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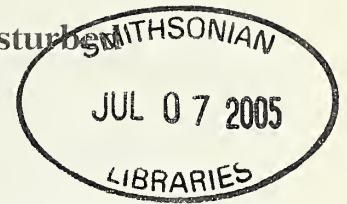
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Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes



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Abstract: The diversity and faunal composition of geometrid moths (Lepidoptera: Geometridae) was investigated at two sites within an anthropogenically disturbed habitat mosaic at 1950 m and 2005 m a.s.l., in the vicinity of intact Andean montane rainforest in southern Ecuador. A total of 629 specimens belonging to 197 species were collected. The results were compared with those from ten sites of undisturbed forest habitats within an elevational range of 1800–2212 m. The local diversity of the moths at disturbed sites was surprisingly high (Fisher's alpha: 86.1 and 86.8; rarefied species number at the level of 250 specimens: 117 and 113; extrapolated species number, estimator Chao 1: 220 and 303). Forest successions and remnants probably serve as habitats for many species, but diversity is possibly overestimated due to the presence of 'tourist species' from adjacent forests. Disturbed habitats were characterized by a low diversity in the genera *Eois*, *Bonatea* and *Herbita*, probably due to the absence of their potential host plants (e.g. *Piper* species). Only three moth species represented by more than three individuals were found exclusively in disturbed habitats (*Eupithecia densicauda*, *Pero obtusaria*, '*Sabulodes muscistrigata*'). Some 25 species profited from disturbance, among these were six species of the genus *Eupithecia*. The proportion of species present with only one specimen was high (56 and 62%), and species dominance was low (Berger-Parker index: 7.9 and 5.8%). In two-dimensional scaling based on the CNESS index of dissimilarity, disturbed sites are separated from the forest sites. The conservation of secondary forest remnants and natural forest appears to be essential for the survival of the very species-rich Andean geometrid moth communities.

Key words: Andes, disturbance, Ecuador, Geometridae, herbivorous insects, moths, Lepidoptera, rainforest

INTRODUCTION

Most tropical rainforests are characterized by their stunning biological diversity. A major proportion of this diversity is formed by insects, the animal group comprising the largest species number on earth. The Andean rainforests are acknowledged to be diversity hotspots on the planet for endemic vascular plants and vertebrate species (Myers et al. 2000). Insect groups such as butterflies are very species rich in the Western Amazon basin and in the Andean foothill region (Robbins & Opler 1997). However, there are surprisingly few studies on insect diversity within the mountain

regions of the Andes (e.g. Janzen et al. 1976, Braun 2002, Brehm 2002, Süßenbach 2003).

Worldwide, pristine habitats are being lost at an alarming rate, and even the remotest areas of the Amazonian rainforest face fragmentation and degradation within the coming decades (Laurance 1998). Most Andean rainforests have already been destroyed and the remnant habitat islands are threatened by fire and logging, and by transformation into pasture or plantations of exotic tree species. The impact of these different land use practices on species-rich insect communities native to the rainforest is largely unknown.

Many studies on the impact of disturbance and management practices have used butterflies as models as these are probably the best known large insect group (e.g. Willott et al. 2000, Hill et al. 2001, Lewis 2001, Stork

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et al. 2003). However, butterflies form only one charismatic fraction of insect diversity, and the responses of this group to habitat alteration might not reflect those of other taxa such as moths (Ricketts et al. 2002). Geometrid moths have been chosen as model group in a number of environmental studies in tropical regions, mainly in South East Asia and Australia (Holloway et al. 1992, Chey et al. 1997, Intachat et al. 1997, 1999, Kitching et al. 2000, Schulze 2000, Beck et al. 2002), but also recently in South America (Brehm 2002), and in Africa (Axmacher et al. 2004). With more than 21,000 described species, Geometridae are one of the three most species-rich moth families. Their taxonomy is relatively advanced (Scoble 1999), and the adults can easily be attracted with blacklight tubes. They have been described as a suitable group in which to study the effects of forestry practices because of their weak flight ability and the high habitat fidelity (Thomas 2002).

Available data suggest that geometrid moths are sensitive to habitat alterations. For example, Kitching et al. (2000) showed that the proportion of geometrid moths among Macrolepidoptera decreased with increasing levels of disturbance in Australia. Holloway et al. (1992) detected a considerable loss of lepidopteran diversity due to logging activities in Borneo, and showed that major groups within the Geometridae belonged to the most vulnerable taxa. A loss of geometrid diversity due to anthropogenic disturbance was also confirmed by Beck et al. (2002) in Borneo. Agricultural areas and young secondary forest had a significantly lower diversity compared with old growth forest.

Few studies have investigated the effects of disturbance on moth communities in the Neotropical region. One of the rare exceptions is that by Ricketts et al. (2001) which found a decreased proportion of geometrid moths in agricultural habitats in Costa Rica. Therefore, we began to investigate the effects of disturbance on geometrid moth diversity in the vicinity of an intact Andean montane rainforest. The aim of this paper is to provide the first quantitative species-level data set from two anthropogenically disturbed sites in this region, and to compare the results with data from ten adjacent forest sites (Brehm 2002, Brehm et al. 2003b). We wanted to test the hypothesis that disturbed habitats have a significantly lower geometrid moth diversity than forest habitats. We expected to find a decline in hostplant specialists

such as members of the genus *Eois* as well as connected shifts in faunal composition. We also assumed that ensembles from the disturbed sites would be separated in ordinations, and that fewer species would reach high relative abundances.

METHODS

Study sites

The study area in southern Ecuador is situated within the Eastern Cordillera of the Andes and belongs to the province of Zamora-Chinchipe. It lies at the northern border of the Podocarpus National Park, which comprises 146,280 ha of mostly undisturbed vegetation at elevations ranging from 1000 to 3600 m above sea level (Madsen & Øllgard 1994). Two sites in disturbed habitats were investigated for this study. The geographical locations of the plots were 3°58.37' S, 79°4.88' W, 1950 m a.s.l. (D1), and 3°58.13' S, 79°4.68' W, 2005 m a.s.l. (D2). Altitude and geographical coordinates were measured using a Garmin GPS III instrument. Both study sites were situated in a landscape mosaic with a variety of land-use types including cattle pastures, bracken fallow, plantations of introduced *Pinus patula*, low-growth secondary forest and large landslide areas induced by road-building. Moth diversity within these disturbed habitats was compared with undisturbed or slightly disturbed forest sites nearby within the same elevational range. An aerial photograph of the study area shows the position of the study sites (Fig. 1).

Results on alpha- and beta diversity as well as on faunal composition of these sites were provided by Brehm (2002), Brehm & Fiedler (2003), and Brehm et al. (2003a, b). From these studies, sites 3a & b, 4a & b, 5a & b, 6a & b and 7a, & b, situated between 1800 and 2212 m a.s.l., were selected for comparison. Geographical information was provided by Brehm (2002) and Brehm & Fiedler (2003). Annual precipitation reached around 2000 mm without a marked dry season, and the average monthly temperature was 15.6°C, as measured at a local climate station at an altitude of 1952 m a.s.l. (P. Emck, personal communication).

Sampling and identification of moths

Moths were sampled manually using portable

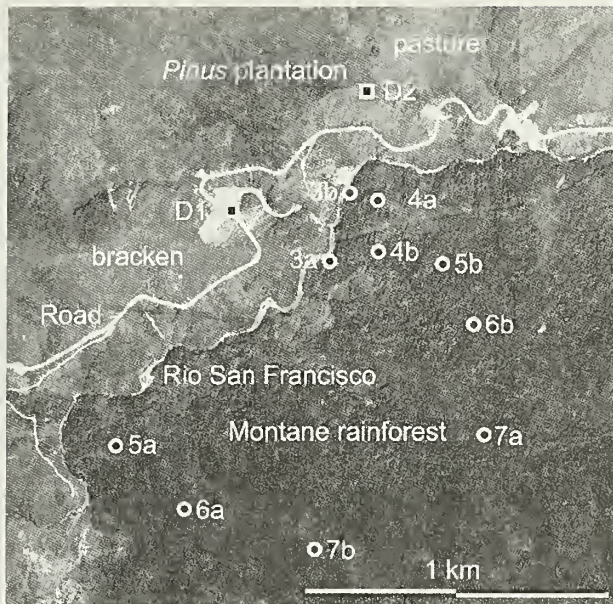


Fig. 1. Aerial photograph of the study area in southern Ecuador, dated from November 2000. Sites 3a (1800 m) to 7b (2212 m) are situated in undisturbed or slightly disturbed montane rainforest at the southern slope of the Rio San Francisco. Sites D1 and D2 are situated in a mosaic of disturbed habitats at the northern slope of the Rio San Francisco. This includes a paved road, large anthropogenically induced landslides, pastures, abandoned farmland with bracken and shrubs, plantations of exotic *Pinus patula*, and secondary forest remnants. Note that the figure is composed of several photographs. Original photographs courtesy of E. Jordan.

light-traps consisting of two 15 W actinic tubes (Sylvania blacklight-blue, F 15 W / BLB-TB and Phillips TLD 15 W 05) and a white gauze cylinder (height 1.60 m, diameter 0.60 m). Sampling methods were described and discussed by Brehm (2002). Light-traps were run during the peak of moth activity at dusk between 18.30 and 21.30 local time. Site D1 was sampled on 17th October and 26th November 2000, and site D2 was sampled on 16th October and 26th November 2000. The number of samples was low, but samples themselves were large, and a meaningful analysis appeared to be appropriate. Forest sites were sampled three to four times in April, May, and December 1999 (Brehm 2002, Brehm & Fiedler 2003). Seasonal effects with regard to changes in moth diversity and species composition in the study area are expected to be of little overall influence (Brehm 2002, Süßenbach 2003).

The moths were identified in the Natural History Museum in London (BMNH), the National Museum of Natural History in Washington D.C. (USNM), the American Museum of Natural History in New York

(AMNH) and the Zoologische Staatssammlung München (ZSM). Of 197 morphospecies collected at the disturbed sites, a noticeably high number of 139 (71%) could be identified provisionally at species level. The remainder were determined to genus. Nomenclature follows Pitkin (2002) for the largest subfamily Ennominae and otherwise follows Scoble (1999). A list of all species sampled at the disturbed sites is provided in Appendix 1.

Statistical analyses of diversity

The choice of appropriate measures of alpha diversity for geometrid moth assemblages from the study area was discussed by Brehm et al. (2003b). In accordance with this study, and in order to ensure the reliability of the results, three different measures were applied here to determine local diversity of the sites: Fisher's alpha of the log-series, rarefied species number, and extrapolated species number (Chao 1 estimator).

