a misinterpretation of de Nicéville's original note. Since the generic term *Hoya* has referred in past nomenclatures to other genera such as *Wattakaka* or *Tylophora*, it is not possible to ascertain the plant species to which de Nicéville referred. Both species of *Hoya* that are found in Sri Lanka (*H. pauciflora* and *H. ovalifolia*) are rare and there are no confirmed records of *Hoya* as a larval food plant.

P. alboflavescens is widely distributed in the wet, intermediate and dry zones and along the coast up to about 1000 m asl (Dassanayake, 1983).

I. iasonia is a forest-loving species that is usually found near streams between 500 m to 2000 m asl, though it also descends to sea level on the southern slopes of the wet zone. The butterfly is absent from many locations where the larval food plant occurs despite the apparent availability of suitable habitats.

On the other hand, *P. alboflavescens* has not been recorded from all areas where the butterfly has been seen (e.g. Agrapatana), which suggests the existence of another larval food plant.

Conclusion

The current study has confirmed some previously recorded larval food plants and has identified some new larval food plants. It has also shown that there are differences between the descriptions of the larva and pupa found in this study and the descriptions that have been done by other authors including those working on Sri Lankan material as well as Indian material. These differences may be due to natural variation or may be associated with the Sri Lankan subspecies. They may also depend on the larval food plant, which is sometimes different than that previously described. Many larval food plants that are used in India are not used by the same species in Sri Lanka or are used less preferentially. It is possible that the Sri Lankan subspecies may have evolved sufficiently to deviate from the larval food plants used in peninsular India and elsewhere. Evidence indicates that populations differ in their preference of larval food plant depending on the climatic region in which they live.

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APPENDIX A – Annotated list of the major scientific publications on the butterflies of Sri Lanka.

1. The Lepidoptera of Ceylon by F. Moore, 1880, 1881. Vol. 1 & Vol. 3 (in part). Descriptions of the adult as well as descriptions of many of the larvae and pupae with larval food plants. Presumably based on Sri Lankan specimens.

2. The Butterflies of India, Burmah and Ceylon by G. F. L. Marshall & L. de Nicéville—Vol. 1, 1882-83; by de Nicéville—Vol. 2, 1886 & Vol. 3. 1890. Descriptions of the larva and pupa of Sri Lankan species largely based on Moore (1880). Few larval food plants listed.

3. The Fauna of British India including Ceylon and Burma: Butterflies by C. T. Bingham, 2 volumes, 1905 & 1907. Information on larval stages and larval food plants of Sri Lankan species mostly quoted from Moore (1880).

4. The Fauna of British India including Ceylon and Burma: Butterflies by G. Talbot, 2 volumes, 1939 & 1947. Talbot included information on larval stages and larval food plants mostly quoted from Bell (1909).

5. Notes on Ceylon Butterflies by W. Ormiston, 1918. Spolia Zeylanica XI (part 40): 1-69 with two plates and XI (part 41): 126-188 with seven plates (II to VIII [*sic*]). Detailed descriptions of adult butterflies and distinguishing characteristics including genitalia but little information on larvae or pupae or larval food plants.

6. The Butterflies of Ceylon by W. Ormiston, 1924. Essentially an edited copy of the 1918 publication with additional information. Appendix B lists larval food plants and the sources are listed as "Mainly taken from the writings of" Moore, de Nicéville and Bell.

APPENDIX A (Cont.)

7. The Identification of Indian Butterflies by W. H. Evans, 1927 & 1932. Mostly identification keys; no immature stages or larval food plants.

8. 8a. The Butterfly Fauna of Ceylon by L. G. O. Woodhouse and G. M. R. Henry,1942. Ceylon Journal of Science [no volume designated]. First complete edition.
8b. The Butterfly Fauna of Ceylon by L. G. O. Woodhouse, 2nd (complete) edition, 1949.
8c. The Butterfly Fauna of Ceylon by L. G. O. Woodhouse, 2nd (abridged) edition, 1950.
All editions included descriptions of larvae, pupae and larval food plants mostly based on Moore (1880) from Sri Lankan material and Bell (1909) from Indian material and with field notes of Tunnard, E. E. Green etc. from Sri Lankan material.

9. The Butterflies of Ceylon by B. d'Abrera, 1998. Descriptions of larvae, pupae and larval food plants mostly based on Woodhouse but with some personal observations.

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Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols

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Abstract. Insects, like most other organisms, are more diverse in tropical than in temperate regions, but standardized comparisons of diversity among tropical regions are rare. Disentangling the effects of ecological, evolutionary, and biogeographic factors on community diversity requires standardized protocols and long-term studies. We compared the abundance and diversity of butterflies using standardised 'Pollard walk' transect counts in the understory of closed-canopy lowland rainforests in Panama (Barro Colorado Island, BCI), Thailand (Khao Chong, KHC) and Papua New Guinea (Wanang, WAN). We observed 1792, 1797 and 3331 butterflies representing 128, 131 and 134 species during 230, 231 and 120 transects at BCI, KHC and WAN, respectively. When corrected for length and duration of transects, butterfly abundance and species richness were highest at WAN and KHC, respectively. Although high butterfly abundance at WAN did not appear to result from methodological artefacts, the biological meaning of this observation remains obscure. The WAN site appeared as floristically diverse as KHC, but supported lower butterfly diversity. This emphasizes that factors other than plant diversity, such as biogeographic history, may be crucial for explaining butterfly diversity. The KHC butterfly fauna may be unusually species rich because the site is at a biogeographic crossroads between the Indochinese and Sundaland regions. In contrast, WAN is firmly within the Australian biogeographic region and relatively low species numbers may result from island biogeographic processes. The common species at each of the three sites shared several traits: fruit and nectar feeders were equally represented, more than half of common species fed on either epiphytes or lianas as larvae, and their range in wing sizes was similar. These observations suggest that Pollard walks in different tropical rainforests target similar assemblages of common species, and, hence, represent a useful tool for long-term monitoring of rainforest butterfly assemblages.

Key words: Barro Colorado Island, Center for Tropical Forest Science, Lepidoptera, tropical rainforest, Panama, Papua New Guinea, Pollard walks, Smithsonian Institution Global Earth Observatories, Thailand.

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Introduction

The structure and high species diversity that characterizes tropical forests has lead many ecologists to overemphasize the similarities among biogeographically distinct forests and to downplay the differences. Although the planet's tropical forests can be categorized in a number of ways, it is clear that rainforest ecosystems have evolved independently several times, providing the opportunity for replicated study of tropical community assemblages while

exploring the unique role of taxa occurring nowhere else (Corlett & Primack, 2006). Cross-continental comparisons of rainforest communities, particularly of insects, are rare, and baseline studies need to be undertaken before anthropogenic incursions makes such studies impossible.

Habitat degradation is currently the biggest threat to tropical insects; however, the effects of climate change may soon be more pervasive (Chen *et al.*, 2009). As indicators of environmental disturbance or environmental change, butterflies are frequently used because they offer a number of logistical advantages over other potential indicator taxa (Thomas, 1991; Ghazoul, 2002; Koh & Sodhi, 2004; Gardner *et al.*, 2008). Primarily, unlike most insect groups, many butterfly species can be identified in the field, often facilitated by field guides. But while butterfly taxonomy is reasonably advanced, understanding of butterfly life histories and ecology lags behind, particularly for tropical taxa, which represent about 90% of all butterfly species. Butterflies and their larvae play important roles in ecosystem functioning, including nutrient cycling and pollination. This implies that tropical butterflies should be studied not just as potential biological indicators, but as targets of conservation in their own right (Bonebrake *et al.* 2010; Schulze *et al.*, 2010).

Unlike temperate areas, no long-term monitoring scheme for butterflies or any other insects has been established in the tropics until recently. In the absence of baseline data, the impact of climate change on butterflies and other tropical insects will be difficult to evaluate (Bonebrake *et al.*, 2010). Further, the diversity and complexity of tropical communities impedes efforts to understand them. Investigating insects in established long-term study plots may capitalize on existing floristic, phenological and climatic data, thus simplifying efforts to study tropical insects and their interactions with plants (Godfray *et al.*, 1999). The network of forest dynamics plots monitored by the Center for Tropical Forest Science (CTFS) is perhaps the most ambitious cross-continental ecological research network coordinated by a single organization (Losos & Leigh, 2004; Corlett & Primack, 2006). This network of permanent rainforest plots provides ample opportunities for long-term monitoring of insect populations and other entomological studies.

There are several methods available to monitor rainforest butterflies, each with their own limitations. Traps baited with rotting fruits are frequently used to attract adult butterflies that imbibe fermenting fruit juice (DeVries & Walla, 2001; Schulze *et al.*, 2001), and have been the subject of considerable interest in tropical conservation biology (Schulze *et al.*, 2001, 2010). However, these traps attract only the subset of species that feed on fruits (Schulze *et al.*, 2001; Caldas & Robbins, 2003). Pollard walks, in which butterflies are counted along timed transects, were pioneered in England over 35 years ago (Pollard, 1977; Thomas, 1983), and today, butterfly monitoring with Pollard walks includes about 2000 transects scattered throughout Europe (van Swaay *et al.*, 2008). Observation counts obtained with Pollard walks are positively correlated with the abundances of individual species as estimated by mark-recapture studies (Pollard, 1979; Thomas *et al.*, 2004), and are therefore deemed to be a faithful measure of abundance. Pollard transects performed in tropical rainforests are often used as a sampling method to (a) assess local butterfly species richness while expending a minimum of effort, often censusing open habitats, because butterfly diversity tends to be higher in these habitats (e.g. Sparrow *et al.*, 1994; Caldas & Robbins, 2003; Walpole & Sheldon, 1999; Hill *et al.*, 2001; Koh & Sodhi, 2004; Tati-Subahar *et al.*, 2007); and (b) compare butterfly species richness in old-growth and disturbed forests or plantations (e.g., Hill *et al.*, 1995; Spitzer *et al.*, 1997; Ghazoul, 2002; Cleary & Genner, 2004).

Examining factors that may explain site-to-site variation in the species richness of butterfly assemblages in primary forests may illuminate changes in disturbed forests. In tropical forests, the high species diversity and reduced visibility in the understory impedes identification of butterflies "on the wing." For this reason, tropical studies often do not include the taxonomically challenging but exceptionally diverse families Hesperiidae and Lycaenidae (e.g., Sparrow *et al.*, 1994; Spitzer *et al.*, 1997; Ghazoul, 2002). Long-term studies with relatively high sampling effort directed at the same locality can alleviate this challenge by focusing taxonomic expertise on problem groups while amassing a suitable reference collection. Further, the use of standardized protocols at different localities is essential to understanding the dynamics of local communities and species assemblages. For this purpose, compilations of museum records and published checklists cannot replace field surveys. Locality data from these sources is unlikely to be detailed enough to assemble a credible list for a particular site, and sampling bias would most likely prevent site-specific extrapolation based on museum records. To the best of our knowledge, no study has yet attempted to compare entire understory butterfly assemblages from closed-canopy tropical rainforests among different biogeographic regions

using standardized sampling.

Several authors also emphasized that various life-history traits of tropical butterfly species, such as geographic range, host specificity, etc., may be correlated with butterfly use of particular habitats and increased vulnerability to disturbance (Bowman *et al.*, 1990; Thomas, 1991; Hill *et al.*, 1995; Spitzer *et al.*, 1997). Thus, a sound comparison of butterfly assemblages at different localities may also contrast possible differences in life-history traits of common butterfly species. Our study, performed at three CTFS permanent rainforest plots in different biogeographic regions (Neotropical, Oriental and Australian), was designed to provide a thorough description of butterfly assemblages in the understory of old-growth forests at these three localities. We compare the faunal composition, species richness, diversity and abundance of these assemblages, as well as the life-history traits of their common species, and then examine whether broad regional differences between our study sites may translate to comparable differences in butterfly species richness.

Methods

Study sites

Neotropical: Barro Colorado Island (BCI) is a 1500 ha island created by the opening of the Panama Canal in 1910-1914. The 50 ha CTFS plot is located in the centre of the island, which is a biological reserve. A detailed description of the setting and of the CTFS plot may be found in Windsor (1990) and Condit (1988). Oriental: the 24 ha CTFS plot at Khao Chong (KHC) is located in protected forest of the Khao Chong Research and Conservation Promotion Station, which is part of the Khao Ban Thad Wildlife Sanctuary in southern Thailand. Australian: the third site is the newly established 50 ha CTFS plot located within the 10000 ha Wanang Conservation Area in Papua New Guinea (WAN). Vegetation at each site can be classified as semi-deciduous lowland moist forest, lowland seasonal evergreen forest, and mixed evergreen hill forest at BCI, KHC and WAN, respectively. At KHC, ridge forests are dominated by large *Dipterocarpus costatus* trees and other characteristic trees include *Shorea gratissima*, *Cynometra malaccensis*, and *Streblus ilicifolius*. Khao Chong forest phenology appears to coincide with the "general flowering" events that occur to the south of peninsular Malaysia (Center for Tropical Forest Science, 2010). Common tree species in the Wanang area include *Pometia pinnata*, *Teijmaniadendron bogorens*, *Chisocheton ceramicus*, *Dysoxylum arborens*, *Celtis latifolia*, *Intsia bijuga* and *Kingiodendron novogunensis*. At all CTFS plots, each tree with a diameter at breast height (DBH) of 1 cm or greater was counted, mapped, and identified to species (Center for Tropical Forest Science, 2010). The three study sites have similar latitude and elevation, but WAN has higher rainfall, BCI has a more severe dry period, and KHC has a steep slope. Tree diversity (in terms of families, genera and species of trees) is higher at KHC and WAN than at BCI (Table 1).

Butterfly transects and identification

At each site, we used Pollard walks to calculate indices of butterfly species abundance along a linear transect that was repeatedly sampled over a given time interval (Pollard, 1977). To reduce trampling, we used concatenated Pollard transects on established trails at BCI and KHC (i.e., narrow understory paths not associated with a canopy opening). At BCI, we designated 10 transect sections each of 500 m, at KHC six transect sections each of 350 m, and at WAN, five transect sections each of 300 m (hereafter transect sections are termed "locations"; the minimum distance between locations was 200 m). To account for the steeper slope at KHC, half of the locations were sited on level terrain (hereafter 'flatland'; 120-160 m) and half on a ridge (255-465 m). During each "walk," one observer walked a transect section (location) at slow and constant pace in about 30 minutes while recording butterflies within 5 m of either side of the trail and to a height of 5-7 m (this was the smallest sampling unit; hereafter, one walk termed "transect"). Butterflies were either identified "on the wing" as accurately as possible (to species, genus or family); netted, identified (at BCI with a home-made field guide; at KHC from memory; at WAN with the pocket guide of Parsons, 1991) and released; or collected for processing and identification in the laboratory. At WAN, field observations of butterfly flight habits and microhabitat preferences made by experienced observers improved the ability to identify specimens in the field.

At all sites, we avoided walks on days with inclement weather (high rainfall or wind, low temperature). Locations were usually walked between 9:00 h and 15:00 h, on different days. Surveys were performed with a weighted frequency of dry/wet periods. At BCI, each location was walked three times during each of four quarterly surveys, from June 2008 to March 2010. At KHC, each transect was walked four times during each of quarterly surveys from August 2008 to November 2009. There was turnover of observers at both sites, but most transects were surveyed by six

Table 1. Salient characteristics of study sites. Sources: Condit, 1988; Windsor, 1990; Center for Tropical Forest Science (2010).

Variable	Barro Colorado Island	Khao Chong	Wanang
Biogeography	Neotropical	Oriental, within the transition zone between the Indochinese and Sundaland regions	Australian
Coordinates	9.15°N, 79.85°W	7.54°N, 99.80°E	5.24°S, 145.08°E
Elevation (m)	120-160	120-330	90-180
Recent history	Island isolated from rising Lake Gatun in 1910-1914	No recent and major disturbance near the permanent plot	No recent and major disturbance near the permanent plot
Annual average rainfall (mm)	2631	2665	3440
Annual average daily maximum air temperature (°C)	28.5	30.9	30.6
Average length of the dry season (days)	136	120	141
Average monthly rainfall during dry season (mm)	64	82	88
Number of tree recorded in CTFS plot with dbh ≥ 1cm	208387	121500	81971*
Stems per ha in CTFS plot	4168	5062	4554*
Number of tree species/genera/families recorded in CTFS plot	298/181/59	593/285/82	553/273/83*
Mean ± s.e. canopy openness (%) †	3.99±0.194a	6.06±0.445b	2.02±0.205c

* Data for the first 18 ha of the 50 ha plot.
† Determined by canopy pictures and spherical densiometer, data not presented here. ANOVA, $F_{2,76} = 20.17$, $P < 0.0001$, significant groups designated by different letters (Tukey-tests, $P < 0.05$).

observers at BCI and three observers at KHC. At WAN, each location was walked biweekly from March 2008 to February 2009 by the same observer. Butterflies were identified using local collections and a variety of sources, including DeVries (1987-1997) and Warren *et al.* (2010) at BCI, Ek-Amnuay (2007) at KHC, and Parsons (1991, 1999) at WAN. Higher classification of butterflies follows Wahlberg (2006), Wahlberg *et al.* (2005, 2009) and Warren *et al.* (2009).

To examine the possibility that species at each site might be cryptic species complexes we sent legs of vouchered specimens to the Biodiversity Institute of Ontario, where cytochrome c oxidase subunit I ('DNA barcode') sequences were sequenced and evaluated using tools in the Barcode of Life Database (BOLD, see Craft *et al.*, 2010). Sequences were uploaded on the BOLD database (http://www.boldsystems.org/) and are publicly available (projects BCIBT, KHCBT and LEGI). Following Craft *et al.* (2010), we refrained from using subspecific names, unless DNA sequences suggested the existence of two or more species. Vouchers have been deposited at the Fairchild Museum, University of Panama (BCI), at the National Museum of Natural History in Washington (WAN), and at the Forest Insect Museum of the Thai Department of National Parks, Wildlife and Plant Conservation (KHC). Representatives of each species will eventually be deposited in museums in the country where they were collected.

Statistical analyses

We compared butterfly assemblages at study sites in terms of (a) subfamilial composition; (b) assemblage structure (abundance, species richness and related variables); and (c) life-history and morphological traits of the most common species (see below). Since transects were longer at BCI and were walked significantly faster than at KHC or WAN (Table 2), we standardized butterfly abundance per 500 m of transect and 30 min duration. Since rainforest butterflies appear to be particularly sensitive to unpredictable differences in climatic conditions between years (Cleary & Genner, 2004), we also compared butterfly abundances at BCI and KHC during the year 2009 (WAN data were collected in 2008 with a different frequency). We used the EstimateS 7.5 software package to calculate Morisita-Horn and Bray-Curtis

Table 2. Differences observed in Pollard walks at the three study sites. Unless stated, data refer to full data sets (values in brackets are for 2009). Mean are reported ± s.e., unless otherwise indicated. For ANOVAs, different letters denote significant different means (Tukey tests, p<0.05).

Variable	BCI	KHC	WAN
Butterfly individuals observed (data for 2009)	1792 (1078)	1797 (863)	3331
No. speces observed (data for 2009)	128 (92)	131 (89)	134
Sampling effort 2008-2010, person-hours (data for 2009), km walked	118 (81), 115	70 (49), 81	56, 36
Percentage of individuals identified to family/genus/species (%)	98.7/67.1/53.8	94.6/37.8/19.4	100/100/100
Percentage of species identified to species (%)	80.4	90.1	100
Percentage of species observed to local known butterfly fauna *	42.6	32.3	68.9
Average Morisita-Horn index of similarity between pairwise locations †	0.859 ± 0.007[a]	0.275 ± 0.046[c]	0.767 ± 0.034[b]
Average Bray-Curtis index of similarity between pairwise locations ††	0.576 ± 0.007[b]	0.212 ± 0.023[c]	0.600 ± 0.017[a]
Average duration of one transect (min.)	32.39 ± 0.0002	27.28 ± 0.0003	28.20 ± 0.0003
Average walking speed (m/min) ‡	15.88 ± 0.24[a]	13.66 ± 0.25[b]	11.02 ± 0.22[c]
Average corrected no. butterflies per transect of 500m and 30 min. ¶	7.40 ± 0.282[c]	12.31 ± 0.729[b]	49.22 ± 2.29[a]
Average corrected no. butterflies per location – 15 transects in 2009 §	109.01 ± 4.18	180.31 ± 20.60	na
Coleman rarefaction for 350 individuals (no. of species ± SD)	77.8 ± 4.74	130.3 ± 1.87	70.5 ± 4.18
Species richness estimate: Chao1 (±SD)	171.7 ± 15.44	186.7 ± 18.05	146.1 ± 6.79
Alpha log series index (±SD) **	39.36 ± 2.14[b]	75.13 ± 6.22[a]	27.99 ± 1.15[b]
Shannon index (±SD) †††	3.51 ± 0.02[b]	4.49 ± 0.05[a]	3.66 ± 0.09[b]
Exponent of bias-corrected Shannon entropy ***	30.98 ± 2.72[b]	64.08 ± 10.07[a]	32.27 ± 4.59[b]
Dominance: Berger-Parker index	0.220	0.069	0.171
Percentage of species observed as singletons (%)	37.0	44.0	16.3

* Sources: BCI: Huntington (1932), 267 spp. but most probably ca 300 spp. (B. Srygley & Y. Basset, unpubl. data); KHC: Pinratana (1981-1988), Pinratana & Eliot (1992-1996), D.L. Lohman unpubl. data, 407 spp.; WAN: Sam (2009), 196 spp.
ANOVAs: † $F_{2,12} = 203.0$, $P < 0.0001$; †† $F_{2,12} = 222.5$, $P < 0.0001$; ‡ $F_{2,324} = 81.2$, $P < 0.0001$; ¶ $F_{2,324} = 430.8$, $P < 0.0001$; ** $F_{2,12} = 74.5$, $P < 0.0001$; ††† $F_{2,12} = 18.8$, $P < 0.0004$; *** $F_{2,12} = 10.53$, $P < 0.0001$.
§ *t*-test: $t = 4.32$, $P < 0.001$.

similarity indices between locations, Mao Tau species accumulation curves, Coleman rarefaction indices, Chao1 richness estimates, Alpha log series diversity indices and Shannon evenness indices, each with 50 randomizations (Colwell, 2005). The Morisita-Horn and Bray-Curtis similarity indices are biased towards common and rare species, respectively (Legendre & Legendre, 1984). We further calculated a relatively unbiased diversity metric with regard to sample size, the exponent of bias-corrected Shannon entropy (Chao & Shen, 2003a), with the software SPADE (Chao & Shen, 2003b).

Common species were defined as the top 15% in a rank-ordered list of species (most to least abundant) at each study site, with the additional proviso that "common species" had to have been collected at each location within a given site (i.e., the total number of individuals observed had to be ≥ 10 at BCI, ≥ 6 at KHC and ≥ 5 at WAN; Appendix S1). Our interpretation gives more weight to the results obtained with common species as our intended monitoring scheme focuses on them. We scored the following suite of life-history traits and morphological characters for common species: adult food resources (fruits or nectar and/or puddle); known host plant species, family and growth form; host specificity (1 = restricted to one plant species; 2 = restricted to one plant genus; 3 = restricted to one plant family; 4 = broad generalist); geographic distribution (see below); use of modified habitats; membership in a known mimicry ring; larval ant attendance; wing colour patterns (system of Burd, 1994: yellow; orange; tiger; red; blue; clearwing; white and black; brown; and fore wing length (mm). Burd's (1994) system was followed to assess possible biases in human observers and/or emphasize different challenges in identifying visually species among sites. We do not use it to discuss the ecological significance of butterfly colour patterns (Schulze *et al.*, 2001). Butterfly traits were compiled from various sources, most notably Pinratana (1981-1988), DeVries (1987-

1997), Pinratana & Eliot (1992-1996), Parsons (1999) and Ek-Amnuay (2007). We also evaluated whether individual butterfly species preferred particular locations, times of day or habitats (flatland or ridge, KHC only) using the indicator value index (Dufrêne & Legendre, 1997). Its significance was tested for each species by Monte Carlo randomization with 1,000 permutations, performed with PC-ORD (McCune & Medford, 1999).

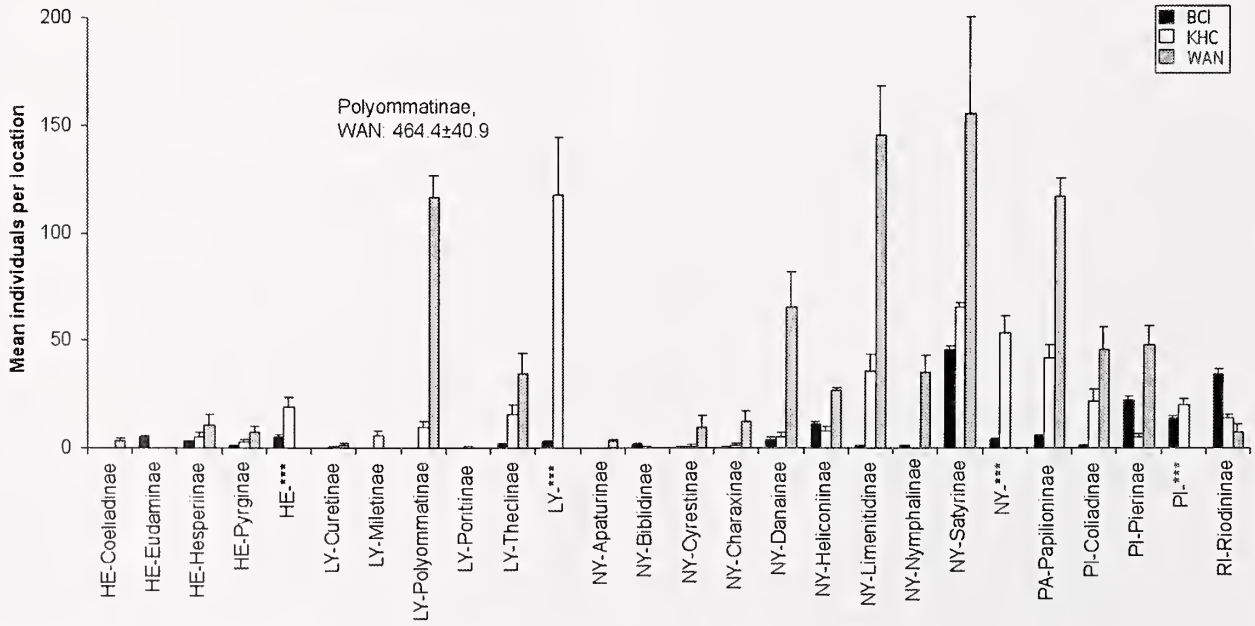
We adopted the system of Thomas (1991) to summarize the geographical distribution of our BCI species (1= endemic to Nicaragua, Costa Rica and Panama; 2= (i) C America, S to Panama, (ii) Nicaragua to NW South America; 3= both regions 2i and 2ii; 4= Neotropics (incl. Brazil, Bolivia and southwards). For KHC species, we modified the system of Spitzer *et al.* (1997) as follows: (1) Myanmar and Thailand excluding the peninsula; (2) zone (1), plus peninsular Thailand, Malaysia and Singapore; (3) Oriental region; (4) Australasian tropics or larger distribution. For WAN species, we modified the system of Parsons (1999) as follows: (1) New Guinea; (2) Australian; (3) Zone 2 plus Indo-Malayan (Sumatra, Java, Borneo, Philippines); (4) Australasian tropics or greater distribution. In these simple analyses, life-history and morphological traits were not corrected for phylogeny, as we wanted to test whether these attributes may differ for a set of common butterfly species as observed with Pollard walks among study sites. The results, irrespective of phylogeny, are important to us as they could point out biases affecting the probability of detecting common species in transects (notably for wing size, wing colour pattern and cryptic life history).

Results

Faunal composition and structure of butterfly assemblages

We observed 1,792, 1,797 and 3,331 individual butterflies representing 128, 131 and 134 species during 7 surveys and 230 transects, 10 surveys and 230 transects, and 12 surveys and 120 transects at BCI, KHC and WAN, respectively. The more inconspicuous Hesperiidae and Lycaenidae represented together 39%, 53% and 44% of observed butterfly species at BCI, KHC and WAN, respectively (χ^2 = 4.97, P = 0.083). Abundance and species richness of families and subfamilies were significantly different across study sites (all χ^2 tests P< 0.0001; Fig. 1). In particular, Eudaminae (*sensu* Warren *et al.*, 2009), Heliconiinae, Pierinae and Riodininae (BCI); Theclinae, Limenitidinae, Papilioninae and Coliadinae (KHC);

Figure 1. Mean number of individuals in each of the observed butterfly subfamilies at BCI (closed bars), KHC (open bars) and WAN (grey bars). Corrected mean (+ s.e.) of individuals observed per location during the whole study period. Abbreviations as follow: HE = Hesperiidae; LY = Lycaenidae; NY = Nymphalidae; PA = Papilionidae; PI = Pieridae; RI = Riodinidae; *** = not assigned to subfamily. For sake of clarity, Polyommatinae at WAN were scaled by a factor 4.0.



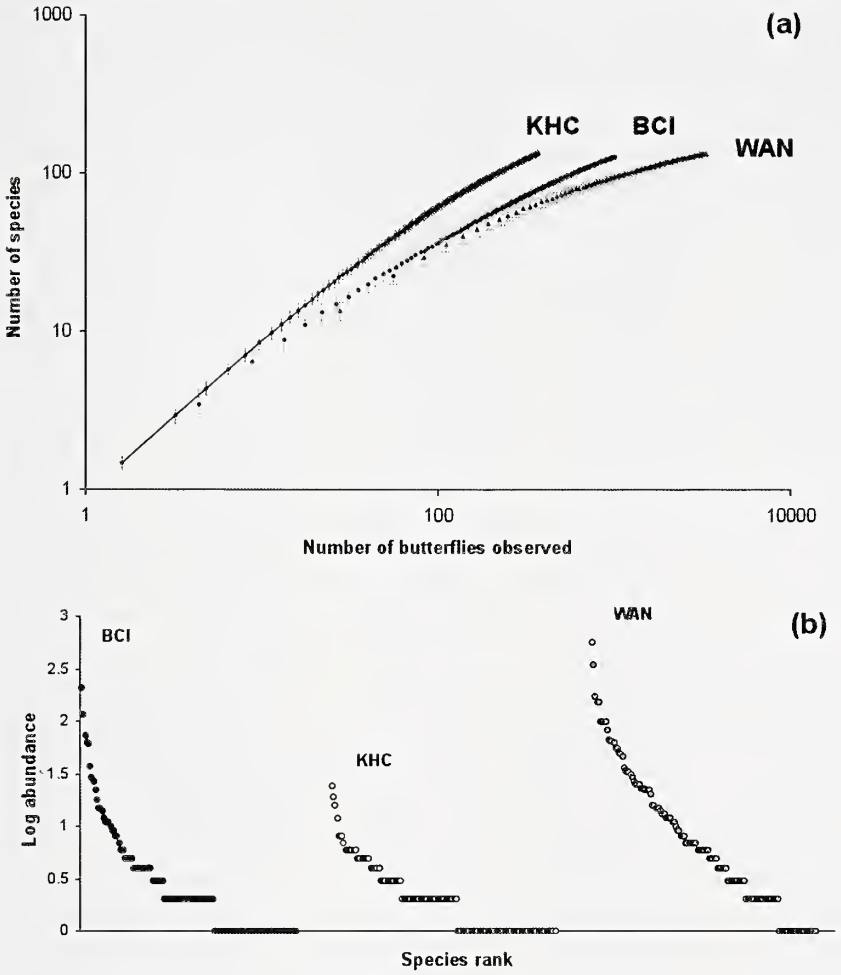


Figure 2. (a) Species accumulation curve against individuals for the BCI, KHC and WAN sites. Mean (±SD, in grey) of 50 randomizations, logarithmic scales on both axes. (b) Species rank abundance plot at BCI (filled circles), KHC (open circles) and WAN (grey circles).

and Polyommatinae, Limenitidinae, Danainae and Papilioninae (WAN) were proportionally well represented at different study sites. The percentage of individuals that could be identified to species was significantly lower at KHC than at BCI and WAN (χ^2 = 3627.9, $P < 0.0001$; Table 2). At WAN, all observed individuals could be identified in the field. Most of the observations at KHC that were not positively identified included unassigned Lycaenidae ($N = 440$) or Nymphalidae ($N = 202$), and generic identifications related to common species. The average faunal similarity between pair-wise locations was significantly different between study sites and particularly low at KHC, irrespectively of giving more weight to common or rare species (Table 2). Appendix S2 lists all species observed at the three study sites.

When corrected for length and duration of transect, butterfly abundance was about seven times higher at WAN than at BCI, and four times higher at WAN than at KHC (Table 2). Our comparison of 15 transects at each location of BCI and KHC in 2009 also indicated a significantly higher abundance of butterflies at KHC than at BCI—nearly twice as many (Table 2). The average diversity (Alpha log series and exponent of bias-corrected Shannon entropy) and evenness (Shannon index) of locations were significantly higher and more even at KHC than at BCI or WAN (Table 2). The Chao1 estimate, the Coleman rarefaction and the steeper species accumulation curve also suggest that the species pool was richer at KHC than at BCI or WAN (Table 2, Fig. 2a). Rank species abundance plots were similar at BCI and KHC, but both plots differed from that of WAN (Kolmogorov-Smirnov two samples tests: $D = 0.125$, $P = 0.27$, $D = 0.344$, $P < 0.001$ and $D = 0.410$, $P < 0.001$, respectively; Fig. 2b), because the proportion of rare

species (as estimated by the number of singletons) was lower at WAN than at other sites (χ^2 = 25.03, P < 0.0001), whereas dominance was highest at BCI (Table 2). At KHC, neither butterfly abundance nor species richness differed significantly between flatland and ridge locations (t-tests, t = 0.05, P = 0.96 and t = 0.47, P = 0.67, respectively). Butterfly abundance did not differ significantly with regard to time of day at BCI (hours tested: 9 am, 10 am, 11 am and noon; Kruskal-Wallis test, W= 4.78, P= 0.189), whereas it did at KHC, where abundance peaked at 11 am and was lowest at 3 pm (hours tested: 10 am, 11 am, noon, 1 pm, 2 pm and 3 pm; W= 20.09, P= 0.001), and at WAN, where abundance peaked at noon and was lowest at 9 am (hours tested: 9 am, 10 am, 11 am, noon, 1 pm, 2 pm; W= 15.44, P= 0.031).

Life-history and morphological traits of common species

Common species included 18, 15 and 20 species, representing 78.8%, 34.4% and 73.3% of individuals identified at BCI, KHC and WAN, respectively. Appendix S1 illustrates common species at the three sites and summarizes life-history and morphological traits. Common species at each of the three sites shared several traits: fruit and nectar feeders were equally represented (G = 0.35, P = 0.84); more than half of common species ate either epiphytes or lianas as larvae (G = 0.16, P = 0.92); and common species were of similar size at the three study sites (ANOVA on forewing length, F= 0.22, P= 0.80). This latter trend persisted when we restricted our comparison to Nymphalidae (F =0.22, P = 0.80) or Satyrinae (F =1.45, P = 0.28), for which we had sufficient data. There were also notable differences between common species at our study sites. At BCI the most common species was the large dark brown Satyrinae (Nymphalidae) *Pierella luna* (Fabricius, 1793), at KHC the most common species was a large, dark brown Amathusiini (Nymphalidae: Satyrinae) *Faunis canens* (Hübner, 1826), and at WAN it was a medium-sized Polyommatinae (Lycaenidae), *Danis danis* (Cramer, 1775). Common species at BCI were more host-specific than at KHC or WAN (Kruskal-Wallis test, W = 8.57, P < 0.05). Common species at WAN showed higher levels of endemicity than at BCI or KHC (W = 38.60, P < 0.0001). At KHC, the proportion of common species that were part of mimicry rings was lower than at BCI or WAN (G = 12.73, P < 0.01), but the proportion of common species that were attended by ants was higher than at the two other study sites (G = 9.20, P < 0.01). Many of the common species at KHC were duller in colour than at BCI or WAN. When grouped into the categories of orange/brown, clearwing and other, there was a significant difference in the distribution of wing colour patterns at all study sites for common species (G = 13.45, P < 0.01). At BCI and KHC, most common species did not show any strong preferences for habitat, locations, or time of day (indicator values and Monte-Carlo permutations tests, Appendix S1). At BCI, only two species significantly preferred locations. At KHC, three species significantly preferred locations, habitat and time of day. At WAN, half of common species showed a significant preference for location, but only three species showed preference for flying at a particular time of day. At BCI, 28% of the common species could be found in anthropogenically modified habitats, the rest were confined to closed canopy forest. Similar data on butterfly habitat use were not available for KHC and WAN.

Discussion

Pollard walks, like other methods for surveying butterfly populations, have advantages and limitations. The main advantages are ease of implementation and the ability to survey both fruit and non-fruit feeding species. This was particularly important in our surveys since more than 80% of all common species were non-fruit feeding butterflies. In contrast, pilot studies with fruit-baited traps in Panama (in the San Lorenzo forest, 25km away from BCI), at KHC and WAN indicated either that the method had low efficiency (Panama, WAN) or that the guild of fruit-feeding butterflies was significantly less diverse at KHC because fruit feeding lineages are weakly represented (D.J. Lohman and N.E. Pierce, unpubl. data). The efficiency of fruit-baited traps and the size of the resulting sample may also be affected by variation in the availability of naturally occurring fruits (Caldas & Robbins, 2003; Walpole & Sheldon, 1999). Fruit-baited traps may be appropriate for monitoring part of local butterfly assemblages at certain rainforest locations (Schulze *et al.*, 2001, 2010), but they appear to be less suitable for comparing butterfly assemblages at locations from different biogeographical regions. Further, Hesperiidae and Lycaenidae represented similar and significant proportions of total numbers of species observed at our three sites (39% to 53%). These diverse families include many camouflaged species with relatively low probability of detection, and these are typically not accounted for in Pollard walks performed in rainforests (Sparrow *et al.*, 1994; Spitzer *et al.*, 1997; Ghazoul, 2002). Our data emphasize that these species should, as far as possible, be recorded in

Pollard walks, for a more representative monitoring of rainforest butterfly assemblages.

However, there are at least four main limitations of Pollard walks when performed in rainforests. First, Pollard walks measure butterfly activity, not abundance, although the two variables are reasonably well correlated (e.g., Thomas, 1983). Second, transect counts may be affected by butterfly apparency and flight behavior (Walpole & Sheldon, 1999) and, thus, relative counts of dull versus apparent species, or smaller species, may be biased. Since the proportion of duller species appeared to be higher at KHC than at other sites, total butterfly species richness at KHC may be higher than that observed. Third, Thomas (1983) suggested that transect counts may be affected by the openness of habitats and visibility of butterflies. While this is an important consideration for comparisons between forested and open sites, this effect was unlikely to bias comparisons, because all three sites were in tall closed wet rainforests (see below). Fourth, butterflies may not be locally amenable to identification in the field with similar level of accuracy. Butterflies were more difficult to identify at KHC, partly because of a large species pool (Table 2) with many similar, dull colored species. A higher proportion of identified butterflies at KHC may have resulted in higher numbers of species observed, thus increasing differences in butterfly richness reported here between study sites. At WAN, additional field observations of butterfly flight habits and microhabitat preferences greatly improved the ability to identify species in the field. We cannot discount an observer effect (e.g., Sparrow *et al.*, 1994), however this effect was weak in multivariate analyses of common species observed in our transects (data presented elsewhere). While taxonomic training and experience was similar for observers, we expect that cultural, educational and/or training differences among observers affect their ability to identify species and may influence their propensity or reluctance to assign names to observed butterflies. We suggest that all observers in a comparative study undergo a minimum level of supervised observational training in the field by an experienced entomologist to reduce the variance among observers. The observer effect may further be reduced by randomization of observers and transect starting points, which was done in our study.

Butterfly abundance was considerably higher at WAN than at other study sites. Our corrected estimates of ca 50 butterflies per 500m of transect (strip of 10x500 m = 0.5 ha) at WAN are commensurate with estimates of 92 butterflies per 0.5 ha derived from independent mark-recapture studies of the common species *Danis danis* and *Taenaris* spp. near the Wanang area. Further, adult survival rates and life spans of these different species at WAN also appeared similar to other tropical butterfly species (P. Vlasanek, unpubl. data). Unusually high short-term densities of butterflies may be attributed to resource concentrations for adults (Young, 1972), but unusually high long-term densities such as reported here may be related to reduced butterfly/caterpillar predation or to mutualisms with ants, which are important arthropod predators in tropical rainforests (Kaminski *et al.*, 2010; Pierce *et al.*, 2002). Since most butterfly taxa were abundant at WAN, and not just those lycaenid taxa associated with ants, this latter explanation is unlikely to be correct. The unusually high butterfly densities at WAN might also be explained by strong differences in the relative occurrence of perching vs. patrolling species (Scott, 1974), but data to test this are lacking. Since air temperature was not notably higher at WAN than at other sites and since a similar protocol was used at all sites, we conclude that differences in butterfly abundance between sites are genuine, but we cannot yet offer a convincing explanation for the observed pattern.

Differences in butterfly species richness observed at our study sites may result from a variety of causes, which may be categorized as local or regional factors. Local factors apply at the level of transects and may include forest gaps, microclimate (air temperature, wind speed and rainfall), presence of larval host plants and adult food sources, flight routes, as well as an observer effect. Analyses of potential local factors affecting our transects are all presented and discussed elsewhere. In particular, small differences in air temperature among transect days, and the occurrence of rain on days preceding a survey were important factors in explaining butterfly abundance and composition; whereas, the presence of forest gaps had only a trivial effect. All our tall closed rainforest sites had overall canopy openness <6% and there was little evidence that canopy disturbance-specialist species were prevalent at our sites (Spitzer *et al.*, 1997; DeVries & Walla, 2001).

Regional phenomena that varied among our study sites include (a) biogeographical factors, (b) recent landscape history, (c) floristics and richness of potential host-plants and (d) annual rainfall and severity of the dry season (Table 1). Our data suggest that the most species-rich site was KHC. This is confirmed by various statistics accounting for species richness and diversity (some less biased towards unequal sample size) and the larger local species pool at KHC (Table 2). This appears contrary to the views that the Neotropical region is more diverse in

butterfly species than the Oriental region and that, in particular, Panama supports a richer butterfly fauna than Thailand (Robbins, 1982, 1992). However, Robbin's (1992) comparisons do not apply specifically to forest understory in these countries. The relatively low species richness of the forest understory compared with disturbed areas is well known, even in the tropics (e.g., Spitzer *et al.*, 1997).

With regard to biogeographical factors (a), KHC (9º 40' N) is located at a biogeographic crossroads between the Indo-Burmese and Sundaland faunal regions, coinciding with a transition from aseasonal to seasonal climatic conditions (Lohman *et al.*, 2011). Immediately to the north of KHC is the Isthmus of Kra (10º 15' N), an ecotone between seasonal evergreen dipterocarp rain forest and mixed moist deciduous forests (Richards, 1996; Corbet & Hill, 1992; Hughes *et al.*, 2003). To the south of KHC is the Kangar-Pattani Line which runs west-east from Kangar, Malaysia to Pattani, Thailand (6° 40' N) and is the most widely recognized Indochinese-Sundaic biogeographic transition for plants (van Steenis, 1950; Richards, 1996). A major transition in butterfly fauna coinciding with the Kangar-Pattani Line was identified by Corbet (1941). Butterfly species recorded from the transition zone between the Isthmus of Kra and the Kangar-Pattani Line contain elements from both biogeographic regions (Ek-Amnuay, 2007). In contrast, Wanang is firmly within the Australian biogeographic region. The southern half of PNG has been part of the Australian plate for around 250 million years. The northern part, which includes Wanang was created by thrust deformation collision in the last 30 million years by the Australian Plate, which is moving north colliding with the north-western moving Pacific Plate (Hall, 2002). The relatively low species numbers at WAN is likely to result from island biogeographic processes (MacArthur & Wilson, 1967).

Recent landscape history (b) may be more relevant to BCI since the island was created by the rise in Lake Gatun in 1910-1914. The depleted butterfly fauna may be partly due to low colonization rates of certain species not able to cross the water channel (nearest forests are 0.5-3.5km distant from the island), although we do not have hard data. With regard to host plants (c), tree species are 2.0 times richer at the KHC and WAN permanent plots than at the BCI plot. We do not have similar data for herbs, lianas and epiphytes, which likely represent a large share of butterfly host-plants at our study sites (as reflected by records for our common species). Just considering tree diversity, the WAN site appeared as floristically diverse as KHC but supported fewer butterfly species. This emphasizes that factors other than plant diversity may be crucial to explaining patterns of butterfly diversity (Hawkins & Porter, 2003). Data not presented here indicated that the effects of seasonality on butterflies (d) were low at all study sites and the wetter site (WAN) was not the most species-rich. Lepš and Spitzer (1990) also emphasized that seasonal effects are relatively low for assemblages of rainforest butterflies, as compared to similar assemblages in disturbed habitats.

Although time of day might explain temporal segregation of feeding activities by particular rainforest butterfly species (Young, 1972; but see Lepš & Spitzer, 1990), few common species showed strong preferences for flying at a particular time within the 9:00 to 15:00 h range of our transects. This suggests that the time of day during which our Pollard walks are performed in tropical forests will not significantly bias the results. Common species at each of the three sites shared several traits: fruit and nectar feeders were equally represented, more than half of common species ate either epiphytes or lianas as larvae, and their range in wing size was similar. There were few differences among our sets of common species at our study sites. Species at KHC appeared on average duller (a factor probably contributing to the low proportion of mimics at KHC), species at BCI were on average more host-specific, and species at WAN on average showed higher levels of endemicity (probably related to the location of the WAN site on a large island, as opposed to the continental locations of the other sites). Although these observations remain tentative, they suggest that Pollard walks in different tropical rainforests may target similar assemblages of common species, and hence, represent a useful tool for long-term monitoring of rainforest butterfly assemblages.

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APPENDICES S1 AND S2 (Available online. URL at http://www.lepidopterarесearchfoundation.org/journals/44/jrl_44_17_28.html)

APPENDIX S1. Dorsal views and details of life-history traits of common butterflies species at BCI, KHC and WAN.

APPENDIX S2. List of all butterfly species collected at BCI, KHC and WAN.

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Note

Nutritional ecology of the mimetic butterfly *Hypolimnas missipus* L. (Lepidoptera: Nymphalidae) in Ghana

Basic information needed for conservation of insect species, especially butterflies and moths, includes larval host plants for various regions. Surprisingly, the identities of even the major larval food plants for many butterflies and moths remain unknown, particularly in the tropics.

One of the most common butterflies in agro ecosystems in Africa is *Hypolimnas missipus* Linnaeus 1764 (Lepidoptera: Nymphalidae) (Owen, 1971). This species is one of the best-studied members of the genus *Hypolimnas* in terms of its distribution, polymorphism, genetics, mimicry and biochemistry (Owen, 1971; Smith, 1976; Vane-Wright *et al.*, 1977; Gordon & Smith, 1989). Food plants reported for *H. missipus* represent at least seven plant families: Convolvulaceae, Malvaceae, Acanthaceae, Amaranthaceae, Portulacaceae, Moraceae, and Palmae (Vane-Wright *et al.*, 1977). With such a broad range of food plants, it is possible that *H. missipus* shows geographical or local adaptation to particular food plants, or that cryptic species are involved.

In this study, larval food plants of *H. missipus* in the Cape Coast area of the coastal zone of Ghana were identified and the performance of the butterfly on each plant was assessed. The nutritional contents of the food plants were analyzed to assess their possible effects on larval growth and development. Field and laboratory studies were carried out to learn which plants were used as oviposition sites by *H. missipus*. It is expected that the results will contribute to the knowledge of the specific resource needs of *H. missipus* and such knowledge will enable better management of the habitat features that help maintain its populations. There are some indications that local populations are declining, though this is yet to be quantified.

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Field studies were carried out from June 2009 to March 2010 in Cape Coast in the coastal zone of Ghana. The area has double rainfall maxima totaling between 750 mm and 1000 mm per year, with the major rainy season between April and July and the minor rainy season between September and November. The mean monthly relative humidity varies between 85% and 99%. The vegetation in the metropolis consists of shrubs about 1.5 m high, grasses, and remnant forest fragments or thickets.

Observations of daily activities of *H. missipus* were carried out in and around the Research Farm (05° 07.926'N, 001° 17.588'W) and Botanical Garden (05° 06. 985'N, 001° 17.744'W) of the University of Cape Coast, and in backyard gardens and lawns of private houses in Cape Coast (05° 06. 567'N, 001° 17.294'W). Records were made of the species of plants on which adult butterflies fed or laid their eggs. Plant species that were already known as larval food plants, from previous studies, were searched for *H. missipus* larvae. Ovipositing females were observed in the field for other plants that served as oviposition sites.

Based on the field observations, *Portulaca oleracea* Linnaeus 1753, *Portulaca quadrifida* Linnaeus 1767, *Asystasia gangetica* (L) T. Anderson 1860 (Acanthaceae), *Acanthus* sp. (Acanthaceae) and *Axonopus compressus* (S.W.) P. Beauv 1812 (Poaceae) were selected to test in the laboratory, their suitability as substrates for oviposition. Female *H. missipus* (assumed already mated) were caught in the field with an aerial net and taken to the laboratory. Each butterfly was placed in a plastic tray containing one of the selected plants. A mixture of *P. quadrifida* and each of the other plants was also set up in a separate tray and a female butterfly placed in the tray. Each tray was covered with a nylon mesh and placed under an incandescent bulb, during the day, to provide light and warmth. Each set-up had 5 replicates. The butterflies were fed on dilute honey solution. The plants were observed for eggs each day for five days.

The common plants in the study area that were known as food plants of *H. missipus* (Vane-Wright *et al.*, 1977) were *P. oleracea*, *P. quadrifida*, *P. foliosa* Ker. Gawl. 1824, *P. grandiflora* Hooker 1829, *Talinum triangulare* (Jacq.) Willd 1799, (Portulacaceae) and *Asystasia*

gangetica (Acanthaceae). *Acanthus sp.* (Acanthaceae) and *Axonopus compressus* (Poaceae) were not known as food plants but were included in this study because female *H. missipus* had been observed flying about them and, on one occasion in Cape Coast, an egg had been found on each of these plants. Larvae were introduced on these plants and their growth monitored until they pupated. Each set-up consisted of a specific food plant and a single neonate larva placed in a plastic cup covered with mesh. The set-up for each food plant was replicated 10 times.