Fisher's alpha (Fisher et al. 1943) is mainly influenced by the frequency of species of medium abundance and has been proven to be sample-size independent and a reliable measure of diversity (Kempton & Taylor 1974, Hayek & Buzas 1997). The fit of the log-series distribution was tested using a program by Henderson & Seaby (2001). While the ensemble in site D1 fits the log-series distributions, that of site D2 does not ($p < 0.005$, 'too many' rare species). However, Fisher's alpha was used because of its proven robustness even if the distributions of relative abundance differ from a log-series (Wolda 1983). Diversity differences between disturbed sites and forest sites were tested for significance with the Solow test implemented in Henderson & Seaby's (2001) program. Rarefied species numbers are particularly useful in samples of different size (Hurlbert 1971). Here, rarefied species numbers at the level of 250 specimens were calculated using a program developed by Kenney & Krebs (2000). The abundance-based estimator 'Chao 1' was applied in a number of studies (e.g. Thomas 1996, Beck et al. 2002, Axmacher et al. 2004). Analyses were performed using the program EstimateS 6.0b1 (Colwell 2000) with the bias-corrected formula.

Faunal composition was measured using the proportions of species numbers of taxa within Geometridae and the two largest subfamilies, Ennominae and Larentiinae. Analysis of faunal

composition is a common method used for comparing the proportions of families of Macrolepidoptera (e.g. Holloway et al. 1992, Chey 2000, Kitching et al. 2000, Ricketts et al. 2001), but still rarely used at the family- or subfamily-level (but see Holloway 1987, Brehm & Fiedler 2003). Geometridae were analyzed at the level of the four subfamilies Ennominae, Larentiinae, Geometrinae and Sterrhinae. Within Ennominae, tribal composition was analyzed, including the tribes Azelinini, Boarmiini, Caberini, *Cratoptera* group, Macariini, Nacophorini, Nephodiini, Ourapterygini, Palyadini, and genera not assigned to tribe. Within Larentiinae, the three largest genera *Eois*, *Eupithecia* and *Psaliodes* as well as the remaining genera were analyzed, since a reliable tribal classification of Neotropical Larentiinae is not currently available.

The two samples from disturbed habitats and the ten samples from forest sites were ordinated using non-metric multidimensional scaling (NMDS). This,

in combination with the NESS or CNESS index of (dis-) similarity, was recommended as an analytical tool by Brehm & Fiedler (2004). The CNESS index was calculated (Trueblood et al. 1994) using the computer program COMPAH (Gallagher 1999). We chose an intermediate value of sample size parameter m of CNESS because the stress value of two-dimensional scaling was the lowest (0.05). The CNESS matrix with m set to 36 showed the best correlation with Kendall's tau with CNESS $m=1$ and $m_{\max}=264$. This optimum of m was determined using a Matlab code written by E. Gallagher (personal communication). Ordinations based on other indices of (dis-) similarity such as Sørensen's index, and Grassle and Smith's (1976) NESS index with different m , as well as correspondence analysis yielded very similar results and are therefore not shown. All standard statistical analyses were performed with the program Statistica 5.5 (StatSoft, Tulsa, UK).

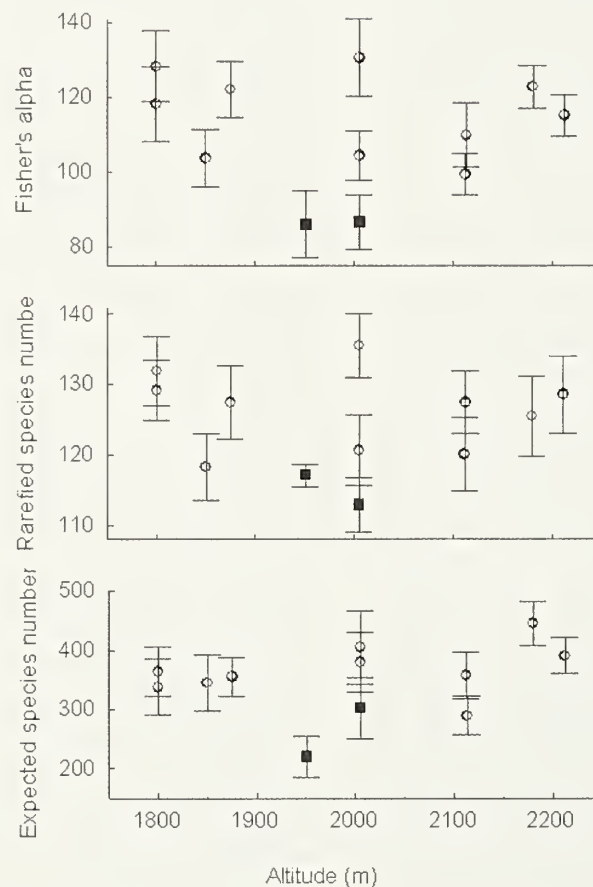


Fig. 2. Alpha diversity of geometrid moths at disturbed sites (two filled squares) compared with undisturbed forest sites (ten open circles) in a montane region in southern Ecuador, using three measures of diversity. Rarefied species number was calculated for a shared number of 250 specimens, and expected species numbers are based on the calculation with the estimator Chao 1. Error bars indicate ± 1 SD.

RESULTS

Alpha diversity

Figure 2 shows geometrid diversity at the two disturbed sites compared with the forest sites. Independent of the measure applied, disturbed sites show a lower diversity than nearly all forest sites. However, the diversity of the disturbed habitats still achieves a very high absolute level, and the difference from many of the forest sites is smaller than it was expected. The results are not fully consistent between the three measures applied.

Fisher's alpha reaches high values of 86.1 and 86.8 for site D1 and D2, respectively, and shows a clear separation between the disturbed sites and the forest sites (Figure 2). However, only eight of the 20 pairwise comparisons are significant according to the Solow test. Forest sites 3a and 5b are significantly more diverse than D1, and forest sites 3a, 3b, 4b, 5b, 7a and 7b are more diverse than D2.

The rarefied species number at the level of 250 specimens is lower at both disturbed sites (117 and 113 respectively) compared with all forest sites. However, these values have a magnitude similar to

those of sites 4a, 5a, and 6a (118, 121, 120 species respectively), and, based on overlapping 95% confidence intervals (which can be estimated as expected species number $\pm 1.96 \times SD$), these differences are not significant.

The extrapolated species number of site D1 is lower (220) than for all forest sites, but the extrapolated species number of site D2 (303) reaches the same magnitude as a number of the forest sites and is even higher than the estimate of site 6b.

Both disturbed sites have a very high proportion of species that were sampled with only one individual (D1: 56%, D2: 62%). Forest sites have a median of 53% singletons with a range between 41% (site 7a) and 63% (site 3a).

Ensemble structure

The faunal composition of geometrid moth ensembles of the disturbed sites shows no fundamental differences from that of the forest sites. Nevertheless, there are some considerable effects with regard to proportional changes and the representation of certain taxa. Table 1 provides

Table 1. Differences in faunal composition (proportions of species and individuals) of disturbed habitats (two sites) compared with undisturbed forest habitats (ten sites). The values of disturbed habitats that do not fall within the range of proportions observed at the forest sites are printed in bold. min – max: minimum and maximum values of forest sites.

	Species		Forest median	min – max	Individuals		Forest median	min – max
	Disturbed D1	D2			Disturbed D1	D2		
Geometridae								
Ennominae	0.40	0.41	0.49	0.42 – 0.57	0.43	0.39	0.54	0.43 – 0.64
Larentiinae	0.41	0.45	0.40	0.31 – 0.45	0.43	0.53	0.33	0.24 – 0.42
Sterrhinae	0.10	0.08	0.06	0.03 – 0.07	0.08	0.06	0.06	0.02 – 0.10
Geometrinae	0.09	0.06	0.06	0.04 – 0.08	0.06	0.03	0.07	0.04 – 0.10
Ennominae								
Azelinini	0.15	0.14	0.04	0.02 – 0.06	0.12	0.09	0.02	0.01 – 0.04
Boarmiini	0.08	0.10	0.14	0.10 – 0.25	0.09	0.18	0.18	0.08 – 0.46
Caberini	0.08	0.07	0.07	0.05 – 0.14	0.04	0.07	0.05	0.04 – 0.18
<i>Cratoptera</i> group	0.02	0.05	0.05	0.01 – 0.07	0.01	0.02	0.02	0.01 – 0.05
Macariini	0.02	0.03	0.01	0.01 – 0.04	0.01	0.01	0.02	0.00 – 0.03
Nacophorini	0.06	0.02	0.05	0.03 – 0.08	0.06	0.04	0.05	0.03 – 0.11
Nephodiini	0.08	0.07	0.11	0.05 – 0.17	0.05	0.03	0.11	0.05 – 0.18
Ourapterygini	0.19	0.24	0.16	0.12 – 0.21	0.12	0.25	0.14	0.08 – 0.19
Palyadini	0.02	0.03	0.05	0.02 – 0.07	0.01	0.01	0.03	0.01 – 0.11
Rest	0.29	0.24	0.31	0.25 – 0.34	0.50	0.29	0.26	0.20 – 0.42
Larentiinae								
<i>Eois</i>	0.16	0.14	0.22	0.15 – 0.41	0.10	0.06	0.28	0.15 – 0.48
<i>Eupithecia</i>	0.44	0.42	0.33	0.20 – 0.48	0.58	0.47	0.30	0.18 – 0.50
<i>Psaliodes</i>	0.10	0.18	0.21	0.14 – 0.27	0.09	0.18	0.18	0.12 – 0.42
Rest	0.30	0.26	0.20	0.12 – 0.22	0.23	0.29	0.15	0.07 – 0.28

information on proportions of different taxa (species, individuals) at the disturbed sites as well as median, minimum and maximum values of the ten forest sites. Specimen proportions do not always perfectly reflect patterns of species proportions, but never show contrasting results.

The species proportion of the large subfamily Ennominae at the disturbed sites is lower than that of all forest sites. This is counterbalanced by higher proportions of Sterrhinae and Geometrinae (D1 only). Specimen proportions of ennomines are also lower at the disturbed sites, whereas more larentiine individuals occur.

Within Ennominae, significantly larger species and specimen proportions of the tribes Azelinini and Ourapterygini (D2 only) are found in disturbed habitats compared with forest sites (Table 1). On the other hand, species of the tribe Boarmiini tend to be underrepresented, with lower values at the disturbed sites compared with the median proportion of the forest sites. Specimens not assigned to genera are overrepresented at site D1. The ennomine genus *Bonatea* (Nephodiini) and the *Herbita* complex (not assigned to tribe) are conspicuously absent at the disturbed sites whereas they occur rather abundantly at the forest plots, with four and six species respectively (Brehm 2002). Other taxa such as two

species of *Pantherodes* (not assigned to tribe) occur in abundance at the disturbed sites and are less common in the forest.

In Larentiinae, species of the very species-rich genus *Eois* are represented by only 14–16% at the two disturbed habitats. Such a low percentage can only be found at one of the highest forest sites (7b: 15%), whereas the median of the proportion of *Eois* species at the forest sites is 22%. The number of *Eois* specimens is also very low compared with forest sites. Higher proportions of other larentiine taxa counterbalance this low proportion of *Eois* species and specimens. The genus *Eupithecia* dominates the larentiine ensembles of the disturbed sites as it does at the uppermost forest plots. However, trends within Larentiinae (*Psaliodes*, remaining genera) are not fully consistent. All four species of the genus *Hagnagora* found in Brehm's (2002) study were also collected at the disturbed sites.

Ensembles from disturbed sites are characterized by a moderate loss of diversity (see above) and by a low number of species exclusive to these habitats. Only a moderate number of species that also occur in forest profits from disturbance, and species dominance was low like at the forest sites.

Among the 197 species found at the disturbed sites, only 20 (10%) were not detected in the forest

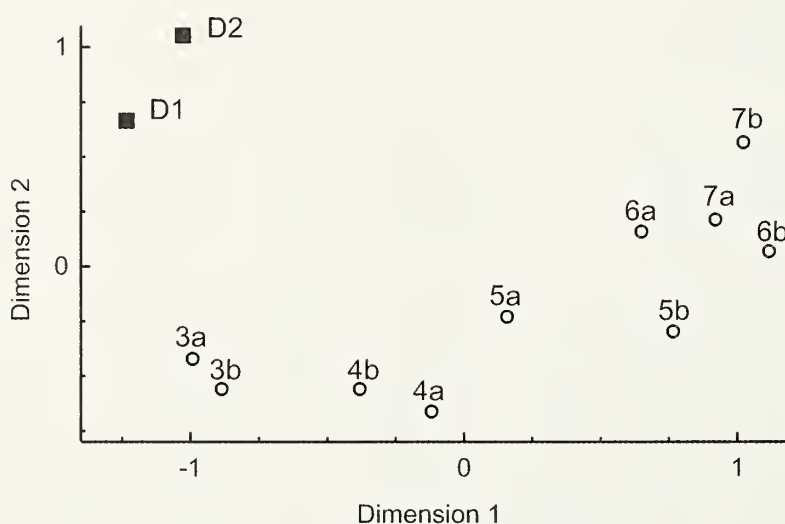


Fig. 3. Non-metric two-dimensional scaling of samples of geometrid moths from two disturbed and ten undisturbed forest sites in southern Ecuador. The ordination is based on the CNESS index with its sample size parameter m set to an intermediate value of 36 (stress: 0.05).

(‘exclusive’ species, Appendix 1). Most of these species were rare: twelve species with one specimen each, and five species with a total of two specimens. One species was collected with a total of three specimens (*Eupithecia densicauda*), one with six (*Pero obtusaria*), and one with seven (*Sabulodes muscistrigata*). Two species were common at the disturbed sites as well as at the forest sites at elevational level 3 (*Sabulodes thermidora*, *Perizoma emmelesiata*). Other species were found in larger numbers compared with forest habitats (figures printed in bold in Appendix 1). These species include (singletons and doubletons discarded): *Budara partita*, *Pantherodes colubraria viperaria*, *P. conglomerata*, *Perisopteryx* sp.nr. *nigricomata*, *Pero semiusta*, *Perusia verticata* (Ennominae), *Euphyia aguada*, *Eupithecia duena*, *E. lachanmei*, *E.* sp.nr. *penicilla*, *Eupithecia* sp., *E. yangana*, *Orthonama effluata*, *Psaliodes inundulata* (Larentiinae) and *Tricentrogyna colustrata* (Sterrhinae).

The two-dimensional scaling (Figure 3), based on the CNESS index ($m=36$), shows an arrangement of the ten forest sites roughly according to their elevational order. Appendix 2 provides the original dissimilarity matrix. As in previous studies (Brehm et al. 2003a), extracted scores of the first dimension of the forest plots correlate highly significantly with the altitude of the sites ($r^2 = 0.87$, $P < 0.001$). In contrast, the two disturbed sites are not arranged according to their elevational position. Rather, they are separated by having lower scores in the first dimension and higher scores in the second dimension than all the forest sites.

DISCUSSION

Possible causes for the high alpha diversity

Anthropogenic disturbance in the study area causes a strong decline in plant diversity (J. Homeier, personal communication). It also leads to a decrease of certain important food resources, such as soft-leaved herbs and understorey shrubs (Paulsch 2002), and to a fundamental change of microclimatic conditions. We therefore expected a significant decline of geometrid diversity as shown e.g. by Beck et al. (2002) in Borneo. However, the results show that local diversity is surprisingly high at disturbed sites, but tends to be lower compared with the forest sites. Values of Fisher’s alpha larger than 86 are still

far beyond those recorded from any temperate site and are among the highest in the world. The values for the extrapolated species number gives an impression of the order of magnitude of actual richness between 200 and 300 species while the results for rarefied species are arranged according to those of the other two measures.

The high diversity of geometrid moths found at the disturbed sites can be explained by (1) suitability of disturbed habitat, and (2) dispersal from adjacent habitats. Disturbed sites in the study area might offer appropriate habitats for a number of species using plants of early successional stages as larval food resources. Lepš et al. (2001) stated that tropical successions could represent a suitable habitat for many insects. In particular, degraded forest remnants might offer a still wider range of resources. On the contrary, open landslides, cattle pastures and bracken fallows provide an extremely impoverished set of potential hosts. It is likely that the dispersal of ‘tourist species’ from adjacent forest sites plays an important role, and that the diversity of the disturbed sites might be overestimated due to this phenomenon. The high number of species represented by only one individual might also indicate an increased proportion of species that only pass through. However, a high rate of singletons is a typical feature of incompletely sampled tropical arthropod communities (Novotny & Basset 2000). Holloway et al. (1992) found that samples from plantations located in the vicinity of secondary forest contained a considerable component of that fauna. Many of the species depended on plants that were not present in the plantation. Thomas (2002) interpreted high values of Fisher’s alpha of geometrid moths at a clearcut site in a Canadian red spruce forest as the consequence of the dispersal of tourist species from unlogged forest. Ricketts et al. (2001) found a relatively high species richness and abundance of moths around forest fragments in Costa Rica. They described the phenomenon as moth ‘halos’ extending more than one kilometer from the forest edge. The disturbed sites in our study area lay within this range (ca. 0.5 km). It is unlikely that moths were attracted from far away by the light-traps, since our study, and those of Ricketts et al. (2001) and Thomas (2002) were conducted with very weak light sources (30, 12, and 22 W, respectively). In order to minimize edge and dispersal effects in further studies, we recommend a study design with large distances between sites which are situated in homogeneous habitats.

Changes in ensemble structure

Some conspicuous patterns have emerged with regard to structure and species composition of the ensembles from the disturbed habitats. The species proportion of the very species-rich genus *Eois* is significantly lower at disturbed sites than at those in the forest, and all twelve species at the disturbed sites were collected only in low numbers (maximum 4, Appendix 1). All known Neotropical *Eois* larvae are specialized feeders on *Piper* species (Brehm 2002, Dyer et al. 2003, L. Dyer & D.L. Gentry, personal communication). Herbs and shrubs of this family are an important component of the understory within the intact forest whereas this resource is largely absent at disturbed sites (J. Homeier, personal communication). Another conspicuous pattern is the absence of the large-bodied ennomine genera *Bonatea* and *Herbita* which also might be associated with missing hostplants. However, available host plant data are still too few for a clear interpretation.

The three more abundant exclusive species *Eupithecia densicauda*, *Pero obtusaria* and '*Sabulodes muscistrigata*' might be regarded as typical components of disturbed habitat, but stochastic sampling effects are likely to play a major role for the remaining exclusive species. The two species common at the disturbed sites as well as at the forest sites at elevational level 3 (*Sabulodes thermidora*, *Perizoma emmelesiata*) could be dispersers from open landscape because these sites are situated at the forest edge.

The high number of species of the genus *Eupithecia* is noticeable, and can be explained by the availability of suitable hosts in disturbed habitats. It is probable that most of these moths had actually developed in disturbed habitats, since Brehm (2003) found larvae of *Eupithecia* of several species in different successional stages on host plants such as the shrub *Baccharis latifolia* (Asteraceae). Species of the larentine genus *Hagnagora* were represented by all four species listed by Brehm (2002) from intact forest. At least two of these species were recorded on *Clethra* hostplants. *C. revoluta* is a common plant in the study area and occurs together with two other *Clethra* species on early successional stages (J. Homeier, personal communication). Other obviously generalist species were common at both disturbed and forest sites. Examples include *Microxydia* sp. nr. *ruficomma*, *Physocleora pulverata*, *Euphyia subguttaria*, *Perizoma zenobia*, *Psaliodes catenifera*, *P. albifascia*, and *Idaea recrenita*.

Against expectations, dominance was low at disturbed sites. The most common species were *Eupithecia yangana* and *Sabulodes thermidora* at site D1 (Berger-Parker index: 5.8%), and *Psaliodes inundulata* at site D2 (Berger-Parker index: 7.9%). This falls within the range of the generally low dominance values of geometrid moths at the forest sites (median 6.7, minimum 4.9, maximum 19.0%). The result stands in contrast to studies showing higher dominance values of ensembles at disturbed habitats, e.g. of geometrid moths in Borneo (Beck et al. 2002).

In the ordination, geometrid ensembles from the two disturbed sites are separated from those at forest sites (Figure 3). On the first axis, ensembles of disturbed sites are not ordinated according to their elevational position as are the forest plots, but are ordinated 'too low'. This result is confirmed when additional ensembles from lower elevations (1380 m, Brehm 2002) are included in the ordination (unpublished results). The pattern might reflect an elevational shift of disturbance ensembles because open habitats could potentially provide warmer conditions as compared to forest habitats. Another explanation is the geographical proximity of sites D1 and D2 to forest sites at elevational levels 3 and 4 (Figure 1). There is a higher chance of dispersal from these nearer plots compared to forest sites at larger distances apart. Further studies could reveal whether physiological adaptations of moth species or geographical proximity of sites play the more important role for the shift along the first dimension. The second dimension might be interpreted as a gradient of 'openness' of vegetation, because trees become smaller and vegetation becomes less dense with rising elevation (Homeier et al. 2002, Paulsch 2002) as well as with rising levels of disturbance.