Based on our preliminary study, *P. oleracea*, *P. quadrifida* and *A. gangetica* were selected for more detailed study. Neonate larvae (from eggs laid on *P. quadrifida*) were introduced on these plants, soon after hatching and before feeding began, and their growth and development were monitored until pupation. Each set-up consisted of a specific food plant and a single neonate larva placed in a plastic cup covered with fine mesh. The set-up for each plant was replicated 50 times. The study was carried out in a laboratory with a constant temperature of 28°C and a relative humidity of 70–85%. The number of molts and the durations of larval and pupal periods were recorded. The lengths of the larvae (at hatching and before pupation) and the wing spans and body lengths of the adults were measured. Weights of day-old larvae, 4th or 5th instars (a day before pupation), and pupae (a day before emergence) were also recorded.

To determine the nutrient contents of food plants, the moisture, crude protein, crude fat, fiber, ash, and soluble carbohydrate levels of *P. oleracea*, *P. quadrifida* and *A. gangetica* were measured as described below.

Samples of each food plant were weighed and dried in an oven at 105°C until constant weights were reached. Moisture content was calculated as

$$\text{Moisture (\%)} = \frac{\text{loss in weight on drying (g)}}{\text{initial sample weight (g)}} \times 100$$

Crucibles were pre-heated in a muffle furnace to about 500°C then cooled in a dessicator and weighed. Crucibles containing 1 g of dry matter of each sample were placed in a cold muffle furnace. The temperature was allowed to rise to 500°C and after 3 hours at 500°C, the crucible was removed, allowed to cool and weighed to determine ash content.

$$\text{Ash (\%)} = \frac{\text{ash weight (g)}}{\text{oven dry weight (g)}} \times 100$$

Total organic nitrogen (N) was determined in the samples by the Kjeldahl digestion and steam distillation procedure as described by Stewart *et al.* (1974).

$$\text{Crude protein (\%)} = \text{N (\%)} \times 6.25$$

In determining the crude fat, 1 g of dry matter from each sample was weighed, placed into a 50 x 10

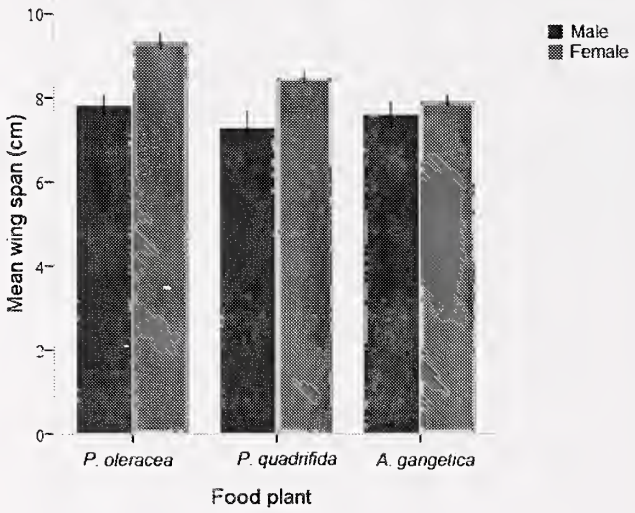

Figure 1. Wing spans of adult male and female *H. missipus* reared from larvae that developed on *P. oleracea*, *P. quadrifida* and *A. gangetica*.

Figure 2. Body lenghts of adult male and female *H. missipus* reared from larvae that developed on *P. oleracea*, *P. quadrifida* and *A. gangetica*.

mm Soxhlet extraction thimble, and then transferred to a 6 ml capacity Soxhlet extractor. About 20 ml of ether was added to a 25 ml round-bottomed flask (B14) containing a glass bead. It was connected to the extractor and extracted for 4 to 6 hours using a heating mantle. The flask was removed and placed in a warm water bath, where the ether was evaporated off using a steam of oxygen-free N_2. It was then placed in a vacuum oven at 40°C for 30 min after which it was cooled in a desiccator and re-weighed.

$$\text{Crude fat (\%)} = \frac{\text{residue in ether extract (g)} \times 10^2}{\text{sample weight (g)}}$$

Soluble carbohydrates were determined in the samples using hot water extraction as described by Stewart *et al.* (1974). For crude fiber content, samples were boiled successively with 1.25% w/v sulphuric acid and 1.25% w/v sodium hydroxide as described by Stewart *et al.* (1974).

The data were tested to verify normality (Shapiro-Wilks test) and the homogeneity of variances. A nonparametric test was used to analyse data that were not normally distributed. Thus the Mann-Whitney and Wilcoxon tests and Kruskal-Wallis test were carried out, as well as multiple comparisons by ranks. The significance of differences between males and females were determined by the Mann-Whitney and Wilcoxon tests, and the Kruskal-Wallis test was used to analyze the growth performances among larvae reared on the three food plants. All statistics were performed by the use of SPSS (version 16) application software.

Adult *H. missipus* were seen feeding on flowers of *Tridax procumbens* L. 1753, *Talinum triangulare* (Jacq.)

Table 1. Development periods of *H. missipus* on three food plants.

Food plant	Larval period (days) †		Pupal period (days) †		Larva-adult (days) †	
	male	female	male	female	male	female
P. oleracea	13.2^{1a}	13.8^{2a}	9.4^{1a}	9.9^{2a}	22.5^{1a}	23.7^{2a}
P. quadrifida	16.7^{1b}	17.4^{2b}	9.1^{1a}	9.6^{1a}	25.8^{1b}	26.9^{2b}
A. gangetica	22.8^{1c}	25^{2c}	8.9^{1a}	9.9^{2a}	31.7^{1c}	34.9^{2c}

† Values in columns not sharing the same letters or in rows within a period not sharing the same numbers are significantly different at the 5% level.

Table 2. Duration of *H. missipus stadia* on three food plants.

Food plant	Period of larval growth (days)				
	1st instar	2nd instar	3rd instar	4th instar	5th instar
P. oleracea	4.5	2.5	1.5	4.5	-
P. quadrifida	6	2.5	2.5	6	-
A. gangetica	4.5	2.5	2.5	6	7

Table 3. Mean weights (± SE) of pupae that developed on three food plants.

Food plant	Mean pupal weight (g) †	
	Male	Female
P. oleracea	$0.77^{1a} \pm 0.02$	$0.95^{2a} \pm 0.01$
P. quadrifida	$0.63^{1b} \pm 0.02$	$0.77^{2b} \pm 0.03$
A. gangetica	$0.64^{1b} \pm 0.01$	$0.73^{2b} \pm 0.02$

† Values in columns not sharing the same letters or in rows not sharing the same numbers are significantly different at 5% level.

Willd.1799, *Melanthera scandens* (Schumach.) Roberty 1954 and *Lantana camara* L. 1753. In the field, the females laid clutches of eggs on *P. oleracea* and *P. quadrifida*. However, in some instances, single eggs were laid on *Acanthus* sp. and *Axonopus compressus*. Larvae were found eating leaves of *P. oleracea* and *P. quadrifida* in the field.

In the laboratory, eggs were laid only on *P. quadrifida* when plants were provided separately. However, eggs were also laid on *P. oleracea*, *Asystasia gangetica* and *Axonopus compressus* when mixed with *P. quadrifida*. Larvae survived on *P. oleracea*, *P. quadrifida* and *A. gangetica* but none of the larvae survived on *P. foliosa*, *P. grandiflora*, *Talinum triangulare* or *Axonopus compressus*.

The eggs of *H. missipus* hatched within 3 to 4 days. There were four instars on *P. oleracea* and *P. quadrifida* but five instars on *A. gangetica* (Tables 1 and 2). Day-old larvae had a body length of about 0.15 cm and weighed less than 0.01 g. Males attained a length of 2.5-3.5 cm and a weight of 0.8-1.0 g while females were 3.0-4.0 cm long and weighed 1-1.2 g before pupation. Larvae that developed on *P. oleracea* produced the heaviest pupae (Table 3) and largest adults, with females having a mean wing span of 9.4 cm and body length of about 3.0 cm while males had a mean wing span of 7.8 cm and body length of 2.7 cm (Figs 1 and 2). Males developed relatively faster than females on all the food plants (Table 1), while female pupae were heavier than male pupae (Table 3).

When reared on *P. oleracea*, male larvae developed 3.5 days faster ($p<0.000$; $\chi^2 = 26.008$) and females 3.6 days faster ($p<0.000$; $\chi^2 = 28.468$) than those reared on *P. quadrifida*. Also, larval period was shorter on *P. quadrifida* than on *A. gangetica* by 6.1 days for males ($p<0.000$; $\chi^2 = 27.854$) and 7.6 days for females ($p<0.000$; $\chi^2 = 17.351$). However pupal periods were similar among all the food plants (male: $p=0.142$; female: $p=0.262$). Larval mortality was lowest on *P. oleracea* (8.7%), followed by *P. quadrifida* (11.1%) then highest on *A. gangetica* (27.1%).

P. oleracea had the highest moisture content and highest levels of almost all the essential nutrients measured. *P. quadrifida* had the most fiber. *Asystasia gangetica* had the highest percentage of crude fat (Table 4).

In the field, *H. missipus* laid eggs on *P. quadrifida* and *P. oleracea*, and larvae survived on both plant species. In the laboratory, however, eggs were laid only on *P. quadrifida* or on other plants when mixed with *P. quadrifida*. *Portulaca quadrifida* and *P. oleracea* may have similar chemical compounds that attracted *H. missipus* for oviposition in the field. However in the laboratory, *P. oleracea* could not attract the butterfly for oviposition. *Portulaca quadrifida* remains fresh for a long period of time and may continue to grow after it has been uprooted. That is not the case for *P. oleracea*, which dehydrates very quickly when out of the soil. Dehydration could cause the breakdown of attractants or the production of stress chemicals that did not attract butterflies. This may explain why in the laboratory, *P. quadrifida* was still able to attract the butterfly for oviposition but *P. oleracea* could not.

In the laboratory, while eggs were laid only on *P. quadrifida* when larval food plants were presented separately, eggs were also laid on other plants when those were mixed with *P. quadrifida*. It appears that ovipositing butterflies are unable to distinguish larval food plants mixed with other plants. This phenomenon, however, is not likely to affect the survival of the larvae in the field, because they are mobile and able to search for the appropriate food plant. Thus even when the eggs are laid on plants that the larvae will not feed on, the neonate larvae may be able to reach preferred food plants, particularly when food plants are not too distant from the oviposition site. This ability was evident in the laboratory when eggs were laid on *Axonopus compressus* that was mixed with *P. quadrifida*. The hatchling larvae did not eat the grass, nor is there any published record of it as a larval food of *H. missipus*. This study provides the first record of an egg laid on *A. compressus* or any grass. The larvae that emerged from eggs laid on *A. compressus* in the laboratory were able to locate and feed on *P. quadrifida* that had been placed in the same container. This behaviour could have survival value

Table 4. Nutrient content of *P. oleracea*, *P. quadrifida* and *A. gangetica*.

Food plant	Nutrient content (%)					
	Moisture	Crude protein	Crude fat	Fibre	Ash	Soluble carbohydrate
P. oleracea	92.5	26.7	11.5	11.2	22.1	15.1
P. quadrifida	88.6	11.4	8	14.1	11.2	6.6
A. gangetica	81.6	25	12.6	12.8	15.8	9.2

in nature, as eggs laid away from larval food might be protected from natural enemies that search for eggs on certain larval food plants.

In the laboratory, larvae developed at different rates on *P. oleracea*, *P. quadrifida* and *A. gangetica*. Nutrients influence all aspects of insect growth, development, and reproduction; *H. missipus* must obtain adequate amounts of the necessary nutrients in a suitable relative balance. Among the three food plants studied, larvae of *H. missipus* performed best on *P. oleracea* in terms of development time and adult size. There is no published report on the essential nutrient requirements of *H. missipus* larvae, but the good performance of larvae on *P. oleracea* indicates the presence of adequate amounts of the essential nutrients required by *H. missipus*. This assessment is supported by the plant nutrient content analysis, which showed that *P. oleracea* had the highest levels of almost all the important nutrients required for insect growth and development. Other studies have shown that *P. oleracea* also contains high levels of Omega-3 fatty acids, in particular alpha-linolenic acid (Simopoulos *et al.*, 1992), which is one of the major fatty acids in insect triglycerides and phospholipids, and is a dietary requirement for lepidopterans (Chapman, 1998). Deficiency of this polyunsaturated fatty acid in lepidopterans can cause failure of pupal or adult ecdysis (Nation, 2008).

The longer development period and smaller size of butterflies when reared on *A. gangetica* may be due to *A. gangetica* not having adequate amounts of the essential nutrients and water required by the larvae for optimum growth and development. Thus it took larvae longer to accumulate the amounts of nutrients necessary to reach pupation. It could also be that the plant did not stimulate the larvae enough to feed properly. Thus the larvae needed more time and an extra instar before they could pupate. Commonly, as food intake increases, development period is extended and insects become smaller and lighter in weight (Chapman, 1998). On nutritionally poor diets, low growth rates are associated with an increase in the number of larval stages. For instance, the caterpillars of *Spodoptera exempta* grew more slowly on *Panicum* and *Setaria* than they did on *Cynodon*, which is more nutritious (Yarro, 1985).

In other countries, including neighboring Côte d'Ivoire, *Talinum triangulare* is known to support development of *H. missipus* (unpublished observations; Vane-Wright *et al.*, 1977) but in our study, larvae did not survive on that plant. Perhaps *H. missipus* may be adapted to different food plants in different localities or geographical areas.

This study has shown that *H. missipus* can survive on *P. oleracea*, *P. quadrifida* and *A. gangetica* but that it develops more quickly and reaches larger size on *P. oleracea*. The information provided about the interactions between *H. missipus* and its food plants is important especially for conservation programs and the mass rearing of *H. missipus* either for research or ecotourism, when choice of appropriate food plants or oviposition materials is necessary. A thorough knowledge in this area is basic to development of an understanding of the butterfly's behaviour, biology and ecology as well as to the development of conservation strategies.

There is a need for further studies on the food requirements of *H. missipus* to fully explain the different larval growth rates recorded for different plants, in this study. Quantifying the amount of food eaten by the larvae on each food plant could demonstrate whether one food plant stimulates feeding better than the others.

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Living on the edge: Habitat and host-plant selection in the butterfly *Lycaena tityrus* (Lepidoptera: Lycaenidae) close to its northern range limit

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Abstract. We here investigate habitat preferences and its variation between the sexes as well as oviposition site selection in a population of the Copper butterfly *Lycaena tityrus* in North-East Germany. Within a continuous habitat, butterflies preferred locations characterized by a higher abundance of nectar plants and a higher proportion of bare ground than found at random, stressing the pivotal importance of adult income and favourable microclimatic conditions. No differences in habitat selection could be detected between males and females, indicating a lack of mutual interference e.g. through male harassment, which is attributed to the relatively low abundance of butterflies in the study area. Females preferentially selected the lowest parts of relatively small (= young) host-plants, growing within relatively low vegetation or in the vicinity of bare ground, for oviposition. Thus, females seem to select high-quality plants and deposit their eggs in the warmest microhabitats available. We suggest that selecting warm microhabitats is an important adaptation for the species' survival under limiting climatic conditions, which is the case for the population studied here being found close to the species' northern distribution limit.

Key words: adult income, habitat preference, habitat quality, host plant, Lycaenidae, microclimate, oviposition.

Introduction

The general needs of any given species can be characterized as a specific set of resources including consumables (such as host-plants) and utilities (such as perch structures; Dennis *et al.*, 2006; Bauerfeind *et al.*, 2009). The presence and abundance of the above resources determines whether a certain habitat patch may or may not support a population of a focal species (Maes *et al.*, 2006; Dennis & Hardy, 2007). However, apart from providing the basic requirements which in either case need to be met, habitat patches may show strong variation in habitat quality. Such differences may crucially affect larval and adult survival, thereby affecting population dynamics (Weiss *et al.*, 1993; Friberg *et al.*, 2008; Turlure & Van Dyck, 2009; Van Dyck & Regniers, 2010). The ability to discriminate between more or less favourable habitats is therefore of pivotal importance for the long-term survival of populations ('preference-performance hypothesis'; e.g. Bonebrake *et al.*, 2010). Unfortunately though, for many if not most species we are currently not able to completely resolve the specific factors involved in determining habitat quality as a crucial prerequisite for successful habitat management (Dennis *et al.*, 2006; Maes *et al.*, 2006; New, 2007 and references therein).

When trying to determine habitat quality, complications may arise from differences in habitat requirements and preferences among sexes (Parker, 1978; Wiklund, 2003; Croft *et al.*, 2006). For instance, the distribution of female butterflies depends on the occurrence of host plants for oviposition (Turlure & Van Dyck, 2009), a factor that is largely irrelevant to males. Also the relevance of other resources such as nectar for adult feeding may differ between the sexes (Fischer & Fiedler, 2001a, 2001b; Turlure & Van Dyck, 2009). Male distribution, on the other hand, should be most strongly affected by the occurrence of receptive

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females. However, male mate location behaviour may in turn impact on female distribution (Parker, 1978). At least in some species females disperse away from areas of high male density in order to avoid male harassment, which may largely exclude females from otherwise suitable habitat (Baguette *et al.*, 1998, Wiklund *et al.*, 2001; Turlure & Van Dyck, 2009).

Finally, it has long been known that larval and adult habitat requirements may strikingly differ (Wiklund, 1977; Dennis *et al.*, 2006). Often, larval habitat requirements are more limiting to population persistence than adult requirements (Elmes & Thomas, 1992; Thomas *et al.*, 2001; Anthes *et al.*, 2003; Wynhoff *et al.*, 2008; Dierks & Fischer, 2009), which has been often overlooked in the past, at least partly because the ecology of pre-imaginal stages is more difficult to observe. Nevertheless such potential differences add further complication to the assessment of a species' habitat requirements.

Against the above background we here investigate (micro-)habitat preferences in the Copper butterfly *Lycaena tityrus* by (1) comparing occupied and vacant habitat patches within a continuous habitat, by (2) investigating potential differences in habitat selection between males and females, and by (3) analyzing oviposition site selection. *L. tityrus* occurs throughout large parts of Eurasia (Tolman & Lewington, 1998). In central Europe it is nowadays a fairly rare species with documented population declines in several regions (Ebert & Rennwald, 1991). Population declines are mainly driven by *L. tityrus* inhabiting different types of grassland, which were subject to substantial agricultural intensification over recent decades.

Materials and methods

Study organism

Lycaena tityrus is a widespread temperate-zone butterfly, ranging from Western Europe to central Asia (Ebert & Rennwald, 1991; Karl *et al.*, 2008). The species is bivoltine with two discrete generations per year in most parts of its range, although populations with one or three generations per year occur (Ebert & Rennwald, 1991; Tolman & Lewington, 1998). *L. tityrus* colonizes different types of unimproved anthropogenic grassland as well as natural grassland such as swampy clearings or mountainous canyons and ridges (Karl & Fischer, 2009). The principal larval host-plant is *Rumex acetosa*, but some congeneric plant species such as *R. acetosella* and *R. scutatus* are utilised as well (Ebert & Rennwald, 1991; Tolman & Lewington, 1998; Karl *et al.*, 2008). The eggs are laid singly on the base of the leaf stem or on the leaf itself (SBN, 1994). Adult butterflies predominantly feed on flowers of composite plants (Asteraceae), but seem to be fairly opportunistic with regard to nectar plant use (Ebert & Rennwald, 1991; Karl & Fischer, 2009). The study was conducted on a relatively dry and sandy fallow field (ca. 40 ha), being currently mown once a year without removing the hay, near the town of Greifswald in North-East Germany. The field work was carried out between May 13th and June 17th during the first and between July 31st and August 15th during the second flight period 2009.

Habitat selection of adult butterflies.

For analysing habitat preferences the following parameters were recorded: slope (in degrees from 0-90°), exposition (in degrees from 1-360°, with 0/360° indicating exposure to the north, 90° exposure to the east etc.), wind exposure (in 3 classes: 1 = sheltered from wind, 2 = intermediate, 3 = strongly wind-exposed), percentage of bare ground in vertical projection, number of vascular plant species, percentage of ground covered by *Rumex* (oviposition) plants, number of *Rumex* plant individuals, availability of nectar flowers (in classes from 0-9, with 0 indicating a lack of flowers and 9 an abundance of flowers), and average vegetation height (as a mean of 16 random, individual measurements). During the first generation, the above parameters as well as *L. tityrus* numbers were scored on 42 randomly selected plots of 5 x 5 m^2, half of which were occupied by butterflies, while the other half was unoccupied during field work. Plot occupation was determined by inspecting each plot repeatedly during the flight period. While in all occupied plots (resting) individuals were repeatedly observed, plots without any *L. tityrus* observation were classified as unoccupied. Records of some of the above parameters, namely percentage of bare ground, number of vascular plant species, percentage of ground covered by *Rumex* plants, and number of *Rumex* plant individuals, were not based on entire plots, but were restricted to four standardised 1 m^2 sub-plots per 25 m^2 plot (for time reasons). In these cases mean values were used for further analysis.

While the above data allowed for a comparison between occupied and vacant patches (within the study area), differences in habitat preferences between the sexes were investigated in the second generation. Therefore, we searched the study area for male and female *L. tityrus* butterflies (n = 31 each). When a butterfly was found, we scored the parameters listed above within plots of 1 m^2, with the place of encounter serving as centre. Habitat parameters were scored as outlined above, except that throughout no sub-plots

were used and that vegetation height was measured at 4 random places within the 1 m^2 plots only.

Oviposition site selection.

For investigating oviposition site preferences individual *L. tityrus* females were followed until they had deposited an egg. Habitat parameters were subsequently scored using the plant chosen for oviposition and a randomly selected, adjacent control *Rumex* plant. In the first generation the parameters measured included distance of the egg from the ground, *Rumex* plant height, length of the (nearest) *Rumex* leaf the egg was laid on (or length of a randomly selected leaf for control plants), height of the surrounding vegetation (mean within a 20 cm radius), and the percentage of bare ground. In the second generation the number of leaves per *Rumex* plant and ambient temperature 1, 10 and 20 cm above ground (next to the plant, measured with a thermocouple) were recorded additionally. As during the whole study butterflies were not marked, we cannot rule out that we occasionally used the same individuals (also above). However, given the size of the whole study area and the size of the population it is highly unlikely that potential double counts significantly affected the results presented here.

Statistical analyses

Comparisons between vacant and occupied patches, male and female habitats, and between oviposition and random *Rumex* plants were analysed using Mann-Whitney U-tests. To further analyse habitat preferences we used general non-linear models (GNLMs) with a binomial (comparing occupied and vacant patches) or ordinal (comparing vacant patches with ones inhabited by a single or more than one butterfly) error distribution. Differences in temperature at the three heights above ground were tested by a Kruskal-Wallis test. Distributions of butterfly eggs across plant height classes were tested against even distributions by chi-square tests. All statistical tests were performed by using Statistica (8.0) and SPSS for Windows (17.0 Student Version).

Results

Habitat preferences of adult butterflies

Only one of the parameters investigated differed between patches occupied by *L. tityrus* and randomly selected patches (Table 1a). The number of nectar flowers available to butterflies was significantly higher in occupied than random patches. However, even the latter difference would be non-significant when applying a Bonferroni correction to the results. When we analyzed the data using a GNLM with a binomial error distribution, we found that the percentage of bare ground (χ^2_1 = 7.0, p = 0.008) and flower availability (χ^2_1 = 3.8, p = 0.052) were the strongest predictors of butterfly occurrence, with the probability of occurrence increasing with a higher percentage of bare ground and higher flower numbers. When using a GNLM with an ordinal error distribution, thus comparing vacant patches with ones inhabited by a single or more than one butterfly, flower availability (χ^2_1 = 4.6, p = 0.031) turned out to be the strongest predictor of butterfly numbers followed by the percentage of bare ground (χ^2_1 = 3.1, p = 0.079). No sexual differences in habitat preferences were detected in second generation butterflies (Table 1b).

Oviposition site preferences

In the first generation, *R. acetosa* plants used for oviposition were significantly smaller than randomly selected *R. acetosa* plants, and the surrounding vegetation was significantly lower at oviposition compared to random sites, while the other two parameters investigated did not differ significantly (Table 2a). The data from the second generation also indicated a significant preference for smaller *R. acetosa* plants, while differences in the height of the surrounding vegetation were not significant here (Table 2b). However, the percentage of bare ground at oviposition sites was significantly higher than at random sites. The remaining parameters, including temperatures measured at different heights above the ground, did not differ significantly between oviposition and randomly selected *R. acetosa* plants. However, temperature decreased significantly with increasing distance from the ground (H_2 = 89.1, p < 0.0001; Table 2b).

In addition to preferring smaller *R. acetosa* plants for oviposition (see above), *L. tityrus* females deposited the vast majority of their eggs quite close to the ground, i.e. between 0 and 5 cm above ground (significant deviation from an even distribution across height classes; χ^2_2 = 55.6, p < 0.0001; Fig. 1a). This pattern was not per se caused by preferring small plants. Females clearly preferred to oviposit on the lowest parts of host plants, as indicated by measuring the position of eggs relative to plant height (significant deviation from an even distribution across height classes; χ^2_3 = 35.2, p < 0.0001; Fig. 1b).

Table 1. Comparison of various habitat parameters (means ± SE) between random and occupied (by *Lycaena tityrus*) patches (a; n = 21 each), and between encounter sites of male versus female butterflies (b; n = 31 each). Significant p-values, as tested by Mann-Whitney U-tests, are given in bold.

Table 1a

Parameter	Random		Occupied		Z	p
	Mean	SE	Mean	SE		
Slope [°]	1.4	1.1	1.7	1.5	0.23	0.8155
Exposition [°]	203.1	88.0	154.4	80.0	-1.70	0.0893
Wind exposure	2.1	0.8	1.8	0.9	-1.29	0.1955
Bare ground [%]	7.2	6.1	13.4	15.8	0.40	0.6869
Plant species [n]	17.6	3.5	19.1	4.6	0.87	0.3838
Rumex acetosa [%]	8.6	5.3	9.9	10.2	-0.53	0.5971
Rumex acetosa [n]	19.5	8.3	15.7	10.2	-1.41	0.1588
Flowers [n]	1.7	1.2	2.7	1.8	2.45	**0.0144**
Vegetation height [cm]	15.0	8.5	13.8	9.2	-0.58	0.5621

Table 1b

Parameter	Random		Occupied		Z	p
	Mean	SE	Mean	SE		
Slope [°]	0.9	0.8	0.7	1.0	1.16	0.2055
Exposition [°]	217.7	99.3	196.0	99.6	0.96	0.3359
Wind exposure	1.8	0.8	1.8	0.6	-0.34	0.7111
Bare ground [%]	5.9	11.7	6.8	11.1	-0.95	0.3153
Plant species [n]	11.6	3.3	11.7	2.8	0.07	0.9436
Rumex acetosa [%]	7.0	7.5	7.5	5.6	-0.97	0.3292
Rumex acetosa [n]	16.0	13.1	19.1	12.8	-0.98	0.3274
Flowers [n]	2.5	2.3	2.5	2.2	0.08	0.9314
Vegetation height [cm]	11.5	10.6	11.5	11.6	0.99	0.3191

Discussion

Within the continuous habitat investigated, very few differences between specific sites occupied or not occupied by *L. tityrus* butterflies could be detected. The only significant predictors of butterfly occurrence in our study were flower availability and the percentage of bare ground. The importance of flowers is hardly surprising, as nectar plays a crucial role in butterflies as flight fuel, and for prolonging longevity and increasing reproductive output (Rusterholz & Erhardt, 2000; Fischer *et al.*, 2004; Bauerfeind & Fischer, 2005). The related Copper butterfly *L. hippothoe* L., for instance, has been shown to rely particularly strongly on nectar intake for egg production (Fischer & Fiedler, 2001a). Accordingly, field studies have shown that availability of nectar plants is positively related to both the number of butterfly species and the number of individuals within species (Feber *et al.*, 1996; Fred *et al.*, 2006; Pyöry *et al.*, 2009).

The preference for places with a higher proportion of bare ground and thus a more heterogeneous vegetation structure is most likely related to beneficial microclimatic conditions. Temperature near the ground is also affected by solar radiation and wind exposure. Associated parameters, however, did not differ significantly between occupied and random patches (Table 1a), probably as a result of the relative homogeneity of the study area with respect to these factors. The same reasoning may apply for the lack of an association between butterfly occurrence and host plant abundance, as *Rumex* plants are abundantly available throughout the whole study area. However,

Table 2. Comparison of various parameters (means ± SE) between *Rumex acetosa* plants used by *Lycaena tityrus* for oviposition and randomly selected (*R. acetosa*) plants in the first (a; n = 22 each) or second flight period (b; n = 30 each). Significant p-values, as tested by Mann-Whitney U-tests, are given in bold.

Table 2a

Parameter	Oviposition		Random		Z	p
	Mean	SE	Mean	SE		
Plant height [cm]	17.8	3.3	28.9	3.3	-2.84	**0.0045**
Leaf lenght [cm]	5.0	0.3	5.1	0.3	-0.21	0.8327
Vegetation height [cm]	20.1	2.2	28.3	2.2	-2.79	**0.0052**
Bare ground [%]	39.5	4.5	43.2	4.5	0.46	0.6472

Table 2b

Parameter	Oviposition		Random		Z	p
	Mean	SE	Mean	SE		
Plant height [cm]	14.4	2.4	21.4	2.4	-2.95	**0.0032**
Leaves [n]	5.7	0.5	4.7	0.5	1.23	0.2170
Leaf length [cm]	4.0	0.4	4.9	0.4	-1.53	0.1260
Vegetation height [cm]	18.9	1.7	20.9	1.7	-1.13	0.2581
Bare ground [%]	55.0	3.7	38.5	3.7	-2.92	**0.0035**
Temperature 1 cm [°C]	30.3	0.5	29.7	0.5	0.82	0.4119
Temperature 10 cm [°C]	26.6	0.3	26.1	0.3	1.13	0.2581
Temperature 20 cm [°C]	25.4	0.3	24.7	0.3	1.77	0.0773

spots of bare ground will warm up more quickly and reach higher equilibrium temperatures compared to ground covered by vegetation, such that these spots are likely to represent the warmest places within our study area. As temperate-zone butterflies typically prefer the warmest spots within their habitats (e.g. Thomas & Lewington, 2010), we believe that the preference for bare ground is caused by its higher temperature.

A bit surprisingly, no differences in habitat selection between male and female *L. tityrus* butterflies could be detected, while studies on other butterflies including lycaenids have shown sex-specific differences (e.g. Baguette *et al.*, 1998; Rusterholz & Erhardt, 2000; Wiklund *et al.*, 2001; Turlure & Van Dyck, 2009). Obviously, both sexes prefer both flower-rich areas and favourable microclimates, without a significant mutual interference between the sexes. The lack of mutual interference is probably caused by the relatively low population density in the study area compared with other *Lycaena* populations (Fischer *et al.*, 1999; Fischer & Fiedler, 2001b). An equally strong preference for nectar plants across sexes is conceivable as both sexes rely on adult income for flight and increased life span (see above). While females furthermore need nectar for egg production, males may set up their territories close to nectar plants awaiting receptive females. Such resource-based territoriality has been shown for *L. hippothoe* (Fischer & Fiedler, 2001b; Turlure & Van Dyck, 2009), and may also exist in *L. tityrus*. The lack of a difference in host-plant abundance at male and female encounter sites is most likely once again related to the abundant and homogeneous occurrence of *Rumex* in the study area.

Our data on oviposition site selection revealed that females clearly preferred to oviposit on fairly small host-plants, on which they deposited their eggs close to the ground (*cf.* Singer & McBride, 2010; Thomas & Lewington, 2010). Females were repeatedly observed to alight on a host-plant, after which they climbed down to reach the parts of the plant close to the ground. While the preference for smaller (= younger) plants is probably related to their higher nutritional quality for hatching caterpillars (more nutrients, fewer secondary plant products; e.g. Begon *et al.*, 1996), the preference for the plants' lower parts is likely to be related to higher temperatures close to the

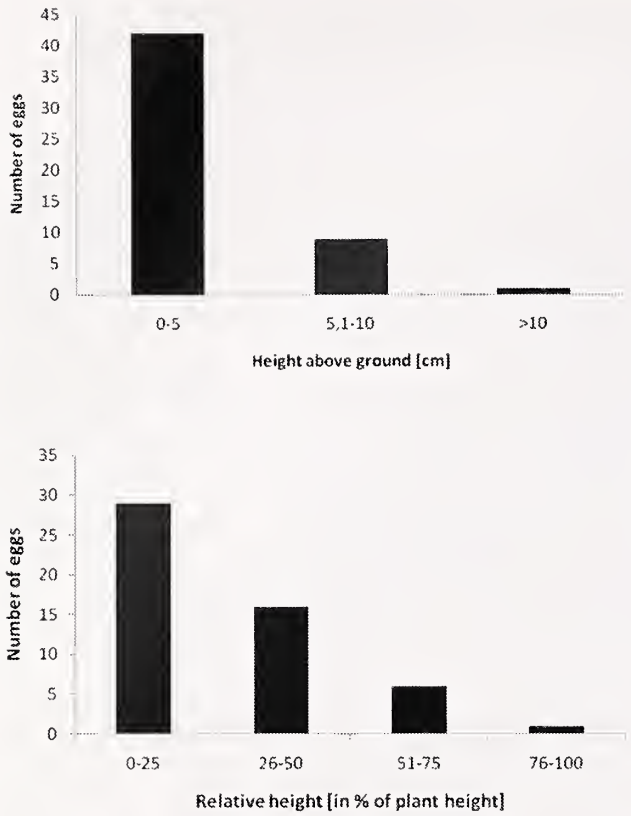

Figure 1. Position of *Lycaena tityrus* eggs on *Rumex* plants as measured as absolute height above ground (a) and relative height in % of total plant height (b; n = 52 each).

ground (*cf.* Table 2b). Such conditions will evidently speed up development. A comparable behaviour was not observed in *L. tityrus* populations in southern Germany or northern Italy, where eggs are laid higher above the ground (KF, personal observations). We therefore hypothesise the existence of population-specific differences in oviposition behaviour, with the females from the population investigated here, which is close to the northern limit of the distribution range of *L. tityrus*, selecting the warmest places for oviposition under relatively poor climatic conditions (Thomas, 1990). Alternatively, such behavioural differences may arise as a consequence of plasticity in oviposition site selection (Gibbs & Van Dyck, 2009).

The findings that lower vegetation (first generation) and bare ground (second generation) were preferred for oviposition further support the notion that *L. tityrus* females prefer warmer sites for egg-laying. Note in this context that the field was mown between the first and the second flight period, which explains why there was no longer a significant effect of vegetation height in the second generation. Why the percentage of bare ground had no significant influence on oviposition site selection in the first generation is unclear, but might be related to the approaching cooler (autumn) conditions after the second flight period. In order to ensure that larvae will reach their hibernation stage before winter, females may have been even more selective in the second generation (*cf.* Thomas & Lewington, 2010 for *Polyommatus bellargus*).

In summary, we found little evidence for pronounced site selectivity in adult *L. tityrus* butterflies within a continuous habitat. Butterflies preferred warm locations rich in nectar plants. However, investigating oviposition plant selection revealed more clear-cut patterns, with females preferring to oviposit on small, high-quality plants and actively seeking to deposit their eggs in warm microclimates. The latter might be a crucial and therefore widespread adaptation in butterflies occurring in cooler climates, as is the case for the *L. tityrus* population studied here which occurs close to the northern limit of the species' range.

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Note

Achiasmy or heterochiasmy: Does meiotic recombination occur in female Lepidoptera?

Sexual dimorphism in the amount of crossing-over and recombination during gamete formation (meiosis) is common in insects (Trivers, 1988; Burt *et al.*, 1991). In many cases, recombination in the different sexes differs not only on sex chromosomes but also on autosomes. In *Drosophila*, for example, genetic exchange between homologous chromosomes is completely absent in males (Morgan, 1914). This phenomenon, called "achiasmy," occurs frequently in Diptera, and in several other insect orders including Lepidoptera (Bell, 1982). According to the Haldane-Huxley rule (Haldane, 1922; Huxley, 1928), when one sex has achiasmate meiosis, it is always the heterogametic sex (XY or WZ). Lepidoptera have WZ/ZZ sex determination; therefore, females, not males should be achiasmate.

Meiotic recombination in Lepidoptera has been studied for decades, and female achiasmy has been found in several Lepidoptera species (Suomalainen *et al.*, 1973; Turner & Sheppard, 1975; Scriber *et al.*, 1995; Heckel *et al.*, 1999). Consequently, the absence of meiotic recombination in females is thought to be a general phenomenon of all butterflies and moths. The pivotal evidence for Lepidoptera achiasmy comes from classical cytogenetic and genetic breeding studies. Advanced cytogenetic imaging techniques have recently been applied to obtain improved and more convincing results (Marec & Traut, 1993; Yoshido *et al.*, 2005). In female meiosis, synaptonemal complexes appear to be modified and are fundamentally different from chiasmata found in males (Marec & Traut, 1993). The absence of normal chiasmata at oogenesis is believed to prevent crossing-over in female butterflies and moths.

Perhaps surprisingly, genetic studies by Carter and Watt (1988) and Wang and Porter (2004) both showed the presence of crossing-over in female *Colias* butterflies. The amount of recombination, however, is considerably less than that in males, with the ratio of female-to-male map length being approximately one third (Wang & Porter, 2004). This situation is called "heterochiasmy" (see Figure 1 for an illustration of the difference), in which both sexes recombine, but with quantitative differences in frequency. Similar to the phenomenon of achiasmy, heterochiasmy tends towards less recombination in the heterogametic sex (Trivers, 1988), which was confirmed by the study of *Colias* butterflies.

Early karyological studies of a few Lepidoptera species, though ambiguous, indicated that chiasmata might actually form in bivalents at oogenesis (reviewed by Robinson, 1971, also refer to Table 1 for a summary). These "exceptional chiasmata," which were documented in the silkworm, appear to occur rarely (Maeda, 1939). It has also been determined

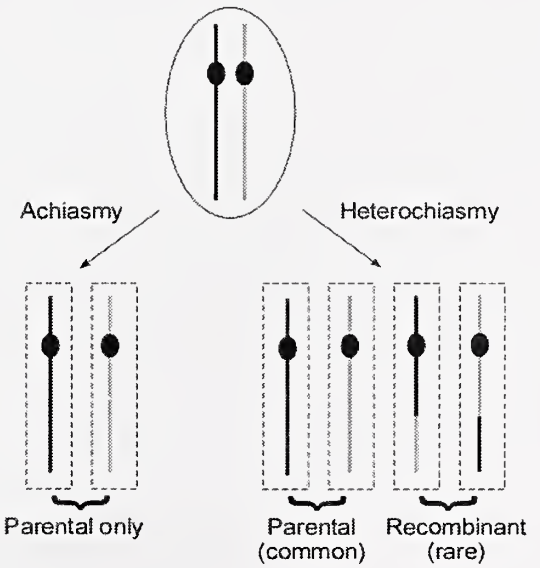

Figure 1. Schematic sketch of gamete formation in female Lepidoptera, illustrating the processes involving achiasmy vs. heterochiasmy. For simplicity, only one pair of chromosomes is shown. In the case of achiasmy, all meiotic products (gametes) are parental type, while gametes of recombinant type are present in the case of heterochiasmy.

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Table 1. Observed cases of heterochiasmy in Lepidoptera.

Species	Evidence	Recombination frequency of females	References
Some race of *Bombyx mori*	karyological observations	0.36%	Maeda, 1939
Trichiura crataegi	microphotographs of chiasmata	unknown	Federley, 1945
Thera obeliscata and *T. variata*	karyological study of the bivalent structures	unknown	Suomalainen, 1953
Philosamia ricini	karyological studies	unknown	Srivastava & Gupta, 1962
Colias eurytheme and *C. philodice*	genetic mapping	1/3 of the frequency of males	Carter & Watt, 1988; Wang & Porter, 2004

that the two sexes of Lepidoptera differ markedly in the number as well as in the position of chiasmata. In females, crossing over is likely to arise only at the ends of the bivalents and terminate shortly thereafter (White, 1954). As a result, recombination is greatly reduced and confined to small chromosomal areas. This is consistent with the results of mapping studies of *Colias* butterflies, where genetic markers clustered in the middle of the linkage groups and longer gaps appeared near the ends (Wang, 2005).

Therefore, the generally held view of female achiasmy in Lepidoptera is not entirely accurate, because, at least for some species, crossing-over is not completely suppressed. Clearly, there is variation in female recombination rates among different Lepidoptera species, some being achiasmatic and others heteroachiasmatic. Such variations may be explained by sex differences in gene epistasis, sexual selection, or gamete selection (Lorch, 2005; Lenormand & Dutheil, 2005). Heterochiasmy is hard to detect and differentiate from achiasmy because the crossing-over events are rare and largely confined to small regions of the chromosomes. The known incidence of heterochiasmy in Lepidoptera may increase as further studies provide a greater understanding of sexual dimorphism in autosomal recombination.

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Book review

A wildlife guide to Chile by Sharon Chester, 2008

Princeton University Press. 392 pp. Paperbound. $19.95. ISBN: 9780691129761 (Also available hardbound and as an e-book.)

Until the publication of this book there was no concise single-volume guide to the remarkable and highly endemic fauna and flora of Chile—not in English, nor in Spanish either, for that matter. Several excellent guides to specific groups are available, of which the best—available in both languages—is Jaramillo's Birds of Chile (2003). For Lepidoptera, the only modern resource has been Peña and Ugarte's Mariposas de Chile (1996, not 1992 as misdated in this book!), which has bilingual text—but it was printed in a very limited edition, as is usual for Latin American books, and is very hard to get. (Try it on-line! I found one copy available.)

So for visitors interested in butterflies and moths, A Wildlife Guide to Chile is the only game in town. And it's not bad. We used to think the Chilean butterfly fauna was really depauperate (except for grass-feeding Satyridae). But then Dubi Benyamini, Zsolt Bálint and Kurt Johnson discovered a wealth of unrecognized Lycaenids, sparking a major reevaluation of evolutionary biogeographical concepts. Fortunately, their work made it into the Peña and Ugarte book—by a whisker. The treatment of butterflies here is explicitly derivative from Peña and Ugarte, but even so, some errors crept in—some via Peña and Ugarte and others *de novo*—and of course, not all the species can be covered, let alone illustrated, in a general book of this sort. So you are encouraged to buy and use Chester, but you might want to make a few corrections in the margins, to wit:

p.92. Not all skipper larvae are green! *Urbanus proteus* does not normally lay eggs in clusters of about 20 (usually singly or at most in twos or threes) and is not restricted to Leguminous vines.

p.94. The descriptions of *Pyrgus* species are wholly inadequate to tell them apart. *P. notatus*, for example, is not "olive-brown with white spots," and even if it were, that wouldn't help identify it. *Erynnis funeralis* may not actually feed on alfalfa, and alfalfa is not a grass, as the text implies it is! ("Larvae feed on alfalfa and other grasses.")

p.95. *Colias vauthierii* does not feed on alfalfa; the name "Colias de la alfalfa" is a misnomer, properly applied to *C. lesbia*, which is sexually dimorphic in pattern but, contrary to the text, has both gray-white and orange females, and is not found in Magallanes. *Colias flaveola*, restricted to a few high-elevation canyons in Coquimbo and across the Argentine border in San Juan, is not a "common species."

p.96. Quintral (*Tristerix*) is a parasite, not an epiphyte. *Hypsochila wagenknechti* (correct spelling) is a high-altitude species, not "common in foothill areas from Coquimbo to Santiago." It's *Infraphulia*, not *Intra-*, and *Phulia nymphula*, not *nimphula*. The descriptions, again, are completely useless, all the more so because they don't even say these Whites are tiny. And there are other high-altitude mini-whites similar to them that are not mentioned at all.

p.98. Users should be aware that much of the Lycaenid diversity of Chile (understandably) cannot be covered here, and brief descriptions are not of much use. (The illustrations in Peña and Ugarte aren't that much better—one needs to access the photos in the original papers describing them, and they are extremely hard to find.)

p.99. It's "Monarca," not "Monarcha." It is by no means established that "South American Monarchs do not migrate." At least Argentine ones almost certainly do. The evolutionary-biogeographic scenario spelled out here is, frankly, gratuitous arm-waving.

p.100-102. The treatment of the Satyrs is pretty good, but again, many species are (necessarily) omitted. Descriptions (e.g. of *Auca coctei*) are of minimal use. The association of many species with bunchgrass in steppe needs to be emphasized.

p.102. The capsule descriptions of the three species of *Yramea* are not useful. *Vanessa carye* is the sister-species of *V. annabella*, not of *V. cardui*! The description of *V. terpsichore* as "paler" than *V. carye* is bizarre and misleading.

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There is a brief overview of moths (pp.103-105) with good illustrations of the few big, showy ones. We do not know that all moths "produce potent pheromones," though many do.

In short: as usual, use with caution. But this book is a good investment for any traveler to Chile with an interest in natural history, and if you are not bilingual, it's a must.

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Book review

Elachistine moths of Australia (Lepidoptera: Gelechioidea: Elachistidae) by Lauri Kaila, 2011

Monographs on Australian Lepidoptera, volume 11, viii + 443 pp. CSIRO Publishing, Collingwood, Australia. ISBN: 9780643103054. Price: AU$ 150.00.

Elachistidae moths are a species-rich clade within the diverse superfamily Gelechioidea. No wonder that such organisms remain severely under-explored in many parts of the world, especially in tropical and subtropical regions. With this present volume, the Finnish Microlepidoptera expert Lauri Kaila now has produced a great leap forward in understanding the diversity and evolution of the subfamily Elachistinae. Representatives of this clade, notably the speciose genus *Elachista*, have considerable ecological importance as one of the globally most diversified lepidopterous taxa that feed on grasses and sedges, usually as leaf miners or stem borers. Some *Elachista* species are notorious pests of agriculturally important grasses like sugar cane or millet.

The present volume, for the first time ever, integrates all taxonomic, morphological, distributional and ecological information available for the Australian species of the subfamily Elachistinae. However, this book is not 'only' a monograph whose relevance would be regionally restricted to Australia. Like other volumes of the same series, this book also provides much information that will be of interest to a far wider readership. The first chapter, co-authored by Kazuhiro Sugisima, is an in-depth analysis of the phylogeny and classification of Elachistinae under a global perspective. The second chapter introduces in detail the morphological and anatomical structures of larvae, pupae and adults, as they have been used to analyze phylogeny and characterize species and clades. There follow two brief chapters on general elachistid biology and on their distribution within Australia. The main part of the book contains detailed accounts of all recognized species, followed by excellent color plates of the adult moths, pupal exuviae and leaf mines, and black-and-white micro photographs of all genitalic structures. Two appendices collate the taxonomic changes taken by the author, and provide the data matrix on which the phylogenetic analyses are based.

This book, like its predecessors in the same series, is extremely well produced. This does not only pertain to its scientific value and content, but also to the quality of printing (especially relevant for the many illustrations) and binding. In view of this, the price (approx. € 100 or US$ 145) is acceptable. Of course, this book will be most interesting to the Microlepidoptera researcher community. But this volume also contains much of interest for a wider audience, from biodiversity research to pest control. To illustrate the progress Kaila has made with a few figures: the number of recognized Australian species in the Elachistinae now amounts to 148. When Kaila started to revise the fauna of that continent, the known species number had been as low as 19 (as published in volume 4 of the Monographs of Australian Lepidoptera series by E. S. Nielsen and colleagues in 1996). Of these, 5 species were just erroneously included in the family Elacistidae. Hence, within 15 years the known species richness within this single moth clade in the Australian fauna increased by one order of magnitude! Not surprisingly, most of these additions are hitherto unrecognized species. These findings now raise Australian Elachistidae richness to the 140+ species level of North America, and even rather close to the far better surveyed European fauna with 200+ recorded species. Such comparisons emphasize how important high quality taxonomic monographs still are for uncovering and understanding biodiversity, even in the age of internet databases. In particular, this volume exemplifies how valuable reference collections in natural history museums are – the materials held in the ANIC (Australian National Insect Collection), together with results of field work by the book's author, form the backbone of this monograph.

This book is to be recommended to all scientists

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with interest in the systematics and biogeography of Microlepidoptera. It should definitely be available in any larger museum or university library. Moreover, one is inclined to hope that further such volumes will continue to appear in that series, in order to improve the documentation of Lepidopteran diversity of the Australian continent.

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Mate–location behavior in *Pereute* Herrich–Schäffer butterflies (Lepidoptera: Pieridae), with a review of male behavior at encounter sites in the subtribe Aporiina

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Abstract. Male butterflies exploit a range of encounter sites, such as larval food resources, adult food resources and landmarks, to detect receptive females for mating. We present preliminary observations on behavior of males of *Pereute* and allied butterflies from South America which suggest that valley floors of ravines and gorges are used as non–resource–based encounter sites to locate mates. Males of *P. callinira* Staudinger, 1884, and *P. telthusa* (Hewitson, 1860) use these landmarks during the morning or around midday, are site tenacious (duration of visitation approx. 1–2 h), exhibit high site defense against conspecifics, and patrol a defined air space (territory): we hypothesize that these components comprise a mate–location tactic to locate receptive females. Similar behavior occurs in the closely related genera *Leodonta, Catasticta* and *Archonias*, although in *Catasticta* and *Archonias* males adopt a perching strategy while waiting at these and other landmarks. A review of available information on mate-location behavior in the Aporiina indicates a diverse array of tactics. Although there is little data on courtship of females and actual matings, non-resource-based sites (landmarks) are used most frequently as putative encounter sites, which as a rule are visited during the morning, and that patrolling behavior amongst males is widespread. Simple optimization of the component of waiting for receptive females in relation to a phylogenetic hypothesis for the Aporiina suggests that patrolling is ancestral and evolved in the common ancestor of the subtribe, whereas perching is derived and evolved relatively recently in the immediate common ancestor of *Catasticta* + (*Archonias* + *Charonias*). The selective forces that may have promoted this evolutionary switch in male behavior within the subtribe are briefly discussed.

Keywords: *Aporia*, butterfly behavior, *Cepora*, *Delias*, landmarks, *Leuciacria*, *Mylothris*, patrolling, phylogenetic history, territory.

Introduction

Butterflies utilize a range of encounter sites for mate–location, including larval food resources (pupation sites where females emerge, oviposition sites), adult food resources (foraging sites such as nectar of flowers), and non–resource–based sites (landmarks) (Thornhill & Alcock, 1983). Rutowski (1991) summarized and reviewed the major components of male behavior at these encounter sites to detect receptive females. These components include visitation times (time of day), site tenacity (duration of visitation), site defense against conspecific males (degree of territoriality), and behavior whilst waiting for receptive females (patrolling or perching). Variation in these components, and hence differences in male–location tactics, is believed to be determined by the spatial and temporal distribution of receptive females (Emlen & Oring, 1977; Thornhill & Alcock, 1983). For the Pieridae, it was concluded that low site tenacity, no site defense and patrolling in this group of butterflies were the rule (Scott, 1974; Rutowski, 1991). However, this conclusion was based on limited data from the Coliadinae and two tribes

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within the Pierinae (Anthocharidini, Pierini); thus, data from a larger breadth of species within this group are likely to be informative. In this review we present preliminary observations on males of *Pereute* Herrich–Schäffer, 1867, from South America, namely *P. callinira* Staudinger, 1884 (Fig. 1) and *P. telthusa* (Hewitson, 1860) (Fig. 2), that are site tenacious, territorial and frequently employ patrolling flight behavior. Mate–location behavior in these species is then compared with related genera in the Aporiina reported elsewhere within the context of an evolutionary history of the subtribe.

Mate–location behavior in *Pereute*

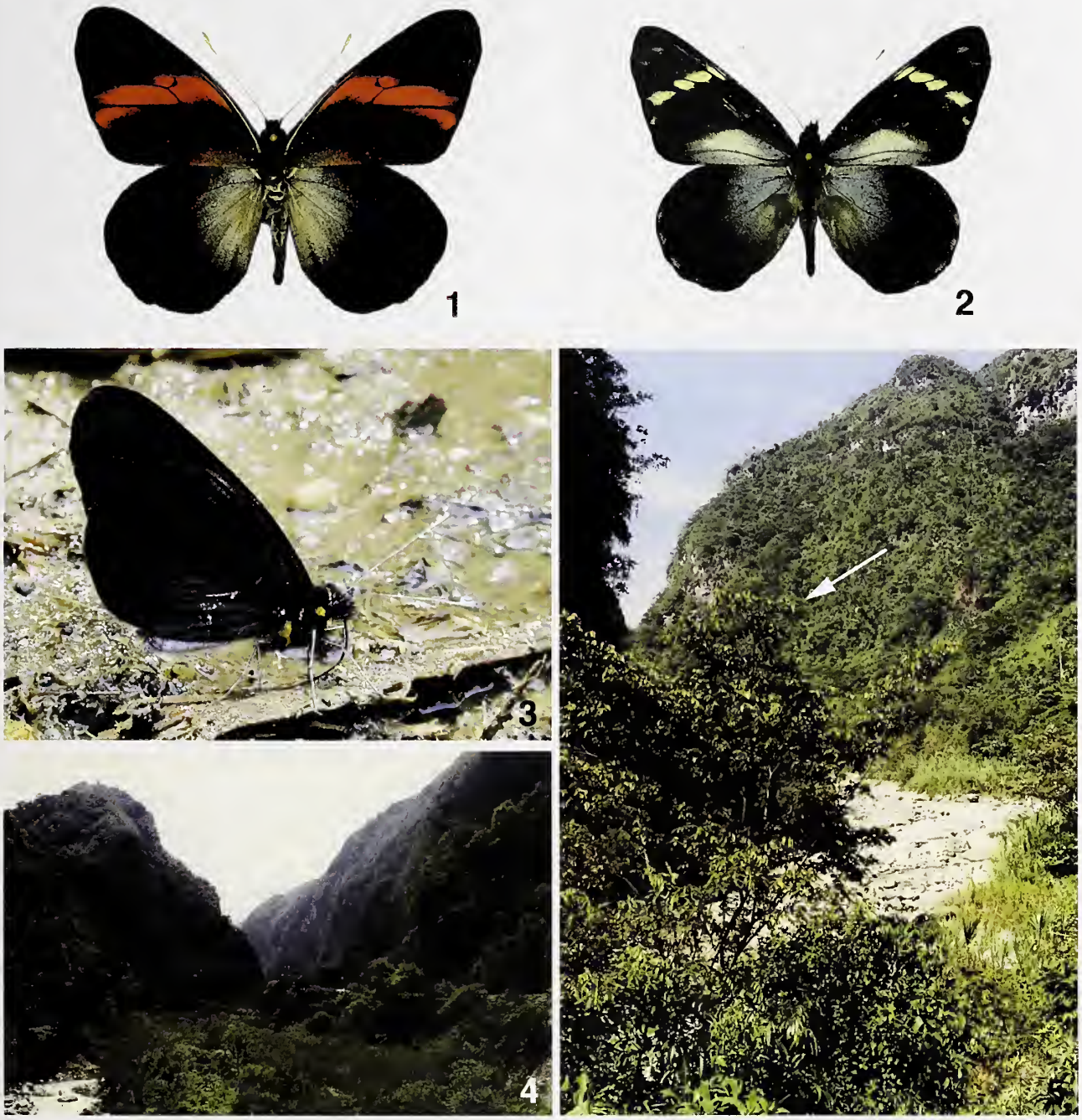
Mate–location behavior among male *Pereute* butterflies was briefly described by DeVries (1987) and W. Haber (personal communication, 2000) for two species from Costa Rica in Central America: *P. charops* (Boisduval, 1836) and *P. cheops* Staudinger, 1884. Males of these butterflies typically select landmarks, which consist of forest edges, light gaps (i.e. prominent openings in the dense forest canopy where light reaches the understorey) or, more usually, the crowns of the tallest trees in the forest. At these landmarks, individuals fly high in the forest canopy with a characteristic and conspicuous slow gliding or sailing flight with shallow wing beats. Each male occupies a defined air space by patrolling in long, circling flights to establish a territory, which is defended against rival males. Patrolling occurs from about mid–morning to midday and may last for several hours without pausing to settle.

In late 2000, opportunistic observations were made in the montane tropical forests of the Chanchamayo district of Peru, South America. The Chanchamayo district lies in the upper Amazon basin on the eastern side of the Andes in steeply dissected country, and is a hotspot for butterfly biodiversity that is readily accessible from the capital Lima, 300 km further west. Five species of *Pereute* fly sympatrically in this area, namely: *P. callinira callinira*; *P. callinice numbalensis* Joicey & Talbot, 1928; *P. leucodrosime bellatrix* Fruhstorfer, 1907; *P. telthusa* and *P. charops peruviana* (Hopffer, 1878) (nomenclature of Lamas 2004). Behavioral observations were made chiefly on two of these species, *P. callinira* and *P. telthusa*, both of which are presumably involved in different mimicry complexes that include species of *Heliconius* (Nymphalidae: Heliconiinae) to which they resemble closely in wing pattern markings and flight behavior.

Field observations were made principally at two sites in the Chanchamayo district: (1) Cataratas de Agua Flor, Río Palca, 15 km SW of San Ramón (11° 10'S, 75°27'W; c. 1400 m a.s.l.); and (2) a tributary (creek) of Río Palca, 10 km SW of San Ramón (11°10'S, 75°24'W; c. 1300 m a.s.l.). Observations were conducted over eight days at the end of the dry season, from 7–10 and 14–17 November 2000. Sites were visited on alternate days, generally from 0800 h to 1600 h (i.e. each site was sampled four times). During 7–10 November, weather conditions were dry, sunny and hot with daytime temperatures reaching their seasonal maximum (c. 28°C). However, considerable rain fell during 11–13 November with the onset of the first pre–wet season storms, and weather conditions after this period were damp, overcast and cooler (c. 22°C), with only limited patches of sunlight around midday.

Pereute callinira Staudinger, 1884

In early November, prior to the pre–wet season storms, males of *Pereute callinira* (Fig. 1) were initially observed flying at the bottom of ravines where they established territories above the river or creek (Fig. 4). Up to six 'older' males (i.e. with slight to worn wing wear) occurred at each site. They typically selected a small sunlit area that included either the open air space above the water and canopy of nearby trees growing along the bank, or an open air space around the canopy of a small tree growing along the bank of the river (Fig. 5). These males flew generally at a height of 5–8 m from the water/ground level, although some males flew much higher, about 12–15 m above the water/ground level, if the flight space was located along steeper, narrower banks. Territories were about 10–20 m in diameter, and distributed linearly along the river or creek at intervals of 50 m or more. Males occupied these territories with a patrolling flight during which they rarely settled. The patrolling flight consisted of a slow sailing or gliding circling flight, with fore wings outstretched and oriented at angles between 135° and 180°, thereby exposing the conspicuous bright red median band, interspersed by a series of slow wing beats. When not interacting with other butterflies, males patrolled the same air space back and forth, but when conspecific males and other similar looking butterflies, for example, *Altinote* and *Abananote* (Nymphalidae: Heliconiinae: Acraeini), were detected they were intercepted and chased out of the flight space (territory). When chasing rival males the resident male often accelerated rapidly and flew at higher speeds. Patrolling behavior was limited to the mid–morning and usually lasted for 60–90 mins when conditions were cool but sunny. Males typically arrived around 0830–0930 h and then departed around 1010–1030 h, by which time



Figures 1–5. Study species and putative encounter sites near San Ramón, Chanchamayo district, Peru. **1**. Male *Pereute callinira*. **2**. Male *P. telthusa*. **3**. Freshly emerged male *P. callinira* puddling. **4**. Ravine showing bottom of valley floor (Río Palca) where encounter sites were established by male *Pereute* butterflies. **5**. Encounter site of *P. callinira*; arrow indicates air space around canopy of tree growing along bank of Río Palca that was used by a particular male.

conditions were warmer. Although not confirmed by mark–release–recapture, resident males appeared to occupy the same territory on successive days during the observation period based on characteristic wing marks of individuals. Between 1010 h and 1100 h, nectar feeding among some of these males was noted to occur, but from 1100 h to 1245 h (hottest part of the day) very few adults were encountered and none flew in open sunlit areas. The only males observed during midday were either settled on leaves of trees or shrubs in deep shade, or were flying very close to the ground along the bank of streams or over the surface of water

in shaded areas of the forest. When settled, males kept their wings closed, concealing the red median band and exposing only the inconspicuous black underside ground color of the hind wing. During the remainder of the afternoon (1245–1600 h) no males were observed flying at the bottom of ravines.

Following pre–wet season storms in mid-November a week after these initial observations were made, the temporal and to some extent spatial behavior of *P. callinira* changed dramatically. Rather than actively flying during the early morning, male activity was limited to a short period around midday, between 1140 h and 1400 h, when conditions were overcast but light levels were somewhat brighter than during the morning or late afternoon. Males also defended light gaps and small open areas in the mid canopy adjacent to the river, as well as open areas above the water.

At the second site, areas up to 400 m upslope from the creek were also surveyed for the presence of the butterfly. No males were detected flying on the steep slopes above the bottom of the valley.

In contrast to the territorial behavior described above, numerous 'younger' males (i.e. freshly emerged with no wing damage) of *P. callinira* (Fig. 3) were observed puddling from creek crossings in cool, shaded microhabitats. Males at these locations drunk water from moist sand and expelled water droplets from their anus, similar to that recorded for *Catasticta* (DeVries 1987). Whilst drinking, the wings remained tightly closed so that the red median band of the forewing remained hidden beneath hind wing, making the butterflies very inconspicuous. Puddling behavior among these newly emerged males occurred throughout much of the day, from around 0830 h to 1600 h.

Pereute telthusa (Hewitson, 1860)

Males of *Pereute telthusa* (Fig. 2) were observed flying in sympatry with *P. callinira* at the second site. Prior to the pre–wet season storms, 'older' males (i.e. all with worn wing condition) of *P. telthusa* were observed in the gorge, with up to five individuals present, displaying patrolling behavior similar to that of *P. callinira*. They typically flew in an open sunny area above a track adjacent to the bank of the creek, about 5–6 m above ground level, with the territories of adjacent males separated by about 30 m. The patrolling flight consisted of a constant speed, flying back and forth over a defined area of about 10 m in length, during which they did not land or settle. The flight consisted of a slow gliding flight, with wings outstretched and open at an angle of approximately 135º. However, when a conspecific male entered the flight space, the resident male flew more rapidly and aggressively chased the intruder from the area, and then returned to the territory to resume patrolling. The behavior lasted for no more than 1 h during the morning and generally occurred earlier in the day than that of *P. callinira*, from around 0820–0830 h to 0900–0930 h. Where the territory partly overlapped that of *P. callinira* (i.e. both species shared the same area in space and time), no interaction was observed, suggesting minimal interspecific competition between the two species.

Following the pre–wet season storms and cooler weather a week later, males were commonly observed patrolling light gaps and open areas in the mid canopy along and adjacent to the creek, but much later in the day, from 1140 h to 1400 h. Unlike *P. callinira*, males were not observed to puddle. However, like *P. callinira*, diurnal activity was restricted to the cooler hours of the day during warmer weather. Limited observations on the steep slopes above the bottom of the valley (up to 400 m upslope from the creek) failed to detect presence of the butterfly.

Discussion

Older males of both *Pereute callinira* and *P. telthusa* were observed to use the air space above creeks and/or light gaps along banks of rivers at the bottom of valley floors of ravines and gorges. Further, their behavior at these sites suggests visitation times varied with temperature (mostly during the morning on hot days, or around midday on cooler days), with moderate site tenacity (duration of visitation approx. 1–2 h each day) and high site defense (resident males established territories and conspecifics were not tolerated), and that patrolling behavior was employed. Although no courtship or matings were observed in either species and no females were observed entering the flight space (territory) of males, we hypothesize that the pattern of male behavior exhibited by these species constitutes a mate–location tactic to locate receptive females and that the valley floors were used as a landmark–based encounter site (see Rutowski, 1991 for review of butterfly mating tactics). The components of this behavior in *P. callinira* and *P. telthusa* are broadly similar to that reported for *P. charops* and *P. cheops*, except the encounter sites differ in that *P. charops* and *P. cheops* utilize crowns of the tallest trees, forest edges or sometimes light gaps (DeVries, 1987; W. Haber, personal communication 2001) that are not necessarily located at the bottom of valleys in ravines and gorges. Salazar (2004) noted that adults of *P. leucodrosime* (Kollar, 1850) in Colombia are active in the morning during sunny

conditions and that they fly 4–7 m above the current of valleys and streams in the Andes, but he did not indicate if such activity comprised male mate–location behavior.

The failure to detect courtship or matings during the observation period is perhaps not surprising given that receptive females are generally very rare relative to searching males among insects, particularly among landmark–based mating systems (Thornhill & Alcock, 1983), and typically many hours are required to detect mating observations (e.g. in the pierid butterfly *Anthocharis pima* 20 h of observation yielded only one mating, while in other species more than 100 h yielded no mating) (Alcock, 1987). Nevertheless, it is puzzling that females of either species were not detected anywhere during the study period, and further observations are needed to ascertain there whereabouts. Presumably they remain in proximity of the breeding areas in search of suitable larval food plants or nectar sources, and that these resources either occur elsewhere in the valley or possibly further upslope from the valley floors. Observations made on males of both species suggest arrival schedules of receptive females may be thermally constrained, and that patrolling behavior is employed whilst waiting for these females, which presumably enter the encounter sites only briefly to mate before departing.

Rutowski (1991) concluded that for species that did not pupate on the larval food plant or feed on relatively small larval food plants, males should focus their mate–locating efforts on non–resource–based encounter sites such as landmarks in the environment. The early stages of *Pereute* are associated with mistletoes (Beccaloni *et al.*, 2008) and the larvae frequently pupate on the trunk of the host tree, usually some distance from the larval food plant (Braby & Nishida, 2010). Mistletoes are small aerial hemiparasitic shrubs in the plant order Santalales and have a patchy distribution in the landscape. These pupation habits and attributes of the larval food plant support Rutowski's generality that *Pereute* adults would be expected to use resources/sites other than mistletoes (i.e. the larval food plant) as encounter sites.

Among the non–resource–based encounter sites, insects have been recorded to utilize a wide–range of landmarks for mate–location. These landmarks are used primarily for mating, not for oviposition or adult feeding, and they include hilltops, gullies and riverbanks, prominent trees or bushes, forest clearings, open water, rock faces, patches of bare ground or places where microclimatic conditions enhance thermal requirements (Thornhill & Alcock, 1983). Hilltops are prominent, elevated landmarks that are frequently used by males of butterflies and other insects as encounter sites to locate receptive females, which are promptly mated on arrival, and this mate–location behavior is characteristic of species that occur in low population density (rare or widely dispersed) (Shields, 1967; Scott, 1968; Alcock, 1987). In contrast, gullies and valley floors of ravines and gorges have been reported as landmarks for mate–location in only a few species. For example, males of the skipper butterflies *Ochlodes snowi* (Edwards, 1877) and *Hesperia viridis* (Edwards, 1883) use gullies for mate-location (Scott, 1973; 1974). In the former species, the males typically perch all day on stones, twigs or low vegetation at the bottom of narrow dry gullies whilst waiting for receptive females, but they do not engage in territorial defense (Scott, 1973). Similar behavior has been noted in males of the spider wasp *Pepsis thisbe* Lucas, 1894, except the encounter sites comprise dry desert washes (Alcock & Johnson, 1990). In this species, the males patrol throughout much of the day, with an apparent peak in activity during mid–morning (0800–1000 h); they also do not establish territories, but fly along routes which stretch for relatively long distances (Alcock & Johnson, 1990). In contrast, in *Pereute* and allied taxa (see below) the males of some species select small areas along valley floors of ravines and gorges in which they engage in territorial defense.

Further studies are needed to determine the extent to which valley floors are used as landmarks for mating. The above examples indicate that a range of insects utilize these landmarks as non–resource–based encounter sites, which suggests that there may be evolutionary convergence of a general landmark–based mating system among distantly related species.

Evolution of male behavior at encounter sites in the Aporiina

Rutowski (1991) concluded that the components of male behavior at encounter sites should be considered separately because they may evolve independently. To test this hypothesis of evolutionary independence, the various attributes of mate-location behavior of *Pereute* were compared with related genera in the *Catasticta* group and more broadly within the Aporiina in an evolutionary context based on review of accounts and reports in the literature and other data, and a published phylogeny for the subtribe (Braby *et al.*, 2007). *Pereute* belongs to a clade of eight genera from the New World, referred to as the *Catasticta* group, which includes *Melete* Swainson, [1831], *Leodonta* Butler, 1870, *Neophasia* Behr, 1869, *Eucheira*

Westwood, 1834, *Catasticta* Butler, 1870, *Archonias* Hübner, [1831] and *Charonias* Röber, 1908. Species of *Melete*, *Pereute*, *Leodonta*, *Catasticta* and *Archonias* occur in the Neotropical Region, are frequently sympatric, and all exploit similar larval food plants, that is, mistletoes (Braby & Nishida, 2010), whereas *Neophasia* and *Eucheira* occur in the Nearctic Region and the larvae feed on host trees that support mistletoes (Braby & Trueman, 2006). The *Catasticta* group is closely related to *Delias* Hübner, [1819] and *Leuciacria* Rothschild & Jordan, 1905, from the Old World and *Aporia* Hübner, [1819] from the Palearctic Region and more distantly related to *Mylothris* Hübner, [1819] from the Afrotropical Region. These genera, together with *Cepora* Billberg, 1820, and *Prioneris* Wallace, 1867, predominantly from the Oriental Region, were placed in the subtribe Aporiina by Braby *et al.* (2006).

Published reports of specific male mate-location tactics and mating behavior in the Aporiina were found to be frequently anecdotal and for most genera several components of male behavior at encounter sites to detect receptive females were not reported. Moreover, courtship behavior and actual matings have rarely been recorded. However, the male flight behavior for most of these genera was well documented, and information on the components of type of encounter site, visitation times and behavior whilst waiting for receptive females (i.e. patrolling or perching) was usually reported.

Available information on mate-location behavior in the Aporiina is summarized at the generic level in Table 1. In general, non-resource-based sites (landmarks) appear to be used most frequently as encounter sites, which as a rule are visited during the morning, and that patrolling behavior amongst males is widespread in the subtribe. The types of landmark vary considerably and include tree canopies, light gaps, valley floors, banks of streams, hilltops and forest edges. The extent of site tenacity and level of site defense at these encounter sites are poorly known, although in the *Catasticta* group these components appear to be of the order of one hour visitation during which a high degree of territoriality is displayed. Further quantitative data and more rigorous observations within the subtribe are needed to confirm these generalities and to test the assumption that the reported landmarks are indeed encounter sites at which courtship and mating takes place. This assumption holds true at least in *Delias* for which freshly emerged females and matings have been recorded at encounter sites in four hilltopping species (see below). Nevertheless, available data suggest that male mate-location tactics are diverse and vary within the group.

Within the *Catasticta* group, the male behavior exhibited by *Pereute* is similar to that noted for *Leodonta* and to some extent *Neophasia*, *Eucheira* and *Melete*. In *Leodonta tellane* (Hewitson, 1860), males use riparian areas at the bottom of valleys and gorges as putative encounter sites, but breeding occurs some distance further upslope (Braby & Nishida, 2010). The males exhibit high territorial behavior by patrolling and defending the air space in prominent light gaps in the mid–canopy of riparian forest by flying rapidly in a small open area, typically at a height of about 5–8 m above the ground near the bank of a river or above water if the gap is located along a steep gully or ravine (Braby & Nishida, 2010). Such patrolling flights by individual males occurs during the morning (0930–1200 h) and may last for 1 h or more during which time they do not settle on foliage or attempt to leave the light gap. The resident male defends the light gap aggressively, chasing off rival males that enter the territory; if a resident male is removed from the light gap, another male soon enters its place and establishes a territory (Braby & Nishida, 2010). In *Neophasia*, Scott (1986) noted that the males of this genus patrol around the conifer larval host trees all day to seek females. Shapiro (2007, p. 102) described the mate–location behavior in *N. menapia* (C. & R. Felder, 1859) in slightly more detail, noting that the "Adults lek around the tops of pines and occasionally other trees, dropping to near the ground and then rising to near the top in a spiraling motion; they repeat the process again and again." Similarly, males of the closely related monotypic genus *Eucheira* never perch, but establish leks around the tops of trees, which include the larval host tree (A. Shapiro and D.L.A. Underwood, personal communication, 2009). In *Melete*, the males of *M. lycimnia* (Cramer, 1777) patrol a defined area along the forest edge, flying 2–8 m above the ground during the morning under sunny conditions, with a slow fluttery flight (DeVries, 1987). Such behavior suggests *Melete* utilizes forest edges as encounter sites, although it is not known if they defend these sites and for how long.

In contrast, the males of several species of *Catasticta* which have been studied, notably *C. teutila* (Doubleday, 1847), *C. sisamnus* (Fabricius, 1793), *C. hegemon* Godman & Salvin, 1889, and *C. flisa* (Herrich-Schäffer, 1858), typically perch with wings closed on foliage and other objects in the understorey, usually a few meters above the ground or at the tops of shrubs, along forest edges, in light gaps or riparian areas during the morning and vigorously defend small territories against conspecific males (DeVries, 1987; Braby & Nishida, 2010). Each site is occupied by a single male, and when an individual is removed from a

Table 1. Character states for various components of male mate-location tactics among the Aporiina. Question mark (?) denotes character state not recorded or there is uncertainty in state. For species which engage in site defense, the degree of territoriality was subjectively classified as either low (conspecific interaction among males noted) or high (conspecific males not tolerated by resident male).

Genus	Encounter site	Visitation time (time of day)	Site tenacity (duration of visitation)	Site defense (degree of territoriality)	Behavior whilst waiting for females	Reference
Prioneris	?	?	?	?	?	
Cepora	larval food plant	morning-midday	?	none	patrolling	M.F. Braby (unpublished data)
Mylothris	landmark (tree canopy)	?	?	low	patrolling	Larsen (1991; 2005), Henning *et al.* (1997)
Aporia	landmark (valley floor)	morning-afternoon	?	?	patrolling	Watanabe (1978), Wickman (1992)
Delias	landmark (hilltop)	morning-midday	?	low	patrolling	Common and Waterhouse (1981), Braby (2000 and unpublished data)
Leuciacria	landmark (tree canopy on ridges and summits)	morning-midday	?	low	patrolling	C.J. Müller (personal communication 2002)
Melete	landmark (forest edge)	morning	?	?	patrolling	DeVries (1987)
Pereute	landmark (valley floor, tree canopy, light gap, forest edge)	morning-midday	1-2h	high	patrolling	DeVries (1987); present paper
Leodonta	landmark (light gap in valley floor or along stream)	morning-midday	>1h	high	patrolling	Braby and Nishida (2010)
Neophasia	larval food plant (tree canopy)	morning-afternoon	?	?	patrolling	Scott (1986), Shapiro (2007)
Eucheira	larval food plant (tree canopy)	?	?	?	patrolling	A. Shapiro and D.L.A. Underwood (personal communication 2009)
Catasticta	landmark (light gap in forest or valley floor, forest edge)	morning	>1h	high	perching	DeVries (1987), Braby and Nishida (2010)
Archonias	landmark (light gap along stream)	early morning	1h	high	perching	DeVries (1987), Brown (1992), Braby and Nishida (2010)
Charonias	landmark (light gap)	morning	?	?	?	DeVries (1987)

particular site, another soon enters the site to take up residency, suggesting limited spatial availability and strong intraspecific competition for these landmarks. In *Archonias*, the males of both *A. tereas* (Godart, 1819) and *A. brassolis* (Fabricius, 1776) are most frequently observed in dense riparian forest along rivers and streams where the males establish and defend small territories early in the morning (DeVries, 1987; Brown, 1992; Braby & Nishida, 2010). They typically perch with wings closed on leaves or tall grass blades close to ground, usually a few meters above ground level, along the banks of rivers or narrow creeks and display aggressive behavior towards conspecific males and other butterflies. Only limited information is available for the rare genus *Charonias*. The males of *C. eurytele* (Hewitson, [1853]) perch in and apparently patrol small light gaps about three meters above ground level during the morning (DeVries, 1987), but it is not known if they establish territories and engage in site defense.

Within the Aporiina, the behavior of male *Pereute* at encounter sites is remarkably similar to the flight behavior exhibited by males of *Delias*, especially species such as *D. harpalyce* (Donovan, 1805), *D.*

nigrina (Fabricius, 1775), *D. argenthona* (Fabricius, 1793) and *D. aganippe* (Donovan, 1805) from eastern Australia. In these species, which feed as larvae on mistletoes and allied plants (Braby, 2006), the encounter sites comprise prominent hilltops where the males congregate, often in large numbers, in the canopy to establish leks (Common & Waterhouse, 1981; Kitching, 1981; Braby, 2000). Although the encounter sites differ from those of the New World taxa, the behavior exhibited by males while waiting is similar in that they usually patrol with a soaring, fluttering flight with wings outstretched. In these four species of *Delias*, freshly emerged females and/or matings have also been recorded at hilltops (M.F. Braby, unpublished data). In *Aporia*, the males exhibit patrolling behavior to find mates (Watanabe, 1978; Wickman, 1992); in species such as *A. hippia* (Bremer, 1861) they typically fly along steep and narrow valleys and ravines throughout the day (Mitsuishi, 1988; Y. Nakamura, personal communication 2010). The flight behavior of *Mylothris*, in which the larvae also utilize mistletoes and related plants in the Santalales (Braby, 2005), is slow and measured (Larsen, 1991; 2005) and both sexes typically exhibit a floating flight (Henning *et al.*, 1997). Moreover, the males of several species, including *M. agathina* (Cramer, 1779), *M. trimenia* (Butler, 1869) and *M. rueppellii* (Koch, 1865), have been observed to flutter and glide for long periods around the canopy of tall trees, apparently supporting the larval food plants, where they establish territories during the warmer hours of the day and on subsequent days (Henning *et al.*, 1997).

The mate–location behavior of *Prioneris*, *Cepora* and *Leuciacria* is not reported in the literature, although unpublished observations for the last two mentioned genera suggest that males of both *Cepora* and *Leuciacria* do not perch but are obligate patrollers. In *Leuciacria olivei* Müller, 1999, from New Ireland, the males fly mainly during the morning, from around 0900 h to 1200 h, with activity ceasing after 1400 h, on the ridges and summits of mountains (C.J. Müller, personal communication 2002). They fly high in the canopy amongst the tops of the highest trees (c. 15 m above the ground) with a fast and direct flight, similar to that of *Delias totila* Heller, 1896, and *D. narses* Heller, 1896, and are highly aggressive, frequently chasing off conspecifics and other pierids. They rarely alight or descend from the treetops (C. J. Müller, personal communication 2002). Similarly, the males of *Cepora perimale* (Donovan, 1805) from Australia never perch (except when basking) during favorable weather, but fly rapidly within a few meters of the ground and appear to patrol the breeding areas in search of females on the larval food plant, *Capparis* spp., which grow as vines or shrubs, from around 0900 h to 1300 h, or sometimes later without engaging in site defense (M. F. Braby, unpublished data). Males of *Prioneris* are well-known for their fast and rapid flight (e.g. Yata, 1985; Corbet & Pendlebury, 1992; Igarashi & Fukuda, 2000), but little is known of their courtship and mating behavior.

In terms of the evolution of the components of male mate-location behavior, data for most attributes in the Aporiina are too fragmentary to be analyzed in an evolutionary context, although it is apparent that there is a diverse array of tactics within the subtribe. However, an exception is the component of waiting for receptive females at encounter sites for which data are available for most genera (Table 1). In male mate–location behavior among butterflies, this component has been categorized into two broad tactics or character states: 'patrolling' and 'perching' (Scott, 1974; Rutowski, 1991; Wickman, 1992). In patrolling species, the males fly almost continuously and either wait or search for mates, whereas in perching species the males sit at characteristic sites and only leave the perch to court passing females or to intercept passing objects such as conspecific males. In some cases, males may adopt both strategies with patrolling employed as an alternative tactic to perching (Scott, 1974), but for the vast majority of species the males are either obligatory patrollers that never perch whilst waiting or they are perchers that typically sit and wait at encounter sites. Scott (2010) recently proposed a new system for describing this behavioral component, with the main objective of distinguishing between species which patrol and those which search whilst in flight; however, it remains to be seen if this system has broader utility and application compared with the present classification.

In the Aporiina, both 'patrolling' and 'perching' tactics for the component of male behavior whilst waiting at encounter sites for receptive females have been recorded. Most genera are patrollers, whereas perching is limited to *Catasticta* and *Archonias* (Table 1). In terms of character evolution, simple optimization of the two states in relation to a phylogenetic hypothesis for the Aporiina indicate that the most parsimonious sequence is that the patrolling strategy is an ancestral state that evolved in the common ancestor of the Aporiina, whereas the strategy of perching is a derived state that evolved relatively recently in the immediate common ancestor of *Catasticta* + (*Archonias* + *Charonias*) (Fig. 6).

The selective pressures that may have promoted this evolutionary switch in mating tactics from patrolling to perching in the Aporiina are unknown and, to our knowledge, it has not previously been

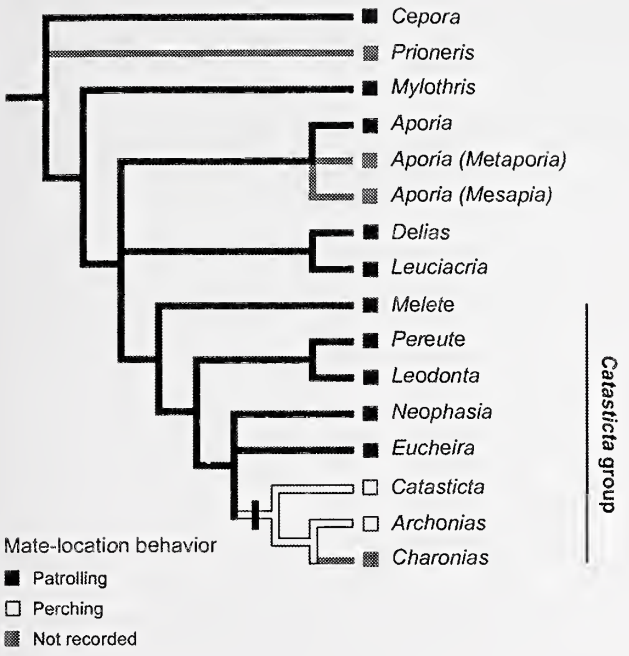


Figure 6. Phylogeny of the subtribe Aporiina (after Braby *et al.* 2007) showing evolution of mate–location tactics in relation to male behavior at encounter sites whilst waiting for receptive females. Vertical bar indicates character state change in male behavior from patrolling to perching.

reported. Several adaptive hypotheses have been proposed to explain the propensity of male butterflies to perch, including avoidance of predators such as birds (i.e. palatability hypothesis) (Wickman, 1992), lower ambient temperature (i.e. thermal constraint hypothesis), and lower male density (i.e. territory economics hypothesis) (Scott, 1974; Kemp, 2001). Alternatively, since patrolling and perching species in the *Catasticta* group appear to utilize different vertical air space, with patrolling species occupying larger areas further from the ground, the alternate tactics may be related to reinforcing reproductive isolation (i.e. reproductive–isolating mechanism hypothesis) (Alcock & Johnson, 1990) or to resource partitioning of microhabitats by courting males so that interference is minimized (i.e. interspecific competition hypothesis) (Scott, 1973). The latter hypothesis may be particularly relevant where the species occur sympatrically; for example, at San Ramón, males of *Pereute*, *Leodonta*, *Catasticta* and *Archonias* all occurred together at the two study sites.

Regardless of the ecological factors that may have shaped the evolution of different mate–location tactics in the Aporiina, the directional change from patrolling to perching is expected to have profound effects on male butterfly design and flight performance due to male competition for mates (Wickman, 1992). The perching genera *Catasticta* and *Archonias* are predicted to have morphological traits associated with higher acceleration ability and speed, such as higher thorax/body mass ratio, higher wing loadings and higher aspect ratios (narrower wings) compared with obligatory patrolling genera *Pereute*, *Leodonta*, *Neophasia*, *Eucheira*, *Melete*, *Delias*, *Aporia*, *Mylothris* and *Cepora*.

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Butterflies, cattle grazing, and environmental heterogeneity in a complex landscape

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Abstract. I investigated the effects of cattle grazing intensity on butterfly species diversity relative to seven other environmental variables in the diverse Cascade-Siskiyou National Monument (CSNM) of southwest Oregon. I sampled twenty-seven transects in 2003 and twenty-nine transects in 2004 in oak savanna and mixed-conifer forests that were subject to different grazing intensities and recorded a total of 89 species across both years. Annual grazing utilization was assessed at each transect using the key-species method, which uses un-grazed palatable reference plants to create a site-specific index of utilization based on the estimated proportion of biomass consumed on grazed plants of the same species. Grazing utilization estimates ranged from low (0-15%) to high (60-75%) on a 5-point scale. Multiple environmental variables were correlated with butterfly community composition and life history characteristics, especially habitat type, plant species richness, the presence or absence of water, and vegetative cover. Cattle grazing utilization did not predict butterfly evenness or total density, and only significantly predicted butterfly species richness in 2003. However, species with grass hostplants (particularly *Cercyonis sthenele*) declined in abundance at higher cattle grazing utilization classes. Management activities related to grazing and butterfly conservation in complex habitats like the CSNM should target specific aspects of butterfly life history, particularly hostplant structure or associated environmental characteristics but those activities cannot be expected to have equivalent effects across species.

Key words: Cascade-Siskiyou National Monument, land management, conservation, life history, species assemblage, ecoregions, *Cercyonis sthenele*

Introduction

Cattle grazing on public lands can create management conflicts, especially in areas of high biodiversity and landscape heterogeneity (Harrison *et al.*, 2003). However, little is known about the interactions between cattle grazing and insect diversity in complex habitat mosaics. The majority of studies examining the influences of livestock grazing and other agricultural practices on insects have been conducted in grassland ecosystems (Swengel & Swengel, 2001; Kruess & Tscharntke, 2002a; Kruess & Tscharntke, 2002b; Saarinen, 2002; González-Megías *et al.*, 2004; Saarinen & Jantunen, 2005; Dumont et al., 2009) where human-mediated grazers and/or native ungulates have been characteristic modes of disturbance for centuries or millennia. Although the large majority of butterfly species studied to date have shown lowered abundance under high grazing regimes, moderate or high grazing utilization has sometimes been shown to locally increase the abundance of insect species adapted to these habitats (Swengel & Swengel, 1999; Weiss, 1999; Swengel & Swengel, 2001; WallisDeVries & Raemakers, 2001; Pöyry *et al.*, 2004; Saarinen *et al.*, 2005), perhaps by maintaining earlier successional conditions (Dover *et al.*, 2011).

At the landscape level, inverse or more complicated patterns are often reported. Heavy grazing regimes are frequently correlated with lowered insect species richness and niche simplification (Swengel 2001; Kruess & Tscharntke, 2002a; Kruess & Tscharntke, 2002b; Boulton *et al.*, 2005), presumably by disrupting trophic interactions between plants and phytophagus insects. Multiple factors appear to simultaneously influence butterfly diversity and composition, and

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the effects of grazing are not uniform across taxa or indices of community composition (Feber *et al.*, 2001; Swengel, 2001; Swengel & Swengel, 2001; WallisDeVries & Raemakers, 2001; Sanford, 2002). Landscape-level variation in management practices may promote diversity (Swengel, 1998; Waltz & Covington, 2004; Pöyry *et al.*, 2005), although landscape-level habitat complexity does not necessarily predict local species composition (Collinge *et al.*, 2003, Krauss *et al.*, 2003).

I studied how variable levels of cattle grazing utilization and other environmental variables were correlated with butterfly diversity and abundance across the ecologically diverse Cascade-Siskiyou National Monument (CSNM), approximately 20 km southeast of Ashland in southwest Oregon, USA. This study was conducted in collaboration with other researchers simultaneously studying the effects of cattle grazing on birds (Alexander *et al.*, 2008), small mammals (Johnston & Anthony, 2008), Greene's mariposa-lily (*Calochortus greenei*) (Frost & Hosten, 2007), and stream habitats and aquatic macroinvertebrates (DellaSala & Barr, 2007). A synthesis of these studies is presented by DellaSala & Barr (2007). This study helps inform grazing prescriptions related to the monument's proclamation (The White House 2000). It also contributes more broadly to the management of ecologically diverse systems where livestock grazing is frequent and butterfly conservation is a concern or rare butterflies have been proposed as indicators of overall environmental health. I asked the following hierarchical questions: 1) Relative to other environmental variables, how important is cattle grazing utilization in affecting local butterfly species richness, evenness, and total density? 2) Do butterflies with similar life history characteristics respond similarly to cattle grazing utilization or other environmental variables? 3) Do individual butterfly species, including those of conservation interest, vary in their responses to cattle grazing utilization and other environmental variables?

Study area

Three ecoregions (the Cascades, Klamath-Siskiyous, and Great Basin) merge in the CSNM (21,427 ha) to create narrow ecotones and complex biodiversity patterns. At least 115 butterfly species are known from the CSNM (Runquist, 1999; 2002; and Runquist unpublished data), representing more than two-thirds of Oregon's known butterfly fauna (Warren, 2005) and one of the most species rich regions in the United States for butterflies. Furthermore, sympatric and synchronic species combinations in the CSNM are often novel and unexpected. Consequently, butterflies are widely cited exemplars of CSNM biodiversity and are federally identified as a research priority for studies on "the impacts of livestock grazing on the objects of biological interest in the monument with specific attention to sustaining the natural ecosystem dynamics" (The White House, 2000).

Grazing by cattle, sheep, and horses on federal lands in the CSNM began in the 1860s, although utilization during the time of this study (an average of 1581 Animal Unit Months between 1995-2004) was approximately 10 times lower than prior to 1960 and only consisted of cattle (USDI Bureau of Land Management, 2005; Hosten *et al.*, 2007a). Free-range grazing began in May at low elevations and gradually moved to higher elevations through summer and ended in October or with the first snowfall.

I studied two broad CSNM habitat types that encompass a range of climatic, structural, and cattle grazing regimes: oak woodlands and mixed-conifer forests. Woodland conditions within the CSNM have increased since European colonization when grasslands were more widespread (Hosten *et al.*, 2007b; Hosten *et al.*, 2007c). Oak woodlands predominate at the lower elevations (730 to 1,250 m) of the southern CSNM and are generally flat, open savannas or shrublands on shallow soils and south-facing hillsides. The climate is Mediterranean with hot, dry summers and mild, wet winters. Summer high temperatures regularly exceed 35°C. Average annual precipitation is about 450 mm. Dominant woody plant species include Garry oak (*Quercus garryana*), California black oak (*Q. kelloggii*), ponderosa pine (*Pinus ponderosa*), western juniper (*Juniperus occidentalis*), and buckbrush (*Ceanothus cuneatus*). Several alien weeds like bulbous bluegrass (*Poa bulbosa*), medusahead (*Taeniatherum caput-medusae*), cheatgrass (*Bromus tectorum*), and yellow star-thistle (*Centaurea solstitialis*) have invaded the understory in many areas, but remnant patches of native bunchgrass habitats remain. Soils are paleosols of thick clay or eroded basalt.

Conifer forests dominate higher elevations (1,100 to 1,870 m) and many north-facing slopes at middle elevations in the CSNM. These forests are multi-layered with unlogged stands generally over 180 years old. Summer high temperatures rarely exceed 32°C. Average annual precipitation is approximately 1,000 mm, largely falling as winter snow. The highest elevations (1,600+ m) are characterized by white fir (*Abies concolor*) forests, and middle elevations are mixed conifer forests consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), ponderosa pine, sugar pine (*P. lambertiana*), white fir, California black oak, and bigleaf maple

(*Acer macrophyllum*). The shrub and herbaceous layer flora are highly diverse, with snowbrush (*Ceanothus velutinus*), blue elderberry (*Sambucus nigra*), choke cherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), oceanspray (*Holodiscus discolor*), common snowberry, (*Symphoricarpos albus*), and giant chinquapin (*Chrysolepis chrysophylla*). Alien weeds include timothy (*Phleum pratense*), bull thistle (*Cirsium vulgare*), and Canada thistle (*C. arvense*). Soils are eroded basalts characteristic of the western Cascades.

Methods

Butterfly sampling

I established 25 butterfly transects in 2003 and conducted 138 total site-visits, averaging 17.6 days (0.55 SE, range of 5–37) between visits (Table 1). In 2004, I added two more transects and conducted 216 total site-visits, averaging 17.8 days (0.07 SE, range of 6–37) between samples. I sampled each transect from April to September following the standard protocols of Pollard & Yates (1993) and Brown & Boyce (1998). This sampling frequency and period effectively captures the entire annual window of butterfly activity, species turnover, and changes in phenology. I identified every butterfly individual observed within 25 perpendicular meters on either side of the baseline transect (a 50-meter wide strip) to species by sight (captured if necessary). I did not include individuals whose specific identity was ambiguous, especially those at far distances. Having studied the butterflies of the CSNM in detail for over 20 years, I have extensive experience with sight-identification of the region's fauna and possess a high degree of accuracy. Taxonomy followed Pelham (2008). Transects were classified by grazing utilization and habitat type: oak woodland (16 in 2003, 17 in 2004) and mixed conifer forest (9 in 2003, 10 in 2004). Mixed conifer transects were largely placed through meadows within the forest matrix because closed-canopy forests had few butterflies and negligible cattle grazing. I could not standardize transect length because of narrow ecotones widespread in the CSNM, and attempted to minimize intra-transect habitat and grazing utilization class variation.

I calculated three measures of butterfly diversity: species richness, evenness, and density. Species richness was standardized across transects using ANALYTIC RAREFACTION 1.3 (Holland, 2003). This method uses the observed distribution of N individuals across species at a site to estimate the number species if only a subset of those individuals had been sampled. Sample size for comparisons was set to equal the number of individuals observed on the transect with the fewest total individuals for each year. Butterfly species richness estimates from rarefaction were log-transformed to satisfy normality. I selected Hill's E5 evenness index to compare the structure of species composition at each transect because this index is less biased by sample size and the addition of rare species (Ludwig & Reynolds, 1988) than other commonly used diversity indices (like the Shannon-Wiener index, H'). I calculated total butterfly density (individuals/ha) at each transect using DISTANCE 4.1,v.2 (Thomas *et al.*, 2003) based on visual estimates of the perpendicular distance of every individual observed off of either side of the transect out to 25 m. I truncated the density data by excluding the farthest 5% of all distance observations at each transect to reduce the influence of potential outliers. This distance sampling method compensates for differences in detectability between sites (Buckland *et al.*, 2001), and has been used successfully in other butterfly studies (Brown & Boyce, 1998; Boughton, 2000). Density estimates were log-transformed.

Environmental variables can influence the composition of butterfly assemblages by potentially constraining the range of life history strategies that can reside in a given habitat (Haddad *et al.*, 2001; Dennis *et al.*, 2004; Haddad *et al.*, 2008). To test this hypothesis, I classified all butterfly species by five life history characteristics: breeding residency, overwintering stage, voltinism (number of generations per year), larval hostplant specialization, and hostplant structure (woody, herbaceous, or graminoid hostplants). I based these classifications on Warren (2005) and personal observations within the CSNM, and assumed that these classifications did not vary across transects. I log-transformed the abundances of each species after adding 1.0 (to avoid irrational numbers for species with zero individuals recorded), and weighted them by their contribution to the overall variance. I conducted multiple mixed ANOVAs in which I nested each species as a random variable within life history characteristics. I only used the abundance data from randomly determined continuous 200 m sections of each transect with 2004 data to standardize sampling effort. I controlled for the false discovery rate to avoid spurious statistical significance due to multiple comparisons when testing for individual species responses using the method of Benjamini & Hochberg (1995). I did not attempt to correct for phylogenetic relatedness between butterfly species in these classifications, which may have the effect of overestimating the importance of some effects because each species cannot be assumed to be an independent replicate of each life history category.

However, the predictive value of evolutionary relatedness between species is often unclear because they may either be more or less likely to utilize related hosts. For example, closely related butterfly species may be expected to be under character displacement pressure to expand host breadth due to inter-specific competition for the same hostplants (e.g. Hesperiinae skippers and *Cercyonis* and *Coenonympha* satyrs all utilize native Poaceae, as well as *Speyeria* and *Boloria* only utilizing *Viola*). Conversely, species may be constrained in their ability to expand host breadth to new hosts due to metabolic limitations to process novel phytochemistry. Furthermore, phylogenetic relatedness is still poorly resolved for many of the species observed in this study and such an effort would be rather speculative.

Habitat structure: Plant species richness and percent cover

I collected plant species richness and percent cover data using point-intercept sampling along randomly located 25-m sub-transects running perpendicular to the primary butterfly transect. Every 50 cm along each sub-transect, I vertically dropped a 2.0 m rod (1 cm in diameter) that had been subdivided into four 0.5 m sections. I recorded intercepts for each species in each section of the rod and estimated species richness and percent cover in four strata up to 2.0 m above the ground. As with the butterfly data, I used rarefaction to calculate plant species richness, with the minimum number of intercepts across transects set as the baseline number of "individuals" for comparison. These estimates were log-transformed to achieve normality. I estimated canopy layer (> 2.0 m above ground) percent cover using the line intercept method along each sub-transect and pooled the data from all sub-transects. I weighted mean percent cover estimates for each vegetation layer by their transect-specific variances. I also recorded the elevation at each transect, and the presence or absence of ephemeral or permanent water sources within 50 m of each transect.

Cattle grazing intensity

In cooperation with the Klamath Bird Observatory (Ashland, OR), I quantified intra-year cattle grazing utilization at each transect in the fall of 2004 using the standard Herbaceous Removal Key Species method (Cooperative Extension Service *et al.*, 1999; Alexander *et al.*, 2003). An ungrazed reference individual of the dominant palatable plant species at each transect was collected, and clipped sections of this reference plant were weighed to obtain a standardized curve relationship between biomass and plant height. Fifty-meter transects were laid out at each butterfly transect and points were established every meter. The height of each member of the reference key species closest to each of these fifty points was measured, and a continuous metric of utilization for the transect was obtained by averaging the biomass estimates across all plants. These protocols and many of the same data points were used in a simultaneous parallel study on the effects of livestock utilization on bird community composition in the CSNM (Alexander *et al.*, 2008).

Dataset robustness and variable selection

Although each transect was sampled multiple times each year, time series analyses are not suitable to test the effects of various environmental effects on the whole of butterfly species richness, evenness, and density because there is a large turnover in species composition and abundance between weeks. Instead, I was interested in the relative effects of these environmental variables on the entire butterfly fauna using weighted least squares linear models. I excluded transect length whenever it was a non-significant main effect, and explored interactions between significant main effects. I placed these interactions into a final model with their main effects to weigh their relative importance. Sampling effort was greater in 2004, so data collected over the two years were analyzed separately. I also partitioned the dataset by habitat type in some analyses to test for differences in effects between oak woodland and mixed conifer forest. All analyses were conducted in JMP 9.0.2 (SAS Institute Inc., Cary, NC, USA). Statistical significance was set at $\alpha = 0.05$, except when controlling for false discovery rate. I selected the following independent variables: transect length, grazing utilization class, elevation (as a continuous surrogate for habitat type), the presence/absence of water, herbaceous layer (0- to 0.5-m) species richness, herbaceous layer weighted percent cover, shrub layer (0.5- to 2.0-m) species richness, shrub layer weighted percent cover, and canopy layer (>2.0 m) weighted percent cover (Table 1). I bracketed mean utilization estimates into ranked intervals of 15% due to high individual variances and grouped transects into the following utilization classes: 0%-14.9% = "1", 15%-29.9% = "2", 30%-44.9% = "3", 45%-59.9% = "4", and 60%-74.9% = "5". No transect had a mean utilization score of more than 75%. These classifications are largely consistent with a coarser landscape-level map of CSNM grazing utilization estimated by Hosten *et al.* (2007a), and additional subjective observations (e.g. "no grazing

Table 1. Butterfly transects by habitat type, grazing utilization ("1" = 0 to 14.9%, ... "5" = 60 – 75%), elevation, the presence/absence of water resources, transect length, and variance-weighted mean vegetation percent cover and log plant species richness in three strata in the Cascade-Siskiyou National Monument, 2004.