CONCLUSIONS

The relatively high diversity of geometrid moths at disturbed sites is probably due to the suitability of secondary forest remnants as habitat and also to the role of immigrating species from adjacent intact forest. However, the diversity of some specialized feeders declined, and disturbed sites added only little to the local species-pool because 90% of the species found at disturbed sites are also present at forest sites. More host plant information is required in order to learn more about the responses of Neotropical moths to

habitat changes. Inventories of caterpillars and their host plants in north-western Costa Rica (D. Janzen, W. Hallwachs et al.) and in northern Ecuador (L. Dyer, D.L. Gentry, H. Greeney et al.) provide such important ecological data.

Our results provide a first impression of the effects of habitat disturbance on a highly diverse arthropod group in a montane rainforest in the Andes. Continuing from this, further studies should investigate the response of geometrid moths to different levels of disturbance and land-use, such as selective logging or the transformation of forest into cattle pasture and plantations in the Andes. The ongoing destruction of Andean rainforests could well have a severe impact on the diversity of geometrid moths. Given that the Andean rainforests are the worldwide hotspot of diversity for Geometridae (Brehm 2002), and for a range of other organisms (e.g. Myers et al. 2000), there is obviously reason for concern from a conservation viewpoint. Strong measures should be taken in order to protect the remaining pristine and secondary habitats.

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APPENDICES

Appendix 1

List of 197 geometrid moth species collected at two sites of disturbed montane habitats in southern Ecuador. Taxonomy follows Pitkin (2002) for Ennominae, and Scoble (1999) for the remaining Geometridae. Taxon numbers refer to data base numbers that are largely identical to the list of species provided by Brehm (2002). Some taxonomic changes have been performed since Brehm's (2002) study because a number of species have been identified in the meantime in the BMNH, USNM and AMNH collections. The column 'exclusive' refers to those species that were not collected by Brehm (2002) in montane forest habitats. Twenty species were collected exclusively at the disturbed sites. sp nr = species near, but not identical with a described species. Numbers printed in bold are those which exceed specimen numbers sampled at any of the 22 forest sites analyzed by Brehm (2002).

Taxon number	Species	D1	D2	exclusive
Ennominae				
292	<i>'Apiciopsis' maciza</i> Dognin	-	1	
73	<i>Argyrotome prospectata</i> Snellen	-	1	
53	<i>Bassania goleta</i> Dognin	-	3	
268	<i>Bryoptera friaria</i> Schaus	1	-	
779	<i>Bryoptera</i> sp nr <i>friaria</i> Schaus	-	1	
774	<i>Budara partita</i> Warren	3	1	
357	<i>Cargolia toulgoeti</i> Herbulot	1	-	x
95	<i>Certima lojanata</i> Dognin	1	1	
253	<i>Certima miligina</i> Dognin	-	1	
90	<i>Cimicodes</i> sp	2	-	
291	<i>Cirsodes casta</i> Warren	-	1	
1040	<i>Cirsodes macilentata</i> Guenée	-	1	
52	<i>Eusarca</i> sp	-	1	x
265	<i>Glena</i> sp nr <i>juga</i> Rindge	-	1	
88	<i>Herbita decurtaria</i> Herrich-Schäffer	-	1	
257	<i>Iridopsis gaujoni</i> Prout	-	1	
256	<i>Iridopsis</i> sp nr <i>subnigrata</i> Warren	3	-	
112	<i>Isochromodes extimaria</i> Walker	2	-	
98	<i>Isochromodes polvoreata</i> Dognin	-	1	
102	<i>Isochromodes</i> sp	-	1	
105	<i>Isochromodes</i> sp	1	2	
106	<i>Isochromodes</i> sp	4	4	
302	<i>Leuculopsis bilineata</i> Warren	-	2	
1030	<i>Leucula</i> sp nr <i>ablinearia</i> Guenée	1	-	
192	<i>Lomographa tributaria</i> Walker	1	1	
768	<i>Macaria lydia</i> Schaus	-	1	
172	<i>Macaria lapidata</i> Warren	1	-	
180	<i>Mesedra</i> sp	1	-	
974	<i>Melanolophia musarana</i> Dognin	1	1	x
695	<i>Microxydia</i> sp nr <i>ruficomma</i> Prout	7	-	
166	<i>Mychonina corticinaria</i> Herrich-Schäffer	1	-	
546	<i>Mychonina</i> sp	-	1	x
170	<i>Neazata fragilis</i> Warren	1	-	
861	<i>Narragodes ochreata</i> Dognin	2	-	x
286	<i>Neodora glaucularia</i> Snellen	-	4	
810	<i>Nephodia clara</i> Dognin	-	1	
216	<i>Nephodia pardata</i> Dognin	1	-	
211	<i>Nephodia occulta</i> Warren	-	1	

Taxon number	Species	D1	D2	exclusive
142	<i>Oenoptila</i> sp nr <i>recessa</i> Dognin	-	1	
232	<i>Opisthoxia</i> sp nr <i>danaeata</i> Walker	1	1	
59	<i>Oxydia</i> <i>augusta</i> Druce	-	1	
60	<i>Oxydia</i> <i>geminata</i> Maassen	1	2	
71	<i>Oxydia</i> <i>optima</i> Dognin	-	2	
72	<i>Oxydia</i> <i>scriptipennaria</i> Walker	1	1	
58	<i>Oxydia</i> <i>trychiata</i> Guenée	1	12	
297	<i>Pantherodes</i> <i>colubraria viperaria</i> Thierry-Mieg	5	13	
298	<i>Pantherodes</i> <i>conglomerata</i> Warren	4	5	
162	<i>Periclina</i> <i>rumiaria</i> Guenée	-	1	
154	<i>Perissopteryx</i> sp nr <i>nigricomata</i> Warren	1	7	
947	<i>Pero</i> <i>algerna</i> Schaus	-	1	
239	<i>Pero</i> <i>buckleyi</i> Butler	3	1	
248	<i>Pero</i> <i>caustomeris</i> Prout	-	1	
472	<i>Pero</i> <i>obtusaria</i> Schaus	3	3	x
245	<i>Pero</i> <i>periculosaria</i> Oberthür	1	-	
924	<i>Pero</i> <i>pretensa</i> Poole	1	-	
928	<i>Pero</i> sp	-	1	x
833	<i>Pero</i> sp nr <i>semiusta</i> Butler	3	4	
791	<i>Pero</i> <i>spectrata</i> Felder & Rogenhofer	-	1	
247	<i>Pero</i> <i>tricaria</i> Poole	1	-	
793	<i>Pero</i> <i>tridenta</i> Poole	1	-	x
792	<i>Pero</i> <i>unfortunata</i> Poole	-	1	
328	<i>Perusia</i> <i>verticata</i> Warren	3	3	
327	<i>Perusia</i> <i>viridis</i> Warren	-	1	
147	' <i>Petelia</i> ' <i>anagogaria</i> Warren	-	1	
630	' <i>Petelia</i> ' sp	1	-	x
49	<i>Phyllodonta</i> <i>caninata</i> Guenée	1	-	
137	<i>Phyllodonta</i> <i>muscilinea</i> Guenée	1	-	
46	<i>Phyllodonta</i> sp nr <i>flabellaria</i> Thierry-Mieg	1	1	
334	<i>Physocleora</i> <i>mniophilaria</i> Guenée	-	1	
333	<i>Physocleora</i> <i>pulverata</i> Warren	5	20	
318	<i>Pynnia</i> <i>gallaria</i> Walker	1	-	
317	<i>Pynnia</i> <i>megara</i> Druce	3	3	
309	<i>Rucana</i> <i>abnormipalpis</i> Warren	1	-	
311	<i>Rucana</i> <i>degener</i> Warren	5	6	
122	<i>Sabulodes</i> sp nr <i>carbina</i> Druce	2	1	
125	<i>Sabulodes</i> <i>thermidora</i> Thierry-Mieg	21	3	
873	' <i>Sabulodes</i> ' <i>muscistrigata</i> Guenée	4	3	x
175	<i>Semiothisa</i> <i>radiata</i> Maassen	-	1	
202	<i>Sericoptera</i> <i>mahometaria</i> Herrich-Schäffer	1	2	
281	<i>Stenalcidia</i> <i>celosoides</i> Dognin	-	1	
275	<i>Stenalcidia</i> sp nr <i>delgada</i> Dognin	1	-	

Geometrinae

761	<i>Lissochlora</i> <i>cecilia</i> Prout	-	1	
351	<i>Lissochlora</i> <i>hoffmannsi</i> Prout	2	-	
352	<i>Lissochlora</i> <i>latuta</i> Dognin	2	1	
355	<i>Nemoria</i> <i>aturia scotocephala</i> Prout	1	1	
345	<i>Nemoria</i> <i>nigrisquama</i> Dognin	2	-	
349	<i>Nemoria</i> sp nr <i>sellata</i> Warren	1	-	
882	<i>Nemoria</i> sp nr <i>erina</i> Dognin	-	1	x
344	<i>Oospila</i> <i>ecuadorata</i> Dognin	1	-	
360	<i>Phrudocentra</i> <i>subaurata</i> Warren	2	1	
341	<i>Poecilochlora</i> <i>minor</i> Warren	1	-	
342	<i>Rhodochlora</i> <i>roseipalpis</i> Felder & Rogenhofer	1	1	
347	<i>Synchlora</i> <i>amplimaculata</i> Herbulot	1	2	
350	<i>Synchlora</i> <i>gerularia</i> Hübner	-	1	
611	<i>Synchlora</i> <i>dependens tumefacta</i> Warren	2	1	

Larentiinae

391	<i>Eois</i> <i>amarillada</i> Dognin	1	2	
1033	<i>Eois</i> <i>apyraria</i> Guenée	-	1	x
392	<i>Eois</i> <i>chasca</i> Dognin	1	1	
1029	<i>Eois</i> <i>chrysocraspedata</i> Warren	2	1	
378	<i>Eois</i> <i>encina</i> Dognin	-	1	
803	<i>Eois</i> <i>muscosa</i> Dognin	1	-	
387	<i>Eois</i> <i>nigricosta</i> Prout	-	1	