	# Sampling Visits							Weighted mean percent cover by layer			Log plant richness by layer	
Transect	2003	2004	Habitat	Grazing utilization class	Elevation (m)	Water	Transect length (m)	Herb	Shrub	Canopy	Herb	Shrub
AF6	5	8	oak	1	1012	No	200	0.12	0.549	0.074	3.807	1.609
BO1	6	8	oak	1	1097	No	500	0.16	0.108	0.102	3.704	1.808
BO2	6	8	oak	1	975	Yes	400	0.22	0.073	0.116	4.237	2.715
OG3	6	8	oak	1	1250	No	250	0.14	0.045	0.099	3.578	1.686
LH1	7	8	conifer	1	1435	No	250	0.08	0.301	0.037	3.98	2.728
LH3	7	8	conifer	1	1463	Yes	450	0.16	0.049	0.044	4.422	2.955
OGH	6	8	conifer	1	1265	Yes	300	0.03	0.116	0.100	4.104	2.728
PR	0	8	conifer	1	1515	No	200	0.12	0.073	0.059	4.132	2.58
AF4	5	8	oak	2	1006	No	200	0.2	0.072	0.147	3.875	1.792
AF5	5	8	oak	2	1006	No	200	0.15	0.143	0.089	3.544	1.74
JC5	5	8	oak	2	967	No	500	0.13	0.167	0.087	4.231	1.589
OG1	6	8	oak	2	1231	No	400	0.32	0.058	0.058	4.029	1.74
OG2	6	8	oak	2	1158	No	500	0.12	0.137	0.067	3.745	1.841
OG4	6	8	oak	2	1052	Yes	500	0.25	0.169	0.181	4.233	2.14
BECR	5	8	conifer	2	1542	Yes	400	0.09	0.05	0.054	4.104	2.407
AF3	6	8	oak	3	1030	No	300	0.42	0.18	0.104	3.437	1.386
JC3	5	8	oak	3	954	Yes	200	0.11	0.131	0.263	3.421	1.504
JC4	5	8	oak	3	938	Yes	400	0.07	0.079	0.104	4.394	2.701
SKCR2	0	8	oak	3	1109	Yes	300	0.16	0.162	0.049	4.038	2.493
SKC1	5	8	conifer	3	1402	Yes	500	0.14	0.052	0.138	4.279	2.625
WIGL	5	8	conifer	3	1570	Yes	400	0.16	0.117	0.056	4.205	2.542
SKCR1	6	8	oak	4	1036	Yes	500	0.16	0.07	0.039	4.265	1.887
KCR	5	8	conifer	4	1189	Yes	200	0.1	0.052	0.083	4.371	2.688
MAR	6	8	conifer	4	1579	Yes	300	0.12	0.103	0.074	3.93	2.389
AF1	6	8	oak	5	1006	No	350	0.25	0.145	0.090	3.638	1.335
AF2	6	8	oak	5	1006	No	300	0.22	0.189	0.165	3.561	1.526
SKC2	5	8	conifer	5	1449	Yes	450	0.09	0.028	0.113	4.264	2.389

observed", "heavily grazed since last visit", etc.). The binning process used to classify transects by their mean grazing utilization estimates is conservative in that it reduces potentially real and biologically significant differences between transects by incorporating the variance around their estimates.

Results

Variable transect lengths led to unequal sampling effort and increasing variance around butterfly and plant species richness estimates on longer transects. Plant species richness of the herbaceous layer was the

only environmental effect biased by transect length ($F1,26 = 6.05$, $P = 0.021$). However, this layer positively covaried with the richness of the shrub layer and with elevation (neither of which were biased by transect length), so significant correlations with species richness in the herbaceous layer are not necessarily invalid. Cattle grazing utilization class was not biased by any environmental variable for either pairwise correlation coefficients or in a nominal logistic model (all $P > 0.05$).

Butterfly diversity and cattle grazing

I recorded 5,423 individual butterflies in 77 species in 2003 and 8,846 individual butterflies constituting 84 species in 2004 (Table 2). I observed a total of 89 species over both years. Species composition was dominated by a few species, and the five most commonly observed species in each year collectively constituted 51.6% and 54.1% of all individuals observed, respectively. Consequently, the majority of the species were rare and/or local.

In the full ANOVA model of all environmental variables listed above, more butterfly species were recorded on transects with moderate grazing (Class 3, 30-45% mean utilization) than those with no or very low grazing (Class 1, 0-15% mean utilization) in 2003, but this trend was not significant in 2004 (Fig. 1, Table 3). Butterfly species richness also increased with elevation (Fig. 3) and herbaceous layer species richness in both years (Fig. 4), and with shrub layer species richness in 2003 (Fig. 5). Butterfly evenness was higher at transects near water in 2004. Total butterfly density was not related to any environmental variable in either year. No effects interacted significantly with grazing utilization class for butterfly species richness, evenness, or total density.

Cattle grazing utilization and butterfly life history characteristics

Since butterflies with similar life history characters may respond in similar manners to environmental variation, I began testing Question #2, by testing the relative predictive value of all eight main effect environmental variables plus transect length and species identity in a full ANOVA model using the log abundance of all 2004 butterfly records. The abundance of each butterfly species was weighted by the inverse of its contribution to overall variance. Only grazing utilization ($F_{4,2171} = 2.49$, $P = 0.041$), water ($F_{1,2171} = 7.90$, $P = 0.005$), and herbaceous layer plant species richness ($F_{1,2171} = 4.36$, $P = 0.037$) significantly predicted butterfly abundance. As in the diversity data, the effect size of cattle utilization (based on the F statistics above) was lower than the effects of water or herbaceous plant richness. I then isolated these three main environmental effects and tested for their interactions with each of the life history categories in reduced ANOVAs described below.

Residency: Permanent breeding residents were more than five times as abundant as species that irregularly immigrate into the CSNM ($F_{1,2171} = 9.79$, $P = 0.002$). No main effects were significant in the

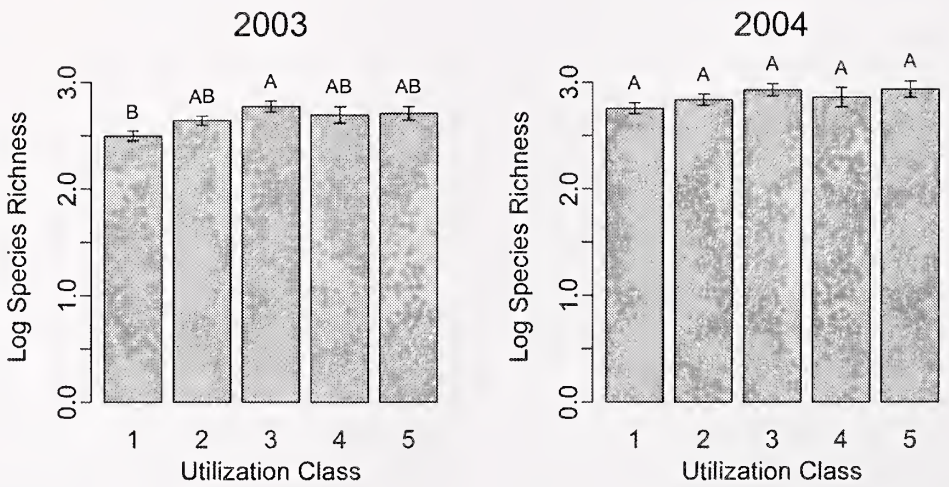

Figure 1. The effect of cattle grazing utilization class on mean log butterfly species richness (+/- SE) in the Cascade-Siskiyou National Monument in 2003 and 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant groups in species richness between utilization classes within each year following post-hoc Tukey tests.

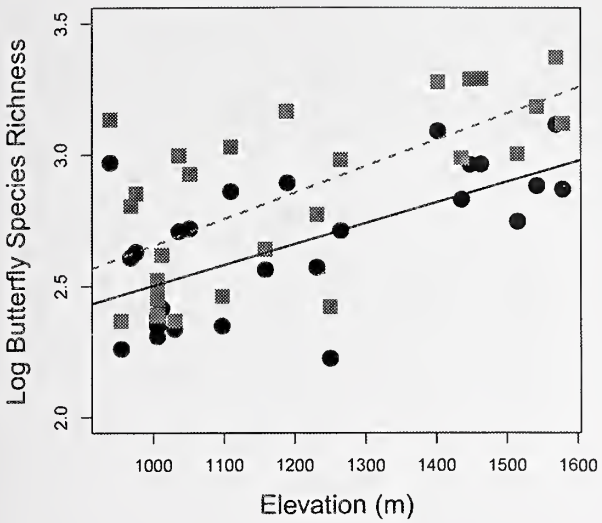

Figure 2. The relationship of butterfly species richness with elevation. Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.

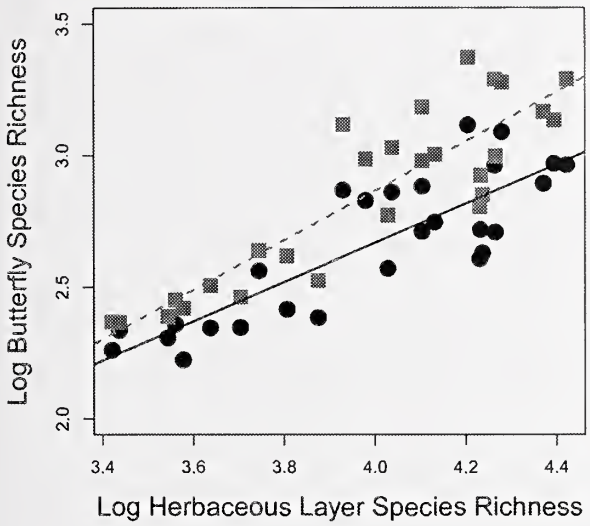

Figure 3. The relationship of butterfly species richness with plant species richness in the herbaceous layer (0-0.5 m from the ground). Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.

reduced ANOVA model, nor were there any significant interactions between main effects.

Overwintering stage: Species that hibernate as larvae were about five times more abundant than those that overwinter in all other stages ($F_{3,2159}$ = 104.75, P < 0.001). Abundance remained positively related to herbaceous layer plant species richness

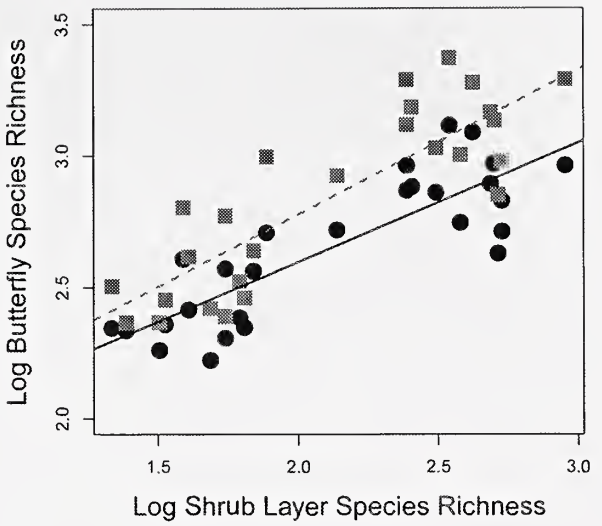

Figure 4. The relationship of butterfly species richness with plant species richness in the shrub layer (0.5-2.0 m from the ground). Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.

in the reduced ANOVA model ($F_{1,2159}$ = 10.78, P = 0.001), but overwintering stage did not interact with any effect.

Voltinism: Butterfly species with one or two broods per year were both about five times more abundant than species with at least three annual broods ($F_{2,2165}$ = 8.40, P < 0.001). Only herbaceous layer richness predicted abundance (positively, $F_{1,2165}$ = 5.29, P = 0.022), and no interactions were found.

Hostplant specialization: Butterfly abundance generally declined with increasing hostplant specificity ($F_{3,2159}$ = 32.52, P < 0.001), although species utilizing multiple plant families as hosts were least abundant (represented by only six species). Grazing utilization class and the presence of water were not important effects, but abundance increased with herbaceous layer richness ($F_{1,2159}$ = 8.12, P = 0.004). However, butterflies using one hostplant genus were less abundant in the presence of water and species with one host family were more abundant around water ($F_{3,2159}$ = 2.99, P = 0.031). Partitioning the dataset by habitat type, this interaction was non-significant in both habitats, and herbaceous layer plant species richness only positively predicted abundance in oak woodlands ($F_{1,1320}$ = 11.13, P < 0.0001). Hostplant specialization was not related to cattle grazing utilization.

Hostplant structure: Butterflies utilizing graminoid hostplants were 2.7 to 3.4 times more abundant than those with woody or herbaceous structured hosts ($F_{2,2165}$ = 179.46, P < 0.001). This difference was

Table 2. Life history characteristics for all butterfly species recorded in 2003 and 2004 and abundance totals for each species by year. Residency: R = overwintering resident, I = non-overwintering immigrant. Overwinter stage: E = egg, L = Larva, P = pupa, A = adult. Voltinism: 1 = one generation annually, 2 = two generations annually, 3 = three or more generations annually. Hostplant Specialization: VH = Utilizing only one hostplant species in the CSNM, H = Utilizing hostplants in one genus, M = Utilizing hostplants in multiple genera in the same family, L = Utilizing hostplants in multiple families. Hostplant Structure: G = Graminoid hostplants, H = Herbaceous hostplants, W = Woody hostplants.

Butterfly Species	Residency	Overwintering-Stage	Voltinism	Host Special.	Host Struct.	2003		2004	
						Total	%	Total	%
Adelpha californica	R	L	2	H	W	20	0.37	99	1.12
Amblyscirtes vialis	R	L	1	H	G	3	0.06	2	0.02
Anthocharis lanceolata	R	P	1	H	H	20	0.37	31	0.35
Anthocharis sara	R	P	1	H	H	19	0.35	33	0.37
Boloria epithore	R	L	1	H	H	34	0.63	46	0.52
Callophrys augustinus	R	P	1	L	W	1	0.02	11	0.12
Callophrys eryphon	R	P	1	H	W	13	0.24	48	0.54
Callophrys gryneus	R	P	1	M	W	70	1.29	120	1.36
Callophrys mossii	R	P	1	H	H			1	0.01
Carterocephalus palaemon	R	L	1	M	G			3	0.03
Celastrina echo	R	P	2	L	W	4	0.07	34	0.38
Cercyonis oetus	R	L	1	M	G	42	0.77	42	0.47
Cercyonis pegala	R	L	1	M	G	322	5.94	572	6.47
Cercyonis sthenele	R	L	1	M	G	167	3.08	587	6.64
Chlosyne hoffmanni	R	L	1	H	H	7	0.13	11	0.12
Chlosyne palla palla	R	L	1	H	H	21	0.39	48	0.54
Coenonympha tullia	R	L	2	M	G	1235	22.77	1686	19.06
Colias eurytheme	I	L	2	L	H	33	0.61	18	0.2
Colias occidentalis	R	L	1	H	H	55	1.01	47	0.53
Danaus plexippus	I	A	3	H	H	1	0.02	16	0.18
Epargyreus clarus	R	P	1	VH	H	1	0.02	1	0.01
Erynnis icelus	R	L	1	M	W	1	0.02	2	0.02
Erynnis persius	R	L	2	L	H	1	0.02	3	0.03
Erynnis propertius	R	L	1	H	W	177	3.26	267	3.02
Euchloe ausonides	R	P	1	M	H	20	0.37	21	0.24
Euphilotes enoptes	R	P	1	H	H	5	0.09		
Euphilotes glaucon	R	P	1	VH	H	1	0.02	2	0.02
Euphydryas chalcedona	R	L	1	H	W	443	8.17	458	5.18
Euphydryas editha	R	L	1	H	H	3	0.06	5	0.06
Euphyes vestris	R	L	1	M	G	7	0.13		
Everes amyntula	R	L	1	L	H	7	0.13	27	0.31
Glaucopsyche lygdamus	R	P	1	M	H			3	0.03
Habrodais grunus	R	E	1	VH	W			1	0.01
Hesperia colorado	R	L	1	M	G	74	1.36	92	1.04
Hesperia columbia	R	L	2	M	G	6	0.11		
Hesperia juba	R	L	2	M	G	6	0.11	17	0.19
Hesperia lindseyi	R	L	1	M	G	405	7.47	1003	11.34
Junonia coenia	I	A	2	L	H	51	0.94	4	0.05
Limenitis lorquini	R	L	1	L	W	95	1.75	150	1.7
Lycaeides anna	R	L	1	M	H	63	1.16	66	0.75
Lycaena arota	R	E	1	H	W			21	0.24
Lycaena gorgon	R	E	1	VH	H	3	0.06	6	0.07

Butterfly Species	Residency	Overwintering. Stage	Voltinism	Host Special.	Host Struct.	2003 Total	2003 %	2004 Total	2004 %
Lycaena helloides	R	E	2	L	H	7	0.13	3	0.03
Lycaena heteronea	R	E	1	H	H	12	0.22	13	0.15
Lycaena nivalis	R	E	1	H	H	138	2.54	88	0.99
Lycaena xanthoides	R	E	1	H	H	38	0.7	39	0.44
Neophasia menapia	R	E	1	M	W	1	0.02	3	0.03
Nymphalis antiopa	R	A	1	H	W	2	0.04	30	0.34
Nymphalis californica	R	A	2	H	W	66	1.22	127	1.44
Ochlodes sylvanoides	R	L	1	L	G	238	4.39	258	2.92
Oeneis nevadensis	R	L	1	M	G	1	0.02	53	0.6
Papilio eurymedon	R	P	1	M	W	7	0.13	59	0.67
Papilio multicaudatus	R	P	2	M	W	8	0.15	49	0.55
Papilio rutulus	R	P	1	L	W	29	0.53	53	0.6
Papilio zelicaon	R	P	2	M	H	4	0.07	14	0.16
Parnassius clodius	R	L	1	VH	H	22	0.41	44	0.5
Phyciodes mylitta	R	L	2	H	H	44	0.81	83	0.94
Phyciodes orseis	R	L	1	H	H	54	1	37	0.42
Phyciodes pulchella	R	L	2	H	H	5	0.09	17	0.19
Pieris marginalis	R	P	1	M	H	5	0.09	4	0.05
Pieris rapae	R	P	3	L	H	1	0.02	3	0.03
Plebejus acmon	R	L	2	L	H	141	2.6	141	1.59
Plebejus icarioides	R	L	1	H	H	3	0.06	24	0.27
Plebejus saepiolus	R	L	1	H	H	270	4.98	491	5.55
Polites mardon	R	P	1	M	G	25	0.46	16	0.18
Polites sabuleti	R	P	1	L	G	1	0.02	2	0.02
Polites sonora	R	P	1	L	G	13	0.24	14	0.16
Polygonia faunus	R	A	1	H	W			6	0.07
Polygonia gracilis	R	A	1	H	W			13	0.15
Polygonia satyrus	R	A	1	H	W			1	0.01
Pontia occidentalis	R	P	2	M	H			2	0.02
Pontia sisymbrii	R	P	1	M	H	3	0.06	2	0.02
Pyrgus communis	R	L	2	L	H	48	0.89	63	0.71
Pyrgus ruralis	R	L	2	M	H	6	0.11	7	0.08
Satyrium californica	R	E	1	H	W	6	0.11	1	0.01
Satyrium saepium	R	E	1	H	W	51	0.94	97	1.1
Satyrium sylvinum	R	E	1	H	W	9	0.17	11	0.12
Satyrium tetra	R	E	1	H	W			1	0.01
Speyeria callippe	R	L	1	H	H	392	7.23	934	10.56
Speyeria coronis	R	L	1	H	H			15	0.17
Speyeria cybele	R	L	1	H	H	3	0.06	5	0.06
Speyeria hesperis	R	L	1	H	H	7	0.13	4	0.05
Speyeria hydaspe	R	L	1	H	H	80	1.48	114	1.29
Speyeria zerene	R	L	1	H	H	134	2.47	257	2.91
Strymon melinus	R	P	3	L	H	1	0.02		
Thorybes pylades	R	L	1	H	H			16	0.18
Vanessa atalanta	R	A	2	H	H	3	0.06		
Vanessa cardui	I	A	3	L	H	8	0.15	10	0.11
Vanessa virginiensis	I	A	2	L	H	1	0.02	1	0.01
Undetermined						100	1.84	17	0.19

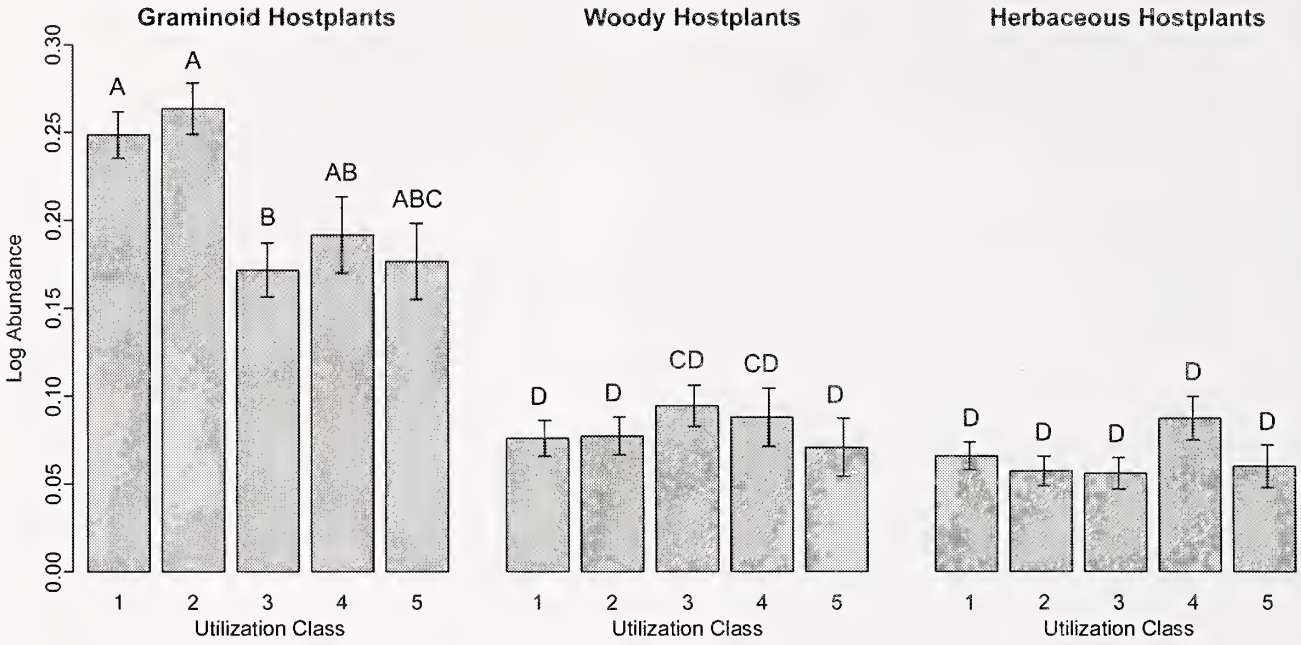

Figure 5. The interaction between cattle grazing utilization class and log butterfly abundance (+/- SE) categorized by butterfly hostplant structure (Graminoid, woody, and herbaceous) in the Cascade-Siskiyou National Monument in 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant differences in mean log abundances across hostplant structures and utilization class following post-hoc Tukey tests.

partially driven by the hyper-abundant grass-feeding *Coenonympha tullia* (Müller, 1764), which represented about one-fifth of all records in both 2003 and 2004. Graminoid-feeding species were less abundant at sites with water sources present while woody- and herbaceous hostplant feeding species were both more abundant near water resources ($F_{2,2165}$ = 4.40, P = 0.012). This interaction was not significant when the dataset was partitioned by habitat type, as well as the main effect of water at mixed conifer forests. Most notably however, graminoid-feeders were 30-33% less abundant at higher grazing utilization classes while the abundances of herbaceous- and woody-feeders were relatively unchanged across utilization levels (Fig. 5; $F_{8,2165}$ = 2.06, P = 0.036).

Individual species responses to cattle grazing

Testing question #3 on the influences of environmental variation and cattle grazing utilization on individual species responses, I found that abundance was significantly related to at least one environmental effect for 34 of the 84 species recorded in 2004 (Table 4). The most widespread effect on individual species abundances was elevation (19 species), highlighting the importance of habitat type in CSNM butterfly diversity patterns. Four species varied significantly with cattle grazing utilization class. Specifically, *Anthocharis lanceolata* Lucas, 1852 ($F_{4,15}$ = 4.22, P = 0.017) and *Euchloe ausonides* (Lucas, 1852) ($F_{4,15}$ = 3.23, P = 0.042) were more common at transects with Class 5 mean utilization than Class 4. *Phyciodes pulchella* (Boisduval, 1852) was more abundant at moderate utilization classes ($F_{4,15}$ = 3.54, P = 0.032). However, these species collectively accounted for less than 1% of all individuals observed in 2004. *A. lanceolata* and *E. ausonides* were also more abundant in mixed conifer forest than oak woodland (both P < 0.01), and only one mixed conifer transect was classified into utilization Class 5. Utilization class is a non-significant effect for these when this transect is excluded. Thus, the significant response of these three species cannot be separated from a site-specific factor unrelated to utilization class. The most notable species response was found with the graminoid-feeding *Cercyonis sthenele* (Boisduval, 1852), which was 70% less abundant at higher grazing utilization transects (Classes 3-5) than low grazing utilization transects (Classes 1 and 2) ($F_{4,15}$ = 5.32, P = 0.007) (Fig. 6), although abundance of this species was statistically significantly higher only at utilization Class 1 transects than at utilization Class 3 transects according to a post-hoc Tukey test. A very similar but slightly non-significant trend was

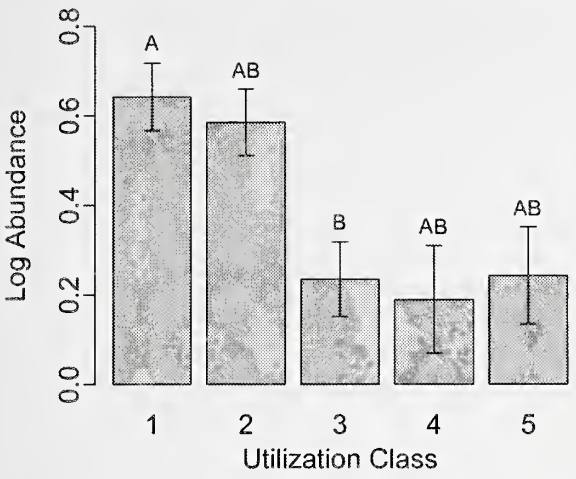

Figure 6. The effect of cattle grazing utilization class on the log abundance of the Great Basin Wood Nymph, *Cercyonis sthenele*, (+/- SE) in the Cascade-Siskiyou National Monument in 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant groups in species richness between utilization class following post-hoc Tukey tests.

also suggested in *Cercyonis pegala* (Fabricius, 1775) ($F_{4,15}$ = 2.37, P = 0.099). Cattle grazing utilization did not significantly predict the abundance of other grass-feeding butterfly species in this way (all P > 0.10).

Since many of the species that I observed were relatively rare in terms of their percentage contribution to the yearly abundance totals (Table 2), it is possible that some statistically significant results are actually artifacts of sampling bias for some or many of these species. When I limited the above analyses to the seven most abundant species (those composing at least 5% of the total observed 2004 individuals; 443+ individuals), four species were related to at least one of the eight environmental variables with α = 0.05. Transect length was unimportant for all these species. However, after correcting for the false discovery rate of incorrectly rejecting true nulls due to multiple statistical comparisons (Benjamini & Hochberg, 1995) (n=7, α = 0.0071,) only two species, *Cercyonis sthenele* and *Hesperia lindseyi* (Holland, 1930), were still significantly related to environmental variables, and *C. sthenele* still significantly declined with increasing grazing utilization class. Although it may be considered a habitat specialist and feeds exclusively on native perennial grasses like Roemer's fescue (*Festuca roemerii*), *C. sthenele* is widespread throughout the western United States and southwestern Canada and is not a species of conservation concern.

Species of special conservation concern

I recorded two species during transect sampling that are listed as being of special conservation concern by the Oregon Biodiversity Information Center (ORBIC 2010): *Polites mardon klamathensis* Mattoon, Emmel, & Emmel, 1998 (ORBIC List 1 and a federal candidate under the U.S. Endangered Species Act) and *Speyeria coronis coronis* (Behr, 1864) (ORBIC List 2). Both of these species were relatively rare on transects, and reasonable statistical estimates on effects of the environmental variables or grazing utilization are not possible. However, subjective evidence based on personal observations and unpublished data suggests that *P. mardon klamathensis* prefers short-statured native meadows dominated by Roemer's fescue and California oatgrass (*Danthonia californica*) and avoids meadows invaded by tall alien grasses like timothy. Light seasonal grazing by cattle may help to maintain the short-statured meadows preferred by *P. mardon klamathensis* since experimental cattle exclusion plots established by the Bureau of Land Management seem to show a long-term transition to tall, timothy-dominated meadows and reductions in *P. mardon klamathensis* abundance. A third rare species, *Callophrys johnsoni* (Skinner, 1904) (ORBIC List 1), is also known from the CSNM. I observed one individual in the vicinity of one transect at the Oregon Gulch headwaters in 2004 (representing only the third known record for the CSNM), but not during a sampling period, and thus was not included in any analyses for this study.

Discussion

Multiple environmental factors, especially plant species richness, contribute to local CSNM butterfly diversity. It is perhaps not surprising that plant species richness consistently provided the strongest predictive value for local butterfly species richness and composition given that butterflies are phytophagous insects. Sites with higher plant species richness and diversity should also be expected to have higher butterfly diversity (Siemann *et al.*, 1998). Similar to Dover *et al.* (2011), cattle grazing utilization class appears to play a secondary role relative to this broader influence and may modulate local butterfly diversity by impacting ecosystem dynamics and plant-insect interactions. For example, cattle are more likely to graze near water sources (Hosten *et al.*, 2007a), and even if these locations do not possess the suitable hostplants, cattle can still affect resource availability by consuming nectar sources and/or alter local hydrology and water availability through trampling

Table 3. Butterfly species richness, evenness (Hill's E5), and total density (individuals ha-1) compared to environmental variables in the Cascade-Siskiyou National Monument in 2003 and 2004 in mixed linear ANOVAs. **Bold** indicates significant effects.

Species Richness			2003			2004	
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	**0.1605**	**4.0876**	**0.0257**	0.0852	1.4374	0.2732
Elevation	1	**0.0663**	**6.7596**	**0.0232**	**0.1791**	**12.0937**	**0.0037**
Water	1	0.0007	0.0756	0.7880	0.0144	0.9739	0.3405
Herb Cover/Var	1	0.0019	0.1976	0.6646	0.0036	0.2419	0.6305
Shrub Cover/Var	1	0.0348	3.5442	0.0842	0.0243	1.6388	0.2213
Canopy Cover/Var	1	0.0007	0.0743	0.7898	0.0083	0.5602	0.4666
Log Herb Richness	1	**0.0489**	**4.9796**	**0.0455**	**0.1771**	**11.9587**	**0.0038**
Log Shrub Richness	1	**0.0487**	**4.9592**	**0.0459**	0.0059	0.3960	0.5393
Length	1	0.0160	1.6259	0.2264	0.0012	0.0801	0.7814

Evenness (E5)			2003			2004	
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	0.0621	0.6100	0.6633	0.0404	0.8752	0.5032
Elevation	1	0.0195	0.7654	0.3988	0.0049	0.4224	0.5263
Water	1	0.0031	0.1217	0.7333	**0.0637**	**5.5202**	**0.0340**
Herb Cover/Var	1	0.0153	0.6022	0.4528	0.0035	0.3075	0.5880
Shrub Cover/Var	1	0.0033	0.1283	0.7264	0.0003	0.0240	0.8792
Canopy Cover/Var	1	0.0076	0.2983	0.5949	0.0289	2.5034	0.1359
Log Herb Richness	1	0.0006	0.0244	0.8784	0.0017	0.1457	0.7084
Log Shrub Richness	1	0.0031	0.1215	0.7334	0.0269	2.3336	0.1489
Length	1	0.0074	0.2914	0.5992	0.0239	2.0722	0.1720

Total Density			2003			2004	
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	0.6098	1.2350	0.3475	1.2377	0.7942	0.5483
Elevation	1	0.0082	0.0666	0.8007	0.0127	0.0325	0.8596
Water	1	0.0077	0.0622	0.8072	0.5390	1.3835	0.2591
Herb Cover/Var	1	0.2461	1.9934	0.1834	0.0857	0.2200	0.6463
Shrub Cover/Var	1	0.0042	0.0342	0.8563	0.2543	0.6527	0.4327
Canopy Cover/Var	1	0.1441	1.1669	0.3013	0.0114	0.0291	0.8669
Log Herb Richness	1	0.2174	1.7609	0.2092	0.1793	0.4603	0.5085
Log Shrub Richness	1	0.0554	0.4491	0.5154	0.1738	0.4461	0.5151
Length	1	0.0403	0.3268	0.5781	0.0572	0.1467	0.7074

Table 4. Significant P values (< 0.05) for the 2004 abundance of butterfly species related to transect length, cattle grazing utilization, and seven environmental variables in the CSNM. Values for utilization and environmental variables are calculated after excluding transect length. **Bold** indicates species that comprise at least 5% of the total 2004 observations and are related to at least one environmental variable (α = 0.05). * = *P* values that are still significant after controlling for the false discovery rate (n=7, α = 0.0071).

					Weighted mean percent cover by layer			Log plant species richness by layer	
Species	Transect length	Grazing utilization class	Elevation	Water	Herb	Shrub	Canopy	Herb	Shrub
Adelpha californica				0.020					
Anthocharis lanceolata		0.017	0.008						
Boloria epithore			0.005						
Cercyonis sthenele		**0.007** *	**<0.001** *						
Chlosyne palla			0.012						
Coenonympha tullia				**0.048**					
Colias occidentalis			0.027						
Erynnis persius				0.016					
Erynnis propertius			0.006						
Euchloe ausonides		0.042	0.005						
Euphilotes glaucon					0.012				
Euphydryas chalcedona			**0.021**	**0.041**					
Euphydryas editha	0.010								
Hesperia lindseyi			**0.005** *						
Limenitis lorquini				0.013					
Lycaena nivalis			0.003						
Papilio multicaudatus			0.002						
Papilio zelicaon				0.030					
Parnassius clodius			0.046						
Phyciodes pulchella		0.032							
Pieris rapae									0.018
Plebejus icarioides			0.007						
Polites mardon			0.024						
Polygonia gracilis			0.008						
Pontia occidentalis								0.030	
Pontia sisymbrii	0.031			0.027					
Pyrgus communis			0.001						
Satyrium saepium						0.050			
Satyrium sylvinum			0.010				0.039		
Satyrium tetra	0.028								
Speyeria coronis	0.029								
Speyeria hydaspe			<0.001						
Speyeria zerene			0.005						
Vanessa cardui							0.039		
No. species	4	4	19	7	1	1	2	1	1

and manure deposition.

The historical grazing and ecological context of the CSNM has important implications for the interpretation of these results (Borman, 2005; Hosten *et al.*, 2007a; Hosten *et al.*, 2007b; Hosten *et al.*, 2007c). For instance, grassland conditions across the CSNM have generally declined since the concurrent decrease of very heavy livestock grazing and advent of strict fire suppression in the 1950s, which has resulted in corresponding increases in Douglas-fir, Ponderosa pine, western juniper, and other woody vegetation. At the same time that native perennial bunchgrasses have increased in some areas under reduced grazing pressure, other locations have seen increases of non-native bulbous bluegrass (Hosten *et al.*, 2007c). While not an aspect addressed in this study, approximately 85% of CSNM forests have also experienced some history of selective timber harvesting (USDI Bureau of Land Management 2002). It is possible therefore that butterflies respond to site-specific factors related to utilization or management history rather than directly to intra-year utilization intensity, such as the long-term conversion of native bunchgrass meadows to non-native annual grasslands by some grazing regimes (Masters & Sheley, 2001; Hosten *et al.*, 2007c). Indeed, the significant difference in butterfly species richness observed in 2003 between Class 1 and Class 3 utilization transects may be largely attributable to the high prevalence of invasive plants like medusahead and bulbous bluegrass, that are unpalatable to both butterflies and cattle, at several oak woodland Class 1 transects. Habitat disturbance effects like cattle grazing can also operate over different spatial and/or temporal scales (Hamer & Hill, 2000), and many butterfly species may be able to disperse over long enough distances to not be significantly sensitive to local variation in intra-year grazing utilization level, particularly if suitable patches are connected (Debinski *et al.*, 2001; Pöyry *et al.*, 2009).

Unrelated species with similar life history characteristics may be predicted to respond in similar manners to these environmental factors. As observed in many European grasslands that have undergone long-term grazing, it is possible that the current CSNM butterfly fauna has been modified such that those species that are tolerant of grazing are in greater abundance now than prior to the influences of cattle grazing. This is particularly relevant given that a primary effect of cattle grazing utilization on butterfly diversity may be to decrease the abundance of species utilizing native graminoid hostplants like *Cercyonis sthenele* at high grazing utilization levels. However, this decrease did not result in a corresponding detectable increase in the abundance of woodland associates.

Comparisons between butterflies and other fauna

Many of the butterfly transects overlapped with the sampling locations used by Alexander *et al.* (2008) and Johnston & Anthony (2008) in their concurrent grazing effect studies on birds and small mammals, so some trends found across taxa can be compared, at least in terms of the effects of cattle grazing utilization. Alexander *et al.* detected significantly fewer birds within several life history suites at high grazing utilization routes than at low utilization routes, and that these effects were more pronounced in oak woodlands. In contrast, Johnston & Anthony (2008) found lower mean diversity and evenness of small mammals in high utilization versus low utilization sites in mixed conifer forest, but no such effects in oak woodlands. Given the decline in grass-feeding butterflies with increased grazing and that most grass-feeding butterfly species were more abundant in oak woodlands, the effects of cattle grazing utilization on butterflies appear to be more similar to birds than to small mammals. Both of these studies found significant and sometimes inconsistent differences between upland and riparian areas in terms of species richness, diversity, and responses by species and/or feeding guilds. Unlike this butterfly study though, Alexander *et al.* (2008) did not collect detailed vegetation data at each of their survey points, and classified grazing as either low (0-40%) or high utilization (>40%). Johnston & Anthony (2008) did estimate forest structure and percent cover, but similarly did not survey plant species richness at each trapping point, and also categorized cattle grazing utilization into subjective "light" or "high" categories. Therefore, this butterfly study incorporates more environmental data into its analyses than either of these bird or small mammal studies.

Management implications

The Presidential Proclamation (2000) establishing the CSNM suggests that high butterfly diversity is a desirable attribute of the CSNM. Management practices that promote local plant species richness should be expected to broadly promote butterfly species richness. However, there is no evidence of a uniform response of individual butterfly species to grazing or other environmental influences given that multiple environmental factors helped explain the trends in the spatial variation in butterfly species composition and abundance. The complex ecological landscape of the CSNM likely amplifies all of these factors, and some underlying patterns may not have been detected. Additional years of

research would likely be necessary to tease out the relative importance of these effects, and help account for long-term population fluctuations (Thomas *et al,*. 2002; Hellmann *et al.*, 2003). Therefore, a diversity of integrative management tools may be necessary since species-specific management frequently creates conflicts in which other species may be adversely affected (Schultz & Crone, 1998; Kwilosz & Knutson, 1999; Panzer, 2002; Huntzinger, 2003; Panzer, 2003).

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Season, sex and flight muscle investment affect take-off performance in the hibernating small tortoiseshell butterfly *Aglais urticae* (Lepidoptera: Nymphalidae)

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Abstract. Flight ability is generally expected to increase with relative flight muscle mass. Changes in weight can therefore be expected to influence the capacity to rapidly take-off, which can determine mating success and predator avoidance. This study examined the influence of relative flight muscle mass, sex, and season on free take-off flight ability in a butterfly model (*Aglais urticae*) that undergoes adult winter hibernation. Mass change and take-off flight ability (velocity and take-off angle), was predicted to fluctuate with season (before, during and after hibernation) and sex (due to reproductive investment). Our results indeed showed changes in take-off ability in relation to both parameters. Females maintained velocity across seasons but reduced take-off angles during and after hibernation. Male flight speed increased during and after hibernation, whereas take-off angles were significantly reduced during hibernation. Finally, we showed that investment in relative flight muscle mass increased velocity in female, but not in male butterflies.

Key words: Flight, diapause, Lepidoptera, predation, body mass, thorax mass.

Introduction

In many species the development of a highly agile body, which may be beneficial as an anti-predation strategy, comes at the cost of reproduction, or vice versa (*e.g.* lizards: Shine, 1980; fish: Plaut, 2002,; Ghalambor *et al.*, 2004; Evans *et al.*, 2007; prawns: Berglund & Rosenqvist, 1986; birds: Swaddle & Witter, 1997; scorpions: Shaffer & Formanowicz, 1996). In winged insects such as butterflies, flight is one of the primary ways of evading an attacking predator. Flight speed has been shown to reduce bird capture rates of butterflies (Chai & Srygley, 1990) suggesting that it is indeed a major determinant of escape ability. Climbing flight (net upward movement), as is common in prey birds (Hedenström & Rosén, 2001), is potentially another way of outmanoeuvring predators. Because winged animals with smaller body masses are aerodynamically favoured during ascent, prey animals may increase their chances of survival by choosing a steeper take-off as their generally larger predators are often unable to match the climbing rate (Hedenström & Rosén, 2001). As butterflies are often targeted by avian predators while feeding or resting (Morse, 1975) managing the transition from perching to airborne may be particularly important. Perching male butterflies also require the ability to quickly depart in order to intercept passing females (Wickman, 1992; Van Dyck, 2003). A high proportion of flight muscle mass relative to body mass is generally expected to enable more precise and rapid flight (Srygley & Dudley, 1993; Almbro & Kullberg, 2008). Insects are, however, highly sensitive to the costs associated with flight (Roff, 1984) suggesting that weight increases (thus reducing relative flight muscle mass) has the potential to markedly influence flight speed or trajectory (Srygley & Dudley, 1993). Our understanding of take-off flight behaviour in a predation context, however, is limited in insects that carry substantial and naturally fluctuating body weight, and has rarely been tested in free flight (but

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see Srygley & Kingsolver, 1998; Almbro & Kullberg, 2008, 2009).

In butterflies, adult winter hibernation demands large amounts of energy (i.e. abdominal fat) to be accumulated prior to hibernation in order to ensure survival until activity is resumed. A lipid content of as much as 25% of body mass is not unusual (Pullin, 1987). Whereas a substantial weight increase prior to hibernation constrains butterfly escape flight speed (Almbro & Kullberg, 2008), no information has been gathered concerning flight ability after hibernation when the demand for flight capacity remains high. Not only should lipid loads be reduced during hibernation (thus increasing relative flight muscle mass), mating would also be expected to result in sex-specific changes in body mass in species in which reproduction occurs after hibernation. Whereas both sexes need to accumulate and deplete lipid loads in relation to hibernation, we would expect females to carry relatively more weight than males after hibernation as substantial gamete related loads are transferred from male to female upon mating (Svärd & Wiklund, 1989). Males on the other hand are likely to increase their relative flight muscle mass as weight is lost following hibernation and mating. However, while the period spent in hibernation may deplete the lipid storage and increase relative flight muscle mass, disuse can result in degeneration of flight muscles (Stegwee *et al.*, 1963) that may hinder the ability to escape predators or locate mates (Layne & Rice, 2003). Adult butterflies occasionally emerge from hibernation for short periods during favourable weather conditions, yet their flight ability at such times has to our knowledge not been tested previously.

In this study we investigated differences in take-off flight performance in relation to sex and season after a simulated predator attack in wild caught small tortoiseshell butterflies (*Aglais urticae*, Linnaeus 1758). Using a 3D-tracking camera system, male and female free take-off flight ability was tested i) before hibernation ii) during hibernation iii) after hibernation. We predicted that flight ability (velocity and take-off angle) would be higher in individuals with a relatively larger flight muscle mass, and that changes in relative flight muscle mass would be related to sex and season. We thus expected male butterflies to increase flight ability with reduced body mass due to lipid depletion during hibernation and mating after hibernation; with the exception for lipid depletion during hibernation, female butterflies were expected to exhibit little or no loss in body mass after hibernation due to reproduction, and thus we did not expect an increase in female flight ability after hibernation.

Materials and method

In Sweden, adult small tortoiseshells hibernate from autumn to spring in dark sheltered areas and emerge in early spring to mate. The butterflies used in this study were collected in winter (January-February) and spring (March-April), 2006 and 2007 (data was pooled as t-tests of morphological measurements revealed no significant differences between years) nearby Tovetorp Zoological Research Station, located in South-East Sweden (58°56'N 17°08'E). Two groups of male and female butterflies were used: i) hibernating butterflies that were collected late in the winter (end of January/early February) whilst sitting in dark, unheated attics and barns near the research station (referred to henceforth as butterflies "during hibernation"), and ii) actively flying individuals captured with a net around the research station in early spring (end of March/early April; referred to henceforth as butterflies "after hibernation").

Butterflies collected during hibernation were kept in a dark incubator (Termaks KB8000, Bergen, Germany) set to 4 ± 0.1°C until treatments commenced around the same time as small tortoiseshells were observed to emerge, and were captured in the wild. The temperature in the incubator was at that point raised to 8 ± 0.1°C and both hibernating and active butterflies were kept in the incubator until used in flight trials. The incubator temperatures approximate outdoor averages for the region during the specified months. Prior to flight trials all butterflies were kept in indoor cages (0.65 x 0.65 x 0.70 m) and allowed to fly for 4 hours. The cages were furnished with moist paper towels to prevent dehydration. In addition to natural light in the room shining through windows, extra light was provided by two Philips Powertone HPI-T Plus 400W light bulbs. Before being subjected to trials, the butterflies spent a minimum of 30 minutes and a maximum of 3 hours in the incubator to facilitate handling. Because all butterflies were transferred back to the incubator at the same time after the allotted 4 hours in the flight cages, some spent more time in the incubator as flight trials were carried out in a randomised order. However, because the butterflies remain inactive whilst incubated, we do not believe that small variations in incubation time in any way affected the flight performance. To further contrast seasonal effects in flight ability, the data from the current study were compared to flight data collected in a previous study on small tortoiseshell butterflies tested prior to hibernation (referred to in the current paper as butterflies 'before hibernation', Almbro & Kullberg, 2008). All methods in the previous study were the same as in the current

study, except that half of the butterflies tested before hibernation had access to sugar water, whereas none of the butterflies tested during/after hibernation were supplied with food. However, food accessibility did not result in differences in body measurements in butterflies before hibernation (Student's t-test; n_{unfed}=14; n_{fed}=11: body mass: t=0.6, p=0.5; abdomen mass: t=1.3, p=0.2; FMR: t=-0.9, p=0.4), nor did fed and unfed butterflies differ in velocity (GLM: F=0.5, p=0.5) or take-off angle (GLM: F=1.9, p=0.2) when controlling for sex, relative flight muscle mass and type of flight (escape/control).

Flight trials

All flight trials were conducted in an indoor experimental area (3 x 4.7 x 2 m) illuminated by eight high frequency natural light fluorescent tubes (Philips TL5 HO 54W) in the ceiling and a spotlight (Philips Broadway MSR 200; high-efficiency hot restrike metal halide lamp with UV-light). Room temperature was maintained at 20 ± 1°C. Biobserve Track-it 3D-camera system (Gmbtl, Bonn, Germany) was used for recording all butterfly flights, providing 50 x-, y-, and z-coordinates per second. Every butterfly was tested once and was either attacked by a model predator or allowed to take off spontaneously. The model predator consisted of a black cardboard box (0.2 m X 0.15 m X 0.15 m) attached to a cart on a rail released 2 m from the butterfly perch at a 14 degree incline (detailed description in Almbro & Kullberg, 2008). All butterflies were allowed to warm up for a minimum time of 3 minutes and a maximum of 5 minutes. After each trial, butterflies were cooled for about 15 minutes, weighed to the nearest mg (Precisa 205A SCS, Dietikon, Switzerland) to obtain body mass (total wet weight), killed by freezing (-18°C), and dissected to obtain thorax and abdominal weights and to determine the sex. Because it consists largely of flight muscles, the weight of the thorax (after wings and legs are removed) is generally considered a reliable proxy for flight muscle mass. Lipids and gametes are located in the abdomen, allowing reliable estimates of lipid accumulation and reproductive load.

Statistical analyses

Butterfly flight data was analysed by using the coordinates provided by the Track-it 3D camera system and via Track 3d (computer software made for analysing space-time data by Ulf Norberg, Stockholm University) calculating velocity and take-off angle for every individual flight at 0.1; 0.2, 0.3; 0.5; 0.7 m from the start. Flight velocity (m/s) was calculated when butterflies passed each of the five distances from the start by measuring the distance between two successive coordinates and dividing by the time between the two recorded coordinates. Take-off angle was calculated for each of the five distances as the angle between horizontal and a line drawn between the perch and the height of the butterfly at that distance. Statistical tests used were ANOVA for morphological comparisons, General linear model (GLM), with the five flight distances as repeated measure, for analysing the effect of sex, season and morphology on flight measurements, and linear regression for analysing correlations between morphological measurements and flight parameters. Body mass was always included as a covariate with thorax mass in the GLMs to analyse relative flight muscle investment and its effect on the measured flight parameters. All data were normally distributed and equality of variances was established with Levene's test. All statistical analyses were made using Statistica version 8.0 (StatSoft, Inc. 1984-2008, Uppsala, Sweden).

Results

A total of 92 hibernated butterflies were used in this study, of which 28 males and 22 females were collected whilst hibernating, and 30 males and 12 females were captured whilst flying actively in the wild after hibernation. To compare flight ability between seasons data from 24 males and 28 females were used from an earlier study on the flight ability of small tortoiseshells prior to hibernation (Almbro & Kullberg, 2008).

Most butterflies took off in a relatively straight manner and headed towards the ceiling or the wall facing them. Only a handful would fly around the room and few flights lasted longer than 5 seconds and most left the tracking area after approximately 1 m. Butterflies that were attacked by the model predator flew faster than control butterflies (GLM with velocity as repeated measurement, and sex, season and type of flight (escape/control) as categorical factors; effect of type of flight: $F_{1,113}$=6.03, p=0.02). Therefore, further statistical analyses were only conducted on attacked butterflies (Females: $N_{\text{before hibernation}}$=17, $N_{\text{during hibernation}}$=13, $N_{\text{after hibernation}}$=10; Males: $N_{\text{before hibernation}}$=8, $N_{\text{during hibernation}}$=16, $N_{\text{after hibernation}}$=9).

Morphological comparisons between sex and season

Male butterflies showed a pattern of reduced body mass after hibernation (Table 1, Fig. 1A), with abdomen mass being highest prior to hibernation and lowest after

hibernation, whereas thorax mass did not change across seasons (Table 1, Fig. 1B-C). Female butterflies showed no change in any of the morphological measurements across seasons (Table 1, Fig. 1 A-C). Male and females butterflies did not differ in body mass before or during hibernation, but males were lighter after hibernation. Thorax mass did not differ between the sexes at any time (Table 1, Fig. 1A-C).

Effect of sex, season and morphology on flight ability

Take-off angle tended to differ between the sexes in butterflies tested after hibernation (Table 2, Fig. 2). Males and females did not differ in velocity across seasons; however, there was an interaction between sex and distance from start which revealed females to fly faster than males, but only later in the flight (at 0.5 m from the start, Table 2).

Female take-off angles were significantly lower both during and after hibernation compared to before hibernation. In contrast, velocity did not differ between seasons in females (Table 3, Fig. 2). There was, however, a significant effect of relative thorax mass on female velocity (Table 3) with linear regression establishing a positive relationship between residual thorax mass and velocity (at 0.5 m: $r=0.46$, $p=0.003$, $r^2=0.23$).

Male butterflies tested before hibernation flew slower than males tested during hibernation (Table 2, Fig. 2), and showed a trend towards being slower than males after hibernation (Tukey HSD, $p=0.09$). Male flight speed significantly increased during hibernation, however, take-off angles during hibernation were significantly reduced compared to before and after hibernation (Table 3, Fig. 2). Although body mass changed with season, relative flight muscle mass in male butterflies did not explain differences in velocity and take-off angle (Table 3).

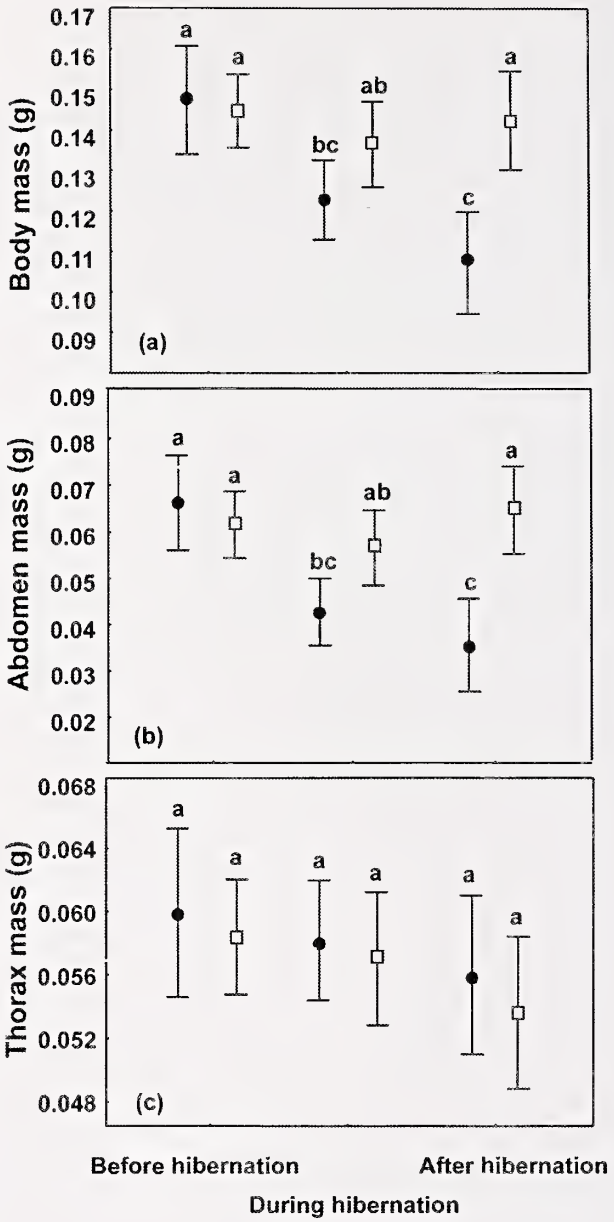

Figure 1. A-C. Mean body mass (A), abdomen mass (B) and thorax mass (C) for male (filled circles) and female butterflies (open squares) across seasons. Different letters indicate significant differences at the 0.05 level established with Tukey HSD.

Discussion

Our results showed that the take-off performance of an adult hibernating butterfly is influenced by season and sex. Male butterflies increased flight speed during hibernation compared to before hibernation, but showed a reduction in take-off angles during hibernation. In contrast, female butterflies maintained flight speed across seasons but showed decreased take-off angles during and after hibernation. Female flight speed was positively correlated to relative flight muscle investment whereas the male flight pattern was mainly explained by season.

The body composition of male butterflies and the flight ability of both male and female butterflies in this study changed across seasons. Male butterflies lost weight during and after hibernation as predicted, with male body mass during hibernation being on average 19.2% less than that of males tested before hibernation, a figure well in line with the estimates of pre-hibernation lipid accumulation made by Pullin (1987). However, despite the expected reduction in male body mass both during and after hibernation, flight speed and take-off angles in males did not

Table 1. Summary statistics from ANOVA with body measurement as dependent variable and sex and season (before, during and after hibernation) as categorical factors. Differences between variables established with Tukey HSD are illustrated in Fig. 1 A-C. P<0.05 highlighted in bold.

		Body mass		Abdomen mass		Thorax mass	
Factor	Df	F	p	F	p	F	p
Sex	1	10.9	**0.002**	12.9	**0.001**	0.9	0.3
Season	2	7.5	**0.001**	7.0	**0.002**	1.7	0.2
Sex x Season	2	5.0	**0.009**	6.8	**0.002**	0.03	0.9

Table 2. Effect of season, sex and flight muscle investment on flight ability in all attacked butterflies. Summary statistics of repeated measures GLM with season (before, during and after hibernation) and sex as categorical predictors, and thorax mass and body mass as continuous predictors. DS=distance from start. Differences between variables established with Tukey HSD are illustrated in Fig. 2. P<0.05 highlighted in bold.

		Take-off angle		Velocity	
Factor	Df	F	p	F	p
Body mass	1	3.2	0.078	0.3	0.558
Thorax mass	1	1.0	0.321	3.2	0.077
Sex	1	3.6	0.062	1.1	0.306
Season	2	9.0	**< 0.001**	3.0	0.059
Sex x Season	2	5.7	**0.006**	2.3	0.110
DS	4	12.5	**< 0.001**	1.0	0.387
DS x Body mass	4	4.9	**0.001**	1.6	0.186
DS x Thorax mass	4	0.4	0.835	2.4	0.051
DS x Sex	4	0.8	0.513	3.0	**0.021**
DS x Season	8	3.1	**0.002**	1.8	0.080
DS x Sex x Season	8	1.2	0.286	0.7	0.660

Table 3. Effect of season and flight muscle investment on male and female flight ability respectively. Summary statistics of repeated measures GLM with season (before, during and after hibernation) as categorical predictor, and thorax mass and body mass as continuous predictors. DS=distance from start. Differences between variables established with Tukey HSD are illustrated for each sex respectively in Fig. 2. P<0.05 highlighted in bold.

		Males				Females			
		Take-off angle		Velocity		Take-off angle		Velocity	
Factor	Df	F	p	F	p	F	p	F	p
Body mass	1	0.1	0.829	0.5	0.472	4.1	0.051	1.4	0.242
Thorax	1	1.6	0.220	0.2	0.703	0.4	0.517	7.3	**0.011**
Season	2	8.5	**0.002**	3.6	**0.046**	9.1	**0.001**	0.1	0.868
DS	4	2.6	**0.041**	1.3	0.276	10.3	**<0.001**	0.8	0.544
DS x Body mass	4	0.3	0.0883	1.3	0.279	5.0	**0.001**	1.4	0.247
DS x Thorax mass	4	0.1	0.984	1.7	0.157	0.4	0.807	2.1	0.089
DS x Season	8	0.7	0.736	2.0	0.054	1.8	0.078	0.9	0.464

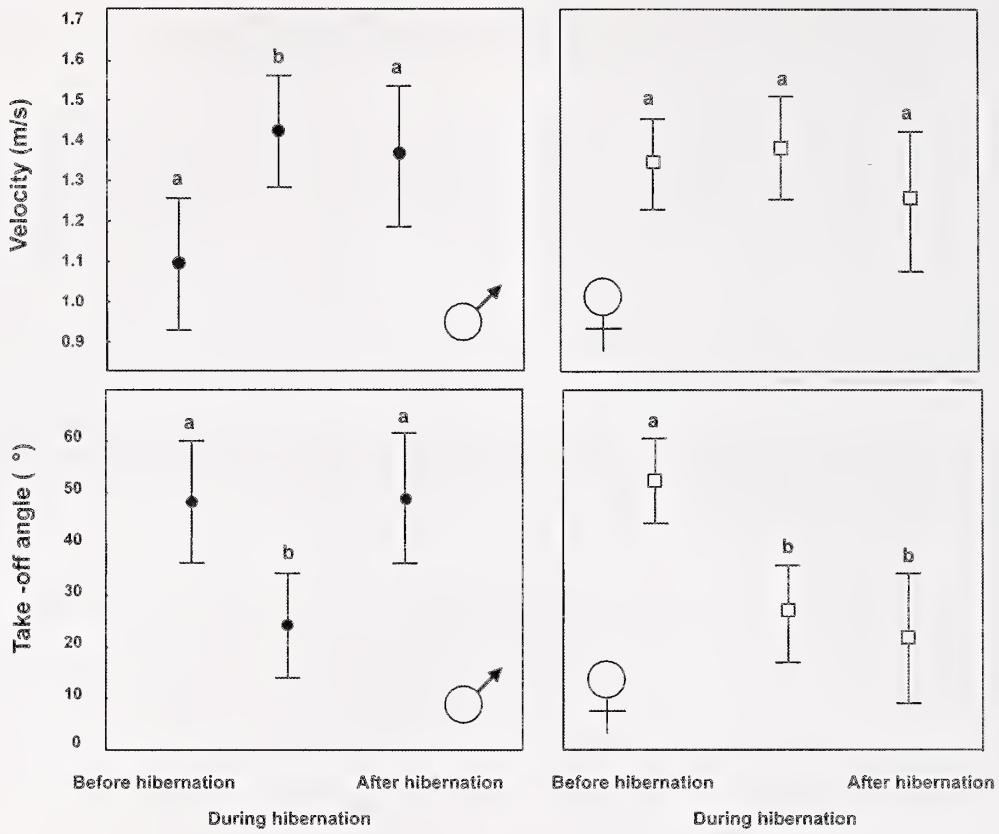

Figure 2. Mean velocity of male (filled circles) and female (open squares) butterflies across seasons (top). Mean take-off angles of male and female butterflies across seasons (bottom). Bars indicate 0.95 C.I and different letters indicate significant differences at the 0.05 level established with Tukey HSD.

directly follow this pattern. Although flight speed and angles were both high after hibernation as expected, the patterns found when we compared flights before and during hibernation were opposing. Whereas escape flights before hibernation were characterised by steeper take-off angles and lower speed, the flights performed during hibernation showed an increase in speed and a reduction in angles. Thus, despite a reduction in load carried which would have increased relative flight muscle mass, male butterflies appeared to maintain flight speed at the expense of take-off angles during hibernation. One explanation for the reduction in take-off angles seen despite weight loss could be that the inactivity of flight muscles during hibernation may have temporarily reduced flight capacity in male butterflies; an explanation supported by work showing that such degeneration in hibernating insects and bats is reversible (Stegwee *et. al.*, 1963; Kim *et al.*, 2000) and the fact that male escape flight after hibernation was both fast and steep, and not explained by a relatively larger flight muscle mass.

In contrast to male butterflies, females did not exhibit any significant change in mass across seasons. Our expectation was that females would experience some reduction in body mass due to lipid depletion at least during hibernation; as females tested after hibernation were most likely mated no body mass reduction was expected. While a lack of body mass loss during hibernation may seem surprising, it must be noted that the butterflies tested before hibernation were sampled in a different year than the butterflies tested during and after hibernation. The years sampled may thus have provided different climate conditions that could have affected for instance lipid accumulation, hibernation length and severity, and general activity levels that could explain why we observed no mass loss in females. Regardless, despite a lack of weight loss, the flight pattern of female butterflies shifted across seasons, showing a significant decrease in take-off angles during and after hibernation. Because there was no observed reduction in flight speed, females, as well as males during hibernation, may have been adjusting take-off angles to promote faster flight. The benefit of a

reduction in take-off angles is conservation of energy as a steeper take-off is more energetically expensive and a lowering of angles also enhances acceleration capacity (Dudley, 2000). As previously mentioned, the reduction in flight angles during hibernation may also have been caused by temporary degeneration of flight muscles. Although abdomen and thorax mass of females did not change across seasons, it cannot be ruled out that the transfer of reproductively related loads between the sexes caused a shift in the centre of mass that may have affected their flight performance (Srygley & Dudley, 1993).

We expected that unless thorax mass had decreased during or after hibernation, flight ability would increase or be unaltered as body mass was reduced or maintained. Neither males nor females in our study differed in thorax mass across seasons, suggesting that resources from the thorax are not used to a large extent as a source of energy or reallocated to reproduction which occurs in some butterfly species (Stjernholm & Karlsson, 2006). The fact that female, but not male, flight speed was positively related to relative flight muscle mass suggests that female butterflies indeed are more sensitive to the trade-off between flight muscle investment and allocation of resources to reproduction than are males (Roff, 1984). Because of the continuous large load carried by females, the energetic cost for flight is probably also much higher than for males (Dudley, 2000). However, such energetic costs imposed on females may be circumvented in the long term as butterflies with relatively low flight muscle mass have been shown to reduce flight activity (Kingsolver & Srygley, 2000), a strategy that perhaps also serves to minimize the risk of encountering predators. Despite their lesser flight muscle investment, female flight during hibernation was equal to that of males, suggesting that females work harder (i.e. increased wing beat frequency) to achieve similar speed and angles. However, a study by Berwaerts and colleagues (2006) on tethered flight in *Pararge aegeria* found no difference in wing beat frequency between the sexes. Butterfly flight is often found to be sex-specific (Berwaerts *et al.*, 2006) but may depend on the type of flight under study. In this study, we focused on take-off flight due to its fitness relevance for predator evasion (Chai & Srygley, 1990) and mate acquisition (Van Dyck, 2003). It is, however, possible that the benefit of investment in relative flight muscle mass in males is revealed under flight types other than take-off; for instance, Nymphalid males such as *A. urticae* often engage in lengthy courtship flights that greatly demand agility and endurance. Furthermore, although their flight ability may exceed that of females during reproduction, males in search for mates spend more time in flight than females (Shreeve, 1984), and may be at higher risk of predation, especially since extensive flight results in suboptimal body temperatures, which impairs take-off ability (Berwaerts & Van Dyck, 2004). It is worth noting that the temperature in the experimental arena and the relatively short time allowed for warm up most likely resulted in suboptimal body temperatures in the butterflies in our study, which may have more clearly revealed differences between the sexes (Berwaerts *et al.*, 2008).

Because the butterflies used in this study were obtained from the field, no reliable data on age could be collected. However, due to the duration of hibernation in this species, there was nonetheless a substantial difference in age across seasons (mainly before and after hibernation, as individuals tested during and after hibernation were of similar age), which may have influenced take-off flight performance. Increased adult age in butterflies has been associated both with lowered flight endurance (Åhman & Karlsson, 2009) and enhanced competitive success in flight contests (Kemp *et al.*, 2006). Flight ability has also been predicted to improve with age as body mass decreases and relative flight muscle mass increases over time (Stjernholm *et al.*, 2005). Males in this study increased relative flight muscle mass and showed no reduction in take-off performance after hibernation; thus, while take-off ability did not appear to be negatively affected by age, it was not explained by relative flight muscle mass in males. The lowered take-off performance of females during and after hibernation, despite the absence of any body mass change, could on the other hand be related to increased age, perhaps due to physiological changes of the functionality of the flight muscles (Saito, 2000) or depleted energy supplies.

Finally, our study confirms previous results showing that butterflies adjust flight effort depending on the perceived predation risk (Almbro & Kullberg, 2008). Kullberg and Lafrenz (2007) found that great tits attacked by a model predator reduced take-off angles in the presence of protective cover which allowed them to perform faster escape flights; in the absence of cover, take-offs were steeper which is suggested to allow a small prey to out climb a large predator (Hedenström & Rosén, 2001). Because the laws of gravity are the same for all flying animals, butterflies may very well differ in their flight response depending on the presence and absence of cover and type of predator. In our study, all flights were carried out without cover, and the significant net upward movement suggest that butterflies aim to out climb their attacker, possibly making the reductions in

take-off angles during hibernation a liability during a predator encounter.

In summary, our results show that butterfly take-off ability was primarily affected by season, sex and perceived predation risk. The importance of investing in a relatively large flight apparatus was evident in female, but not in male butterflies. Female flight ability after hibernation was characterised by maintained speed but lowered take-off angles whereas males shifted from low speed and steep angles before hibernation to low angles and higher speed during, with a surge in angles again after hibernation. Finally, our study confirmed that butterflies attacked by a model predator flew at greater speeds than during routine take-off.

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On the status of *Pseudomylothris* Neustetter, a supposed endemic butterfly genus from the Uluguru Mountains of Tanzania (Lepidoptera: Pieridae)

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Abstract. The nominal butterfly genus *Pseudomylothris* Neustetter, 1929, is confirmed to be a junior subjective synonym of *Mylothris* Hübner, 1819 (Lepidoptera: Pieridae). The status of its type species, *Mylothris leonora* Krüger, 1928, variously treated as an endemic species to the Uluguru Mountains of Tanzania, an endemic subspecies of *M. crawshayi* Butler, 1896, or a more wide-ranging subspecies of *M. crawshayi*, is discussed. It is concluded that *M. leonora* represents a Tanzanian endemic species belonging to the *M. sagala* species-group, the significance of which is discussed with respect to the endemicity and irreplaceability of the Uluguru conservation area. *Mylothris crawshayi* sensu stricto, from Malawi, is demonstrated to be very distinct from *M. leonora*. *Mylothris sagala seminigra* Berger (December 1980) is noted as a homonym and new synonym of *M. sagala seminigra* D'Abrera (September 1980).

Key words: New synonymy, endemism, Eastern Arc Mountains, Africa, biodiversity, taxonomic status, *Mylothris leonora*.

Introduction

The Uluguru Mountains of Tanzania, situated south of Morogoro town at approximately 7–8° S and 37–38° E, lie close to the centre of the Eastern Arc Mountains, a biodiversity hotspot (Myers *et al.*, 2000). Major efforts are being made to conserve the fauna and flora of the Ulugurus and other Eastern Arc mountains, particularly to prevent further deforestation (e.g. Arc Journal, 2005). In support of protection it is helpful to be able to point to endemic taxa, the presence of which renders an area 'irreplaceable' (Pressey *et al.*, 1993; Margules & Pressey, 2000).

According to Burgess *et al.* (2002), the Ulugurus have over 130 species of endemic plants, while Burgess *et al.* (2007) noted as many as 81 endemic or "near-endemic" species of vertebrates. However, if we focus on strictly endemic bird and mammal species, these numbers do not look quite so impressive. According to Hansen (2005: 11), there is just one strictly endemic species of bird (Uluguru Bushshrike, *Malaconotus alius* Friedmann), and supposedly two strictly endemic mammals: the Geata Mouse Shrew, *Myosorex geata* (Allen & Loveridge), and Telford's Shrew, *Crocidura telfordi* Hutterer (Hansen, 2005: 51). But even of these two, *C. telfordi* is also said to occur in the Udzungwa Mountains (Wilson & Reeder, 2005; Mammals of Tanzania, 2011). According to Burgess *et al.* (2007: 216), the total of all full species of vertebrates considered strictly endemic to the Ulugurus is 13 (but this number appears to include *C. telfordi*).

If endemic taxa are very distinct, such as genera or families, a 'premium' can be added (Vane-Wright *et al.*, 1991; Isaac *et al.*, 2007). The genus *Malaconotus* includes 6 species, *Myosorex* 15, while *Crocidura* has well over 150 species. Neustetter (1929) proposed the genus *Pseudomylothris* to receive *Mylothris leonora*, a pierid butterfly that had been described as a new species from the Uluguru Mountains the previous year (Krüger, 1928). Klots (1933) was unconvinced but, without access to material, tentatively treated

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Pseudomylothris as a subgenus of *Mylothris* Hübner, 1819. However, its separate status was endorsed by George Talbot who, after examining the type material of *leonora*, commented "This genus possibly forms a link between *Mylothris* and [the Indo-Australian genus] *Delias*" (Talbot, 1944: 184).

The restriction of an entire genus to a single mountain block would be unique among African Pieridae and, despite Talbot's view, *Pseudomylothris* is either ignored in recent printed taxonomic catalogues (e.g. Kielland, 1990; d'Abrera, 1997; see also Braby *et al.*, 2006), or treated explicitly as a synonym of *Mylothris* (e.g. Berger, 1980b; Ackery *et al.*, 1995; Braby, 2005a).

Currently, however, *Pseudomylothris* appears as a seemingly valid genus on more than a dozen electronic databases accessible on the 'web' (WWW, 2011). Although online databases do not have 'priority' over printed taxonomic literature, this leads to uncertainty. The purpose of this paper is to examine the taxonomic status of Neustetter's genus and its single included species, to determine to what extent this insect does or does not represent a further significant argument for conservation in the Ulugurus.

Mylothris Hübner, 1819

Mylothris Hübner, 1819. Type species by selection of Butler: *Papilio poppea* Cramer, 1777. [See Hemming, 1967: 302.]

Pseudomylothris Neustetter, 1929: 191. Type species: *Mylothris leonora* Krüger, 1928, by original designation and monotypy. Synonymy with *Mylothris* here confirmed.

Mylothris ? subgenus *Pseudomylothris* Neustetter: Klots, 1933: 225.

Pseudomylothris Neustetter: Talbot, 1944: 155, 184.

Mylothris Hübner, 1819: Carcasson, 1962: 61; Berger, 1980b: 872; Ackery, Smith & Vane-Wright, 1995: 217; Braby, 2005: 12; Williams, 2010. [*Pseudomylothris* Neustetter cited as a junior subjective synonym.]

Why should *Pseudomylothris* be regarded as a subjective synonym of *Mylothris*?

Together with his short original description, Neustetter (1929) provided a venation diagram showing only nine veins reaching the forewing margin, including two radials. According to Talbot (1944: 184), "The main distinction between *Mylothris* and *Pseudomylothris* is the absence in the latter of vein 10 of the fw., which is also the case in *Delias*." However, in *Delias* Hübner ten veins, including three branches of the radius, reach the forewing margin (e.g. Bascombe *et al.*, 1999: fig. 7.8, pl. 170). Comparison of Neustetter's figure with van Son's (1949: fig. 115, p. 214) diagram for *Mylothris chloris* (Fabricius) indicates that the supposed difference is better referred to, using the Comstock-Needham system, as the loss of R_2, or its complete fusion with R_1 (to form R_{1+2}).

Neustetter (1929) not only figured nine forewing veins for *Pseudomylothris*, but confirmed this in his description ("dass die Vorderflügel nur 9 Rippen besitzen"). Such a venation would be unique among the Pierinae, which otherwise all have 10, 11 or 12 forewing veins. This immediately raises the possibility of misinterpretation, or that the type material of *leonora* was aberrant. Long ago Carcasson (1962) showed that the latter seems to be the case. In November 1959 the late Arthur Rydon collected three males and a female *leonora* in the Uluguru Mountans. Carcasson found that all four new specimens had the normal *Mylothris* venation, with ten veins reaching the forewing margin. He then asked T.G. Howarth at the Natural History Museum in London (BMNH) to re-examine the two *leonora* type specimens. Howarth reported that one was normal, with ten veins, but the other apparently lacked one of the radials. As all other characters of *leonora*, including male genitalia, were consistent with *Mylothris*, Carcasson had no hesitation in declaring *Pseudomylothris* a synonym of *Mylothris* (a conclusion with which we are entirely in agreement), and suggesting that Neustetter must have based his venation diagram on the aberrant individual (the paralectotype—see below). Carcasson's action was duly noted in the Zoological Record for 1962.

Our own examination of the aberrant individual suggests that rather than being entirely missing, veins R_1 and R_2 appear to run exceptionally close throughout their length, almost touching, and therefore appearing at modest magnifications like a single vein. Radial veins that run extremely close together have caused confusion in other butterflies (e.g. the genus *Bia* Hübner: Vane-Wright & Boppré, 2005)—and so it appears in this case, as both Neustetter and Talbot were misled.

Mylothris leonora Krüger, 1928, stat. rev.

Mylothris leonora Krüger, 1928: 21. Lectotype female, TANZANIA: "D.-Ost-Afrika, Ukami" (BMNH), here designated. [Examined.]

Pseudomylothris leonora (Krüger); Neustetter, 1929: 191; Talbot, 1944: 184.

Mylothris leonora Krüger; Carcasson, 1962: 61–62; Carcasson, 1964: 142; Berger, 1980a: figs 7,8; Berger, 1980b: 872; Berger, 1985: 109, pl. 5 figs 3,4,6; Ackery *et al.*, 1995: 220; d'Abrera, 1997: 108, 109; Williams, 2010: 54.

Mylothris crawshayi leonora Krüger: D'Abrera, 1980: 94; Carcasson, 1981: 128; Kielland, 1990: 66, 269; de Jong & Congdon, 1993: appendix 8.2.

Mylothris leonora form *bondwa* Berger, 1985: 109, pl. 5 fig. 6. TANZANIA: "Bondwa (Mts Uluguru)".

Mylothris crawshayi: Collins *et al.*, 2007.

Mylothris leonora was described from two female specimens (syntypes), from Ukami, German East

Africa. Two female specimens (Figs 1–4) now in the Natural History Museum, London (BMNH), although they do not carry data labels that correspond precisely with the published description, have long been accepted as Krüger's original material. One of them, referred to by Talbot (1944: 184) as the "type" and by Carcasson (1962: 61) as the "holotype" (Figs 1, 2) bears the following labels: "Uluguru Berge O. Afr. / Myl. leonora Kr. Type ♀ / 18.28 [Joicey accession number] / Joicey Bequest Brit. Mus. 1934-120 / Type H.T. [attached by Joicey curator]" This specimen is hereby designated the lectotype of *Mylothris leonora* Krüger, 1928, and has been labelled accordingly.

The second specimen (Figs 3, 4), referred to by both Talbot (1944: 184) and Carcasson (1962: 61) as the "paratype", bears the following labels: "Uluguru Berge O. Afr. / Myl. leonora ♀ einzige Cotype / 31.28 [Joicey accession number] / 34/ Joicey Bequest Brit. Mus. 1934-120 / Type P.T. [attached by Joicey curator]" This specimen is hereby designated paralectotype of *Mylothris leonora* Krüger, 1928, and has been labelled accordingly.

M. leonora ♀ f. bondwa Berger differs from the typical female in having the hindwing suffused with orange, rather than plain, clear yellow. It seems possible that this butterfly exhibits female-limited polymorphism (class 7: Vane-Wright, 1975). However, both the lectotype and paralectotype of *leonora* have a distinctly orange cast to the hindwing (in contrast to the clear yellow of males), although this is not as extreme as in 'bondwa'.

Distribution. Other than records given by de Jong & Congdon (1993; see below), *leonora* has only been recorded from the Uluguru Mountains, in the Morogoro district of Tanzania (Carcasson, 1992; Kielland, 1990). The only specific localities known to us are Ukami (Krüger, 1928), Lukwangule Plateau (Berger, 1980b) and Mount Bondwa (Berger, 1985). According to Kielland (1990), the butterfly occurs in montane forest and forest-grassland mosaic, at 1200–2640 m. Berger (1980b) records it from Lukwangule, South Ulugurus, at 2200–2500 m. Nothing is known about the early stages (Williams, 2010; see Braby, 2005b).

What species-rank status should be accepted for *Mylothris leonora* Krüger?

There are three main possibilities concerning the rank of *M. leonora*, all of which have been listed or supported by various authors since Krüger first proposed this taxon as a new species: a species restricted to the Ulugurus (endemic species hypothesis), a restricted subspecies of a more widespread species-group taxon (endemic subspecies hypothesis), or a population of a more widespread species-group taxon (non-endemic hypothesis, including the possibility that *leonora* is a synonym of an earlier-established species or subspecies from elsewhere in Africa).

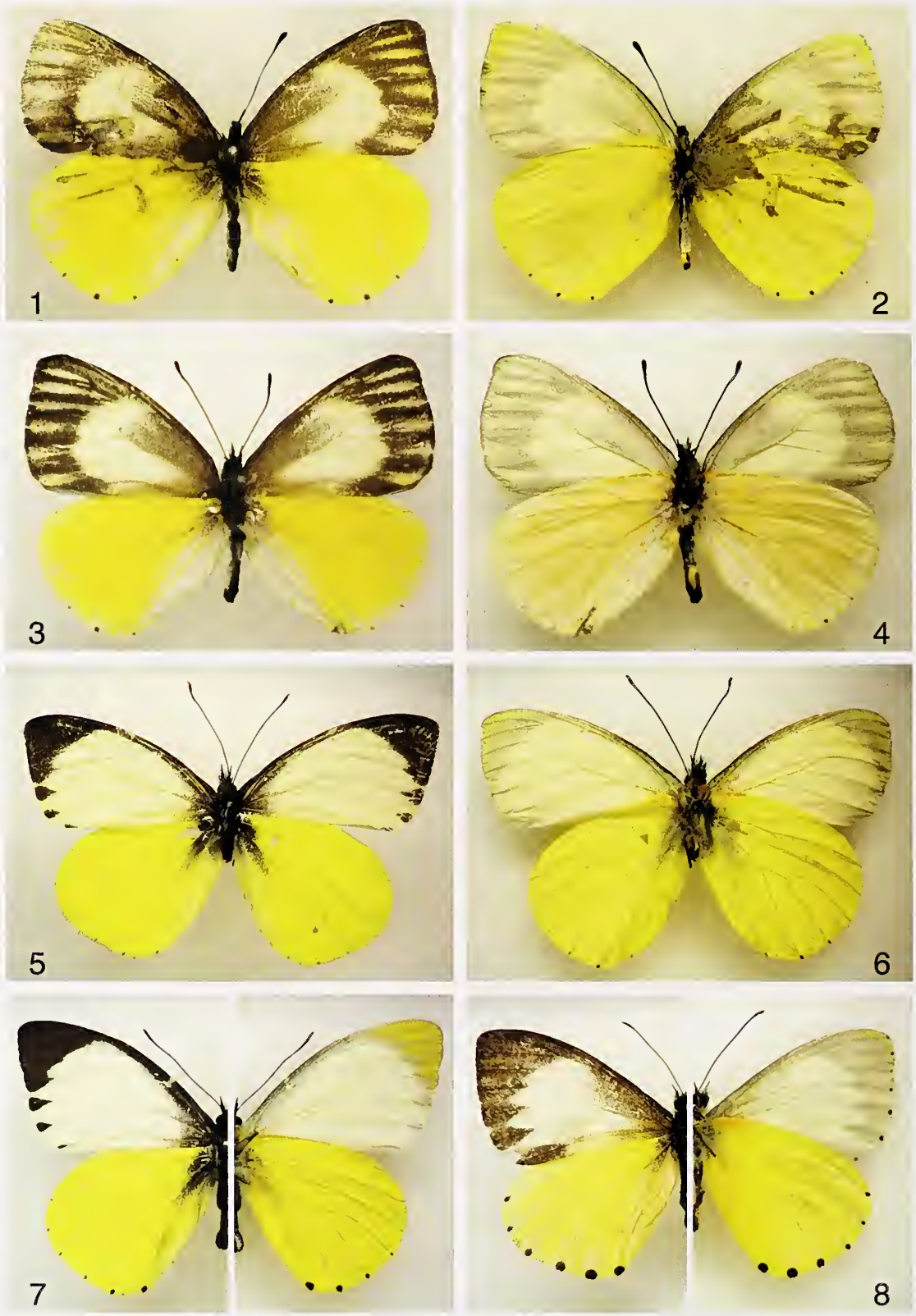
Endemic species hypothesis

This was clearly assumed by Talbot (1944), but more significantly it was accepted by Carcasson (1962) and Berger (1980b, 1985). One might also cite d'Abrera (1997) and Ackery *et al.* (1995) as further support for this hypothesis, but these works were based on various drafts of Carcasson's catalogue of Afrotropical butterflies (see Carcasson, 1981), and only differed where the authors had their own reasons to do so.

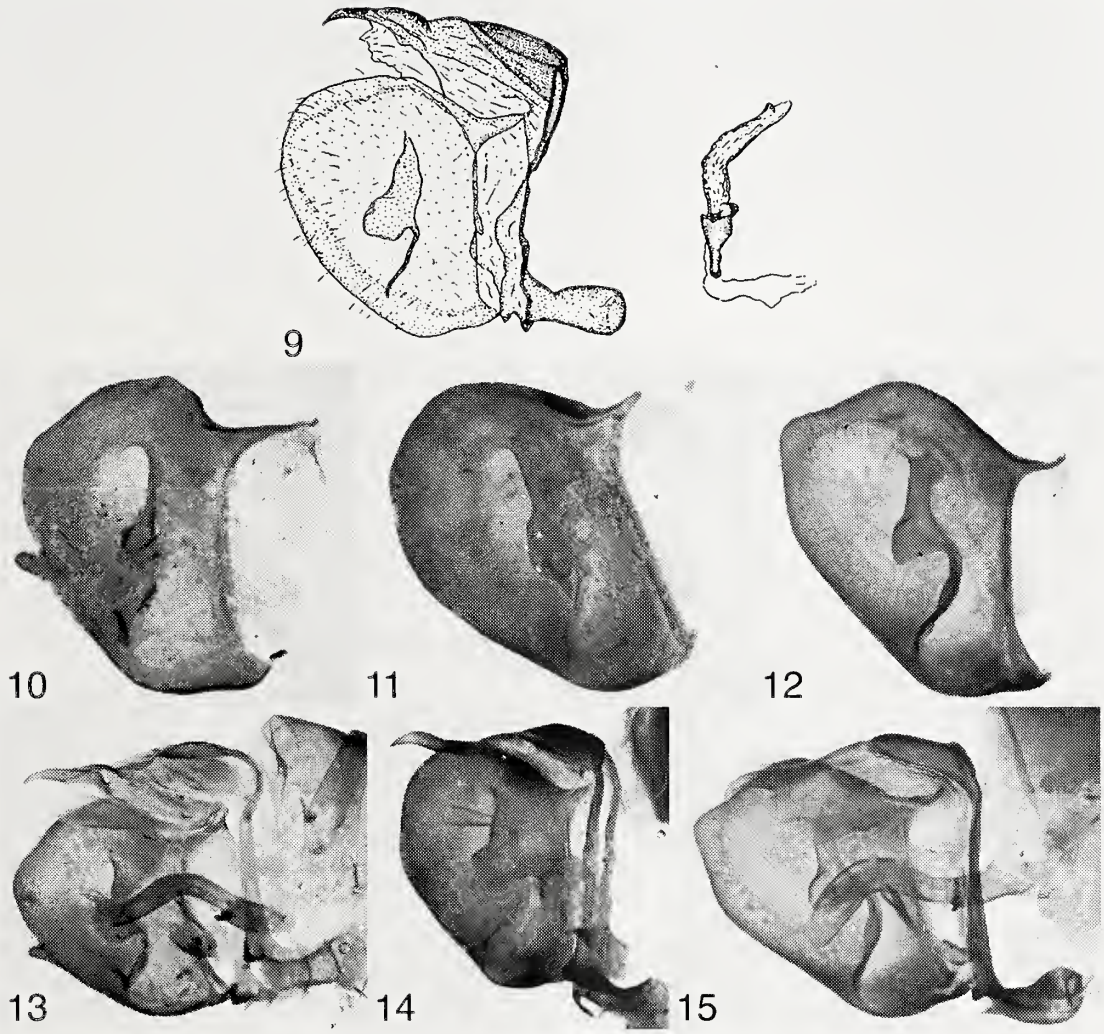
The most important account of the separate species hypothesis is given by Berger (1980b), who discussed three members of Talbot's (1944) *Mylothris sagala* Grose-Smith species-group found in the Ulugurus: *M. sagala seminigra* D'Abrera, September 1980 (= *M. sagala seminigra* Berger, December 1980, homonym, syn nov.), *M. leonora*, and *M. crawshayi bunduki* Berger, 1980. Berger noted that in these mountains he never encountered *M. sagala* outside the range 1400–1800 m, and that the single known specimen (holotype) of *crawshayi bunduki* was found at one of the *sagala seminigra* localities, Bunduki, at 1500 m. In contrast, *M. leonora* was only encountered in the more southerly Lukwangule Plateau, at 2200–2500 m. In addition to these apparent ecological differences between *crawshayi* and *leonora*, Berger (1980b, 1985) noted phenotypic differences in wing coloration pattern (both sexes), wing shape, and morphology of the genitalia (see discussion below).

Endemic subspecies hypothesis

Despite his earlier treatment, Carcasson (1981) placed *leonora* as the Uluguru subspecies of *Mylothris crawshayi* Butler, 1896, evidently believing he was the first person to make this change in status, marking his checklist entry "stat. nov." However, in print at least, he was anticipated by D'Abrera (1980). Neither author offered any explanation for the change in status (it is likely that D'Abrera was informed of Carcasson's intention through correspondence). Kielland (1990: 66) arrived at the same conclusion, perhaps independently: "I feel this taxon [*leonora*] is no more than a race of *crawshayi*. The only difference is in the female with the very wide and even marginal band, always interrupted by internervular white or pale-yellow streaks. Streaks are also present in the



Figures 1–8. *Mylothris* butterflies. **1-6**, *M. leonora* Krüger: **1, 2**, lectotype female ("Uluguru Berge"), upperside (1), underside (2); **3, 4**, paralectotype female ("Uluguru Berge"), ups (3), uns (4); **5, 6**, 'neallotype' male (Carcasson, 1962) ("Ulugurus, Nov. 1959, A.H.B. Rydon"), ups (5), uns (6). **7, 8**, *M. crawshayi* Butler: **7**, male, Malawi ("R. Crawshay, 96-156, Kasungu Mt., Nyika, 2.3.96"), ups/uns; **8**, female syntype, Malawi ("R. Crawshay, 95-143, Nyankowa Mt., 6500 ft. alt., Apr. 9th [18]95"), ups/uns.



Figures 9–15. Male genitalia of *Mylothris* species (all specimens in BMNH). **9**, *M. leonora*, 'neallotype' (Tanzania, Uluguru Mountains, A.H.B. Rydon; figures reproduced from Carcasson, 1962: fig. 17 (phallus inset), BMNH Rhoplaocera Slide no. 3222). 10–12, right-hand valves, interior faces, reversed: **10**, *M. crawshayi* (Malawi, Kantorongondo Mt., Nyika, 5900 ft, 15.iv.1895, R.W. [Crawshay], topotype, BMNH Rhopalocera Vial no. 8919); **11**, *M. sagala cf. narcissus* Butler (Tanzania, Tanga, West Usambara Mts, Magamba Forest, 1800 m, 22.x.2001, S.D. Liseki, BMNH Rhopalocera Vial no. 8918); **12**, *M. ruandana* Strand (Burundi, Kabira Forest, 7000 ft, i.1924, T.A. Barns, BMNH Rhopalocera Vial no. 8917). 13–15, terminalia, right-hand valves removed, phalluses *in situ* (all data as Figs 10–12): **13**, *M. crawshayi*; **14**, *M. sagala cf. narcissus*, **15**, *M. ruandana*.

population from Nguru Mts. and in some specimens in the U[d]zungwa Range, but with much more dentate inner-side of the marginal band. I cannot detect differences in the genitalia of *leonora* and *crawshayi*."

With respect to the male genitalia, Carcasson (1962) compared *Mylothris leonora* with *M. sagala* (of which, no doubt following Talbot, 1944, he considered *M. crawshayi* to be a subspecies, or even only a form), noting that, in comparison, the uncus of *leonora* was more pointed, its valve less rounded, and the harpe more irregular. His illustration (Carcasson, 1962: fig. 17) is reproduced here as Fig. 9. In describing the new species *M. kiellandi*, Berger (1985) stated that its genitalia differed from *M. crawshayi* in having a small apophysis on the dorsal margin of the valve longer and finer than that seen in *crawshayi*, and also had a more trapezoidal-shaped harpe. Berger (1985) also stated that *M. leonora* completely lacked the dorsal apophysis, commenting that Carcasson's (1962) figure was "exact." These statements cannot be reconciled with Kielland's comment that the genitalia of *leonora* and *crawshayi* are indistinguishable (see discussion, below).

Despite noting some similarities between true *leonora* females and females of *crawshayi* from the

Ngurus and Udzungwas, Kielland (*loc. cit.*) was quite clear that in his view subspecies *leonora* was confined to the Ulugurus, while the nominate race of *crawshayi* occurred in the Nguru, Ukaguru and Udzungwa ranges and Mt Image in south-eastern Tanzania, as well as adjacent Nyika Plateau of northern Zambia (Heath *et al.*, 2002) and northern Malawi (Gifford, 1965, as a form of *sagala*).

Non-endemic hypothesis

This is the position adopted by de Jong & Congdon (1993), who listed *Mylothris crawshayi leonora* as a subspecies from the Nguru, Uluguru, Ukaguru, Rubeho and Udzungwa mountains, with nominate *Mylothris crawshayi crawshayi* restricted to the Nyika Plateau in northern Malawi (the type locality) and eastern Zambia. No argument is offered in support of this interpretation, but it is equivalent to synonymising *M. crawshayi bunduki* Berger, sensu Ackery *et al.* (1995) and Williams (2010) (who regarded all Tanzanian populations of *M. crawshayi* as attributable to subspecies *bunduki*), with *M. leonora*.

Discussion of the alternative hypotheses

Wing shape and pattern characters

The taxa *Mylothris crawshayi*, *M. leonora* and *M. kiellandi* appear similar, and are plausibly closely related (Kielland, 1990). Phenotypically, *M. leonora* differs from typical *M. crawshayi* in the shape of the outer marginal dark forewing border of the female. This border is broader in *leonora* (about 6–7 mm instead of ca 5 mm in most *crawshayi*), with an irregular but not clearly dentate proximal margin, enclosing five or six, usually very distinct pale streaks (Figs 1 & 3, *cf.* Fig. 8). As observed by Kielland, some females from the Nguru and Udzungwa Mts that he included in (subspecies) *crawshayi* do have pale streaks, but these are less clear, and the proximal margin of the band, even when widened in some individuals, is always dentate (Kielland, 1990: pl. 13).

Despite some variation, as proposed by Berger (1980b, 1985), within an extended *Mylothris sagala*-group (see below), three diagnosable taxa supposedly related to *crawshayi* can be separated on colour pattern and wing shape characters, according to the key below.

Female *M. leonora*, as characterised above, are readily diagnosable, although the males hardly differ in colour pattern from typical *M. crawshayi* except with respect to the colour of the forewing apex beneath. However, were we to accept the arrangement of de Jong & Congdon (1993), on available characters, the various populations of '*M. crawshayi leonora*' would be phenotypically heterogeneous.

Male genitalia characters

Talbot (1944) noted that characters of the male genitalia, notably the form of the harpe and the presence or absence of an apical projection (distal projection of Klots, 1933: 226) to the valve, offer useful characters at species and species-group levels. He divided the genus into four very unequal species groups, all the species of interest here supposedly belonging to the sagala group (but see observations below on *M crawshayi*).

With respect to the male genitalia of the sagala group, Talbot (1944: 163) stated: "Valve without any apical projection . . . Harpe very broad, short and rounded, similar to that of [*trimenia*] (see Talbot, 1946) and unlike that of other groups." Within the *sagala* group Talbot included only two species, *sagala* (Fig. 11) and *ruandana* Strand (Fig. 12). However, to this must now be added *M. carcassoni* van Son, 1948, from

Key for separation of *Mylothris crawshayi*, *M. leonora* and *M. kiellandi*.

1. Posterior section of male upperside forewing outer margin lacking a complete dark border continuous with the black forewing apex, the tips of veins Cu_{A1}, Cu_{A2} and 1A being marked only with separate black chevrons (Figs 5, 7); sexually dimorphic species.....2
– Male upperside with a continuous, solid black border along entire forewing outer margin, about 6 mm in width, from apex to termen; inner margin of this border more or less distinctly dentate but occasionally not so (Berger, 1985: fig. 5); males and females similar in colour pattern (West Usambara Mts).....*M. kiellandi* Berger, 1985
2. Underside male forewing almost entirely white, only obscurely yellowed at apex; female with broad dark border running along the entire forewing outer margin, about 6 mm in width, always with at least five but usually six pale longitudinal streaks, with inner margin of the border, although irregular, not distinctly dentate; outer margin of female forewing (and to some extent male) slightly but distinctly sinusoidal, not straight or evenly rounded (Uluguru Mts) (Figs 1–6).....*M. leonora* Krüger, 1928
– Underside male forewing mostly white but with clear yellow apex; female forewing with slightly narrower dark border, about 5 mm in width, occasionally marked with more or less distinct longitudinal streaks but normally all dark, with the posterior section of the inner margin of the border normally distinctly dentate (but not so in type specimen of *M. crawshayi* female form *iringa* Berger, 1985); border element at tip of vein 1A often detached; outer margin of female forewing usually straight and then evenly rounded towards the apex, only rarely slightly sinusoidal (from Nguru Mts southwest through Udzungwa Mts to north-eastern Zambia and northern Malawi) (Figs 7, 8).....*M. crawshayi* Butler, 1896

the border area between Mozambique and Zimbabwe, which also completely lacks an apical projection (van Son, 1948), and the South African endemic *M. trimenia* Butler, 1869, which Talbot excluded due to a muddle over genitalia dissections (Talbot, 1946). In making this confusion explicit, van Son (1949: 228, figs 124, 126) even suggested that *trimenia* and *sagala* might be conspecific. Further, Talbot placed *crawshayi* within *sagala* as merely a form of *M. sagala dentatus* Butler, 1896, but all more recent authors have treated *crawshayi* as a separate species (*dentatus* does belong to *sagala*). Part of the earlier confusion may also be due to Aurivillius (1910: pl. 11d), who illustrated what is clearly a form of the very variable *M. sagala* misidentified as *M. crawshayi*. As shown below, true *M. crawshayi* is abundantly distinct, and probably does not even belong to the *sagala* group sensu stricto.

As already noted, Berger (1980b) discussed *M. leonora* as a member of the *sagala* group, to which it conforms based on the male genitalia (Fig. 9, *cf.* Figs. 11, 14). With respect to *M. kiellandi*, Berger (1985) described his new species as close to *M. leonora* and *M. crawshayi*. In particular, he compared the male genitalia of *M. kiellandi* with *M. crawshayi*, stating that the valve of *kiellandi* carries a small "dorsal [*sic*] apophyse" that is longer and finer than that of *crawshayi*. We do not have access to material of *kiellandi* that we can dissect, nor have we found any published diagram for this species. Kielland (1990) states only that it is closest to *crawshayi*. How are we to interpret "dorsal apophyse" – is this the apical (or distal) projection (apophysis), or was he referring to the dorsal articulating connection of the valve to the vinculum? If the former, which seems more likely, this would suggest that, based on a typological approach to the characters of the male genitalia, that neither *kiellandi* nor *crawshayi* belong to the *sagala* group.

We have been able to confirm this for nominate *crawshayi* (Fig. 10, 13). The preparation, made from original but non-type material collected by Richard Crawshay from one of the two original type localities in Malawi, shows that the valve of *crawshayi* has a well-developed apical projection, unlike *M. sagala* or *M. leonora*. Moreover, the valve has a very different overall shape and harpe. We can confirm that, by microscope examination but without dissection, all the male type specimens of *M. crawshayi* have the apical projection, which is easily and clearly seen in posterior view.

From this we can conclude that *M. crawhayi* and *M. leonora* are entirely separate, possibly not even belonging to the same species group. If so, then the similarity in colour pattern between the two would seem remarkable and unexplained. Alternatively, the characters of the male genitalia are specific, and offer little or no information regarding 'higher' taxa, such as the species groups proposed by Talbot. On present evidence, if we regard the absence of an apical projection (when coupled with a more or less rounded valve outline) as a loss-apomorphy (the vast majority of *Mylothris* species have an apical projection: Talbot, 1944: figs 1–26), then *M. leonora* plausibly belongs to a small monophyletic group that includes *M. sagala, M. carcassoni, M. trimenia*, and possibly *M. ruandana* (Figs. 12, 15), but excludes *M. crawshayi* and, it would seem, *M. kiellandi* – but this reformulated *sagala* group might nonetheless be nested within a slightly larger group including *M. crawshayi*. Then the similarities in colour pattern might simply be plesiomorphous. Molecular data would surely be the most rapid and effective way to confirm or refute such suggestions.

We are left with a puzzle, however. What was Jan Kielland comparing when he stated "I cannot detect differences in the genitalia of *leonora* and *crawshayi*" (Kielland, 1990: 66)? The differences between the two (Figs 9, 10) are very clear. Kielland would surely have been comparing *leonora* from the Ulugurus with what he considered to be *crawshayi* from elsewhere in Tanzania, not from Malawi. Is it possible that other, perhaps all Tanzanian populations previously attributed to *crawshayi* are in fact *leonora*? In other words, *M. leonora* is not endemic to the Ulugurus, but is a more widespread Tanzanian endemic. This would be equivalent to the "non-endemic hypothesis" of de Jong & Congdon (1993), but with the Malawi (Nyika) and Tanzanian "subspecies" raised to wholly separate species status.

In this context the original material of *M. crawshayi bunduki* becomes very significant. This taxon was based on a single male supposedly collected at Bunduki, Uluguru Mountains, in December 1913 (Berger, 1980b: 874). Berger collected in the same area during May–August 1971, but did not encounter this butterfly. It would be very desirable to confirm or refute this old record, as the presence of true *crawshayi* in the Ulugurus (although in a different biotope to *M. leonora*) would be of considerable importance in further confirming their separate status. Kielland (1990) made no mention of *crawshayi bunduki*, or its supposed presence in the Ulugurus. Unfortunately, extensive efforts to trace the holotype of *bunduki* in the Musée Royal de l'Afrique Centrale (Tervuren) have not met with success. Were the holotype of *bunduki* be found to have *leonora*-like genitalia, and this also applied to other Tanzanian material currently regarded as *M. crawshayi*, then it would seem that *M. leonora* could no longer be regarded as a species narrowly endemic to the Uluguru Mountains. If on the other hand all such specimens were found to have *crawshayi*-like male genitalia, then this would confirm

M. leonora as a narrow endemic. Unfortunately, we currently do not have access to any such material, so this must wait for the future.

In conclusion, *M. crawshayi* sensu stricto and *M. leonora* cannot be regarded as the same species, as clearly pointed out by Berger (1980a,b; 1985). They should continue to be regarded as separate, as listed by Ackery *et al.* (1995), d'Abrera (1997) and Williams (2010). What remains uncertain is the identity of the Tanzanian *Mylothris* populations from the Nguru, Ukaguru, Image and Udzungwa mountains attributed by Kielland (1990) to *M. crawshayi.* Are these also *M. leonora*? It may be significant that of these populations Kielland (1990: 66) states "flight very rapid for a *Mylothris*", the very same point made by Berger (1980b: 873, 874) concerning *M. leonora* while, at the same time, pointing to Richard Crawshay's original observation, noted by Butler (1896), that the flight of *crawshayi* is "weak". Even so, however attractive this hypothesis may seem to explain Kielland's otherwise paradoxical statement about the genitalia being inseparable, Berger (who examined the genitalia of these insects) was equally emphatic that two separate, *crawshayi*-like species occur in Tanzania. More work is needed, both morphological and molecular.