Taxon number	Species	D1	D2	exclusive
404	<i>Eois obada</i> Druce	1	-	
416	<i>Eois olivacea</i> Felder & Rogenhofer	1	2	
424	<i>Eois paraviolascens</i> Dognin	3	1	
419	<i>Eois</i> sp nr <i>odatis</i> Druce	1	-	
961	<i>Eois</i> sp nr <i>tegularia</i> Guenée	-	1	
482	<i>Euphyia aguada</i> Dognin	4	5	
952	<i>Euphyia infundibulata</i> Guenée	-	2	
633	<i>Euphyia psyra</i> Druce	1	1	
465	<i>Euphyia</i> sp	1	-	
462	<i>Euphyia</i> sp nr <i>fringillata</i> Guenée	-	3	
460	<i>Euphyia subguttaria</i> Herrich-Schäffer	1	4	
813	<i>Euphyia violetta</i> Warren	3	1	
623	<i>Eupithecia anita</i> Warren	2	3	
554	<i>Eupithecia casta</i> Warren	-	2	
512	<i>Eupithecia densicauda</i> Warren	2	1	x
559	<i>Eupithecia disformata</i> Dognin	-	1	
556	<i>Eupithecia duena</i> Dognin	3	15	
677	<i>Eupithecia higa</i> Dognin	3	1	
679	<i>Eupithecia hilaris</i> Prout	1	1	
569	<i>Eupithecia hormiga</i> Dognin	2	-	
563	<i>Eupithecia lachaumei</i> Herbulot	9	11	
661	<i>Eupithecia nigrithorax</i> Warren	3	-	
653	<i>Eupithecia nigrodiscata</i> Herbulot	-	2	
562	<i>Eupithecia penicilla</i> Dognin	-	2	
550	<i>Eupithecia rubellicincta</i> Warren	2	4	
674	<i>Eupithecia sobria</i> Prout	3	-	
580	<i>Eupithecia</i> sp	-	1	
586	<i>Eupithecia</i> sp	-	1	
926	<i>Eupithecia</i> sp	-	1	x
604	<i>Eupithecia</i> sp	2	8	
609	<i>Eupithecia</i> sp	2	2	
622	<i>Eupithecia</i> sp	-	2	
624	<i>Eupithecia</i> sp	-	2	
645	<i>Eupithecia</i> sp	3	5	
646	<i>Eupithecia</i> sp	1	-	
658	<i>Eupithecia</i> sp	1	-	
664	<i>Eupithecia</i> sp	1	-	
666	<i>Eupithecia</i> sp	-	2	
876	<i>Eupithecia</i> sp	1	2	
900	<i>Eupithecia</i> sp	1	-	
572	<i>Eupithecia</i> sp nr <i>contexta</i> Schaus	1	-	
574	<i>Eupithecia</i> sp nr <i>contexta</i> Schaus	1	1	
561	<i>Eupithecia</i> sp nr <i>penicilla</i> Dognin	2	9	
615	<i>Eupithecia</i> sp nr <i>saphenes</i> Prout	-	1	
555	<i>Eupithecia</i> sp nr <i>sobria</i> Prout	-	1	
570	<i>Eupithecia versiplaga</i> Warren	-	1	
667	<i>Eupithecia yangana</i> Dognin	21	9	
435	<i>Hagnagora anicata</i> Felder & Rogenhofer	-	2	
434	<i>Hagnagora croceitincta</i> Dognin	-	1	
433	<i>Hagnagora ephestris</i> Felder & Rogenhofer	1	1	
436	<i>Hagnagora mortipax</i> Butler	1	-	
468	<i>Hammaptera praderia</i> Dognin	1	-	
469	<i>Hammaptera</i> sp	2	-	
475	<i>Hydriomena</i> sp nr <i>cydra</i> Druce	1	2	
951	<i>Obila umbrinata</i> Guenée	1	-	
441	<i>Orthonama effluata</i> Snellen	3	7	
492	<i>Perizoma basiplaga</i> Schaus	-	1	
486	<i>Perizoma emmelesiata</i> Snellen	1	14	
487	<i>Perizoma zenobia</i> Thierry-Mieg	5	3	
894	<i>Pocophora rufisticta</i> Warren	-	1	x
489	<i>Psaliodes albifascia</i> Dognin	2	2	
524	<i>Psaliodes castanea</i> Warren	-	1	
496	<i>Psaliodes catenifera</i> Warren	3	1	
539	<i>Psaliodes cedaza</i> Dognin	1	1	
538	<i>Psaliodes confusa</i> Warren	-	1	
532	<i>Psaliodes crassinota</i> Dognin	-	2	
488	<i>Psaliodes inundulata</i> Guenée	3	21	
698	<i>Psaliodes nictitans</i> Warren	-	1	
541	<i>Psaliodes perfuscata</i> Bastelberger	-	2	
501	<i>Psaliodes</i> sp	1	-	

Taxon number	Species	D1	D2	exclusive
499	<i>Psaliodes</i> sp nr <i>endotrichiata</i> Snellen	-	6	
393	<i>Psaliodes</i> sp nr <i>philetus</i> Schaus	-	1	x
518	<i>Psaliodes strigosa</i> Warren	-	1	
33	<i>Scotopteryx fulminata</i> Dognin	-	1	
513	<i>Smileuma plagifracta</i> Prout	-	1	
440	<i>Triphosa affirmata</i> Guenée	1	-	
Sterrhinae				
29	<i>Cyclophora acutaria</i> Walker	-	1	
8	' <i>Cyclophora</i> ' <i>gracilinea</i> Warren	-	1	
11	' <i>Cyclophora</i> ' <i>lancearia</i> Felder & Rogenhofer	-	1	
36	<i>Idaea arhostiodes</i> Warren	1	-	
40	<i>Idaea fimbriata</i> Warren	-	1	
41	<i>Idaea quadrirubata</i> Warren	-	1	
34	<i>Idaea reclinata</i> Prout	3	2	
35	<i>Idaea</i> sp nr <i>iridaria</i> Schaus	2	-	
38	<i>Lobocleta costalis</i> Dyar	1	-	
972	<i>Pleuroprucha</i> sp	1	-	
880	<i>Scopula privata</i> Walker	2	-	x
704	<i>Scopula</i> sp	1	-	x
595	<i>Scopula</i> sp	1	1	x
987	<i>Scopula</i> sp	2	-	x
27	<i>Scopula</i> sp nr <i>subquadrata</i> Guenée	-	1	
23	<i>Semaeopus dentilinea</i> Warren	1	-	
21	<i>Semaeopus verbena</i> Dognin	-	1	
42	<i>Tricentrogyna collustrata</i> Snellen	5	10	
39	<i>Tricentrogyna nigricosta</i> Warren	1	1	

Appendix 2

Dissimilarity matrix based on the CNESS index ($m = 36$) for two disturbed sites and ten undisturbed sites of montane rainforest in southern Ecuador. Note that CNESS may attain a potential maximum of the square root of 2 = 1.414.

	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b	D1
3b	0.68	0									
4a	1.03	1.04	0								
4b	0.93	0.99	0.75	0							
5a	1.06	1.03	0.89	0.98	0						
5b	1.19	1.16	1.01	1.07	0.83	0					
6a	1.17	1.13	1.04	1.11	0.91	0.82	0				
6b	1.25	1.23	1.11	1.14	1.01	0.94	0.77	0			
7a	1.19	1.10	1.13	1.13	1.00	0.95	0.73	0.74	0		
7b	1.23	1.21	1.18	1.17	1.05	0.99	0.77	0.88	0.78	0	
D1	1.07	1.08	1.16	1.13	1.14	1.22	1.20	1.26	1.22	1.25	0
D2	1.12	1.17	1.16	1.16	1.18	1.21	1.20	1.25	1.22	1.24	0.83

Colony survivorship of social caterpillars in the field: A case study of the small eggar moth (Lepidoptera: Lasiocampidae)

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Abstract: We investigated survivorship of 100 caterpillar colonies of the tent-building central place-foraging moth, *Eriogaster lanestris*. Our aim was to demonstrate if survival patterns match those reported for the related eastern tent caterpillar, *Malacosoma americanum*, which has a similar social system. The field experiment took place at four sites in northern Bavaria, Germany, in May and June 2002. Egg clusters were obtained from females mated in the laboratory and were exposed in the field just before hatching of the young caterpillars. Establishment of larval tents and survivorship on the colony level was then monitored until completion of larval development. In total, 52% of colonies had at least one larva surviving until pupation, with no significant differences between the four study sites. Colony-level mortality rate was constant over time and did not drop markedly during the last two larval instars, when *E. lanestris* larvae develop urticating hairs that are presumed to confer protection against vertebrate predators. The inability to build an initial tent, or the later loss of the tent, accounted for 71% of the observed total colony losses. Strong rainfall had a severe influence on the constitution of tents and increased the likelihood of colony failure. Overall, maintenance of an intact tent emerged as the single most important predictor of colony survival.

Key words: colony survivorship, *Eriogaster lanestris*, Germany, predation, rainfall, tent-building caterpillars

INTRODUCTION

Lepidopteran larvae are most vulnerable in the earliest stages of their lives. Natural enemies are often the dominant cause of mortality (Cornell et al. 1998). Only few Lepidopteran caterpillars (<3% of the species worldwide, Costa & Pierce 1997) live gregariously or 'socially', sometimes in groups of several hundreds of individuals. Gregarious caterpillars may benefit from living in groups, for example by maximizing growth through efficient thermoregulation (Joos et al. 1988; Ruf & Fiedler 2000, 2002b) or by social feeding facilitation (Clark & Faeth 1997; Denno & Benrey 1997). However, since they are very conspicuous at the same time, caterpillar groups may incur a high risk of predation once they have been detected by visually hunting predators

like birds, or by predators that recruit further nest-mates to food (e.g. ants, wasps).

Many gregarious species show warning coloration (Sillén-Tullberg 1988; Vulinec 1990) and are suggested to be chemically or structurally defended, which enables them to behave conspicuously (Heinrich 1979, 1993). The effect of aposematism may be enhanced by gregarious life habits because grouping renders the aposematic signal more effective by generating a greater aversion in predators (Gamberale & Tullberg 1996, 1998). Nevertheless, unless unpalatability is tested explicitly for any species an assumption of chemical defense always remains doubtful. In addition, the effectiveness of any defensive structures may vary according to the larval stage as well as between various types of predators.

We here study larval survivorship of the tent-building small eggar moth, *Eriogaster lanestris* (Linnaeus 1758) under the influence of natural predation and adverse

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weather conditions. *E. lanestris* caterpillars hatch in spring a few days after budbreak. They live together in and on a silken tent until the very end of their development, when they finally leave the tent and pupate some meters away (Ruf et al. 2003). Females lay all their eggs in one single cluster and siblings stay together for their whole development. Caterpillars start building the tent right after hatching, and expand it throughout development. Tents may achieve a volume of 750 cm³. Since the tent does not include any resources, caterpillars must leave it for every food intake, i.e. they are central-place foragers according to Fitzgerald & Peterson (1988). Individuals are highly site tenacious and always return to the tent after feeding even if this has been severely damaged. Young caterpillars (L1-L3) are totally black (to the human observer) and bear white setae, whereas fourth instar caterpillars develop additional tufts of shorter red urticating hairs, which become even more pronounced in the fifth (last) instar.