Eendemism of Uluguru butterflies

Hansen (2005: 54) states that butterfly endemism in the Uluguru Mountains is 27%. This would be remarkable, but seems to reflect a misrepresentation of the data, or a misreading of de Jong & Congdon (1993). Congdon & Bampton (2001) list seven species strictly endemic to the Ulugurus. Collins *et al.* (2007) note a total of 349 butterfly species from the whole mountain block. Among these the following eight appear strictly endemic at species level: *Celaenorrhinus kimboza* Evans (Hesperiidae), *Celaenorrhinus uluguru* Kielland (Hesperiidae), *Chondrolepis* sp. nov. Larsen & Congdon MS (Hesperiidae), *Anthene montana* Kielland (Lycaenidae), *Baliochila citrina* Henning & Henning (Lycaenidae), *Harpendyreus bergeri* Stempffer (Lycaenidae), *Uranothauma lukwangule* Kielland (Lycaenidae), and *Uranothauma uganda* Kielland (Lycaenidae). Two species listed as endemic by de Jong & Congdon (1993) not included here are *Charaxes mccleeryi* van Someren (Nymphalidae) and *Pseudathyma uluguru* Kielland (Nymphalidae), both of which have now been recorded (at species level) beyond the Ulugurus (Collins *et al.*, 2007).

If only the eight strict endemics listed above are counted, butterfly endemism in the Ulugurus, measured as a percentage of the total Uluguru butterfly fauna, is 2.3% (8/349 x 100). This rises modestly to 2.6% if *Mylothris leonora* is recognised as a separate species, as we argue here that it should be—one of the 134 species of butterflies listed as endemic to Tanzania as a whole (Williams, 2010). As a separate species, *M. leonora* thus offers further support for the irreplaceable nature of the Uluguru Mountains—but it certainly does not represent a higher taxon, and might only prove eventually to be the nominate subspecies of a more widespread Tanzanian endemic. However, this must be assessed in the context that no higher taxon of vertebrates or butterflies is restricted to the Uluguru conservation area.

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Editor's note

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Host plants of Lycaenidae on inflorescences in the central Brazilian cerrado

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Abstract. A list of lycaenid butterflies reared on inflorescences is provided and discussed. Over 13,000 inflorescences from 35 plant families of the cerrado (a region with savanna-like vegetation) of Distrito Federal, Brazil, were examined. Larvae were reared in the laboratory and 321 adults from 38 lycaenid species were obtained from 55 plant species belonging to 24 families. A compilation of the host plant records is also presented based on data available in the literature. Our study points out that the sampling effort for obtaining immature stages of lycaenids in cerrado vegetation is crucial for a better understanding of the diversity and biology of these butterflies. Many species listed in this paper are widespread and tend to be locally polyphagous (using inflorescences of more than one plant family) or oligophagous (restricted to only one plant family). Some plant families, such as Proteaceae, Malpighiaceae, and Vochysiaceae, showed higher species richness and abundance of larvae than has been observed in Rubiaceae. Host plant records are provided for the first time for seven species of lycaenids.

Key words: *Cyanophrys*, Eumaeini, florivory, *Nicolaea*, oligophagy, *Paiwarria*, sampling effort, *Strymon*, Theclinae, Vochysiaceae.

Introduction

The feeding specificity of herbivorous insects is a central topic in the discussion of factors behind the mega-diversity of tropical insects (May, 1990; Odegaard *et al.*, 2000; Novotny *et al.*, 2006; Dyer *et al.*, 2007, Condon *et al.*, 2008; Lewinsohn & Roslin, 2008). Despite our increasing knowledge of phytophagous insects and their host plants, some recent catalogs (Pastrana, 2004; Santin, 2004; Beccaloni *et al.*, 2008) have shown that much work remains in the neotropics. For example, Beccaloni *et al.* (2008) estimate that there are records of host plants for only 26% of the approximately 8,000 species of neotropical butterflies. However, it is important to note that collecting information on the diet of herbivorous insects is a time-consuming activity that demands extensive field sampling, rearing immatures in the laboratory, depositing testimony material in collections, and precise species identification (Gaston, 1993; Godfray *et al.*, 1999).

Lycaenidae (Lepidoptera, Papilionoidea) are distributed worldwide and include at least 1,200 neotropical species in three subfamilies: Lycaeninae, Polyommatinae, and Theclinae (Lamas, 2004; Robbins, 2004a). Despite its high species richness, this family is comparatively less well known (Fiedler, 1995a; 2001; Pierce *et al.*, 2002; Robbins, 2004b) than other groups of butterflies (e.g., Pieridae, Papilionidae, and frugivorous nymphalids). However, the number of studies on the neotropical lycaenids is growing rapidly (e.g., Hall *et al.*, 2005; Nicolay & Robbins, 2005; Prieto & Dahners, 2006; Vila & Eastwood, 2006; Duarte & Robbins, 2010; Robbins *et al.*, 2010; Rodrigues *et al.*, 2010), but information on immature stages, host plants, and biology is still scarce (Duarte *et al.*, 2005; Duarte & Robbins, 2009; Kaminski *et al.*, 2010; Kaminski & Freitas, 2010).

Most phytophagous lycaenids are generalist feeders

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with a broad diet, especially in the tropics (Fiedler, 1995a). The tropical Theclinae may use ephemeral food resources, including expanding leaves, flower buds, and flowers (Robbins & Aiello, 1982; Chew & Robbins, 1984; Fiedler, 1995b; Feinstein *et al.*, 2007; Vargas & Parra, 2009), and in an ecosystem where the climate facilitates reproduction for several months a year, such predilections for nitrogen-rich plant parts may encourage polyphagy (Monteiro, 1991; Fiedler, 1995a).

The aim of this study was to sample larvae of Lycaenidae from inflorescences found in an area with savanna-like vegetation (cerrado) in central Brazil. Host plant records for 37 species of Theclinae and one species of Polyommatinae are presented, with a compilation of the host plant information available in the literature for these species. The huge sampling effort required to obtain lycaenid larvae in the cerrado vegetation and the polyphagy observed in the family are discussed.

Methods

Study area

The study was conducted in cerrado areas of the Fazenda Água Limpa (15°55'S-47°55'W), with sporadic surveys in three other nearby localities: Reserva Ecológica do IBGE (RECOR), Parque Nacional de Brasília and the campus of the Universidade de Brasília, Distrito Federal, Brazil. Fazenda Água Limpa (FAL) is an experimental and protected area with approximately 5,000 ha. It belongs to the Universidade de Brasília, and together with the Jardim Botânico de Brasília and the RECOR, it forms the core of the Environmental Protected Area known as "APA Gama e Cabeça de Veado" with approximately 20,000 ha.

The region is characterized by altitudes of around 1,050 m, an average annual temperature of 22ºC, an average annual rainfall of 1,416.8 mm (RECOR Meteorological Station), and a marked seasonality, with a lengthy dry season from May to September and a wet season from October to April. The vegetation includes many phytophysiognomies that range from grassland to gallery forest (for illustrations, see Goodland, 1971; Oliveira-Filho & Ratter, 2002), with predominance of cerrado *sensu stricto* (Ratter, 1980, Felfili & Silva Junior 1993).

Larval surveys

Larvae of Lycaenidae were sampled from inflorescences from the FAL area of the cerrado beginning in 1999 (Diniz & Morais, 2002, Morais *et al.*, 2009). Three data sets were analyzed in the present work: (a) quantitative samplings of inflorescences without visual inspection for larval presence (1999-2009), (b) quantitative samplings with visual inspection for larval presence (between March 2009 and March 2010, only those inflorescences with at least one larva were collected), and (c) inflorescence samplings conducted between April and December 2010. The first two data sets (the quantitative surveys) were considered to evaluate the field sampling effort of larvae, and the host plant records were compiled for each reared species. The cerrado vegetation is primarily characterized by shrubs and herbaceous plants, which allow direct examination of the inflorescences. Up to five inflorescences per plant were collected or examined in the field. From taller plants, the inflorescences were collected with the aid of a pruning hook. Plants with inflorescences were collected and examined with no prior selection of plant species.

All inflorescence samples were transferred to the laboratory and kept in individual plastic containers covered with thin fabric. Each inflorescence branch was inserted into a bottle containing water. The containers were checked and cleaned every two days, and any consumed inflorescences were regularly replaced by fresh ones. The plants were identified with the support of the Herbário da Universidade de Brasília (UB). The butterflies were deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP) and at the Coleção Entomológica do Departamento de Zoologia of the Universidade de Brasília.

Results

Sampling effort

In the quantitative samplings (data sets "a" and "b described in the Methods), 11,445 inflorescences belonging to 89 species and 31 families were analyzed. In the laboratory, 202 adults of Lycaenidae were obtained (Table 1). This sampling effort revealed an average of 1.8 adult lycaenids per 100 inflorescences. The inflorescences that were collected without prior visual inspection (n = 8,220) yielded 119 adult lycaenids, or 1.4 individuals per 100 inflorescences, and the active search for larvae (n = 3,225 examined inflorescences) revealed 83 adult lycaenids or 2.6 individuals per 100 inflorescences.

In total (data sets "a", "b", and "c" described in the Methods), over 13,000 flowers belonging to 95 species and 35 plant families were examined. The 321 adult lycaenids obtained under laboratory conditions emerged from 55 species on 24 plant families (Table 2). A compilation of published records of larval host

Table 1. Sampling effort for Lycaenidae larvae in inflorescences in the cerrado of the Distrito Federal, Brazil, number of adults reared in laboratory. The nomenclature and authorship of the species are as given by Cavalcanti & Ramos (2001). The arrangement of the families follows the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/APweb/).

Examined Plants		Examined or collected inflorescences	Number of Lycaenidae (adults)
Family	Species		
Annonaceae	*Annona coriaceae* Mart.	1	0
Velloziaceae	*Vellozia squamata* Pohl	15	0
Arecaceae	*Syagrus flexuosa* (Mart.) Becc.	5	0
Proteaceae	*Roupala montana* Aubl.	595	16
Celastraceae	*Plenkia polpunea* Reissek	2	0
Connaraceae	*Rourea induta* Planch.	447	7
Calophyllaceae	*Kielmeyera* spp. (2 species)	214	2
Caryocaraceae	*Caryocar brasiliense* Camb.	653	8
Euphorbiaceae	*Delachampia caperonioides* Baill.	50	0
Euphorbiaceae	*Maprounea guianensis* (Aubl.) Müll. Arg.	4	0
Salicaceae	*Casearia sylvestris* Sw.	148	4
Malpighiaceae	*Banisteriopsis* spp. (2 species)	105	0
Malpighiaceae	*Byrsonima* spp. (6 species)	471	20
Malpighiaceae	*Heteropterys* spp. (3 species)	67	4
Malpighiaceae	*Peixotoa* spp. (2 species)	153	4
Malpighiaceae	*Pterandra pyroidea* A. Juss.	30	2
Ochnaceae	*Ouratea hexasperma* (St.Hil) Baill.	279	3
Fabaceae	*Calliandra dysantha* Benth.	19	4
Fabaceae	*Chamaecrista* spp. (3 species)	277	0
Fabaceae	*Dalbergia miscolobium* Benth.	55	0
Fabaceae	*Dimorphandra mollis* Benth.	100	0
Fabaceae	*Galactia* sp.	2	0
Fabaceae	Fabaceae spp. (2 species)	37	2
Fabaceae	*Mimosa* spp. (4 species)	527	22
Fabaceae	*Periandra* sp.	265	3
Fabaceae	*Pterodon pubescens* (Benth.) Benth.	123	1
Fabaceae	*Stryphnodendron adstringens* (Mart.) Cov.	33	0
Lythraceae	*Diplusodon* sp.	60	4
Melastomataceae	*Leandra aurea* (Cham.) Cogn.	35	0
Melastomataceae	*Miconia* spp. (5 species)	1378	26
Myrtaceae	*Blepharocalyx salicifolius* (H., B. & K.)	100	0
Myrtaceae	*Myrcia* spp. (3 species)	23	0
Vochysiaceae	*Qualea grandiflora* Mart.	851	24
Vochysiaceae	*Vochysia elliptica* Mart.	553	11
Anacardiaceae	*Anacardium humile* St.Hil.	36	0
Burseraceae	*Protium ovatum* Engl.	100	0
Rutaceae	*Spiranthera odoratissima* St. Hil.	16	0

Table 1. Cont.

Malvaceae	*Eriotheca pubescens* (Mart.&Zucc.) S. & E.	100	0
Malvaceae	*Pavonia rosa-campestris* St. Hil.	10	0
Loranthaceae	*Phthirusa ovata* (DC.) Eichler	191	0
Primulaceae	*Cybianthus detergens* Mart.	196	0
Primulaceae	*Rapanea guianensis* Aubl.	162	0
Styracaceae	*Styrax ferrugineus* Ness & Mart.	100	1
Rubiaceae	*Chomelia ribesioides* Benth.	203	2
Rubiaceae	*Ferdinandusa elliptica* Pohl	4	0
Rubiaceae	*Palicourea coriacea* (Cham.) K. Schum.	798	0
Rubiaceae	*Tocoyena formosa* (C. & S.) K. Schum.	3	0
Bignoniaceae	*Arrabidae brachypoda* (DC.)	5	1
Bignoniaceae	*Jacaranda ulei* Bureau & K. Schum.	52	0
Bignoniaceae	*Zeyhera montana* Mart.	8	0
Lamiaceae	*Hyptis* sp.	100	0
Lamiaceae	*Aegiphila lhotzkiana* L.	3	0
Verbenaceae	*Lippia rotundifolia* Cham.	34	0
Solanaceae	*Solanum lycocarpum* St. Hil.	287	4
Asteraceae	*Aspilia foliacea* (Spreng.)	65	1
Asteraceae	Asteraceae spp. (2 species)	5	0
Asteraceae	*Eremanthus* spp. (2 species)	118	0
Asteraceae	*Gochnatia* sp.	2	0
Araliaceae	*Schefflera macrocapa* (Cham. & Schltdl.)	1170	26
	TOTAL	11445	202

plants for these butterflies is also given in Table 2.

Lycaenidae and their larval host plants

In this study, 37 species of Theclinae (Eumaeini) and one species of Polyommatinae were reared from 55 plant species (Table 2). *Calycopis mimas* (Godman & Salvin, 1887), *Chalybs hassan* (Stoll, 1790), *Cyanophrys acaste* (Prittwitz, 1865), *Ostrinotes empusa* (Hewitson, 1867), *Strymon cyanofusca* K. Johnson, Eisele & MacPherson, 1990, and *Rekoa stagira* (Hewitson, 1867) are the first records for the Distrito Federal, central Brazil (see also Emery *et al.*, 2006; Pinheiro & Emery, 2006; Pinheiro *et al.*, 2008). *Qualea grandiflora* Mart. (Vochysiaceae) is recorded for the first time as a larval host plant of *Thepytus thyrea* (Hewitson, 1867) (see Robbins *et al.*, 2010); for six other eumaeines, *Ignata norax* (Godman & Salvin, 1887), *Nicolaea socia* (Hewitson, 1868), *Paiwarria aphaca* (Hewitson, 1867), *Strymon crambusa* (Hewitson, 1874), *Strymon cyanofusca*, K. Johnson, Eisele & MacPherson, 1990, and *Tmolus cydrara* (Hewitson, 1868), host plant records were not found in the literature (Table 2). Illustrations of larvae and adults with biological notes (e.g., myrmecophily and parasitism) will be presented elsewhere.

Discussion

Sampling effort

Our larval surveys of the central cerrado show that the frequency of immature stages of Lycaenidae is relatively low when compared to two other South American habitats. Vargas and Parra (2009) obtained an average of 2.4 larvae of three lycaenid species in 50 inflorescences of *Acacia macracantha* Willd. (Fabaceae) in northern Chile. In a two-year study

of the restinga vegetation of Rio de Janeiro (Brazil), Monteiro (1990) obtained 500 eggs and larvae of *Rekoa marius* (Lucas, 1857) and 150 eggs and larvae of *Rekoa palegon* (Cramer, 1780).

The number of adults obtained in laboratory depends on the frequency of larvae observed in the field and on the rearing success. Even if we consider a high mortality rate of 50%, the frequency of lycaenid larvae found by our quantitative samplings remained low.

Visual inspections of the inflorescences contributed to the successful capture of larvae and the ability to observe their interactions with ants. The collection and maintenance of the flowers in the laboratory allowed us to observe larvae with internal development in reproductive plant tissues, a possible generalized behavior for juvenile larvae of Eumaeini (e.g., Pierce & Easteal, 1986; Kaminski *et al.*, 2010). The larvae of several species of lycaenids are cryptic, as their colors are similar to the consumed inflorescence (Monteiro, 1991; Grimble & Beckwith, 1993; Kaminski & Freitas, 2010). Thus, the methods used in this study complement the field collection of immature stages of these butterflies.

Use of cerrado plants by Lycaenidae

Our experience collecting larvae on leaves and flowers in cerrado, which has stretched over a decade, corroborates evidence from Chew and Robbins (1984) that indicates a predilection of the Eumaeini larvae to feed on flowers, fruits and, more rarely, on leaves (Morais *et al.*, 2009).

The occurrence of *Rekoa palegon* on inflorescences of several species of Asteraceae confirms the observations of Robbins (1991a) and Monteiro (1991) relating to this plant family. Monteiro (1990) noted that the reproduction of *R. palegon* was concentrated in April and June, which coincides with the flowering of their major host plants in the resting area of Rio de Janeiro: *Mikania hoehnei* B. L. Rob., *M. stipulacea* Willd., *Eupatorium laxum* Gardner and *Vernonia scorpioides* (Lam.) Pers. *Rekoa marius* were highly polyphagous as observed by Monteiro (1991) and Robbins (1991a). Monteiro (1990) noted the frequent use of one species of Bignoniaceae and one species of Fabaceae. Despite the high polyphagy of this butterfly, Monteiro (1990) did not succeed in rearing larvae in Asteraceae species. *Rekoa stagira* appears as the first record for the Distrito Federal, Brazil, and this supports the observations of Robbins (1991a) regarding the rarity of this species when compared to its closest relatives.

Electrostrymon endymion (Fabricius, 1775) and *Kisutam syllis* (Godman & Salvin, 1887) may be facultative detritivores like other species in the subtribe Calycopidina (see Duarte & Robbins, 2010). *Kisutam syllis* is one of the most common eumaeine species and is especially abundant around decaying fruit on the wet forest floor (Duarte & Robbins, 2010). The present study observed that both species use flowers lying on the ground (the feeding habit is known as saproflorivory *sensu* Feinstein *et al.* 2007). However, two other Calycopidina species, *Calycopis mimas* and *C. calor* (H. H. Druce, 1907), were found on inflorescences, and Duarte and Robbins have additional unpublished data suggesting that the lineage to which these two species belong is not detritivorous.

There are many taxa of tropical lycaenids that tend to be polyphagous, especially on groups with obligate ant association and the flower- and fruit-feeders (e.g., Fiedler, 1994; Pierce *et al.*, 2002). For the neotropical Eumaeini, however, this perspective seems to be influenced by the occurrence of common species with wide geographical distributions and information on host plants collected in various regions.

Information scattered in the literature on a number of neotropical Eumaeini suggests a higher occurrence of oligophagy than has been previously reported. This is exemplified by the association of *Ministrymon azia* (Hewitson, 1873) with Fabaceae, *Michaelus thordesa* (Hewitson, 1867) with Bignoniaceae (Table 2), *Allosmaitia strophius* (Godart, [1824]) with Malpighiaceae (Kaminski & Freitas, 2010) and the genus *Arawacus* Kaye with Solanaceae (Robbins & Aiello, 1982; Robbins, 1991b; 2000; Gentry, 2003; Beccaloni *et al.*, 2008; Janzen & Hallwachs, 2010). However, Asteraceae is cited as a host plant for two species of *Arawacus*, *A. ellida* (Hewitson, 1867) and *A. binangula* (Schaus, 1902) (Robbins, 2000). In addition, Fabaceae is referred to *A. tarania* (Hewitson, 1868) (Robbins, 2000; Beccaloni *et al.*, 2008). All of these species have a wide geographical distribution: *M. azia* is found from the USA to Argentina, *Allosmaitia strophius* is found from south Texas to southern Brazil, and *Arawacus ellida* is found throughout South America.

Some species are locally highly polyphagous, occurring on at least five plant families at one cerrado site: *Kolana ergina* (Hewitson, 1867), *Nicolaea socia*, *Parrhasius polibetes* (Stoll, 1781), *Strymon mulucha* (Hewitson, 1867), and *Tmolus echion* (Linnaeus, 1767). Some species have a wide geographical distribution, including *K. ergina* (South America), *P. polibetes* (Mexico to Uruguay), *S. mulucha* (Mexico to Argentina), and *T. echion* (South Texas to Argentina).

Table 2. Lycaenidae species whose caterpillars were found and reared on host plants in cerrado of the Distrito Federal, Brazil. Information on host plants families from others areas was compiled from other sources.

Lycaenidae Species	Adults in lab.	Food resource	**Families** and species of hostplants in cerrado	Families of hostplants in other areas	References
Theclinae - Eumaeini					
Allosmaitia strophius (Godart, [1824])	51	Inflorescence and young fruits	**Malpighiaceae** (*Byrsonima pachyphylla, B. subterranea, B. verbascifolia, B. viminifolia, Heteropterys procoriacea, Heteropterys* sp., *Peixotoa goiana, Pterandra pyroidea,* species not identified)	Malpighiaceae	Kaminski & Freitas 2010
Arawacus ellida (Hewitson, 1867)	1	Inflorescence	**Solanaceae** (*Solanum lycocarpum*)	Asteraceae	Robbins 2000
Calycopis calor (H. H. Druce, 1907)	19	Inflorescence	**Calophyllaceae** (*Kielmeyera coriacea, Kielmeyera* sp.), **Caryocaraceae** (*Caryocar brasiliense*), **Vochysiaceae** (*Qualea grandiflora*)	Malpighiaceae; genus with some facultative detritivores species	Duarte *et al.* 2005, Duarte & Robbins 2009, Torezan Silingardi 2007
Calycopis mimas (Godman & Salvin, 1887)	1	Inflorescence	**Lythraceae** (*Diplusodon* sp.)	Melastomataceae, genus with some facultative detritivores species	Beccaloni *et al.* 2008, Duarte *et al.* 2005, Duarte & Robbins 2009
Chalybs hassan (Stoll, 1790)	2	Inflorescence	**Araliaceae** (*Schefflera macrocarpa*), **Malpighiaceae** (*Peixotoa goiana*)	Fabaceae	Beccaloni *et al.* 2008
Chlorostrymon telea (Hewitson, 1868)	4	Inflorescence	**Fabaceae** (*Pterodon pubescens*), **Proteaceae** (*Roupala montana*)	Sapindaceae, Sterculiaceae	Beccaloni *et al.* 2008, Janzen & Hallwachs 2010
Cyanophrys herodotus (Fabricius, 1793)	14	New leaves and inflorescence	**Araliaceae** (*Schefflera macrocarpa*), **Proteaceae** (*Roupala montana*), **Rubiaceae** (*Chomelia ribesioides*)	Adoxaceae (= Dipsacaceae), Anacardiaceae, Asteraceae, Boraginaceae, Malvaceae, Sambucaceae, Verbenaceae	Robbins & Duarte 2005
Cyanophrys acaste (Prittwitz, 1865)	1	Inflorescence	**Fabaceae** (*Dalbergia miscolobium*)	Asteraceae, Ulmaceae	Robbins & Duarte 2005, Beccaloni *et al.* 2008
Electrostrymon endymion (Fabricius, 1775)	1	Fallen flowers	**Vochysiaceae** (*Qualea grandiflora*)	Detritivores	Duarte & Robbins 2010
Erora aff. *biblia* (Hewitson, 1868)	1	Inflorescence	**Melastomataceae** (*Miconia fallax*)	--	
Erora aff. *gabina* (Godman & Salvin 1887)	4	Inflorescence	**Melastomataceae** (*Miconia albicans, M. pohliana*), **Vochysiaceae** (*Qualea grandiflora*)	--	
Gargina aff. *thyesta* (Hewitson, 1869)	1	Inflorescence	**Proteaceae** (*Roupala montana*)	--	
Ignata norax (Godman & Salvin, 1887)	1	Inflorescence	**Caryocaraceae** (*Caryocar brasiliense*)	Not found in the literature	
Kisutam syllis (Godman & Salvin, 1887)	6	Fallen flowers	**Vochysiaceae** (*Qualea grandiflora*)	Anacardiaceae, Combretaceae; facultative detritivores species	Beccaloni et al. 2008, Duarte & Robbins 2010
Kolana ergina (Hewitson, 1867)	7	New leaves and inflorescence	**Araliaceae** (*Schefflera macrocapa*), **Connaraceae** (*Rourea induta*), **Malpighiaceae** (*Byrsonima pachyphylla*), **Melastomataceae** (*Miconia albicans*), **Ochnaceae** (*Ouratea hexasperma*), **Vochysiaceae** (*Vochysia elliptica*)	Araliaceae, Malpighiaceae (leaves of *Byrsonima sericea*)	Flinte *et al.* 2006, Kaminski 2010

Table 2. Cont.

Michaelus thordesa (Hewitson, 1867)	3	Inflorescence	**Bignoniaceae** (*Jacaranda ulei*), **Fabaceae** (*Bauhinia* sp.)	Bignoniaceae	Kaminski *et al.* 2010, Monteiro 1990, Zikán & Zikán 1968
Ministrymon azia (Hewitson, 1873)	22	Inflorescence	**Fabaceae** (*Mimosa foliosa, M. lanuginosa, M. radula*)	Anacardiaceae, Fabaceae	Miller & Miller 1997, Vargas & Parra 2009
Nicolaea cauter (H. H. Druce, 1907)	3	Inflorescence	**Proteaceae** (*Roupala montana*), **Vochysiaceae** (*Vochysia elliptica*)	Ochnaceae	Beccaloni *et al.* 2008
Nicolaea socia (Hewitson, 1868)	18	Inflorescence	**Araliaceae** (*Schefflera macrocarpa*), **Caryocaraceae** (*Caryocar brasiliense*), **Connaraceae** (*Rourea induta*), **Malpighiaceae** (*Byrsonima verbascifolia*), **Melastomataceae** (*Miconia ferruginata*), **Proteaceae** (*Roupala montana*) **Vochysiaceae** (*Qualea parviflora, Vochysia elliptica*)	Not found in the literature	
Ocaria ocrisia (Hewitson, 1868)	3	Inflorescence	**Proteaceae** (*Roupala montana*)	Fagaceae, Ochnaceae, Polygonaceae, Sapindaceae	Beccaloni *et al.* 2008, Canals 2003, Monteiro 1990
Olynthus aff. *punctum* (Herrich-Schäffer, [1853])	3	Inflorescence	**Caryocaraceae** (*Caryocar brasiliense*)	--	
Ostrinotes empusa (Hewitson, 1867)	5	Inflorescence	**Malpighiaceae** (*Byrsonima coccolobifolia, Peixotoa goiana*), **Proteaceae** (*Roupala montana*)	Sterculiaceae	Beccaloni *et al.* 2008
Paiwarria aphaca (Hewitson, 1867)	6	New leaves and inflorescence	**Celastraceae** (*Salacia crassifolia, Salacia* sp. ?)	Not found in the literature	
Parrhasius polibetes (Stoll, 1781)	45	New leaves and inflorescence	**Araliaceae** (*Schefflera macrocarpa*), **Bignoniaceae** (*Arrabidea brachypoda*), **Lythraceae** (*Diplusodon* sp.), **Malpighiaceae** (*Byrsonima coccolobifolia, B. verbascifolia,* species not identified), **Melastomataceae** (*Miconia albicans, M. fallax, M. ferruginata*), **Ochnaceae** (*Ouratea hexasperma*), **Proteaceae** (*Roupala montana*), **Styracaceae** (*Styrax ferrugineus*), **Vochysiaceae** (*Qualea grandiflora, Q. parviflora*)	Araliaceae, Bignoniaceae, Chrysobalanaceae, Combretaceae, Euphorbiaceae, Fabaceae, Malpighiaceae, Malvaceae, Melastomataceae, Myrtaceae, Sapotaceae, Sapindaceae, Styracaceae	Beccaloni *et al.* 2008, Kaminski *et al.* 2010, Rodrigues *et al.* 2010, Torezan Silingardi 2007
Pseudolycaena marsyas (Linnaeus, 1758)	2	Inflorescence	**Ochnaceae** (*Ouratea hexasperma*)	Anacardiaceae, Combretaceae, Fabaceae (Papilionoideae), Meliaceae, Myrtaceae, Polygonaceae, Resedaceae, Rosaceae, Sapotaceae, Sterculiaceae, Ulmaceae	Beccaloni *et al.* 2008
Rekoa marius (Lucas, 1857)	7	Inflorescence	**Fabaceae** (species not identified), **Malpighiaceae** (species not identified), **Melastomataceae** (*Miconia fallax*), **Ochnaceae** (*Ouratea hexasperma*), **Proteaceae** (*Roupala montana*), **Vochysiaceae** (*Qualea grandiflora*)	Apocynaceae, Araliaceae, Bignoniaceae, Boraginaceae, Combretaceae, Fabaceae, Malpighiaceae, Melastomataceae, Myrtaceae, Ochnaceae, Polygonaceae, Sapindaceae, Verbenaceae	Kaminski 2010, Monteiro 1991, Robbins 1991a, Torezan Silingardi 2007

Table 2. Cont.

Rekoa palegon (Cramer, 1780)	4	Inflorescence	**Asteraceae** (*Aspilia foliacea, Baccharis dracunculifolia, Chromolaena pedunculosa, Lepdaploa* sp., species of Eupatorie not identified)	Araliaceae, Boraginaceae, Euphorbiaceae, Fabaceae, Melastomataceae, Ochnaceae, Polygonaceae, Solanaceae, Verbenaceae, Ulmaceae	Beccaloni *et al.* 2008, Kaminski 2010, Monteiro 1990, Robbins 1991a
Rekoa stagira (Hewitson, 1867)	1	Inflorescence	**Proteaceae** (*Roupala montana*)	Araliaceae, Malpighiaceae, Fabaceae	Kaminski 2010, Robbins 1991a
Strymon bazochii (Godart, [1824])	8	Inflorescence	**Verbenaceae** (species not identified)	Lamiaceae, Verbenaceae	Beccaloni *et al.* 2008, Janzen & Hallwachs 2010
Strymon bubastus (Stoll, 1780)	1	Inflorescence	**Fabaceae** (*Galactia* sp.)	Boraginaceae, Convolvulaceae, Fabaceae, Malvaceae, Portulacaceae	Beccaloni *et al.* 2008
Strymon crambusa (Hewitson, 1874)	1	Inflorescence	**Oxalidaceae** (*Oxalis* sp.)	Not found in the literature	
Strymon cyanofusca K. Johnson, Eisele & MacPherson, 1990	5	Inflorescence	**Gentianaceae** (*Calolisianthus speciosus*)	Not found in the literature	
Strymon mulucha (Hewitson, 1867)	43	Inflorescence	**Connaraceae** (*Rourea induta*), **Fabaceae** (*Bauhinia* sp., *Calliandra dysantha, Galactia* sp., *Periandra* sp.), **Malpighiaceae** (*Heteropterys procoriacea, Peixotoa goiana,* species not identified), **Malvaceae** (*Pavonia rosa-campestris*), **Ochnaceae** (*Ouratea hexasperma*), **Salicaceae** (*Casearia sylvestris*), **Sapindaceae** (*Serjania* sp.)	Alstroemeriaceae, Bignoniaceae, Malvaceae, Melastomataceae, Orchidaceae	Beccaloni *et al.* 2008, Canals 2003, Monteiro 1990
Thepytus thyrea (Hewitson, 1867)	1	Inflorescence	**Vochysiaceae** (*Qualea grandiflora*)	No previus record of hostplant	Robbins *et al.* 2010
Tmolus cydrara (Hewitson, 1868)	1	Inflorescence	**Vochysiaceae** (*Qualea grandiflora*)	Not found in the literature	
Tmolus echion (Linnaeus, 1767)	11	Inflorescence	**Campanulaceae** (*Amazonia hirta*), **Connaraceae** (*Rourea induta*), **Ochnaceae** (*Ouratea hexasperma*), **Solanaceae** (*Solanum lycocarpum*), **Vochysiaceae** (*Qualea grandiflora, Q. multiflora*)	Acanthaceae, Anacardiaceae, Boraginaceae, Fabaceae, Gesneriaceae, Lamiaceae, Malpighiaceae, Malvaceae, Ochnaceae, Sapindaceae, Solanaceae, Verbenaceae	Beccaloni *et al.* 2008, Canals 2003, Monteiro 1990, Robbins & Aiello 1982
Tmolus venustus (H. H. Druce, 1907)	11	Inflorescence	**Fabaceae** (*Galactia* sp.), **Malpighiaceae** (*Peixotoa goiana, Pterandra pyroidea,* species not identified), **Melastomataceae** (*Miconia ferruginata, M. pohliana*), **Ochnaceae** (*Ouratea hexasperma*)	Malpighiaceae	Torezan Silingardi 2007
Polyommatinae					
Hemiargus hanno (Stoll, 1790)	3	Inflorescence	**Fabaceae** (*Galactia* sp.), **Malpighiaceae** (species not identified)	Fabaceae, Oxalidaceae	Beccaloni et al. 2008, Duarte *et al.* 2001

In contrast, *N. socia* is currently restricted to the cerrado vegetation (see also Brown, 1993, where the species is cited as *Thecla socia*).

Some cerrado plant species support a high species richness of lycaenids (Table 2): *Roupala montana* Aubl. (Proteaceae) supports 10 species, *Qualea grandiflora* supports nine species, *Ouratea hexasperma* (St. Hil) Baill. (Ochnaceae) supports seven species, *Peixotoa goiana* C.E. Anderson (Malpighiaceae) supports five species, and *Caryocar brasiliense* Camb. (Caryocaraceae), *Rourea induta* Planch. (Connaraceae) and *Schefflera macrocarpa* (Seem) D. C. Frodin (Araliaceae) each support larvae of four different species. Except for *Q. grandiflora*, all of these plants show some taxonomic isolation, as each family is represented by up to four species in the cerrado of the Distrito Federal (Cavalcanti & Ramos, 2001). Large families of flowering plants, such as Fabaceae, Myrtaceae, and especially Asteraceae, were proportionately less sampled. Genera of large families that were conspicuous in the study area, such as *Byrsonima* Rich. (Malpighiaceae), *Miconia* Ruiz & Pav. (Melastomataceae), *Palicourea* Aubl. (Rubiaceae) and *Qualea* Aubl. (Vochysiaceae), were relatively well sampled (Table 1). Interestingly, the nearly complete absence of larvae feeding on Rubiaceae contrasts with the high number of lycaenid species on Vochysiaceae. The low number of lycaenids associated with Rubiaceae is in accordance with the information presented by Fiedler (1995b); in contrast, our results with Vochysiaceae may be the first in the literature.

Roupala montana, *S. macrocarpa* and *R. induta* do not have extra floral nectaries, but the two first species, as well as *Byrsonima* (revised by Kaminski & Freitas, 2010), often present hemipterans attended by ants on their inflorescences. Other genera, such as *Banisteriopsis* C.B. Rob., Peixotoa A. Juss. (Malpighiaceae), and *Qualea* present foliar extrafloral nectaries (Oliveira & Leitão-Filho, 1987). *Caryocar brasiliense* was the only species with considerable Lycaenidae species richness in our study, bearing extrafloral nectaries on their inflorescences (Oliveira, 1997). The cerrado vegetation is composed of a high proportion of species and individuals with extrafloral nectaries (Oliveira & Leitão-Filho, 1987), but the vast majority of plants have nectaries on their leaves. Thus, the influence of the extrafloral nectaries on plant consumption by florivorous lycaenids must be small. However, characteristics of the inflorescences, such as size and structure, and the presence of ants associated with hemipterans may be important factors for the choice of host plants (Monteiro, 1990; Oliveira & DelClaro, 2005; Rodrigues *et al.*, 2010).

An understanding of the immature stages of Lepidoptera is of major importance to studies of phylogeny and taxonomy (e.g., Lafontaine *et al.*, 1982; Aiello, 1984; Epstein, 1996; DeVries *et al.*, 2004; Hebert *et al.*, 2004; Warren *et al.*, 2009), particularly in taxonomically complex groups such as the tribe Eumaeini (Lycaenidae, Theclinae). As noted by Duarte *et al.* (2005) and in the present study, the immature stages of the eumeines are not readily found in the field. One interesting alternative for the study of all immature stages of some species, especially those that feed on artificial diet as larvae (Duarte *et al.*, 2005; Duarte & Robbins, 2009), is to obtain the eggs and rear them in laboratory. However, this methodology does not allow describing patterns of host plant use by larvae. Therefore, more fieldwork and laboratory rearing are necessary to understand the biology and habitat restrictions of these butterflies and for their conservation in critically threatened biomes such as the Brazilian cerrado. Information gathered from this type of work may contribute to the development of further biological and morphological studies of the immature stages of Lycaenidae and, in some cases, help to resolve a number of taxonomic uncertainties largely relating to incorrect associations between males and females of dimorphic (or polymorphic) species (Robbins *et al.*, 2010).

This work reports 113 records of host plants for 38 species of lycaenids, with host plant records mentioned for the first time for seven of these species. Also, it adds six species of Lycaenidae to the lists of butterflies from Distrito Federal. Although, butterflies are considered a well-known group of insects, it is surprising how little is still known about their host plants (Beccaloni *et al.*, 2008). Thus, collecting juveniles on inflorescences can supplement adult collection for documenting the fauna of a region. Despite the restricted study area, there is much work to be done in view of the high species richness of Lycaenidae and plants.

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Book review

Guia dos Sphingidae da Serra dos Órgãos, sudeste do Brasil. A guide to the hawkmoths of the Serra dos Orgaos, south-eastern Brazil by Alan Martin, Alexandre Soares and Jorge Bizarro, 2011

REGUA Publications, Oxford, 143 pp. Avaliable from NHBS, UK (www.nhbs.com). ISBN: 9780956829108. Price: £ 24.99 (approx. US$ 41 or € 28).

Sphingidae, or hawkmoths, arguably are the globally best known representatives of (mostly) nocturnal moths. They are taxonomically well known, and the wealth of biogeographical as well as ecological information available for them render hawkmoths ideal subjects of evolutionary, macro-ecological and biodiversity studies. Moreover, many hawkmoths play important roles as pollinators of flowering plants and a small number also achieve, at least occasionally, importance as agricultural or silvicultural pests. As with most insect groups, the Sphingidae attain maximum species richness in the tropics, yet species identifications of tropical hawkmoths are still hampered by the lack of affordable regional guides for many areas within South America or tropical Africa.

This new guide covers 110 Sphingidae species recorded thus far from a rather small subarea of the state of Rio de Janeiro in south-eastern Brazil. The study region harbours substantial remnants of the formerly extensive Mata Atlantica forest, a global biodiversity hotspot of high conservation concern. This hotspot score of the study region is also supported by the fact that almost 50 % of all hawkmoths known to occur in Brazil have been recorded from this small area. The book starts with four short introductory chapters (bilingual in Portuguese and English). These are followed by detailed accounts (in English only) of the 110 observed plus four more suspected hawkmoth species of the area. On 37 photographic color plates spread specimens (both sexes of all species) are depicted in dorsal and ventral view. Additional 10 color plates contain photographs of living moths attracted to light sources. While the former are more useful for identification and comparison, they suffer from the fact that quite a number of specimens show faded colors. In contrast, coloration of the living specimens is more intense, and therefore it is really helpful to have them both available in the book. Appendices on the English-born naturalist Henry R. Pearson (who started research on hawkmoths in the region and collected many of the figured specimens), on the reserve REGUA, on locality details of all figured specimens, on larval host-plant affiliations, and species lists broken down to localities and months of the year complement the book.

This is a useful addition to the recent literature on Neotropical moths. A minor draw-back is the lack of scale bars included with the figures – it is thus impossible to get an idea about body sizes directly from the plates (all moths are figured in the same size, but fore wing length data are provided in the species accounts). For the international reader it would have been more rewarding to cover the entire hawkmoth fauna of Brazil, or at least of the whole state of Rio de Janeiro, instead of focusing on such a small arbitrarily limited area. These are, however, minor criticisms. Relative to another recent regional faunal treatment from the Neotropical region (Ecuador, 142 of 172 known species figured in color: Guevara *et al.* 2002) the new guide compares favorably with its more informative text, higher quality of color plates, the inclusion of host-plant data, and the more modest price.

Overall, this book can be recommended to every lepidopterist with an interest in hawkmoths from the southern half of South America. Many widespread Neotropical species are covered, but the narrow regional restriction somewhat reduces the versatility of the book for readers with a broader interest, e.g. extending into Amazonian or Andean ecosystems. Nevertheless, guides like this are most needed to stimulate further research in

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the documentation and understanding of tropical moth biodiversity. It is hoped this volume will play its role in that regard.

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BOOK REVIEW

Distribution atlas of butterflies in Europe by O. Kudrna, A. Harpke, K. Lux, J. Pennerstorfer, O. Schweiger, J. Settele and M. Wiemers, 2011

Gesellschaft für Schmetterlingschutz, Halle, Germany, 576 pp. ISBN: 978-3-938249-70-3. Distributed by Gesellschaft für Schmetterlingsschutz e.V. (contact: meb-gfs@ufz.de) and authorized booksellers. Recommended retail price: € 65.00.

Butterflies are arguably the best known insects in the world with regard to their taxonomy and distribution. If anywhere on Earth, this applies to Europe with over 250 years history of butterfly research since Linnean times. One might therefore ask what niche a novel distribution atlas for European butterflies might fill on the book market. This question seems even more suggestive given that the senior author of this present volume, Otakar Kudrna, published a first such atlas less than 10 years ago (Kudrna, 2002). The clear answer to such skeptical conjecture is: YES, this new atlas IS a valuable addition to the butterfly literature. The book is based on an international mapping campaign spanning almost all European countries. Only Belarus and the European fraction of Russia are not covered. This project was solely coordinated, in an enormous personal effort and essentially without any support from external or institutional funds, by Kudrna over some 25 years. The earlier atlas published in 2002 was the first significant outcome of this enterprise and attracted somewhat controversial commentaries in the lepidopterological community (see C. M. Naumann, 2002, Entomologische Zeitschrift 112: 340; vs. Z. Kolev, 2003, Nota lepidopterologica 25: 280–283). This new version is based on a very much advanced data set and, with the assistance of a number of co-authors most shortcomings of the first atlas have been overcome.

The book starts with a short preface to set the stage of the whole "Mapping European Butterflies" adventure. Then, in a general part Kudrna introduces the sources of data and the data-basing system behind. This system is a slightly critical issue since records were electronically stored with the help of 9145 pre-selected "reference localities" (RL) instead of precise geographic coordinates. Each 'true' locality of a butterfly record was substituted by its nearest RL. This procedure by necessity introduced some fuzziness in the data when later being represented on maps. This was one of the major critical points raised by Kolev (*loc. cit.*), but on a large pan-European scale this slight imprecision appears negligible. For scientists with regional or national interests, however, this procedure decreases the value of the mapping program because on such smaller spatial scales the extent of transmission errors may be unacceptably large. As an example, there are records of various alpine butterflies indicated on the maps to occur in lowland areas of easternmost or northern Austria (*Pyrgus cacaliae*, *Colias phicomone*, *Euphydryas cynthia*, *Boloria pales*, *Plebejus orbitulus*) – which in all likelihood are just distorted representations of data points due to the use of the RL system.

The subsequent chapter outlines the systematic and taxonomic arrangement of butterfly species used in the atlas. Kudrna's version of European butterfly systematics will not go without critiques. For example the decision whether a certain group of species deserves genus rank or not is still a matter of debate (and sometimes taste), even in the era of molecular systematics. The same applies to the recognition of local forms as valid species, or just as genotypes within species boundaries. On the genus level, Kudrna accepts, in a rather coherent manner, an inclusive approach, i.e. he (laudably) disregards many of the atomized 'genera' that have been popular in European butterfly books after about 1950. On the species level, his solution is less coherent: some allopatric island or mountain forms of debatable taxonomic rank are treated as distinct 'good' species (like *Plebejus aquilo*, *pyrenaicus*, *dardanus*, and *zullichi* as species distinct from *P. glandon*), whereas in other cases such forms are lumped into one (e.g. the taxa around *Polyommatus eros* and *P. eroides*). But these are minor issues relative to the major thrust of the atlas, which is the presentation of distribution maps. They form the main part of the book (pp. 45-483), printed

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in color and arranged in alphabetical order. Color codes allow to distinguish records from three temporal horizons (pre-1950; 1950-1980; and post-1980). These maps give an unprecedented and comprehensive overview of the butterflies' European distributions, even though such maps will never be 'complete'. The authors themselves emphasize and honestly admit some sources of incompleteness (e.g. insurmountable problems with data migration between different storage systems, or the validation of literature records). Kudrna and his co-workers also strictly adhered to the concept "if in doubt, leave it out", which resulted in the deliberate omission of records that were not substantiated well enough to be adopted.

By browsing through the maps some few obvious omissions struck me. *Zerynthia polyxena* had historically been recorded in SE Germany (Bavaria, near river Danube), but is missing for the whole country on the map – whereas other nationally extinct species are covered (*Polyommatus semiargus* and *Lycaena dispar* in Great Britain). *Polyommatus amandus* has no records from all over Romania, and *Maculinea* (*Phengaris*) *nausithous* does not appear for Bulgaria, though records do exist in both cases. A comparison with a rather recent and well documented butterfly atlas from the Czech Republic (Benes *et al*,. 2003) revealed that for quite a number of endangered butterfly species (e.g. *Parnassius apollo*, *Neptis sappho*, *Lycaena helle*) critically revised and confirmed historical records cover far larger fractions of that country than indicated on the new maps. Hence, for species of international conservation concern the situation indeed may look duller than one might extract from the new European atlas. Some other errors relate, for example, to *Aricia agestis* (mapped to occur in southern Norway, but the species is not mentioned to be part of the Norwegian fauna: Aarvik *et al.*, 2009) or to *Scolitantides baton* (mapped to occur all over the Iberian peninsula, but it only occurs in the northernmost parts of Spain: García-Barros *et al.*, 2004). Overall, however, such errors are minor relative to the huge amount of information that can be extracted from this new volume, be it for subsequent use in ecology, biogeography, or conservation.

The book concludes with a synthesis chapter that touches upon diverse aspects such as status of recording, biogeographical and macro-ecological patterns, and conservation issues. A references list, a gazetteer of the reference localities used for data storage and management, a glossary of terms and abbreviations, and a taxonomic index are appended.

This new butterfly atlas will be an indispensable resource of distributional information for any researcher with a detailed and deep interest into the European butterfly fauna. It will come as surprise for many readers how many European butterfly species have strikingly narrow distributional ranges. For many more general readers, however, another book from largely the same team of authors (Settele *et al.*, 2008, available as Open Access publication for free download) will possibly remain more interesting, since this latter volume also contains ecological and photographic portraits of all species besides distribution maps (though based on less actual and fewer data) and modeled maps of expected ranges under different climate change scenarios. Yet, in contrast to the new atlas by Kudrna and co-workers this earlier volume gives distribution maps only for the more widely distributed species. Overall, this new atlas will remain as an important reference source for many years to come – a must for university and museum libraries, and a highly recommended work for biogeographers and conservationists alike.

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New and revised descriptions of the immature stages of some butterflies in Sri Lanka and their larval food plants (Lepidoptera: Papilionidae)

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Abstract. The immature stages and larval food plants of 13 of the 15 species of butterflies of the family Papilionidae, subfamily Papilioninae in Sri Lanka are presented. The immature stages and larval food plants of two species remain unknown. The immature stages of one species in Sri Lanka is reported for the first time. The larval food plant of another species in Sri Lanka is documented for the first time. The immature stages of the remaining 12 species that have been previously described from Sri Lankan material are compared to the findings of the current study and additional observations are presented. For these 12 species, new larval food plants are reported for the first time. For 7 of these 12 species, larval food plants previously reported in Sri Lanka are confirmed. This study provides the basic information for further studies on the biology of these species. It also provides information for conservation management programs for butterflies in Sri Lanka.

Keywords: Immature stages, larval food plants, Sri Lanka, Ceylon, Papilionidae, Lepidoptera, butterflies, conservation.

Introduction

In the current study (conducted from 2004 to the present and ongoing), we have documented the immature stages and larval food plants of 162 of the 245 known species of butterflies in Sri Lanka. For more details on the background and approach, see van der Poorten and van der Poorten (2011). In this paper, we present the immature stages and larval food plants of 13 of the 15 species of the family Papilionidae. The immature stages and larval food plants of two species remain unknown. The immature stages of 12 species covered here have been previously described from Sri Lankan material, though most of the descriptions are very brief and are only of the final instar of the larva and the pupa. These older descriptions are compared to the findings of the current study and additional observations are presented. For 12 species, new larval food plants are reported for the first time, while for 7 species larval food plants previously reported in Sri Lanka are confirmed. Where information on the duration of developmental stages is given, these data were obtained in rearings at ambient temperatures (25–31°C) at Bandarakoswatte (07.37.01N, 80.10.57E), 70 m asl, North Western Province, Sri Lanka. Conventions used (applied to both the larva and the pupa): Segments are numbered S1 to S14 (S1—the head; S2 to S4—the 3 segments of the thorax; S5 to S14—the 10 segments of the abdomen).

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Results and discussion

Tribe Leptocircini

Graphium nomius nomius (Esper, 1799). Spot Swordtail.

The immature stages of *G. n. nomius* have not yet been described in Sri Lanka but detailed accounts of the final instar larva and pupa of *G. nomius* based on Indian specimens were given by Davidson and Aitken (1890) and Bell (1912b). Woodhouse (1949) quoted a brief description from Talbot (1939) who quoted from Jordan (1909). In the course of this study, we have not yet found the larva or pupa of this species.

Larval food plants: There are no reports of the larval food plants in Sri Lanka though the report of *Polyalthia longifolia* (Annonaceae) by Jordan (1909)

may have been based on information from Sri Lanka. In India, Bell (1912b) reported *Saccopetalum tomentosum* [now *Miliusa tomentosa*] (Annonaceae) for *G. nomius.*

Miliusa tomentosa is very local in dry forests around Bibile on the eastern side of the island. *Polyalthia longifolia* is also found on the eastern side of the island but is more widespread, especially along rivers, in dry forests. The columnar form of *P. longifolia* is also planted widely around the island, including the wet zone, as an ornamental (Dassanayake, 1985).

G. n. nomius occurs on the eastern side of the island, as far north as Trincomalee and Kantalai, south to Monaragala, Wellawaya, Wasgamuwa, Udawalawe, Kataragama and Yala, and as far west as Ritigala, and Kumbukgolla near Dambulla. It is seasonally common.

It is likely that *M. tomentosa* and/or *P. longifolia* are larval food plants. It is also likely that other species of *Miliusa* and *Polyalthia* are used because the distributions of *M. tomentosa* and *P. longifolia* do not fully cover that of the butterfly.

Graphium antiphates ceylonicus (Eimer, 1889). Fivebar Swordtail. Endemic subspecies.

The immature stages of *G. antiphates ceylonicus* have not yet been described in Sri Lanka but detailed accounts of the final instar larva and pupa of *G. antiphates* based on Indian specimens were given by Davidson *et al.*, (1897, later quoted in Woodhouse 1949) and by Bell (1912b). In the course of this study, we have not yet found the larva or pupa of this species.

Larval food plants: There are no reports of larval food plants in Sri Lanka except those given by Woodhouse (1949). He listed "*Unona lawii* [now *Desmos lawii*], *U. elegans* [now *Desmos elegans*] and *U. zeylanica* [now *Desmos zeylanica*]" (Annonaceae) without references, so it is not clear whether or not these are records from Sri Lanka. While *D. elegans* and *D. zeylanica* do occur in Sri Lanka, *D. lawii* does not, though it was reported as a larval food plant of *G. a. naira* in India (Davidson *et al.*, 1897). There is one report of *G. a. ceylonicus* ovipositing on *Xylopia championii* (Annonaceae) (M. Silva, pers. comm.) but larvae have not been reared or observed on this plant.

D. elegans is locally common at the edges and in clearings in lowland dipterocarp forest to about 300 m asl especially along streams, while *D. zeylanica* is found in dipterocarp forest of the wettest parts of the lower hill country from 200–800 m asl (Dassanayake, 1985).

G. antiphates ceylonicus is rare, but there are two disjunct populations. One is confined to the wet dipterocarp forests of the south-west (Sinharaja, Morapitiya, Kanneliya, Kottawa, and the Peak Wilderness Sanctuary). The other population occurs in the eastern half of the dry zone (Anuradhapura, Sigiriya, Wasgamuwa, and Dambulla).

It is possible that *D. elegans* or *D. zeylanica* are used as larval food plants by the populations in the forests of the south-west. However, the populations in the eastern dry zone probably use a different larval food plant as no species of *Desmos* are found there. There are, however, several other species of Annonaceae that might be used.

Note: Many current publications and websites list "*Annona lawii*" as a larval food plant for *Graphium doson* (e.g. Kunte, 2000), but *Annona lawii* is not listed in the botanical literature. The plant referred to as *Annona lawii* may well be *Unona lawii* (now *Desmos lawii*).

Graphium sarpedon teredon (C. & R. Felder, 1865). Common Bluebottle.

The final instar larva and pupa of *G. sarpedon teredon* were described very briefly by Moore (1880) from Sri Lankan material. The larva and pupa of *G. sarpedon* was described briefly by Davidson and Aitken (1890) and by Bell (1912b) who quotes from Jordan (1909) based on Indian material. *G. teredon* was described in detail by Bell (1912b) from Indian material. Woodhouse (1949) quoted from these sources and briefly from a report by Tunnard in Sri Lanka. These descriptions agree with the findings of the current study except for the following points: in *G. s. teredon*, the larva has a brown form and a green form in the 3rd (Fig. 1a, b), 4th (Fig. 1c, d) and 5th instar (Fig. 1e, g). Both forms are mottled with fine, indistinct, small cream-colored spots. The head of the brown form is a light sandy-brown with an orange patch posteriorly (Fig. 1h). The head of the green form (Fig. 1f) is as described by Bell (1912b) for *G. teredon* in India. We have recorded the green form of the pupa (Fig. 1i) but have not yet encountered the brown form as described by Tunnard (Woodhouse, 1949).

Additional notes on immature stages: Egg: white, spherical (Fig. 1j). 1st instar: newly emerged larva ate eggshell, abdomen dark smoky green, khaki green filaments on S3, S4 and S14 (Fig 1k). Length of mature larva 35 mm. Duration of immature stages (days): Egg (3–4); 1st instar (1–3); 2nd (3); 3rd (4); 4th & 5th (not recorded); pupation (1); pupa (12–15); egg–adult (32–39).

Larval food plants: In Sri Lanka, Moore (1880) reported "*Cinnamomeum* [*sic*]" [*Cinnamomum*], and *Tunnard* (Woodhouse, 1949) reported "several, those bearing aromatic leaves being favored, such as wild cinnamon, etc." Woodhouse (1949) also reported

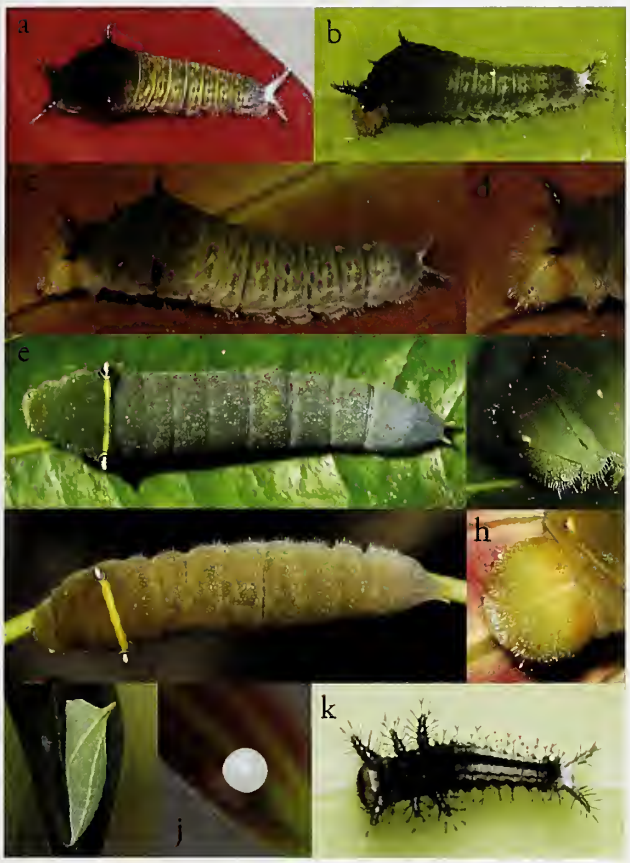

Figure 1. *Graphium sarpedon teredon.* **1a:** Larva, third instar, brown form. **1b:** Larva, third instar, green form. **1c:** Larva, fourth instar, brown form. **1d:** Larva, fourth instar, brown form, close up of head. **1e:** Larva, fifth instar, green form. **1f:** Larva, fifth instar, green form, close up of head. **1g:** Larva, fifth instar, brown form. **1h:** Larva, fifth instar, brown form, close up of head. **1i:** Pupa, green form. **1j:** Egg. **1k:** Larva, first instar.

"*Machilus odoratissima* [now *Persea odoratissima*], *Cinnamomum, Alseodaphne semecarpifolia, Litsea sebifera* [now *Litsea glutinosa*], and especially *Camphora officinalis* [now *Cinnamomum camphora*] where this tree has been imported" from Indian reports in Talbot (1939). The current study showed for the first time that the following are larval food plants in Sri Lanka: *Cinnamomum verum*, *C. capparu-coronde*, *C. dubium*, *Neolitsea cassia* and *N. fuscata* (Lauraceae). We have not been able to confirm whether or not *Litsea glutinosa* is used—if it is, it is likely to have been reported because it is a common plant. We have not been able to confirm whether or not *Cinnamomum camphora* (which is an introduced plant in Sri Lanka as well) or *Alseodaphne semecarpifolia* are used. "Wild cinnamon" may refer to *Neolitsea cassia.*

Cinnamomum species are widely distributed in Sri Lanka especially in the moist lowlands and central hills: *C. verum* is found in the wet low country to 700 m asl; *C. dubium* is found in the wet country to 1800 m asl; *C. capparu-coronde* is common in the wet hills from 400–1400 m asl. There are no *Cinnamomum* species in the dry zone. *Neolitsea cassia* is found in the wet lowlands of the southwest and also in the hills of the intermediate zone (including Ritigala). *Neolitsea fuscata* is very common in the upper montane zone (Nuwara Eliya, Horton Plains). *Persea odoratissima* is not found in Sri Lanka; the only species of *Persea* found in the island is *P. macrantha* which is found in the wet zone from 200–1000 m asl.

G. sarpedon teredon is a common butterfly in the wet zone (the central hills and the south-west) but smaller populations are also found in the mountain ranges of the intermediate and dry zones (e.g. Ritigala).

The distributions of the known larval food plants match that of *G. sarpedon teredon* except for the populations in the mountain ranges of the intermediate and dry zones. In these areas, other species of *Neolitsea* may be used (there are no *Cinnamomum* species in these areas). It is likely that other members of the Lauraceae (including possibly *P. macrantha*) are eaten as well.

Graphium doson doson (C. & R. Felder, 1864). Common Jay. Endemic subspecies.

The immature stages of *G. d. doson* have not been described from Sri Lankan material. However, the final instar larva and pupa of *G. doson* were described briefly by Davidson and Aitken (1890) and by Talbot (1939, after Jordan 1909) and in detail by Bell (1912b) from Indian material. Woodhouse (1949) quoted from these sources. These descriptions of the larva agree with the findings of the current study except for the following points: Davidson and Aitken (1890) described the larva as black or smoky in the first four instars. In the current study, *G. d. doson* is a dull chocolate brown in the 2nd instar (Fig. 2a); a darker chocolate brown in the 3rd instar (Fig. 2b); light cinnamon brown (Fig. 2c) or dark chocolate brown in the 4th instar; and green (Fig. 2d) or smoky purplish-brown (Fig. 2e) in the 5th instar. Bell (1912b) described the larva as "black in the early stages with tail points of pure white." In the current study, the 2nd instar of *G. d. doson* has S14 white and the tail points brown; the amount of white on S14 decreases with each subsequent instar until the 5th when S14 is mostly green or smoky purplish-brown. The historical descriptions of the pupa agree with the findings of the current study (Fig. 2f).

Additional notes on immature stages: Egg: globular, smooth, pale bluish-white when laid, soon turning pale yellow (Fig. 2g).

Figure 2. *Graphium doson doson.* **2a**: Larva, second instar. **2b**: Larva, third instar. **2c**: Larva, fourth instar. **2d**: Larva, fifth instar, green form. **2e**: Larva, fifth instar, smoky purplish-brown form. **2f**: Pupa, lateral view. **2g**: egg.

Duration of immature stages (days): Egg (4–5); 1st instar (1); 2nd (2); 3rd (2); 4th (7); 5th (6); pupa (12).

Larval food plants: In Sri Lanka, Woodhouse (1949) reported "*Cinnamomum*, *Polyalthia* and other Annonaceae" (likely after Talbot 1939). The current study showed for the first time that the following are larval food plants in Sri Lanka: *Polyalthia cerasoides* (H. D. Jayasinghe, pers. comm.), *Polyalthia korinti*; and, in the lab, the larvae ate the tender leaves and flowers of *Miliusa indica* (Annonaceae). We have not observed any species of *Cinnamomum* being used as a larval food plant in Sri Lanka.

Polyalthia cerasoides is locally abundant in dry forests of the east, south-east and south. *Polyalthia korinti* is widespread and common in the dry and wet zones to 300 m asl. *Miliusa indica* is widespread from sea level to 1000 m asl in the dry, intermediate and wet zones (Dassanayake, 1985).

G. d. doson is widely distributed over the whole island, except in north, and is seasonally very common. Though the distribution of the known larval food plants matches the distribution of *G. d. doson*, it is likely that there are other larval food plants as the ones identified so far are not that common as to account for all breeding populations.

Graphium agamemnon menides (Fruhstorfer, 1904). Tailed Jay.

The final instar larva and pupa of *G. agamemnon menides* were described very briefly by Moore (1880) from Sri Lankan material. The larva and pupa of *G. agamemnon* were described briefly by Davidson and Aitken (1890), in detail (all instars) by Bell (1912b) and briefly by Talbot (1939) based on Jordan (1909) from Indian material. Woodhouse (1949) quoted from these sources and also reported details of the egg and all instars from Tunnard using Sri Lankan material. These descriptions agree with the findings of the current study except for the following points: Bell (1912b) reported a white doubled subspiracular line. In the current study, in *G. a. menides*, the subspiracular line is often absent; if present, it is not distinct and consists of two dark-colored bands with a lighter band in-between (bands the same color as the ground color). Two forms are found in the final instar: green (Fig. 3a), and ochre-yellow with a greenish tinge (Fig. 3b) in agreement with Talbot (1939, after Jordan, 1909). The description of the 1st instar agrees with that of Tunnard rather than that of Jordan.

Additional notes on immature stages: Egg: pale yellow when first laid, later turning orangish with blotches (Fig. 3c). 1st instar: dark brown when newly hatched; turns greenish-brown the next day (Fig. 3d). 2nd instar: ground color varies from dark green (Fig. 3e) to almost black (Fig. 3f). 3rd instar: ground color varies from olive green (Fig. 3g) to greenish-brown. 4th instar: ground color varies from grayish-green (Fig. 3h) to brownish-green. Pupa: the green form (Fig. 3i) seems to be the most common as we have not yet observed the brown form reported by Tunnard. Duration of immature stages (days): Hatching to pupation (20–21); pupation (1); pupa (10–12).

Larval food plants: In Sri Lanka, Moore (1880) reported "Magnoliaceae and Anonaceae [*sic*]" and, after Mackwood, "Soursop [*Annona muricata*] and Cinnamon." Woodhouse (1949) reported various Annonaceae as reported from Indian sources as well as *Annona cherimola* reported by Tunnard from Sri Lankan material. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Persea americana* (N. Kamalgoda, pers. comm.), *Polyalthia cerasoides* (H. D. Jayasinghe, pers. comm.), *Annona squamosa*, *A. reticulata*, *A. glabra*, *Polyalthia suberosa*, *Uvaria macropoda*, *U. sphenocarpa*, *Artabotrys hexapetalus*, *Miliusa indica* and *M. tomentosa* (Annonaceae) and *Michelia champaca* (Magnoliaceae). The current study also confirmed that *Annona muricata* is a larval food

Figure 3. *Graphium agamemnon menides*. **3a**: Larva, fifth instar, green form. **3b**: Larva, fifth instar, ochre-yellow with a greenish tinge form. 3c: Ova. 3d: Larva, first instar, newly hatched. 3e: Larva, second instar, dark green form. 3f: Larva, second instar, black form. 3g: Larva, third instar, olive green form. 3h: Larva, fourth instar, grayish-green form. 3i: Pupa, green form.

plant in Sri Lanka. We have not been able to verify the use of *A. cherimola* but Tunnard is undoubtedly correct in his identification. We have not been able to verify that any species of *Cinnamomum* ("Cinnamon", Lauraceae) are used as a larval food plant.

Persea americana, *Annona reticulata*, *A. muricata* and *Michelia champaca* are cultivated plants that are commonly grown in the low and mid-country wet and intermediate zones. *A. glabra* is abundant and naturalized along the south-west coast. *A. squamosa* is naturalized and cultivated in the northern part of the dry zone. *Polyalthia suberosa* is locally common, especially near the coasts, in the dry and wet zones. *P. cerasoides* is locally abundant in dry forests, mostly in the east and southeast. *Uvaria macropoda* is widely distributed in the dry and intermediate zone but is not found in the lowlands of the south-west. *U. sphenocarpa* is an endemic plant found locally in the dry, intermediate and wet zones up to about 700 m asl in disturbed forests. *Artabotrys hexapetalus* is uncommon in the forests of the dry zone. *Miliusa indica* is widespread from sea level to 1000 m asl in the dry, intermediate and wet zones (Dassanayake, 1985, 1987).

G. agamemnon menides is common and widely distributed over the whole island except for the north. Though the distributions of the known larval food plants match that of *G. agamemnon menides*, it is likely that other species of Annonaceae are used as well.

Tribe Troidini

Pachliopta jophon Gray, [1853]. Sri Lankan Rose. Endemic species.

The egg and final instar larva of *P. jophon* were described and illustrated by Green from Sri Lankan material in Moore (1884-1887). Green described the egg as "tawny, globular, ridged." In the current study, the egg is pink and smooth but overlaid with a rough, ridged, discontinuous orange coating (Fig. 4a). Since Green's drawing and description account for only 13 segments in the larva, we redescribe the thorax and abdomen of the larva: the filaments (crimson unless otherwise stated): S3–S14, 1 pair (subdorsal, white on S7); S2–S5, 1 pair (lateral); S3–S12, 1 pair (subspiracular, white on S7); S3–S12, 1 pair (below subspiracular, highly reduced in some individuals). The white band on S7 does not meet on the dorsum as it does in *P. aristolochiae ceylonica* (Figs. 4b, c). Otherwise Green's description of the larva agrees with the findings of the current study except for the following points: in *P. jophon*, a) some larvae have a white subdorsal interrupted band and extensive white markings below the subdorsal spines that run obliquely to the posterior margin of the previous segment (Figs. 4d, e); b) other individuals have white on the anterior edge of the subdorsal spines; and c) S2 has a light-orange anterior transverse band with 1 pair of subdorsal whitish protuberances, a dark purple posterior band and a black, shiny shield between (Fig. 4f). The pupa has not yet been described. In the current study, however, the few field-collected larvae were parasitized and died prior to pupation though the pupa is reported to be very similar to that of *P. hector*.

Additional notes on immature stages: The eggs were laid singly on the branches and twigs of the larval food plant, and occasionally on a leaf. 1st instar: newly emerged larva ate the eggshell. 2nd instar: same as 5th but filaments somewhat shorter (Fig. 4g). 3rd & 4th: not recorded. Duration of immature stages (days): Egg (7).

Larval food plants: In Sri Lanka, a plant belonging "to the Aristolochiaceae family" was reported by Woodhouse (1949). The current study showed for

Figure 4. *Pachliopta jophon.* **4a**: *ova.* **4b**: Larva, fifth instar. **4c**: Larva, fifth instar. **4d**: Larva, fifth instar. **4e**: Larva, fifth instar. **4f**: Larva, fifth instar, close up of head and S2. **4g**: Larva, second instar.

the first time that the following is a larval food plant in Sri Lanka: *Thottea siliquosa* (Aristolochiaceae). *T. siliquosa* is fairly common but found only in the wet zone where it grows under dense shade (Dassanayake, 1999).

P. jophon is a rare forest-dwelling butterfly but may appear in fair numbers during the season (May–July). Its distribution matches that of *T. siliquosa*, which is probably its only larval food plant.

Pachliopta hector Linnaeus, 1758. Crimson Rose.

The final instar larva of *P. hector* was described by Moore (1880) only as being "very similar" to that of *P. aristolochiae ceylonica* based on Sri Lankan material. Based on Indian material, Davidson and Aitken (1890) described the larva briefly while Bell (1911) described the larva and pupa in detail. Talbot (1939) quoted Bell (1911); Woodhouse (1949) quoted Talbot (1939). These descriptions agree with the findings of the current study except for the following points: a) in some individuals, the filaments are dark purplish-brown and reduced in size, and the markings are highly reduced making the larva appear almost black (Fig. 5a); b) subdorsal spots on S7–S11 are variable in size and placement, and are sometimes obsolete; c) lateral spots on S8–S11 are reduced or absent; d) S7 has 1 pair of spots on the anterior margin and one pair of elongated spots on the posterior margin (Fig. 5b, c). In addition, the placement of the filaments is at variance with these descriptions so a complete description of the filaments is given here: S2–S14, 1 pair (subdorsal, S2 & S14 very short); S2–S12, 1 pair (subspiracular); S2–S5, 1 pair (lateral); S3–S12, 1 pair (below subspiracular); the filaments are slightly constricted below the apex which is bulbous.

Additional notes on immature stages: Egg: orange, smooth and globular, transversely ribbed with a rough, orange, discontinuous coating, apex slightly pointed (Fig. 5d). 1st instar: newly emerged larva ate the eggshell, abdomen light purplish-red. Next day—head reddish-brown, abdomen purplish-red, fading to reddish-orange from S11–S14, filaments (same color as body, each with several long, black spines): S2–S12, 2 pairs (subdorsal and subspiracular); S3 & S4, 1 pair (lateral); S2 with anterior and posterior light yellowish-brown transverse bands which meet at the sides, dark brown dorsally between the bands (Fig. 5e). 2nd instar: head black, filaments without spines, uniform purplish-red, S2-S13, 1 pair (subdorsal); S2-S4, 1 pair (lateral); S3-S12, 1 pair (subspiracular); S14, 1 pair (Fig. 5f). 3rd instar: head black, abdomen velvety purplish-black; filaments: S2–S13, 1 pair (subdorsal); S3–S12, 1 pair (subspiracular); S2–S4, 1 pair (lateral); S2–S4, 1 pair (spiracular), filaments same as body color except subdorsal ones on S2, S11, S12, S14 and base of S11 light orange; S2 with anterior and posterior margins elevated enclosing a black space; anterior transverse band with 1 pair of orange transverse streaks, posterior transverse band with 1 pair subdorsal filaments, pinkish-white streak on the base of filaments on S11 and S12 (Figs. 5g, h). 4th instar: similar to 3rd except with an additional spot on S7–S10, anterior to the lateral filaments (Fig. 5i). Pupa: dark purplish-brown right after pupation, later turning light pinkish-brown, broader in the first four segments than that of *P. aristolochiae ceylonica* and the lateral extensions of the arrow-shaped ridge on the dorsal surface of S4 are more pointed (Figs. 5j-l). Length of mature larva 38 mm. Duration of immature stages (days): 1st instar (2); 2nd (4); 3rd (2); 4th (3); 5th (7); pupation (2); pupa (usually 15–17, up to 104).

Larval food plants: In Sri Lanka, Moore (1880) reported "*Aristolochia.*" Woodhouse (1949) reported *Aristolochia indica* based on Talbot (1939), which was based on Bell (1911) reporting from India. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Aristolochia indica* and *A. bracteolata* (Aristolochiaceae). *A. indica* is widespread over most of the island up to 1000 m asl (Dassanayake, 1999). *A. bracteolata* is restricted to dry sandy regions (Jaffna, Mannar, Trincomalee and Batticaloa). Larvae were found feeding on *A. bracteolata* on the bund of Giant's Tank at Mannar. *A. bracteolata* grows in the open, scrambling along the ground; the larvae feeding on the plant were quite exposed.

Figure 5. *Pachliopta hector.* **5a**: Fifth instar, dark individual with reduced markings. **5b**: Fifth instar, dorso-lateral view. **5c**: Fifth instar, dorsal view. **5d**: Egg. **5e**: First instar, newly emerged. **5f**: Second instar. **5g**: Third instar, dorsal view. **5h**: Third instar, lateral view. **5i**: Fourth instar, lateral view. **5j**: Pupa, lateral view. **5k**: Pupa, dorsal view. **5l**: Pupa, ventral view, close up of head region.

P. hector is common over most of the island. Its distribution matches that of *A. indica* and *A. bracteolata* well. These are probably the only two larval food plants in Sri Lanka. However, it is possible that the larvae also feed on *A. ringens*, a naturalized introduction that is found in the central hills though there are reports that this plant is poisonous to the larva (H. D. Jayasinghe, pers. comm.). It may also feed on *Thottea siliquosa* (Aristolochiaceae), which is found in the wet zone, and which is used by *P. aristolochiae ceylonica.*

Pachliopta aristolochiae ceylonica (Moore, 1881). Common Rose. Endemic subspecies.

The final instar larva and pupa of *P. aristolochiae ceylonica* were described very briefly by Moore (1880) from Sri Lankan material. The larva and pupa of *P. aristolochiae* were described by Davidson and Aitken (1890), Moore (1901-1903), Bell (1911) and Talbot (1939) from Indian material. Woodhouse (1949) quoted these sources and also included a brief description of the Ceylon subspecies. These descriptions agree with the findings of the current study except for the following points: in *P. a. ceylonica*, a) the band on S7 is not pale flesh-colored (as per Moore, 1880) or pinkish (as per Davidson & Aitken, 1890) but white to cream-colored, and sometimes with a sand-colored or pinkish tinge especially on the filaments; b) some individuals do not have a spot on S8 or on S11 (as per Davidson & Aitken, 1890); c) although Woodhouse (1949) used the same system of numbering as the current study, he reported that the white band was on S6 but it is on S7; and d) some individuals have 2 crimson streaks on the adfrontal area of the head. The descriptions of the filaments given by Moore are at variance with the current study and are also somewhat different from those reported by Bell; therefore we redescribe them here: S3–S14, 1 pair (subdorsal); S2–S12, 1 pair (subspiracular); S2–S4, 1 pair (lateral); S2, 1 pair (spiracular); all filaments evenly tapered to the apex (Figs. 6a, b).

Additional notes on immature stages: Egg: light pink, smooth and globular, transversely ribbed with a rough, orange, discontinuous coating, apex slightly pointed (Fig. 6c). 1st instar: newly emerged larva (Fig. 6d) ate the eggshell, head black with black spines, abdomen reddish-brown, filaments (each with numerous black spines)— S3–S13, 1 pair (subdorsal, those on S3, S4, S7, S8, S11–S13 orangish, those on S5, S6, S9, S10 dark purplish-black); S2–S12, 1 pair (subspiracular, those on S2, S3, S11, S12 orangish, those on S4–S10 purplish); S2, 1 pair (lateral, reddish-orange); and a slight white protuberance on S14; S2 with an anterior white transverse dorsal band and posterior dark brown transverse band; next day—head black, abdomen purplish-brown, filaments with numerous black spines, subdorsal filaments on S7 white, on S3 & S4 orangish, on S5 & S6 and S8–S10 purplish brown, on S11–S13 light orange, subspiracular filaments on S7 tipped with white, rest of filaments purplish brown (Fig. 6e). 2nd instar: head black, abdomen velvet purplish-black, all filaments devoid of spines, placement and number of filaments as in the 1st instar but S3 & S4 with an additional lateral pair of filaments; the white on S7 now continues in a transverse band across the dorsum and down the sides almost meeting the subspiracular filament and with a black patch laterally; S2 with an orange anterior transverse band and a purplish posterior transverse band with 2 orange lateral spots, black between the bands which meet at the lower lateral edge (Fig. 6f). 3rd instar: similar to the 2nd but all filaments are longer and of the same color (dark reddish-purple) except for S7 which is white, ground color a darker, uniform purplish-brown (Fig. 6g). 4th instar: ground color purplish-black, filaments longer than in 3rd instar, white filaments on S7 tinged with red, and white transverse band on S7 interrupted on the dorsum (Fig. 6h, i). Pupa: similar to other *Pachliopta*, but the lateral processes of the head are horizontal (Fig. 6j-l). Length of mature larva 35–40 mm. Duration of immature stages (days): Egg (5); 1st instar (2); 2nd (2); 3rd (3–4); 4th (3–4); 5th (not recorded); pupation (2); pupa (13–15).

Larval food plants: In Sri Lanka, "*Aristolochia*" was reported by Moore (1880). Woodhouse (1949) quoted "various species of *Aristolochia*" based on

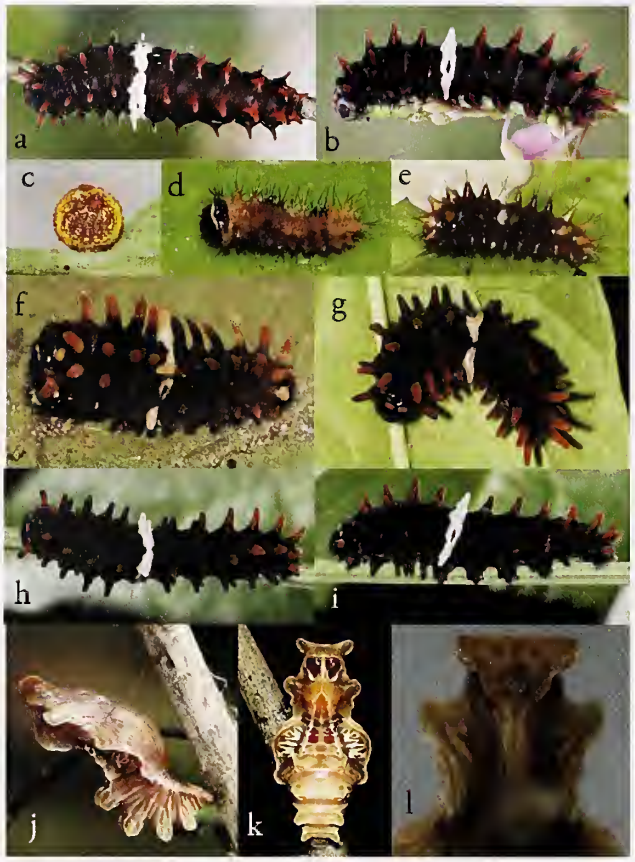

Figure 6. *Pachliopta aristolochiae ceylonica*. **6a**: Larva, fifth instar, dorsal view. **6b**: Larva, fifth instar, lateral view. **6c**: Egg. **6d**: Larva, first instar, newly emerged. **6e**: Larva, first instar, two days old. **6f**: Larva, second instar. **6g**: Larva, third instar. **6h**: Larva, fourth instar, dorsal view. **6i**: Larva, fourth instar, lateral view. **6j**: Pupa, lateral view. **6k**: Pupa dorsal view. **6l**: Pupa, close-up, ventral view.

Talbot (1939) from Indian sources. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Aristolochia indica*, *A. bracteolata* and *Thottea siliquosa* (Aristolochiaceae). The use of *T. siliquosa* was recorded only once in the field and the larva grew slowly and produced a dwarf individual. *A. indica* is widespread over most of the island up to 1000 m asl and is the most extensively used larval food plant. *A. bracteolata* is restricted to dry sandy regions (Jaffna, Mannar, Trincomalee and Batticaloa). *T. siliquosa* is distributed mainly in the wet zone where it grows under dense shade (Dassanayake, 1999).

P. aristolochiae ceylonica is common and distributed over most of the island. The distribution of the three known larval food plants matches the distribution of this species well. It is possible though that *A. ringens*, a naturalized introduction that is found in the central hills, is also used as a larval food plant though this plant is reported to be poisonous to the larva of *P. hector* (H. D. Jayasinghe, pers. comm.).

Troides darsius (Gray, [1853]). Common Birdwing. Endemic species.

The final instar larva and pupa of *T. darsius* were described by Moore (1880) from Sri Lankan material. This description of the larva agrees with the findings of the current study except for the following points: in *T. darsius*, a) the streak on S7 and S8 is pale pink to ivory ("pale pink" in Moore) and b) the ground color in some individuals is light brown (not just dull purple brown as in Moore) (Figs. 7a, b). In addition, the description of the filaments is not clear and they are re-described here: S3–S14. 1 pair (subdorsal); S3–S5, 1 pair (dorso-lateral); S2–S6, 1 pair (lateral, shorter); S2–S13, 1 pair (subspiracular) and a filament on each proleg (S7–S10). Most of the filaments are white-tipped. The description of the pupa agrees with the findings of the current study except for the following: in *T. darsius*, the pupa shows much greater variation in color: in addition to the pale purplish-ochreous color recorded by Moore (that additionally has lateral orange patches) (Figs. 7c,d), the pupa also may be greenish-gray with golden yellow patches on the dorsum, and shadings in between (Figs. 7e, f).

Additional notes on immature stages: Egg: globular, pink with a rough, discontinuous orange covering, a dark-colored micropyle and distinct orange cement (Fig. 7g). 1st instar: newly hatched larva ate the eggshell, head purplish-brown, abdomen purplish-brown except S11–S14 orange, dorso-lateral filaments with fine black spines on each segment from S2–S14, anterior edge of S2 bordered by yellow (Fig. 7h). 2nd instar: dark purplish-brown, filaments S2–S13, 1 pair (subdorsal, same color as ground color except for those on S8 and S11 which are pinkish with a dark tip); S3–S5, 1 pair (dorsolateral); S2–S14, 1 pair (lateral, those on S7 and S11–S14 whitish); head and legs black (Fig. 7i). 3rd instar: not recorded. 4th instar: same as 5th. Length of mature larva 55 mm. Duration of immature stages (days): Egg (7–8); 1st instar (3); 2nd (4); 3rd (8); 4th & 5th (not recorded); pupation (2); pupa (26); egg–adult (56).

Larval food plants: In Sri Lanka, "*Aristolochia*" was reported by Moore (1880) and "*Aristolochia* and the Betel leaf" by Moore (1901-03) after Tennent (1861). Woodhouse (1949) reported "plants of the family Aristolochiaceae and Betel leaf" after Talbot (1939) who quoted from Moore. Igarashi and Fukuda (2000) stated that *Aristolochia indica* was used. Matsuka (2001) reported seeing larvae, eggs and oviposition on *A. indica* and additionally listed *A. tagala* as a larval food plant but without a reference. Igarashi and Fukuda (2000) further reported that "formerly, the larva of this butterfly has been believed to feed on *Aristolochia tagala*" but without a reference. No other authors have reported *A. tagala* as a larval food plant for this species. The current study confirmed that

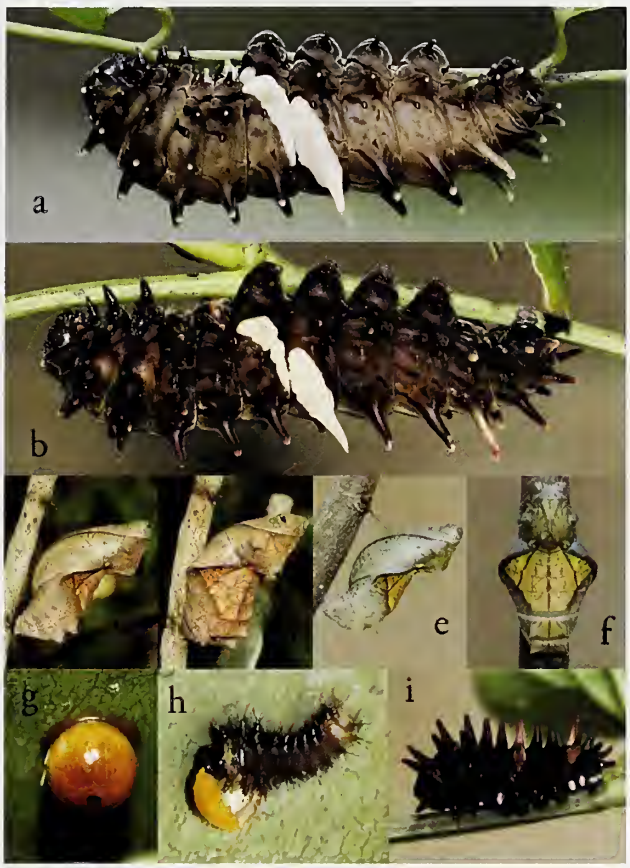

Figure 7. *Troides darsius.* **7a**: Larva, fifth instar, brown form. **7b**: Larva, fifth instar, purplish-brown form. **7c**: Pupa, purplish-ochreous form, lateral view. **7d**: Pupa, purplish-ochreous form, dorso-lateral view. **7e**: Greenish-gray form, lateral view. **7f**: Pupa, greenish-gray form, dorsal view. **7g**: Egg. **7h**: Larva, first instar. **7i**: Larva, second instar.

Aristolochia indica (Aristolochiaceae) is a larval food plant in Sri Lanka. The scientific name of the "betel leaf" plant likely refers to *Piper betle* (Piperaceae). We have not been able to confirm whether or not *Piper betle* is used as a larval food plant. However, it is unlikely because there are no records of any species of the Troidini using any species of Piperaceae. We have not been able to confirm the use of *A. tagala* as a larval food plant. Igarashi and Fukuda (2000) stated that in Moore (1880-81), there is an illustration of *A. tagala* as the food plant. However, the illustration that they refer to is inaccurate—it is little more than a sketch of a branch and what appear to be unopened flower buds. It is unclear on what basis they identified it as *A. tagala.* Further, *A. tagala* does not occur in Sri Lanka (Dassanayake, 1999; Trimen, 1895) though several references (for example, Murugan *et. al.*, 2006) claim erroneously that it does.

T. darsius is fairly common and widespread as is its larval food plant, *A. indica.* It is likely that this is the only larval food plant in Sri Lanka. However, the closely related *T. minos* in India feeds on *Thottea siliquosa* which is also found in Sri Lanka; it is possible that this is used as a food plant in Sri Lanka as well. It is also possible that *T. darsius* might use *A. ringens,* which has been introduced into the central hills where *T. darsius* is also found. The only other native species of *Aristolochia* in Sri Lanka is *A. bracteolata.* It is unlikely that this is used as a larval food plant because it is a low-growing vine found in the hot, dry coastal areas where *T. darsius* is very rarely seen.

Tribe Papilionini

Papilio clytia lankeswara Moore, 1879. Common Mime. Endemic subspecies.

The final instar larva and pupa of *P. clytia lankeswara* were described by Moore (1880) as *Chilasa dissimilis* and *C. lankeswara* from Sri Lankan material. The final instar larva and pupa of *P. clytia* were described by Moore (1903-1905), Davidson and Aitken (1890) and Bell (1912a) from Indian material. Woodhouse (1949) quoted from Talbot (1939) who quoted from Bell (1912a). These descriptions of the larva agree with the findings of the current study except for the following: in *P. clytia lankeswara,* a) the ground color of the abdomen varies from almost black to dark grayish-green to, rarely, light blue, and is studded with black spots; b) the larvae with a blue ground color have pink to white bands while the others have yellow bands as described. Further, the filaments and crimson spots are not well described and are described here: filaments black; S3 & S4, 1 pair (subdorsal, short); S3–S13, 1 pair (just outside this, still subdorsal); S3–S5, 1 pair (lateral); and S5 & S6, 1 pair (subspiracular, crimson). Crimson spots: laterally, single spot on each of S3–S6 and S8–S10; spot (variable in size) at base of each filament on the inner margin on S3–S11; single subspiracular spot on S5–S12. What Moore describes as the "posterior band" is a very wide subdorsal band on S11–S14 (Figs. 8a-c). These descriptions of the pupa agree with the findings of the current study except for the following: in *P. clytia lankeswara,* the pupa varies from light brown to dark grayish-brown (Figs. 8d, e).

Additional notes on immature stages: Egg: smooth, spherical, light green with a discontinuous rough orange coating (Fig. 8f). 1st instar: head black, abdomen more or less square in section, broadest at S2 tapering to S14; ground color black; brown dorsal patch on S2–S4, dorsal white patches on S7, S8, S12 and S13; dorsal row of filaments armed with spines on S2–S13; those on S7, S8, S12 and S13 white; filaments on S2 more prominent than the rest (Fig. 8g). 2nd instar: similar to the 1st, ground color shades of glossy reddish-brown; abdomen broadest at S4; spines on filaments much

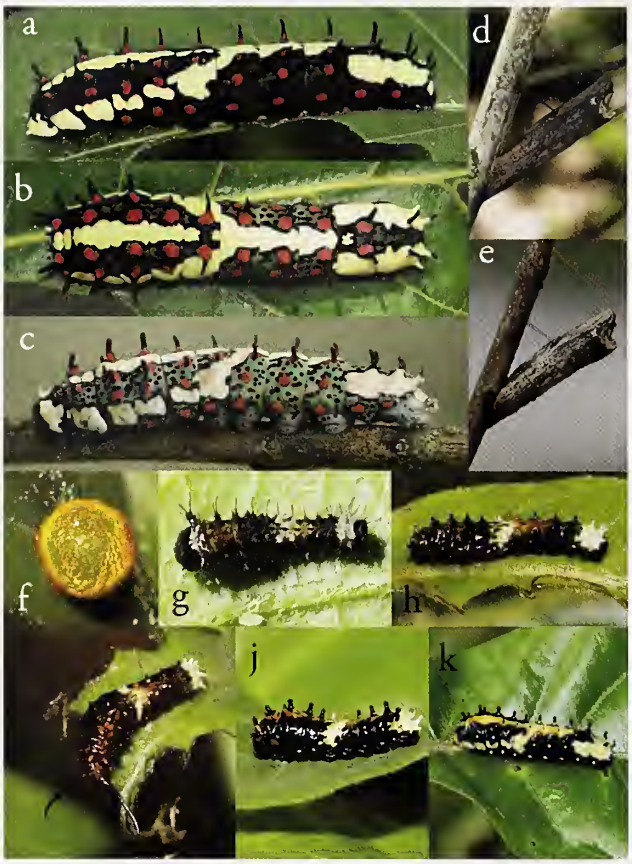

Figure 8. *Papilio clytia lankeswara*. **8a**: Larva, fifth instar, dorso-lateral view. **8b**: Larva, fifth instar, dorsal view. **8c**: Larva fifth instar, blue colored form. **8d**: Pupa, dark brown. **8e**: Pupa, light brown. **8f**: Egg. **8g**: Larva, first instar. **8h**: Larva, second instar. **8i**: Larva, second instar, osmeterium everted. **8j**: Larva, third instar. **8k**: Larva, fourth instar.

reduced; dorsal and dorso-lateral white markings confined to S7/S8 and S12/S13 (Figs. 8h, i). 3rd instar: Ground color black with a bright orange irregular dorsal band; white patches similar to those of 2nd instar. Light-blue subspiracular spots S5–S12 (Fig. 8j). 4th instar: similar to 3rd but dorsal band cream-colored (Fig. 8k). Length of mature larva 38–43 mm. Duration of immature stages (days): Egg (2–3); 1st instar (3–4); 2nd (not recorded); 3rd (2–3); 4th (1–2); 5th (4–5); pupation (2); pupa (11–18 though some individuals remained in the pupal stage for 2 months or more); egg–adult (25–34, up to 80).

Larval food plants: In Sri Lanka, Moore (1880) reported "*Tetranthera*" [now *Litsea*] as the larval food plant and also quoted from Mackwood who said it feeds on "cinnamon." Woodhouse (1949) quoting from Talbot (1939) after Bell (1912a) from Indian sources wrote "various Lauraceae (laurels), and various species of *Cinnamomum*, *Nauclea cadamba* [now *Neolamarckia cadamba*], *Litsea sebifera* [now *Litsea glutinosa*]." d'Abrera (1998) reported that the larvae were "easy to rear on camphor laurel (Sinh[alese]: kapuru)" [possibly referring to *Cinnamomum camphor* or *Cinnamomum capparu-coronde*]. The current study confirmed *Litsea glutinosa* (Lauraceae) as the most widely used larval food plant in Sri Lanka. It also showed for the first time that *Cinnamomum verum* (Lauraceae) is a larval food plant in Sri Lanka, but the only larva on this plant grew slowly. We have not been able to confirm the use of *C. capparu-coronde* which is an endemic species found in the wet zone or *C. camphora* which is an introduced plant (Lauraceae). *N. cadamba* (Rubiaceae) is not likely to be a larval food plant: Moore (1903-05) seems to be the source of this record and none of the usual authors (Davidson & Aitken, 1890; Bell, 1912a) mentioned it. Further this species has not been recorded in Sri Lanka (Dassanayake, 1987).

Litsea glutinosa is very common in the forested and non-forested areas in the wet, dry and intermediate zones to 1000 m asl. In non-forested areas, the plants are frequently cut which causes them to flush a new set of leaves which are ideal egg-laying sites for *P. clytia lankeswara*. *Cinnamomum verum* is found in the wet low country to 700 m asl (Dassanayake, 1995).

P. clytia lankeswara is common all over the island at lower elevations to about 700 m asl. Though the distribution of the known larval food plants matches that of *P. clytia lankeswara*, it is possible that there are other larval food plants since this species is so common and so widely distributed.

Papilio polymnestor parinda (Moore, [1881]). Blue Mormon. Endemic subspecies.

The final instar larva and pupa of *P. polymnestor parinda* were described by Moore (1880) from Sri Lankan material. The larva and pupa of *P. polymnestor* were described very briefly by Davidson and Aitken (1890) and in detail by Bell (1912a) from Indian material. Woodhouse (1949) quoted Talbot (1939) (after Moore (1880) and Bell (1912a)) and from Tunnard and Fryer (1911) both of whose works were based on Sri Lankan material. These descriptions of the larva agree with the findings of the current study but in addition, after the 4th molt, for a day or two, the larva is a light bluish-green with yellow markings laterally (Figs. 9a, b). These descriptions of the pupa agree with the findings of the current study except for the following: in *P. polymnestor parinda*, the color of the pupa varies from green, to brown, to brown mottled with green (Figs. 9c-e).

Additional notes on immature stages: Egg: round and light yellow (as per Tunnard in Woodhouse 1949). 1st instar: head black, dark brown at the margin, covered with short black bristles; abdomen more or less square in section, dark greenish-brown with a diamond-shaped white dorsal patch from S6–S11; S2 with 1 pair of long anterior lateral filaments and a smaller pair posteriorly, a white band between the filaments; S3 and S4

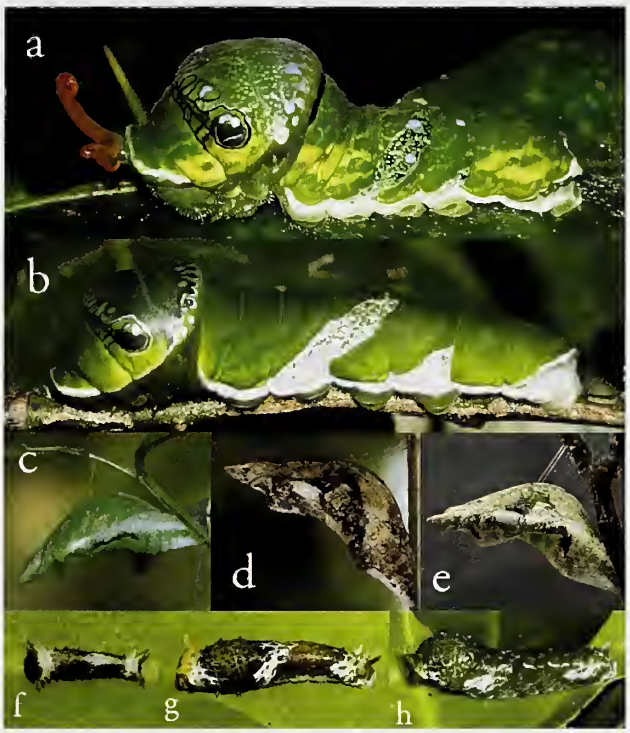

Figure 9. *Papilio polymnestor parinda*. **9a**: Larva, fifth instar, after molt, osmeterium everted. **9b**: Larva, fifth instar, late in instar. **9c**: Pupa, green. **9d**: Pupa, brown. **9e**: Pupa, brown with green. **9f**: Larva, first instar. **9g**: Larva, third instar. **9h**: Larva, fourth instar.

with shorter, black filaments with short hairs, 3 pairs (subdorsal, lateral, subspiracular); S5–S11, filaments black or dark brown, 2 pairs (subdorsal, subspiracular), progressively shorter posteriorly; S12 with a pair of white subdorsal filaments and entire segment with a white transverse band; S13 with 1 pair long, light brown filaments subdorsal (Fig. 9f). 2nd instar: not recorded. 3rd instar: head light greenish-brown, abdomen brownish-green, widest at S4 and circular in transverse section; white irregular patch ascending obliquely to the dorsal line on S4–S6; a similar white irregular patch from S11–S13, white irregular patch on S2 and S3 confined to the lateral margin. Filaments highly reduced except those on S2, S12 and S13; those on S2 are the most prominent and light-orange in color including the area behind them; S3 and S4 with knobby, short filaments, 1 pair subdorsally, 2 pairs laterally; S5 with similar knobby filaments but without the lowest pair of lateral filaments; S12 and S13 filaments white and well-developed but shorter than on S2 (Fig. 9g). 4th instar: head yellowish-green, abdomen brownish-green and minutely speckled with white spots; white patches on abdomen similar to 3rd instar; filaments greatly reduced, S12 carries a very small pair of subdorsal filaments and S13 a larger pair, both sets white; 2 pairs of light blue lateral spots on S4, S5 and S8; usually one pair on S9; S6–S14 with a white band along the margins below the spiracular line (Fig. 9h). Duration of immature stages (days): Egg (4–9); 1st–5th instar (not recorded); pupa (11–15); egg–adult (40–44; except for 1 ♀ – 33). In the higher hills (1100 m asl), where the temperatures are much cooler, Tunnard (Woodhouse 1949) recorded much longer durations for the immature stages.

Larval food plants: In Sri Lanka, Moore (1880) listed "*Citrus decumana* [now *C. grandis*] &c"; Tunnard (Woodhouse, 1949) listed "orange tree" and Fryer (1911) listed "Rutaceae....and *Citrus*." The current study confirmed *Citrus grandis* as a larval food plant in Sri Lanka. It also showed for the first time that the following are larval food plants in Sri Lanka: *Citrus reticulata, C. aurantifolia* and *C. sinensis* in disturbed and cultivated areas, and *Atalantia ceylanica, A. monophylla* and *Paramignya monophylla* in the forests of the dry and intermediate zones (all Rutaceae).

Citrus grandis, C. reticulata, C. aurantifolia and *C. sinensis* are commonly cultivated around the island. *Atalantia ceylanica* is found in forests of the intermediate and dry zones (Rattota, Yala, Knuckles). *A. monophylla* is found on rocky coasts and towards the interior in dry areas (Wilpattu, Uma Oya, Yala). *Paramignya monophylla* is widespread in the drier areas at low and moderate altitudes (Medawachchiya, Yala, Trincomalee) but also in the wetter areas (Rambode, Kandy) (Dassanayake, 1985).

P. polymnestor parinda is found throughout the year, all over the island to about 1000 m asl in all zones. The distributions of the known larval food plants match that of *P. polymnestor parinda*. However, other Rutaceae may be used.

Papilio crino Fabricius, 1793. Common Banded Peacock.

The final instar larva and pupa of *P. crino* were described briefly by Moore (1880) from a pencil-sketch of a specimen found in Sri Lanka. Both Bell (1912b) and Woodhouse (1949) quoted from Moore (1880). These descriptions are so brief that we describe all instars and the pupa in detail.