Various aspects of group living in *E. lanestris* have been analyzed in recent years, but mostly in the laboratory (Ruf & Fiedler 2000, 2002a, b; Ruf et al. 2001a). Data on the survival of caterpillars in the field are crucial for understanding the costs associated with sociality in this species, since the destruction of a colony means the total loss of a female's offspring. We here investigate survivorship in *E. lanestris* at the colony level under field conditions, with special reference to the timing and impact of predation as well as to the effects of heavy rainfall. In line with earlier findings by Costa (1993) on the related Eastern tent caterpillar, *Malacosoma americanum* (Fabricius 1793), and in view of the development of advanced chemical defense (= urticating hairs) in older instars of *E. lanestris* we expected mortality to be highest in young instars (especially before a tent has been fully established) and to level off when caterpillars approach maturity.

MATERIAL AND METHODS

Study sites

Study sites (Table 1) were situated in the region around Bayreuth (Germany, northern Bavaria). All were xerothermic habitats on limestone with blackthorn (*Prunus spinosa* Linnaeus, Rosaceae) bushes and/or hedgerows. At sites HP and PB we

found naturally occurring tents of *E. lanestris* several times between 1999 and 2002. The site HL had previously been only scarcely covered with blackthorn bushes but presently blackthorn shrubs rapidly spread over the whole site. The site BB is a former military training area managed through regular grazing by sheep and goats but also experiences massive encroachment by blackthorn. For BB the occurrence of *E. lanestris* was reported for at least the end of the 1970s (Wolf 1982).

Animals

One-hundred egg clusters laid on small twigs were attached between 8-10 May with small pieces of wire to branches of blackthorn, a preferred natural host-plant in southern Germany (Ebert 1994). We chose the top of smaller bushes (height <ca. 1.7 m) or the sun-exposed side of higher plants (height 2-3 m). Egg clusters were placed 0.5-1.5 m above ground (depending on the height of the plant) and were marked with small numbered labels for later relocation and identification. The number of egg clusters exposed per site varied (Table 1) depending on the size of the area and the availability of suitable blackthorns. All egg clusters stemmed from a laboratory bred stock (third laboratory generation, original animals from site HP).

Monitoring and acquisition of data

After exposure of egg masses at the field sites hatching of the caterpillars and development was monitored once a week (Table 2). Due to the distance between sites, it was not possible to census all sites at one day. Experimental egg clusters were not attached to the blackthorns before budbreak to prevent caterpillars from hatching too early. Two naturally occurring field colonies (sites HP and HL) were one larval stage ahead at the onset of the experiment. Nevertheless, some experimental colonies finished development before the younger one of the natural colonies. Thus, experimental colonies were largely synchronous with the natural populations and experienced predation and weather in much the same way as these.

We here focus on colony, rather than individual, survivorship since even under high solar irradiation usually only a fraction of colony members can be observed on or outside the tent (Ruf & Fiedler 2002b). Moreover, the proportion of larvae active outside the tent strongly varies during molting

Table 1. Study sites, numbers of exposed *Eriogaster lanestris* egg masses, and survivorship of colonies during a field experiment in May and June 2002 in northern Bavaria, Germany.

Site	Latitude	Longitude	Altitude (m)	Exposure	Colonies surviving to 5 th instar/ total number exposed	Proportion colonies surviving
BB	49°59'40''	11°38'00''	490	SW and plateau	22 / 5	44%
HP	49°48'50''	11°26'50''	615	plateau	10 / 15	67%
PB	49°46'40''	11°27'10''	460	S	9 / 15	60%
HL	49°48'20''	11°24'20''	560	SW	11 / 20	55%
Total					52 / 100	52%

Table 2. Exposure dates, census dates and progress of larval development for 100 experimental *E. lanestris* colonies.

	Site BB		Site HP, HL, PB	
Start	8-9 May	exposure	10 May	exposure
Census 1	15 May	first caterpillars hatched	20 May	60% of colonies hatched
Census 2	22 May	L1, most tents established	26 May	L1, most tents established
Census 3	28 May	L1/L2	1 June	L1/L2
Census 4	4 June	L2/L3	9 June	L2/L3
Census 5	12 June	L2-L4 (most L3)	16 June	L2-L4 (most L3)
Census 6	19 June	L3-L5 (most L4)	22 June	L3-L5 (most L4)
Census 7	26 June	most tents abandoned	29 June	L5 or abandoned

Table 3. Descriptors for the condition of colonies (pertinent to either egg cluster or tent).

Descriptor	Explanation
hatched	caterpillars just hatched, no tent yet established
infertile	no caterpillars hatched from the egg clusters within three weeks
no tent	caterpillars without tent (just after hatching, because of small number of caterpillars, or after destruction of tent)
intact	tent with no physical damage
repaired	tent was obviously damaged, but new silk has been spread over the holes
damaged	egg cluster: parts are missing; tent: shows holes, not yet repaired
destroyed	egg cluster: no eggs left; tent: completely destroyed, but caterpillars still alive
abandoned	tent abandoned, occasionally fifth (=final) instar caterpillars in the nearby surroundings
extinct	colony completely destroyed, no caterpillars nearby

Table 4. Monthly mean temperature and mean sum of precipitation in Bayreuth (northern Bavaria, Germany) in May and June between 1971 and 2001, and in the year of the study.

	May 1971-2001	June 1971-2001	May 2002	June 2002
Temperature [°C]	12.0	14.9	14.1	17.5
Sum of precipitation [mm]	56.3	78.9	76.5	113.4

periods (Ruf et al. 2001b). Thus, a reliable census of tent-mates cannot be achieved without severely damaging the colony.

The condition of colonies was evaluated using the descriptors listed in Table 3. If possible, the cause of the damage of a tent was recorded. Predation by invertebrates does not leave obvious marks on the tent. Predation by birds leaves large holes in amidst the silk mats of the tent. Damage caused by rain is clearly distinguishable from that by birds since ruptures due to rain arise from the edges of the mats and stretch in the direction of the silk filaments.

Climatic data were provided by the meteorological station at Bayreuth University (49°55'45"N 11°35'10"E, 365m asl). These data depict the regional weather conditions during the time of the study (all study sites are less than 20km away from the station). Minor local variation in temperature or the extent of rainfall was not considered.

RESULTS

During the period of observations, mean daytime temperature (7a.m.-7.p.m.) was 18.9°C, mean

nighttime temperature (9p.m.-5a.m.) was 11.3°C. Maximum temperature was 33.0°C and nighttime minimum temperature was always above 0°C (minimum: 2.8°C) (Fig. 1). Mean temperature and the sum of precipitation were higher in May and June 2002 compared to the average of the last 30 years (Table 4). On June 6 unusually strong rainfall occurred with 43l/m²×h. Compared to other years (1992-2001) the monthly sum of rainfall varied considerably among years but such extreme rainfall events in May and June are exceptionally rare in the study region (Ruf 2003).

Most caterpillars hatched between May 15 and May 20 (about one week after exposure in the field) and left their tents around the end of June (colonies at site BB a few days ahead compared to the colonies at the sites HL, HP, and PB). Thus, the complete development of the caterpillars lasted approximately 6-7 weeks (caterpillars pupate very soon after leaving the tent: C. Ruf, *pers. obs.*).

Five of 100 egg-batches failed to eclose. Obviously, these eggs were not fertile. Two egg clusters disappeared prior to hatching from unknown reasons. In 94.2% of all colonies that were successful in building a tent (N=69), the tent was directly built on

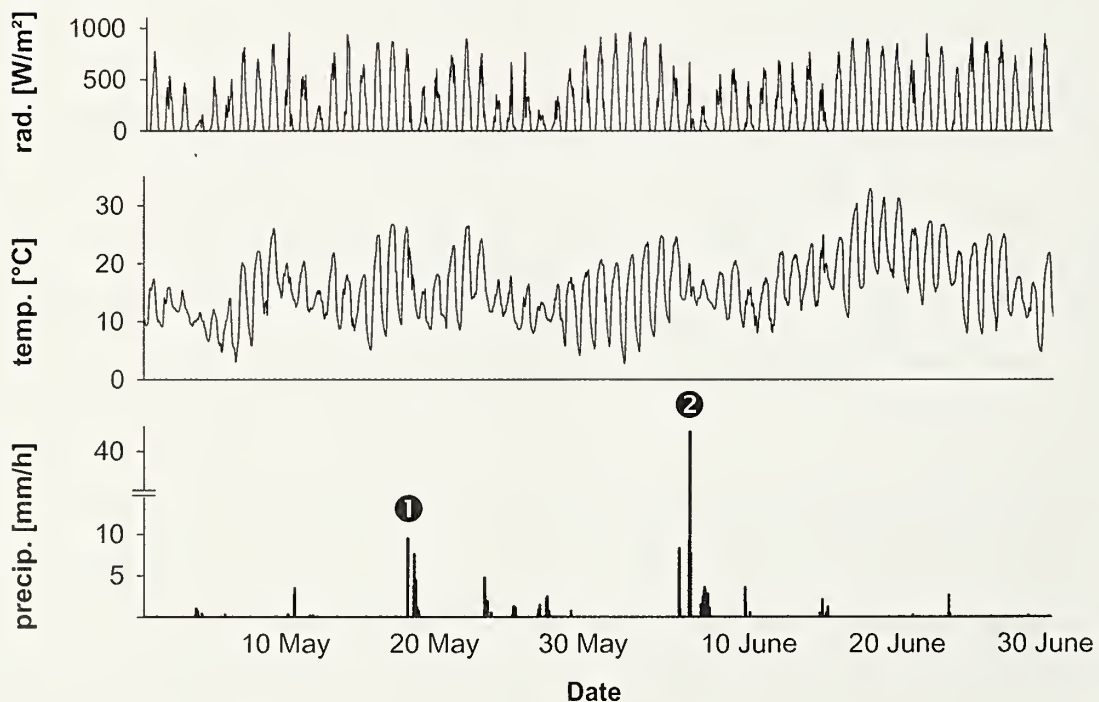


Fig. 1. Climatic conditions (short-wave radiation, temperature, and precipitation) in Bayreuth, May and June 2002. Note the interruption of the y-axis in the lowest graph. Numbers: 1 = raining period during hatching time. 2: heavy rainfall events during instars L2/L3.

the egg mass. Only four colonies built their tent about 30cm above the egg mass. In most cases, the same tent was used (and expanded) over the whole development period. Occasionally (N=6 colonies), caterpillars moved to a web of the ermine moth *Yponomeuta padella* (Linnaeus 1758) (Yponomeutidae) to start tent-building for a second time. Loose *Yponomeuta* webs were sometimes extremely abundant on blackthorn. Such webs were then expanded.