Additional notes on immature stages: Egg: spherical, smooth, pale greenish-yellow (Fig. 10a). 1st instar: newly emerged larva ate most of the eggshell, head pale brownish-gray with moderately long hairs laterally; abdomen more or less square in section, broadest at S2, ground color grayish-white, gray dorsally; dorsal line grayish-green to brownish; dorso-lateral band black to dark brown; pair of dorso-lateral filaments armed with spines on S2–S13; filaments on S2 and S13 longest, brown; S2 with an additional pair of short white filaments posterior to the brown pair and with a white dorsal patch behind the filaments; filaments on S3–S10 progressively smaller and greenish-brown; filaments on S11 longer and greenish-brown; those on S12 longer and white; filaments with spines from S2–S4 laterally, filaments about as long as those on S12; a black lateral band from S4–S10; dark brown to black below spiracular line (Fig. 10b). 2nd instar: similar to the 1st; lateral filaments on S3 and S4 more prominent, those on the dorso-lateral band reduced in size; S2–S5 more rounded and broadest at S4; S3 and S4 grayish-green dorsally, this color extending faintly along the dorsal line and along the side, enclosing the black bands (Fig. 10c). 3rd instar: similar to the 2nd but much greener overall with dorso-lateral filaments on S3–S12 barely visible; lateral filaments on S3 and S4 small; filaments on S2, S12 and S13 still prominent; larva turns darker green toward the end of the instar and the black lateral line becomes faint (Figs. 10d, e). 4th instar: similar to 3rd, ground color light grayish-green with faint black lateral

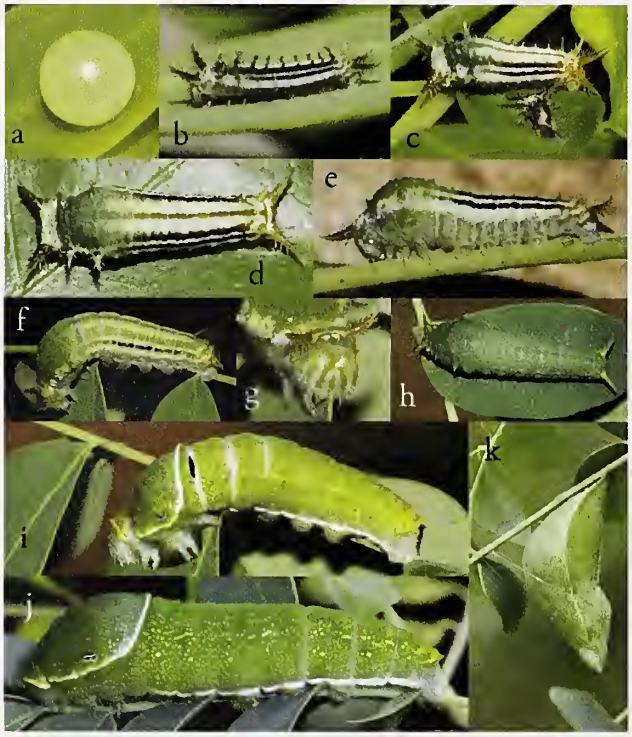

Figure 10. *Papilio crino.* **10a**: Egg. **10b**: Larva, first instar. **10c**: Larva, second instar with molt. **10d**: Larva, third instar, dorsal view. **10e**: Larva, third instar, lateral view. **10f**: Larva fourth instar, lateral view. **10g**: Larva, fourth instar, close up of face. **10h**: Larva, fourth instar, green form. **10i**: Larva, fifth instar, right after molt, black mark on S5 visible. **10j**: Larva, fifth instar. **10k**: Pupa.

line from S7–S12 that is flanked on either side by cream-colored line that extends to S2; rather indistinct cream-colored subdorsal line; head grayish-green with faint white bands on adfrontal area and side of clypeus (Figs. 10f, g); towards the end of this instar, some individuals lose the cream-colored and black bands i.e. they become all green speckled with light cream spots (Fig. 10h). 5th instar: head blue-green; abdomen paler green speckled with minute cream-colored spots; S2–S5 convex and shield-like dorsally with a white border; S4 with a prominent lateral white spot with two black transverse bands; S6–S12 with a prominent white band at the base of each segment above the prolegs; S12 with greatly reduced subdorsal amber-colored filaments; spiracles slit-like, grayish, small; black slit-like mark dorso-laterally at the posterior end of S5, which is evident only when the abdomen is stretched (Figs. 10i, j). Pupa: green, with distinct cream colored lateral and dorsal lines, series of subdorsal and lateral black spots from S5–S12; female pupae distinctly broader and more rounder than those of males; well concealed among the leaves (Fig. 10k). Length of 2nd instar (11 mm); length of mature larva 30–40 mm. Duration of immature stages (days): Egg (3–5); 1st instar (3–6); 2nd (2–3); 3rd (3–5); 4th (4–5); 5th (6–9); pupation (1); pupa (11); egg–adult (32–38).

Larval food plants: In Sri Lanka, *Chloroxylon swietenia* was recorded by Moore (1880) based on a report by J. Pole. d'Abrera (1998) also reported *C. swietenia* based on a personal communication from P. B. Karunaratne in Sri Lanka. The current study showed for the first time that the following are larval food plants in Sri Lanka: *Toddalia asiatica* and *Clausena indica* (Rutaceae). It also confirmed *Chloroxylon swietenia* (Rutaceae) as a larval food plant in Sri Lanka.

Chloroxylon swietenia is fairly common in the dry deciduous forests of the dry and intermediate zones at lower elevations and very sparse in the wet zone. *Toddalia asiatica* is more widespread: it is rather common in montane forests (Pussellawa, Hakgala, Horton plains) and quite common in the dry and intermediate zones (Dambulla, Wilpattu, Jaffna, and Trincomalee). *Clausena indica* is locally common in the dry and intermediate zones (Kurunegala, Hunnasgiriya, Dambulla, Mannar, Jaffna, Wellawaya) (Dassanayake, 1985).

P. crino is a common species, found all over the island up to about 1000 m asl. The distributions of the known larval food plants match that of *P. crino* well. *C. swietenia* is the preferred larval food plant in the dry and intermediate zones, despite the availability of *Toddalia asiatica* and *Clausena indica.* In the wet zone, where *C. swietenia* is very rare, *Toddalia asiatica* is used.

Papilio helenus mooreanus Rothschild, 1895. Red Helen. Endemic subspecies.

The final instar larva and pupa of *P. helenus mooreanus* (as *Charus helenus*) were described briefly by Moore (1880) from Sri Lankan material. The larva and pupa of *P. helenus daksha* were described briefly by Davidson and Aitken (1890), and in detail by Bell (1912a) from Indian material. Woodhouse (1949) quoted from Moore (1880) and from Tunnard in Sri Lanka. The descriptions of the larva (Figs. 11a-d) and pupa (Figs. 11e, f) in Moore and by Tunnard agree with the findings of the current study.

Additional notes on immature stages: Egg: spherical, pale yellow (Fig. 11g). 1st instar: newly hatched larva ate eggshell, description not recorded. 2nd instar: not recorded. 3rd instar: bird-dropping type, head reddish-brown; abdomen dark orange-brown with white transverse band mottled with brown on apical one-third of S6, all of S7 and basal one-third of S8; S11–S13 white; S2 dorsally light brown. Filaments (very small except those on S2, color same as ground color except where noted): S2, 1 pair (subdorsal); S3, 2 pairs (subdorsal and lateral); S4, 3 pairs (dorsal, subdorsal and lateral); S5, 2 pairs (subdorsal and lateral, lateral filaments posterior to subdorsal ones); S6–S11, 1 pair each (subdorsal, brown); S12 & S13, 1 pair each (subdorsal, white) (Figs. 11h, i). 4th instar: bird-dropping type; two color forms: form 1—green & white; form 2— amber & white. Form 1—head green, ground color white, S2 yellow anteriorly with 2 small filaments of similar color, S3 with 2 pairs of dorsal and dorso-lateral raised yellowish spots; S4 with 6 spots (the 4 outer ones with a pale blue spot inwardly); S5 with 6 spots but the two center ones are displaced anteriorly and outer 4 spots with pale blue inwardly; S3–S5 convex and shield-like dorsally; S7–S9 with one oblique

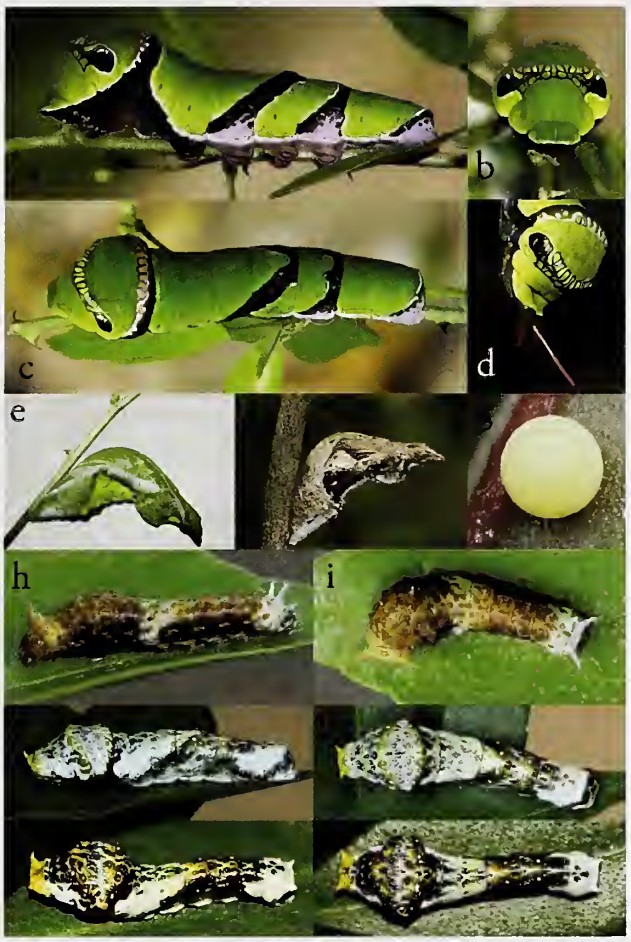

Figure 11. *Papilio helenus mooreanus.* **11a**: Larva, fifth instar, lateral view. **11b**: Larva, fifth instar, close up of face. **11c**: Larva, fifth instar, dorsal view. **11d**: Larva, fifth instar, osmeterium everted. **11e**: Pupa, green form. **11f**: Pupa, brown form. **11g**: Egg. **11h**: Larva, third instar, dorso-lateral view. **11i**: Larva, third instar, dorsal view. **11j**: Larva, fourth instar, green and white form, lateral. **11k**: Larva, fourth instar, green and white form, dorsal. **11l**: Larva, fourth instar, green, white and amber form, lateral. **11m**: Larva, fourth instar, green, white and amber form, dorsal.

broad irregular greenish-brown band, S10 with shorter oblique broad irregular greenish-brown band; S9 with 4 slightly raised, greenish-yellow, spots (2 subdorsal and 2 lateral), each spot with a pale blue spot inwardly; S10 with 2 subdorsal raised yellowish spots, each with a pale blue spot inwardly; S13 with small white dorsal filaments; abdomen narrowest at S11, broadest at S5, widens from S1–S5, narrows from S5–S11 and then broadens again (Figs. 11j, k). Form 2—ground color white, markings similar but pale yellow spots on S3–S5 amber-colored (still with pale blue spots); bands on S7–S10 amber-colored; S2 bright yellow (Figs. 11l, m). Length of mature larva 54 mm. Duration of immature stages (days): Egg (4); 1st instar (3); 2nd (6); 3rd (3); 4th & 5th (not recorded); pupation (1); pupa (16–21); egg–adult (45–50). In the higher hills (1100 m asl), Tunnard (Woodhouse, 1949) reported longer durations for all stages.

Larval food plants: In Sri Lanka, "Rutaceae...and *Citrus*" were reported by Fryer (1911). The current study showed for the first time that *Toddalia asiatica* (Rutaceae) is a larval food plant in Sri Lanka. There are reports of it feeding on *Citrus sinensis* (Rutaceae) in captivity but no records of it ovipositing on this plant in the field.

Toddalia asiatica is quite widespread: it is rather common in montane forests (Pussellawa, Hakgala, Horton Plains) and quite common in the dry and intermediate zones (Dambulla, Wilpattu, Jaffna, and Trincomalee) (Dassanayake, 1985). *P. helenus mooreanus* is not uncommon in submontane and montane regions of the wet and intermediate zones and on the southern slopes to 500 m asl. The distribution of *Toddalia asiatica* matches that of *P. helenus mooreanus* well but there may be other plants used.

Papilio polytes romulus Cramer, [1775]. Common Mormon.

The final instar larva and pupa of *P. polytes romulus* were described by Moore (1880) and by Tunnard (Woodhouse, 1949) from Sri Lankan material (Fig. 12a-c). The larva and pupa of *P. polytes* were described briefly by Davidson and Aitken (1890) and Davidson *et al.* (1897), and in detail by Moore (1901-1903) and Bell (1912a) from Indian material. Woodhouse (1949) quoted from Talbot (1939) (who quoted from Bell (1912a) and Jordan (1909)) from Indian material and from Tunnard from Sri Lankan material. The 4th instar of *P. polytes* was described by Moore (1901-1903). These descriptions of the larva agree with the results of the current study except for the following point: in *P. polytes romulus*, some individuals in the 4th instar have a brown head (Fig. 12d). These descriptions of the pupa agree with the results of the current study except that the pupa can be green, or brown mottled with gray (Figs. 12e, f).

Additional notes on immature stages: Egg: spherical, pale yellow. 1st instar: head light brown; abdomen greenish-brown; diffuse light-yellow broad dorsal stripe S3–S11; S2 pale-yellow; filaments: S2, 2 pairs (anterior pair, lateral, long, brown, posterior pair subdorsal, small, white); S3 and S4, 3 pairs (subdorsal, lateral, subspiracular, shorter, light brown, with fine hairs); S5–S11, 2 pairs (subdorsal, lateral (light brown)); S12, 1 pair (subdorsal, white); S13, 1 pair (subdorsal, light brown and white) (Fig. 12g). 2nd instar: almost identical to 4th (Fig. 12h). 3rd instar: almost identical to 4th (Fig. 12i). Duration of immature stages (days): Egg (1–4); 1st–4th instar (not recorded); 5th (5); pupation (1); pupa (10–12); egg–adult (34).

Larval food plants: In Sri Lanka, Woodhouse (1949) reported *Toddalia asiatica* and "all types of *Citrus* trees" after Tunnard, and *Murraya koenigii*. The current study confirmed the following as larval food plants in Sri Lanka: *Toddalia asiatica, Murraya*

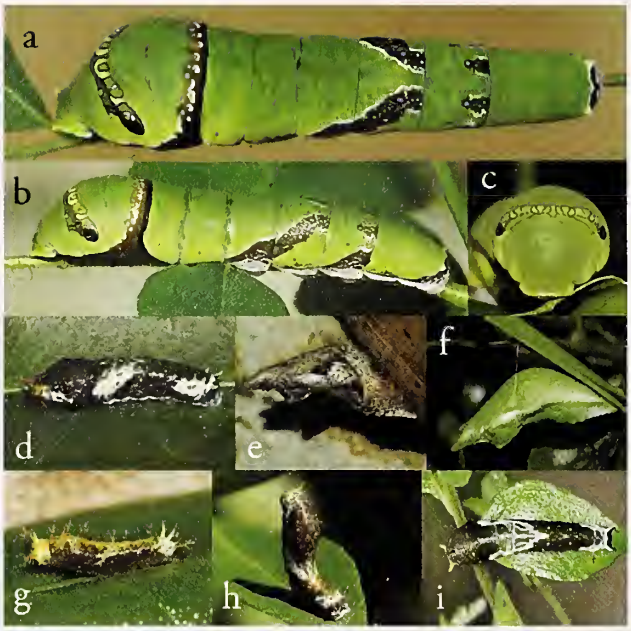

Figure 12. *Papilio polytes romulus*. **12a**: Larva, fifth instar, dorsal view. **12b**: Larva, fifth instar, lateral view. **12c**: Larva, fifth instar, close up of face. **12d**: Larva, fourth instar. **12e**: Larva, pupa, brown form. **12f**: Larva, pupa, green form. **12g**: Larva, first instar. **12h**: Larva, second instar. **12i**: Larva, third instar.

koenigii, Citrus sinensis, Citrus aurantifolia and *Citrus limon* (Rutaceae). It also showed for the first time that the following are larval food plants in Sri Lanka: *Micromelum minutum* (H. D. Jayasinghe, pers. comm.), *Atalantia ceylanica, Pleiospermium alatum*, and *Glycosmis pentaphylla* (Rutaceae).

Toddalia asiatica is quite widespread: it is rather common in montane forests (Pussellawa, Hakgala, Horton plains) and in the dry and intermediate zones (Dambulla, Wilpattu, Jaffna, and Trincomalee) (Dassanayake, 1985). *Atalantia ceylanica* is found in forests of the intermediate and dry zones (Rattota, Yala, Knuckles). *Pleiospermium alatum* is common in the low country dry zone. *Glycosmis pentaphylla* is fairly common in the low country especially in the dry and intermediate zones. *Micromelum minutum* is found in the low country, especially in the dry and intermediate zones. *Murraya koenigii*, although widely cultivated around the island, is restricted to the low country, especially in the dry and intermediate zones. *Citrus sinensis, Citrus aurantifolia* and *Citrus limon* are widely cultivated around the island.

P. polytes romulus is widely distributed over all the island, including up to the highest hills. The distributions of the known larval food plants match the distribution of *P. polytes romulus* well. However, other species of Rutaceae, such as *Glycosmis angustifolia*, may also be larval food plants.

Papilio demoleus demoleus Linnaeus, 1758. Lime Butterfly.

The final instar larva and pupa of *P. demoleus* were described briefly by Moore (1880) and of *P. d. demoleus* by Tunnard (Woodhouse 1949) from Sri Lankan material. The larva and pupa of *P. demoleus* were described in detail by Bell (1911) from Indian material. Woodhouse (1949) also quotes from Talbot (1939) who quoted from Bell (1911) reporting from India. These descriptions of the larva agree with the findings of the current study except for the following points: in *P. d. demoleus*, a) Moore (1880) described "dorsal bands" on S3 and S4 but these are more correctly described as transverse bands and they are on S4 and S5. Further he describes the bands as yellow but in the current study, they were found to be white, brown, black or dark orange or absent or reduced to spots; b) Moore (1880) described a pale lateral streak on S8 and S9 but in the current study, the lateral streak is either entirely absent or reduced in varying degrees and is colored white, or brown or a mottled mix of white and brown; c) Moore (1880) described an upright streak on S10 but in the current study, the streak is either entirely absent or reduced in varying degrees and is colored white, or brown, or a mottled mix of white and brown; d) the filaments on S2 and S13 are brown to reddish-brown and the tips are a lighter shade (this feature distinguishes the larva of *P. d. demoleus* from that of *P. polytes romulus*); e) "the pale yellow lower lateral line" described by Moore (1880) is sometimes white or can be absent, replaced by a series of subdorsal black spots from S9–S12; f). Moore (1880) described the ground color as green but in the current study, the ground color varied from light green to yellow-green and to blue-green. Of all the Papilioinidae in Sri Lanka, the final instar of *P. d. demoleus* is the most variable in color and markings (Figs. 13a-h), a fact that has not been noted by any previous authors. These descriptions of the pupa agree with the findings of the current study (Fig. 13i).

Additional notes on immature stages: Egg: pale yellow and smooth (Fig. 13j). 1st instar larva: newly hatched larva ate all the eggshell, head light brown, ground color dark brown to black, S2 light brown, S7 and S8 with a light yellowish dorsal patch that extends laterally, S12–S14 dark amber-colored, S2–S13 with dark brown filaments (except where noted), 1 pair subdorsal and 1 pair spiracular, each of which has many black spines, S2 and S13 with the longest, subdorsal, brown filaments, S7and S8 with yellowish subdorsal filaments, spiracular filaments almost black and very small (Fig. 13k); next day, abdomen lighter colored and mottled with white especially on S7 and S8. 2nd instar: agrees with the description of Chaumette reporting from Lucknow in

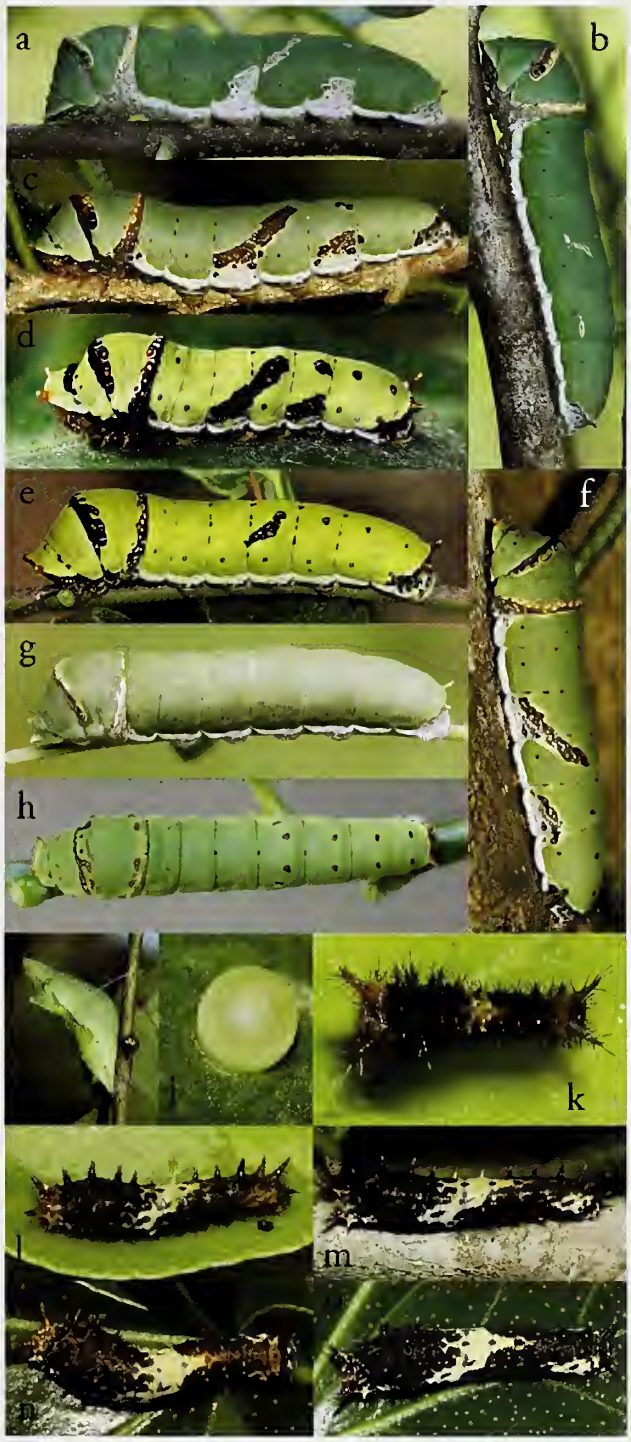

Figure 13. *Papilio demoleus demoleus*. **13a**: Larva, fifth instar. **13b**: Larva, fifth instar. **13c**: Larva, fifth instar. **13d**: Larva, fifth instar. **13e**: Larva, fifth instar. **13f**: Larva, fifth instar. **13g**: Larva, fifth instar. **13h**: Larva, fifth instar. **13i**: Pupa, lateral view. **13j**: Egg. **13k**: Larva, first instar. **13l**: Larva, second instar. **13m**: Larva, third instar. **13n**: Larva third instar. **13o**: Fourth instar, dorsal view.

India (Moore, 1901-1903) except that the ground color is dark brown to black not pale olive-green (Fig. 13l). 3rd instar: same as the 2nd (Figs. 13m, n). 4th instar: agrees with the description of Chaumette except that the ground color is dark brown (not green or bright olive); there is no lateral line over the legs, S3 and S4 have no orange markings, the v-shaped patch on S7 and S8 is whitish and is united on the back, and S9 has only a white mid-dorsal patch (Fig. 13o). Length (mm) of 1st instar (4); 2nd (8); 3rd (15); 4th (22). Duration of immature stages (days): 1st instar (2); 2nd (1); 3rd (2); 4th (2–3); 5th (5); pupation (1); pupa (10).

Larval food plants: In Sri Lanka, Tunnard (Woodhouse, 1949) reported "lemon (*Citrus* [*limon*])". Woodhouse (1949) reported "*Aegle marmelos*, orange [*Citrus sinensis*], pomelo [*Citrus grandis*], lime [*Citrus aurantifolia*], *Zizyphus* [*sic*] *jujuba* [now *Ziziphus mauritiana*], *Glycosmis pentaphylla*" after de Nicéville (no reference) and "also known to be *Feronia elephantum*" [now *Limonia acidissima*]. The current study showed for the first time that *Chloroxylon swietenia* (Rutaceae) and *Cullen corylifolium* (Fabaceae) are larval food plants in Sri Lanka. It also confirmed the following as larval food plants in Sri Lanka: *Citrus aurantifolia*, *Limonia acidissima*, *Citrus limon*, *Citrus sinensis* and *Aegle marmelos*. We have not observed the use of *Glycosmis pentaphylla*, *Ziziphus mauritiana* and *Citrus grandis* as larval food plants. It is unlikely that *Ziziphus mauritiana* (Rhamnaceae) is used: it is a common plant and so likely to have been recorded if used. *Glycosmis pentaphylla* is also a common plant whose use has not been recorded. *Citrus grandis*, which is cultivated, is a possible larval food plant.

Chloroxylon swietenia is fairly common in the dry deciduous forests of the dry and intermediate zones at lower elevations. *Limonia acidissima* is common in the dry zone though lately it has been cultivated in the intermediate and wet zones as well. These two plants are the preferred larval food plants in the dry and intermediate zones. *Cullen corylifolium* is common in the arid zone but found only sparingly in the dry zone. *Citrus limon*, *Citrus sinensis* and *Aegle marmelos* are found only in cultivation, largely in the dry and intermediate zones but also in the wet zone, where the cultivated *Citrus* species are the preferred larval food plants.

P. d. demoleus is widely distributed and common in intermediate, dry and arid zones, but is uncommon in the wet zone. The distributions of the known larval food plants match the distribution of *P. d. demoleus* well but there may be other larval food plants as well.

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NOTE ADDED IN PROOF

Pachliopta jophon. Ceylon Rose.

We were finally able to raise the larva of *P. jophon* to the pupal stage (Fig. 14a–c). It is similar to that of *P. hector* and *P. aristolochiae ceylonica* but can be distinguished by the following: the fronto-clypeus is invaginated dorsally at the centre, the edges are rounded and point downwards; the dorsal ridge on the mesothorax divides to form a bell-shaped ridge; the prothorax has one pair of large rectangular red spots bounded by white; it is a more slender pupa.

Figure 14. *Pachliopta jophon.* **14a.** Pupa, lateral view. **14b.** Pupa, dorsal view. **14c.** Pupa, ventral view, close-up of head area.

Graphium nomius nomius. Spot swordtail.

Eggs and larvae were collected by S. Sanjeeva and raised to the adult stage. The description by Bell (1912) of the first instar agrees with the results of this study. The description of the final instar larva by Davidson and Aitken (1890), by Bell (1912) and by Jordan (1909) as quoted in Talbot (1939) differ somewhat from the findings of this

study. These references describe the larva as black, banded on the sides with narrow white stripes except for the first 3 or 4 segments, which are rusty-red, and sometimes the larva is entirely green. We did not encounter a larva of this description. In the current study, two color forms of the final instar larva were encountered: a green form and a brown form (Figs. 15a–c). The green form has a green ground color, a white supraspiracular line from S2–S14 that has an orange spot at the centre of the line at the centre of each segment, some orange spots have a tinge of red; ventral and lateral margins of S14 are dark reddish-maroon; S4 reddish-brown dorsally above the supraspiracular line; S2–S4, S14 with 1 pair of black spines each, very short and sharp; spiracles pale greenish-yellow bounded by a black ring; S2 dorsally greenish-orange; dorsum with a ferruginous cast on all segments. The brown form has a light brown ground color above the orange supraspiracular line and light green below; S5–S14 with 2 transverse white bands per segment above the supraspiracular line, S4 black dorsally; white subspiracular line and ground color below this is light greenish-yellow. The descriptions of the pupa agree with the results of the current study (Fig. 15d). Though the larva was raised in the lab, it migrated to the base of the container and pupated under a dried leaf so it is likely that in the wild it pupates under stones and in crevices as described by earlier authors. The larval food plant in Sri Lanka is confirmed to be *Miliusa tomentosa* (Annonaceae).

Figure 15. *Graphium nomius nomius*. **15a**. Larva, final instar, green form, lateral view. **15b**. Larva, final instar, green form, dorsal view. **15c**. Larva, final instar, brown form, lateral view. **15d**. Pupa, dorso-lateral view. Photographs 15a-c by S. Sanjeeva.

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Note

Discovery of the previously unknown female of *Salanoemia shigerui* Maruyama (Lepidoptera: Hesperiidae) from Peninsular Malaysia

The genus *Salanoemia* was erected by Eliot (in Corbet & Pendlebury, 1978) for a group of skipper butterflies formerly placed under *Plastingia* Butler, 1870. It is distributed from India to Sundaland (Corbet & Pendlebury, 1992). Two new species have been added to the genus in the last decade (Maruyama, 2000; de Jong, 2006), among them *Salanoemia shigerui*, which was described from a single male from Peninsular Malaysia (Maruyama, 2000) and is also known from a single male from east Sumatra (de Jong, 2006), but for which the female has remained unknown. The male of this species (Figs. 1 A & B) can be readily distinguished from males of other species of *Salanoemia* by the creamy-white colour on the basal two thirds of the hindwing underside, as well as the creamy-white discal patch on the hindwing upperside. On both sides of the forewing, there is also a similarly coloured streak along the basal half of the dorsum, and yellowish scaling along the basal half of the costa.

Females of this species were found during a butterfly survey in Panti Forest Reserve (located near the town of Kota Tinggi in the state of Johore, Malaysia) by two of the authors (C.-K. Phon and L.G. Kirton) in July 2010. Two males and three females were collected together. The males are very similar to the male described by Maruyama (2000) but are slightly smaller in size (forewing length 17.2 mm compared with 19.3 mm). The female (Figs. 1 C & D) differs from the male in a number of respects. The specimens are larger (forewing length 19.4–20.6 mm), and the areas that are creamy-yellow in the male are, in the female, orange-yellow on the upperside and yellow on the underside. On the underside of both wings, the yellow markings are overlaid with orange scaling that is more prominent in spaces 1, 1b and 8 of the hindwing. The veins crossing the discal patch on the hindwing upperside are not dark dusted. The tornal cilia of the hindwing are longer and more orange. The brown band along the margin of the hindwing underside is not as dark as in the male and is more ferruginous in colour. In addition, the female has a more yellowish brown scale and hair colour on the thorax and abdomen; in the male, these hairs are a lighter shade of yellow- or grey-brown.

Although the colour of the markings in the male has been described as creamy-white (Maruyama, 2000), the hindwing upperside discal patch is actually creamy-yellow in space 4 and below vein 2, while the creamy-white area on the hindwing underside is overlaid with yellowish scales, particularly in spaces 1, 1b and 8. Consequently, the colour in the male is somewhat yellowish, as implied in de Jong (2006), which is more obvious in fresh than in worn specimens. However, the yellow to orange colouration is stronger in the female.

A key to the males of the known species of *Salanoemia* is given in de Jong (2006). *Salanoemia shigerui* is also included in an updated key to both sexes of the Malayan species (Eliot, 2006) that is based on the key in Corbet and Pendlebury (1992). However, the key is no longer applicable because the female of *S. shigerui* has yellow markings. The key is, therefore, revised as shown overleaf.

As far as is known, *Salanoemia shigerui* was in the past only known from a specimen from east Sumatra and the holotype collected from Jason Bay, Malaysia (Fig. 2). The specimens collected from Panti Forest Reserve in 2010 are, like the holotype, also from the south eastern extreme of Peninsular Malaysia (south east Johore; Fig. 2), an area that together with east Sumatra and west Borneo belongs to a biogeographical subregion called the Riau pocket (Corner, 1978; Fig. 2). This area is thought to comprise remnants of low-lying forests and swamps that existed during glacial periods when sea levels were lower. However, two years prior to its discovery in Panti Forest Reserve, a female *S. shigerui* was photographed in the wild (Fig. 3) by one of the authors (L.-C. Goh) in Shah Alam, Selangor, which is in the central west of the

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Key for the separation of the Malayan species of *Salanoemia*

1. Upperside hindwing unmarked brown....2
- Upperside hindwing with a yellowish to cream coloured discal area....3
2. Upperside forewing without subapical spots....*S. sala*
- Upperside forewing with one or two subapical spots....*S. fuscicornis*
3. Upperside forewing cell spots subequal....4
- Upperside forewing upper cell spot absent or very small....*S. similis*
4. Underside hindwing without a prominent, brown marginal band; upperside hindwing discal area and underside hindwing ground colour yellow....*S. tavoyana*
- Underside hindwing with a wide, brown marginal band from tornus to termen; hindwing with discal area of upperside and basal two thirds of underside cream coloured in ♂, yellow in ♀....*S. shigerui*

Peninsula (Fig. 2). As this site is an agricultural park, it is uncertain whether the species was resident in the secondary forest of this area or was introduced on rattans or ornamental palms during the development of the park.

In Panti Forest Reserve, *Salanoemia shigerui* was observed to fly faster and in more open vegetation, such as clearings, compared with *S. sala* (Hewitson, [1866]) and *S. fuscicornis* (Elwes & Edwards, 1897), which were both present at the same location, but nearby in more shaded forest. In Selangor, *S. shigerui* was encountered under shade in secondary forest. *Salanoemia shigerui* appeared to be sporadic in occurrence at Panti Forest Reserve, as it was not found on subsequent visits. *Salanoemia sala* was the commonest and most regularly encountered species of the genus.

Acknowledgements

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Figure 1. *Salanoemia shigerui* collected from Panti Forest Reserve, Johore, Malaysia, in the collection of the Forest Research Institute Malaysia. A) Male, upperside. B) Male, underside. C) Female, upperside. D) Female, underside.

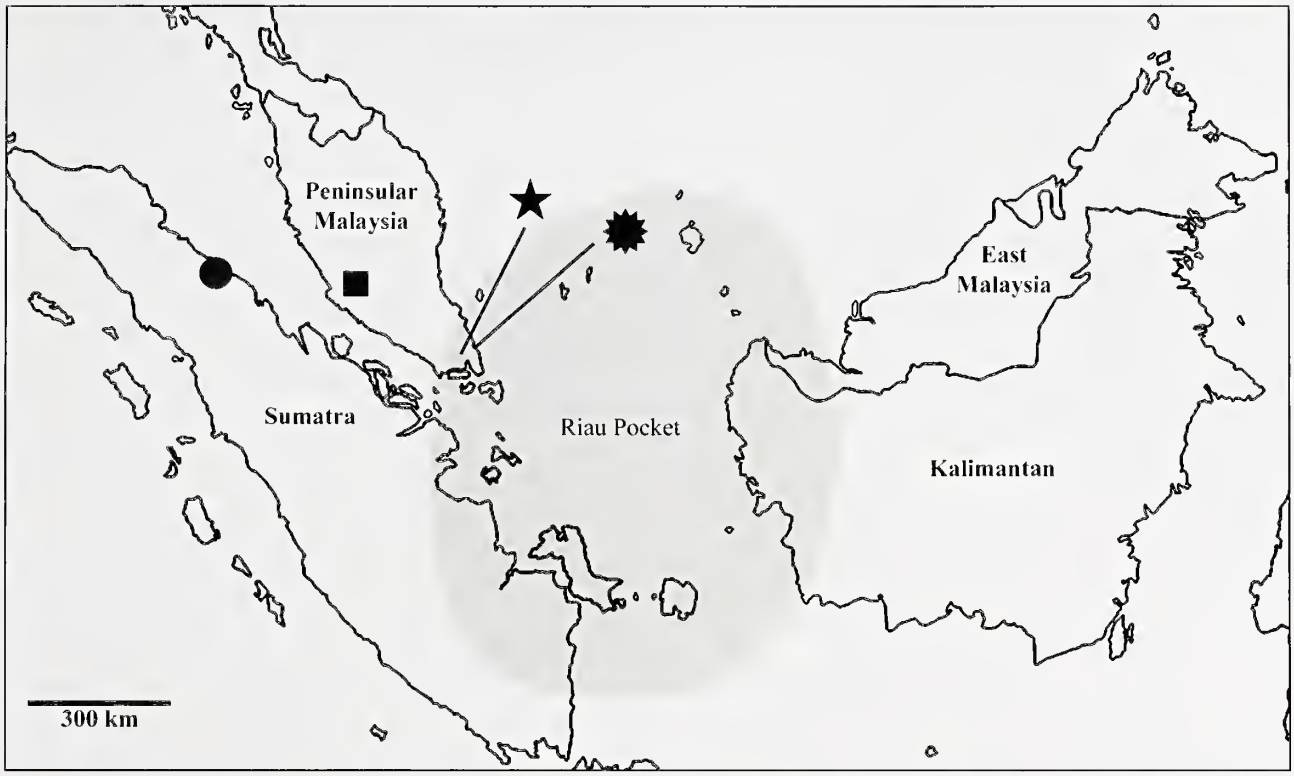

Figure 2. Known occurrences of *Salanoemia shigerui*. Peninsular Malaysia: ✹ Jason Bay, Johore (type locality); ■ Shah Alam, Selangor; ★ Panti Forest Reserve, Johore. Sumatra: ● Laut Tador. The shaded region is the Riau Pocket.

Figure 3. *Salanoemia shigerui* female photographed at Bukit Cahaya Seri Alam Agricultural Park, Shah Alam, Selangor, Malaysia. Photo: L.-C. Goh.

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Editorial

In August 1962, William 'Bill' Hovanitz founded the *Journal of Research on the Lepidoptera* (JRL). Ever since, JRL has served as a prominent venue for scientists from around the globe to publish their research results. JRL has established itself as one of the few scholarly edited, truly international journals devoted entirely to the species-rich order Lepidoptera. Over the past five decades JRL matured in the company of, and usually friendly competition, with a few similar-aimed scientific periodicals as the *Journal of the Lepidopterists' Society* (started in 1947), *Lepidoptera Science* (formerly Transactions of the *Lepidopterological Society of Japan*, or earlier *Tyô to Ga*; issued since 1949), and *Nota lepidopterologica* (from 1977 onwards; published by Societas Europaea Lepidopterologica, SEL).

Hovanitz was editor until his premature death in 1977. Rudi Mattoni then was selected editor of the journal as well as president of *The Lepidoptera Research Foundation*. The *Foundation* owns the JRL and provides the resources for its production. Under the Mattoni's auspices JRL continued for over 30 years, from Volume 16 through to Volume 43. In the 49 years since the establishment of JRL, the approach to scientific publishing has changed so radically that nobody could have even remotely anticipated these developments. In the 1960's manuscripts were in reality still typescripts (often with subsequent amendments in hand-writing) which had to be fully re-typed for printing – a time-consuming and error-prone procedure. In the 1980's personal computers and word processing appeared and changed publishing forever. Authors soon were expected to provide manuscripts in electronic form. But still much of the publication process, especially submission and reviewing, required the physical transfer of paper copies. I well recall my first own submission to JRL that required me to deliver a number of paper copies for reviewing, plus a now extinct diskette, from Germany to California. There was substantial cost for the mailing as well. This happened on 15th January 1990. Almost exactly two months later, after reviewers' comments had been received and incorporated, I was able to send the revised manuscript package a second time to Rudi. Again, months later, after receiving and returning proofs, the paper finally appeared in print (*Journal of Research on the Lepidoptera* 28: 239–257, 1991).

Yet, submitting papers as data files that could be directly used for printing, once revised and finally edited, was the first step towards electronic publishing. With the exponential growth of the worldwide web in the 1990's the next revolution commenced. In 2010, with Volume 43, JRL responded to this new world by becoming a fully open-access online journal, available free to anyone anywhere on Earth with an interest in the Lepidoptera. This critical step was still completely guided by Rudi, but at this juncture he sought a person to take responsibilities for JRL into the future. At the XVIIth *European Congress of Lepidopterology*, held at Luxemburg from May 9 to 14, 2011 under the auspices of SEL, a number of colleagues who already served the new expanded Editorial Board of JRL convened and the role of the Editor was formally handed over to me. I accepted this honor and obligation with respect and pleasure.

Hence, with Volume 44, now finalized, we have published the last group of papers edited and processed by Rudi, and the first collection of papers guided by the new editor and his colleagues from the board. Rudi Mattoni continues as the president of the *Foundation*. I am most thankful to my predecessor and good friend Rudi, as well as my eminent colleagues on the board for their confidence and support – to further develop JRL and to increase its standards of excellence as a scholarly scientific periodical on the international scene. This is the crucial goal for me in the years to come and I solicit cooperation from everyone.

Scientific publishing has turned into 'big business' in recent years, but now is experiencing an increasingly severe crisis. Many 'classical' journals have become so expensive that ever fewer institutional libraries (and indirectly taxpayers) are able and willing to pay these costs. Printing, mailing and processing hardcopies has simultaneously become so costly that more and more scientific information is mainly, if not exclusively, stored or at least transmitted over the internet. At the same time, new journals are sprouting

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like mushrooms everywhere, many of them with poor quality control and many of them exclusively on websites with no guarantee of their content availability over the long run. JRL continues to produce printed hardcopies for subscribers and life members. We also deliver hardcopies of each individual publication with nomenclatorial relevance to 9 internationally prominent institutions, simultaneous with online publication, to meet the criteria of the *International Code of Zoological Nomenclature* with regard to the availability of suggested names or name changes. Otherwise, the publication process of JRL is completely web-based with the final product open accessible and free to all under the premises of Creative Commons license agreements (http://creativecommons.org/).

Manuscripts are submitted through e-mail, are distributed to reviewers via e-mail, with all subsequent steps of editing and finalizing manuscripts handled this way. Once authors have sent the last corrections with their proofs to us, the formatted paper is published online on our website at once, and the paper is sent by e-mail to our life members and subscribers. All this smooth and quick handling can only be achieved through the help of our editorial manager, Nancy Vannucci. She deserves my sincere thanks for her efforts and excellent support!

Even though electronic technologies facilitate and speed up communication, we continue to strive for scholarly quality of the papers to be published in JRL. Therefore, each submitted manuscript is reviewed by at least two independent peers, usually one from the editorial board and one colleague from outside. This is in practice the most time-demanding step since all potential reviewers are burdened with manifold obligations. The editorial team of JRL therefore apologizes for any delay that authors may sometimes be confronted with, but according to our policy scientific quality takes precedence over speed.

In the last decade, another threat to scientific publishing has emerged from the ever increasing tendency of institutions and funding agencies to evaluate scientists on the grounds of so-called 'bibliometric' indicators. Scientists are thereby pushed to publish their findings in as many (and as small) pieces as possible to increase the length and 'impressiveness' of their publication lists. Concomitantly, their papers only 'count' if these are published in periodicals listed by the *ISI Web of Science*®, run by the company Thomson Reuters. Only ISI-listed journals receive a so-called 'impact factor' IF, and only papers with IF are meaningful when it comes to decisions about offering tenure positions to young scientists. Even though this use of impact factors has long been recognized as misuse (e.g. Kokko & Sutherland, 1999; Amin & Mabe, 2000; Leimu & Koricheva, 2005, Falagas *et al.*, 2008; Retzer & Jurasinski, 2009), journals not listed in ISI data bases are increasingly unattractive, at least for young scientists who need to care for a perspective in science, to publish their research results. We are striving for getting JRL listed by ISI and also by Scopus®, an alternative and widely used database run by the publishing company Elsevier.

Even though JRL is not (yet) listed by ISI, many papers published in our journal have been cited widely and can be traced via the 'Cited Reference Search' menu of that data base. The five top-cited articles (as of 12th December 2011) are: O. Shields (Hilltopping: An ecological study of summit congregation behavior of butterflies on a Southern California hill, 6: 69–187, 1967, cited 127 times); J. A. Scott (Mating of butterflies, 11: 99–127, 1973, cited 51 times), P. J. DeVries (Stratification of fruit-feeding butterflies in a Costa Rican rainforest, 26: 98–108, 1988, cited 50 times); R. L. Rutowski (Sexual selection and the evolution of butterfly mating behaviour, 23: 125–142, 1984, cited 37 times); and R. A. Raguso & J. Llorente-Bousquets (The butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, revisited: Species-richness and habitat disturbance, 29: 105–133, 1991, cited 37 times). Using the Google Scholar® routine retrieves an even larger number of scientific papers and books wherein articles published in JRL have been cited. These brief examples substantiate that JRL is recognized as an important source of scientific information by the lepidopterist community around the globe.

What is the way to go from here? It is relevant to recall and emphasize that JRL neither has a regional focus nor any editorial bias with regard to taxa within the order Lepidoptera. We therefore encourage all scientists with an interest in the Lepidoptera (butterflies and moths) to submit their research results for publication in JRL. Papers from all relevant disciplines, be it morphology or ecology, systematics or conservation biology, behavioral biology or applied entomology, are welcome. Besides full research papers we also accept, at our editorial discretion, short notes. There are only two restrictions, viz. scholarly quality and relevance of each contribution beyond a very narrow readership. For example, single distribution or host-plant records of individual species will fall into consideration only if they are of extraordinary significance in a broader conceptual context, such as biogeography or evolution. Likewise, mere species lists are typically not considered, even though they may have their relevance and merits on a regional or national level, for example in nature conservation and management. Beyond that, pending of course the

outcome of mandatory peer review, we offer to our authors quick open access online publication free of cost, including color illustrations. Accordingly, papers published in JRL are visible worldwide from the day they are presented online.

We hope that with this editorial policy, which is in place since Volume 43, JRL will overcome the irregularity of its appearance in print that was at times a problem in past years. JRL offers, since almost 50 years, to the worldwide community of lepidopterists a unique venue to publicize their scholarly research findings in an international framework. It depends on the resonance within the community whether we will be able to continue with that service for the decades to come, despite and in view of all the ongoing revolutions in scientific publishing. In the era of a global biodiversity crisis and given the prominent role charismatic animals like butterflies and moths can play in fostering the scientific understanding of biodiversity at large, the need is out there. Will there be continual demand for our service?

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Editorial footnote

I cannot say enough in praise of Konrad Fiedler as editor of the JRL. Although reluctant to recognize my mortality, the future of the JRL clearly depended on finding a suitable replacement to assure the future of the venture. Although some of my biomedical friends assure me immortality may be achievable in the future because of the large effort is being spent, it is unlikely to be soon enough. A pragmatic approach was necessary. I have known Konrad since his graduate student days and am very gratified with his achievements in our field, not only in research but in education as well. He has a distinguished career as a scholar and certainly is dedicated to bring the highest level of performance with the JRL. Konrad is a true academic. They are becoming harder to find.

Although the primary goal of the *Foundation* is support of the JRL, our overriding concern is with promoting research in addition to disseminating its results. The world now faces an uncertain future with limits of growth of many key materials clearly in sight. Entrained climate change and other macro-trends will provide additional interest. The next 20 years will be completely unlike the past 20 years and likely not pleasant. In the meantime the *Foundation* should persevere and hopefully provide continuing support. We will need help here at some point to maintain direction, operationality and support. We will keep you informed.

In the past there has been some concern that the *Foundation* was competitive with the great societies in our field, especially the *Lepidopterists Society* and the SEL. There was a hint of this in the original organization, but we have long not been a membership society. We in fact sincerely support these societies. Our goal is education and publication. We are formulating an initiative to provide of travel funds for graduates to meetings. We have funded research efforts of several students in the past and a survey project. Not to be outdone, we supported a butterfly and arts exhibition and seminar in Buenos Aires. The projects are all described on our website, which we strive to improve, in addition to developing contacts through the social networking sites as Facebook, and have started a listing of professional Lepidopterists of the world. The latter has accumulated over 400 names, but has been bogged down in defining "professional." The number of colleagues at this level was astonishing, yet still quite incomplete, but happily indicates a large set of like minds out there.

We have also published two notable books in the past: the revision of the giant silkmoth genus *Attacus* by Richard Peigler, and the Butterflies of Baja California by John Brown, Herman Real and David Faulkner. Then there are the small field guide and poster, Butterflies of Greater Los Angeles by your former editor that sold nearly 10,000 copies, the

Garden Butterflies of Buenos Aires by Rudi Mattoni and Nancy Vannucci (in English and Spanish), and the Big Moths of Buenos Aires and Southern Uruguay by Rudi Mattoni and Fernando Penco (at printers), available from the *Foundation*. Last but not least, the Pelham Catalogue of the Butterflies of the United States and Canada, published as Volume 40, is available as a separate. This 600 page tome represented a two year effort with Andy Warren as editor and rewrites Nancy Vannucci thought would never end.

Business has been managed by Leona Mattoni since 1977, and all such inquiries should be addressed to her. However, Leona has been exhausted by the years of dedicated effort and the arrangement must change soon. In the meantime, send checks to her or pay by Paypal. Bioquip products has performed some business and has most inventory of our books and past journals. So little printed material is selling, we are unclear on the future of the arrangement as the costs or storage may not be worth the effort as the Gutenberg mass era is obviously in its twilight as print formats become very specialized.

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Instructions to authors

Submission of Manuscripts. Papers must be written in English. We encourage all non-native English speaking authors to have their manuscripts read by native English speaking colleagues. Your initial manuscript must be submitted as an electronic version by e-mail to the editor in Rich Text Format (rtf), 12 point Times New Roman preferred, double-spaced. **Do not format the text and do not justify the right margin.** Use only the regular and italic fonts, with the italic font only for the scientific names of the genus and species. Do not use boldface or vary type size for any sections or headers. **Put returns only at the end of paragraphs, not at the end of each line.** Use one tab to indent each paragraph. At the time of initial submission, all images (black and white or color) should be sent in digital form, preferably in medium quality JPEG format, for easy upload.
Upon acceptance of a paper, high quality images will be requested. Files will be submitted by e-mail. Digital images must be TIFF or maximum quality JPEG files. Should you have further queries on this subject, please contact the technical editor.

Title material. All papers must include complete title, author's name(s), institution(s), and addresses for correspondence and all e-mail addresses. A family citation must be given in parentheses (Lepidoptera: Hesperiidae) for referencing.

Abstract. Max. 300 words. No citations or figure references.

Key words. Max. 10 words in addition to those in the title.

Text. The text of a regular research paper should be clearly structured: e.g. introduction, materials and methods, results, discussion, etc. with acknowledgements and literature cited at the end. Papers to be considered as Notes, Opinion pieces, or Book Reviews do not follow this structure. A note with four or fewer references should have these cited in the body of the text.

Name citations and systematic works. The first mention of any organism should include the full scientific name with unabbreviated name of author(s) and year of description. Taxonomic descriptions must comply with the rules of the ICZN (4th edition).

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Larsen, T. B. 1990. The butterflies of Egypt, Apollo Books, Svendborg. 112 pp. Figurny-Puchalska E., R. M. E. Gadeberg & J. J. Boomsma. 2000. Comparison of genetic population structure of the large blue butterflies *Maculinea nausithous* and *M. teleius*. Biodiversity Conservation 9: 419-432.
Thomas, J. A., R. T. Clarke, G. W. Elmes & M. E. Hochberg. 1998a. Population dynamics in the genus *Maculinea* (Lepidoptera: Lycaenidae), pp. 262-290. *In*: Dempster, J. P. & I. F. G. McLean (eds.), Insect populations. Kluwer Academic Publishers, Dordrecht.

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