Fifty-two colonies survived until census 7 when the caterpillars had reached their final instar (Table 1). Survival here means that we traced at least one mature caterpillar which we could unequivocally attribute to a given colony. Survival curves varied between sites, but not significantly so (Kaplan-Meier survival analysis: $\chi^2_{3df} = 0.50$, $p = 0.92$). While on the sites HP, PB and HL no colony became extinct after 9 June 2002, losses of colonies continued to occur at site BB until the end of the larval period. Pooling the data from all sites reveals that mortality occurred almost equally throughout larval development (Fig. 2). We noted somewhat higher incidences of colony failure about 30 days after exposure (i.e., after torrential rainfall of June 6), and from June 12 to June 19 at site BB.

Successful construction of a tent emerged as most

crucial factor for the survival of the caterpillars (Fig. 3). Of 24 caterpillar groups that had not been successful in building an initial tent by the second census (i.e. within approximately one week after hatching) 18 became extinct. This amounts to 43.9% of all total losses that occurred after hatching. From the remaining six hatchling groups without a tent only two were able to establish a tent later during the second instar. The other four groups survived without having built a tent, but dwindled to a final group size of only one individual each until census 7. Also later in the larval life, complete destruction of the tent strongly increased the extinction risk of these colonies (Fig. 3). Only two out of 15 colonies that had lost their tent between census 3 and 7 succeeded in rebuilding a tent and two further such colonies survived without a tent, whereas the other eleven colonies died out within 1-3 weeks after tent destruction. Thus, 70.7% of the colony mortality after hatching was caused by or associated with the loss or lack of a tent. Probability of survival was significantly higher (nearly 3-fold) after the successful construction of a tent and again significantly increased (nearly 3-fold) when the tent remained intact or when the caterpillars were able to repair the

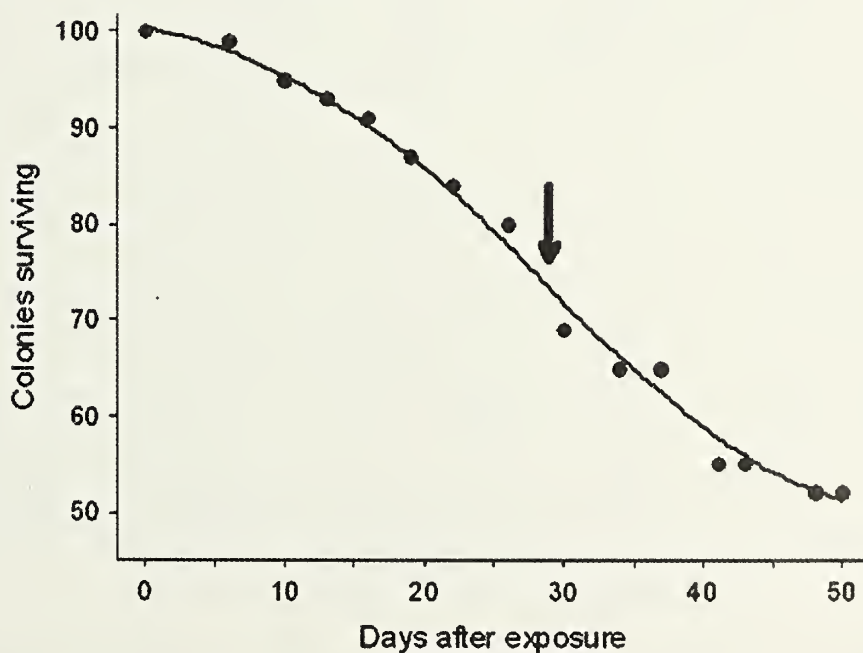


Fig. 2. Number of colonies surviving (initially: $n=100$ egg batches), summed over the four study sites. Time axis: 0 = exposure day of egg batches. Arrow: day of heavy rainfall. Curve fitted by distance-weighted least-squares regression.

tent before it was totally destroyed (see statistics in Fig. 3).

Although the weekly observations of the colonies provided only snapshots and observations lack completeness, predation was observed by ants (*Lasius* sp., *Formica* sp.), bugs (Miridae), spiders, and beetles (Cantharidae) during the earlier larval stages. Only two of 11 colonies at which predation by invertebrates was directly observed became extinct by the next census. Both these colonies had no tent for their protection. Predation by birds directly at the tents was not noted before census 5 at site HP and census 6 at site BB (i.e. when pre-final instars equipped with

urticating hairs were present). None of the tents with obvious damage by birds (N=5) was completely lacking caterpillars, and in no case did bird attacks lead to the complete extinction of a colony.

Heavy rain had a severe impact on the condition of the colonies in our experiments. Fig. 4 shows that all tents at site BB and the majority of tents at the sites HP, PB and HL were damaged after the severe rainfall on June 6. Most tents showed a noticeable reduction of volume at census 5 compared to census 4 and tents were probably temporarily (i.e. until the damage was repaired and the tent was newly expanded again) not habitable for the caterpillars.

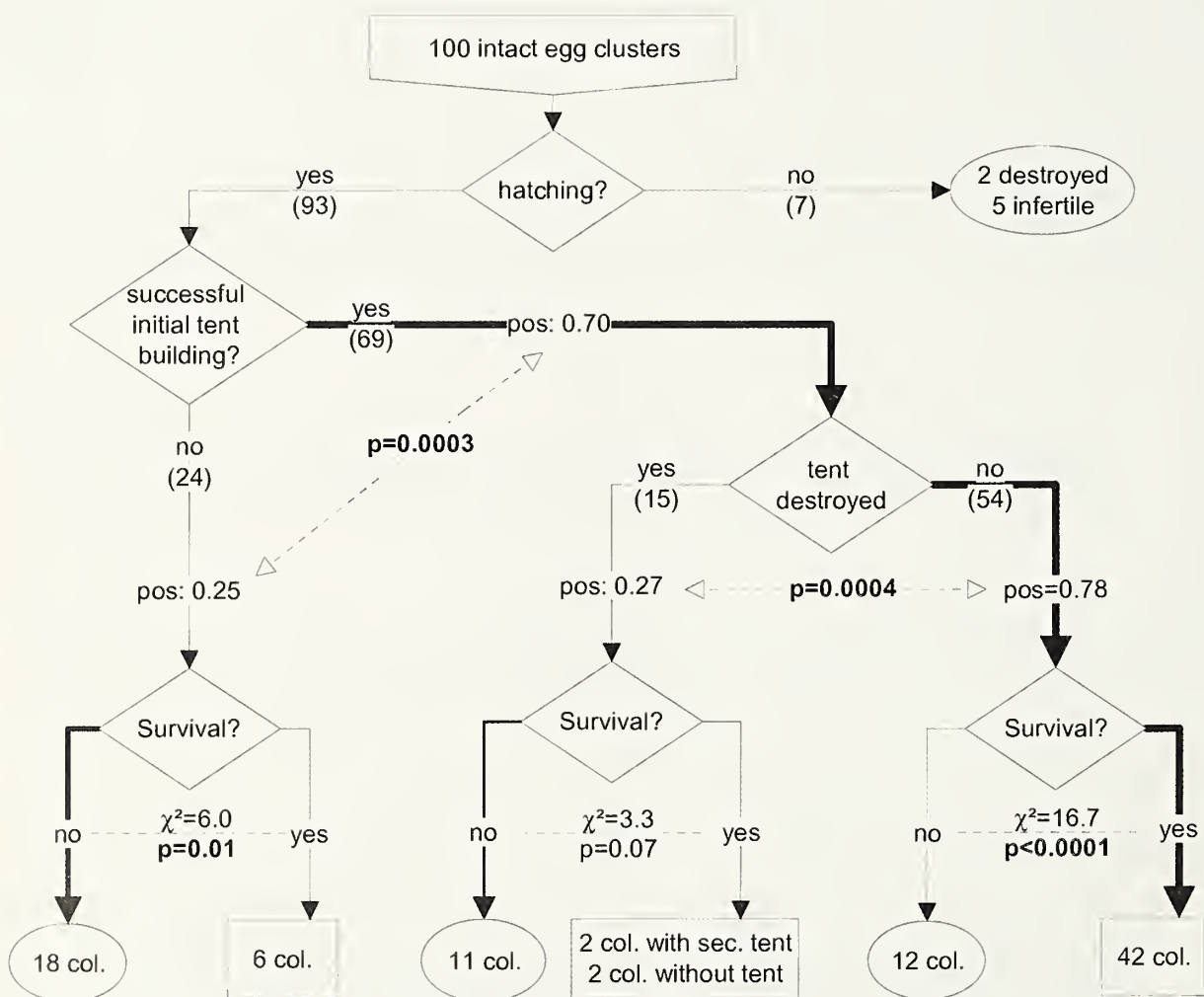


Fig. 3. Flow-chart diagram illustrating the fate of the colonies. Numbers in parentheses = number of colonies. pos = proportion of surviving colonies. Statistics: Comparison of actual survival probabilities at a given point: Fisher's exact test; for deviation of pathways from equal proportions: chi²-test (1df). Probability values printed in bold are significant ($p < 0.05$) after sequential Bonferroni correction. Different width of arrows indicates pathways with significant differences in survival.

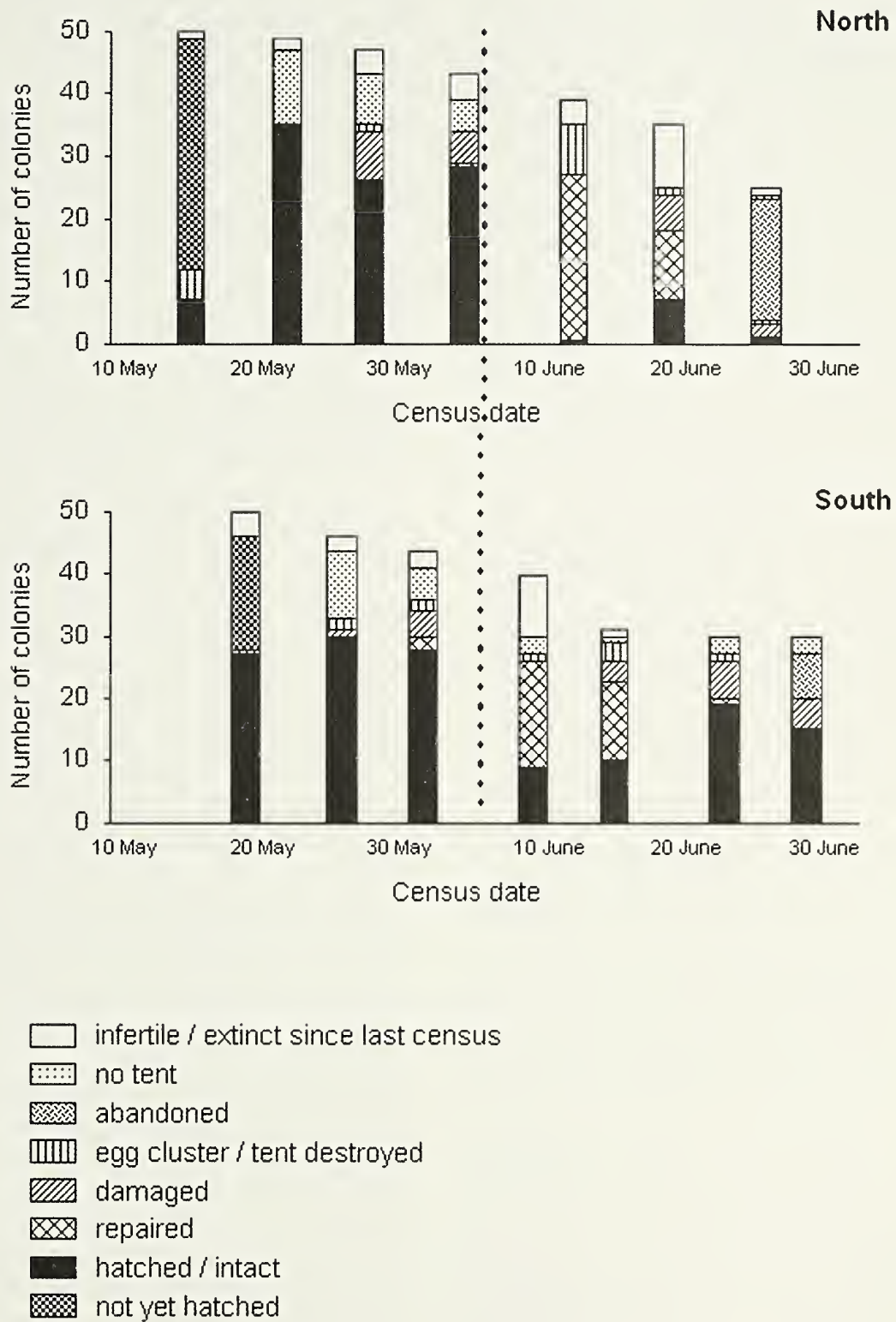


Fig. 4. Condition of colonies during the seven censuses at each site. The dashed line indicates the start of the heavy rainfall that severely damaged most tents. North: Colonies at site BB, South: Colonies at sites HL, HP, PB (these were pooled because of their geographic proximity and to homogenize sample sizes; see Table 1).

DISCUSSION

Colony mortality was not restricted to, nor particularly intense, during early instars in *E. lanestris* in our study, but was rather constant over time. Although older larvae possess defensive urticating hairs, colony mortality did not attenuate in the last two larval stages. Comparable data from other social, tent building caterpillars are rare. In a field study conducted in Georgia, USA, caterpillars of *Malacosoma americanum* finished their development within 7-8 weeks (Costa 1993). Climatic conditions in the Georgia piedmont in March and April and in the region of Bayreuth in May and June are similar with respect to mean temperature (Georgia: March: 13.7°C, April: 16.0°C), whereas precipitation is higher in Georgia (March: 207.5mm, April: 54.6mm; Georgia State Climatology Office 2003).

In contrast to our findings, *M. americanum* experienced significant early-instar mortality but negligible mid- to late-instar mortality. Overall, one third of the *M. americanum* colonies was destroyed by the third to fourth instar but no colony became extinct later on. We assume that the relatively higher mid- and late-instar mortality of *E. lanestris* in our study was predominantly due to the damage of the tents after the heavy rainfall on June 6, which led to the extinction of whole colonies. Climatic conditions did not contribute to mortality in *M. americanum*, perhaps because precipitation was evenly spread without distinct peaks in the year of Costa's (1993) study (i.e. 1990).

Rain seriously affected the constitution of the silk which became brittle leading to large ruptures and holes at the edges of the tent. Additionally, the multiple layers of the tent stuck together after being soaked by heavy rain, which forced the caterpillars to stay outside. Damage at tents may have contributed to higher mortality through facilitation of predation as well as by constraining the tent's thermoregulatory properties (Ruf & Fiedler 2002b).

Climatic factors may also have contributed to first instar mortality. The five day period (15-20 May) with cool weather (daily maximum <20°C) and with substantial precipitation (Fig. 1) most likely constrained mobility of the small caterpillars and retarded the construction of the initial tent just after hatching. Under laboratory conditions (ca. 20°C constantly) without precipitation caterpillars build a tent, in which all caterpillars may hide, within 1-2 days

after hatching (C. Ruf, pers. obs.). Besides the direct impact of rain and associated low temperatures which retard mobility, foraging, and digestion (Ruf & Fiedler 2002a), it is very likely that those groups that were not able to build a tent fast enough were decimated by invertebrate predators. As a consequence, too few individuals (10-20) were left which would not be able to construct a tent any more. Those groups are very likely to become extinct.

The impact of weather on the abundance of insects has been analyzed for many species (e.g. Roy et al. 2001 for British butterflies), often showing positive associations with low rainfall. Extreme weather events (e.g. rainstorms) may severely affect butterfly populations, but by their very nature such events lack reproducibility (Dennis & Bardell 1996).

Mortality rates of social caterpillars vary enormously. In two other *Malacosoma* species colony mortality was 40%, or higher than 95%, respectively (Shiga 1979 cited after Fitzgerald 1995; Filip & Dirzo 1985). While our and other studies on social, tent-building caterpillars focused on colony mortality only and not on mortality of individuals, the latter is probably several times higher. In the tent building pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller 1775) (Notodontidae), Schmidt et al. (1990) calculated a mean reduction by 62% of the individuals from the mean number of eggs in a cluster to the mean number of mid-instar caterpillars per colony counted in the field. Unfortunately their study disregarded those colonies that had been completely destroyed between egg deposition and the detection of the colony. Another study on web-building caterpillars (*Hyphantria cunea* (Drury 1773), Arctiidae) found mortality rates of 77-100% during the fourth and fifth stadium by birds and wasps (Morris 1972). Myers (2000) showed that survival of western tent caterpillars (*Malacosoma californicum* (Packard 1864)) varied with the natural 6-11 years periodicity of this species. Highest survival rates were measured in early phases of the population increase and survival was lowest during the population decline. Since our study was confined to one single year, we cannot even guess whether such variation might also occur in *E. lanestris*. However, population cycles have never been reported for *E. lanestris*.

We did not control for the impact of parasitism and virus or bacterial infections on the survival of colonies but no colony showed obvious signs of strong

parasitism (e.g. many larval carcasses on the outside of the tents) or disease (heterogeneous multi-instar colonies, shrunken dead caterpillars). Over the years, we observed very few parasitoids emerging from field-collected *E. lanestris* larvae (rates of parasitoid infestation in colonies from site HP <5% in 1999, own unpublished data).

Possession of an intact tent emerged as the strongest predictor of colony success. Overall, 71% of colony failures were related to the loss of the tent. Functions of the tent are numerous (thermoregulation: Joos et al. 1988; Breuer & Devkota 1989; Fitzgerald & Underwood 2000; Ruf & Fiedler 2002b; communication: Fitzgerald & Costa 1999, Ruf 2003; water balance: Wellington 1974). Since caterpillars often rest on the surface of the tents, these structures are expected to be only marginally effective in reducing the overall impact of predators and parasitoids (Fitzgerald 1995), but sophisticated studies controlling for the sole effect of the tent as a refuge from invertebrate predators are missing so far. We suppose that tents serve as a shelter for at least part of the time because many invertebrates (e.g. bugs, wasps, ants) did not enter tents as long as these remained physically intact (C. Ruf, pers. obs.). Destruction of the tent thus means the simultaneous loss of multiple functions enhancing development and communication among the caterpillars. In view of the marked differences in timing and extent of mortality between species with social caterpillars (see above), it is quite likely that the relative importance of various mortality risk factors differs between species and also depends on population density.

Silken tents are a costly investment for herbivorous caterpillars (Berenbaum et al. 1993; Craig et al. 1999; Stevens et al. 1999). The importance of the tent is obvious since *E. lanestris* caterpillars repaired the tent whenever it had been destroyed but normally did not leave it. The only cases where a replacement of the tent was observed were associated with the expansion of an already existing *Yponomeuta* web, thus saving costs for a completely new tent.

In a meta-analysis comparing published survival curves for gregarious and solitary Lepidoptera and Symphyta, Hunter (2000) showed that gregarious caterpillars are less likely to die during the earlier instars than solitary caterpillars, but mortality rates rise during the later development (last, solitary instars, pupal phase). Overall, in the comparative analysis survival (from egg to adult) was not

significantly different between solitary and gregarious species whereas the timing of mortality differed between the two classes. Our data conform to this pattern, with rather low rates of colony failures during early stages, and slightly more frequent losses later on.

In highly social caterpillars, where tent-building can only be achieved by large numbers of cooperating siblings, colony mortality reduces a female's individual fitness to zero even though mean survival may be high on the population level. Thus, there must be a strong trade-off for tent-building in highly social Lepidoptera between high benefits, primarily by developmental advantages, and high costs due to the risk of complete reproductive failure. Most mature *E. lanestris* tents we found in the field contained more than 200 larvae. Since the mean fecundity of an *E. lanestris* female is about 325 eggs (Ruf et al. 2003) survival must be quite high once the hatchlings have established their tent and no extreme weather events influence the caterpillars' development. Thus, in *E. lanestris* the benefits of sociality usually outweigh the high risk of losing the whole offspring. As we have shown here, possession of an intact tent plays the most important role in that regard.

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Two phylogenetically significant new *Calycopis* species (Lycaenidae: Theclinae: Eumaeini)

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Abstract: *Calycopis sullivanii* Robbins & Duarte is described from wet lowland rain forest on the Atlantic Coast of Central America, and *Calycopis cicero* Robbins & Duarte is named from cloud forest on the eastern slope of the Andes of Ecuador. Both new species and *C. caesaries* have the ductus ejaculatorius entering the penis ventrally, a character state that has not been reported for the Eumaeini. These three species and *C. cerata* share muted blue color dorsally in males. The phylogenetic positions of *C. caesaries* and *C. cerata* were unstable in ongoing phylogenetic analyses, and the two new species are described because we are adding them to the analyses.

Key words: butterflies, hairstreaks, Lepidoptera, Neotropics.

INTRODUCTION

Calycopis Scudder is the largest genus of the thecline tribe Eumaeini (Lycaenidae). It contains 62 described species, 12 undescribed species, and many more names of uncertain status (Robbins 2004). In preliminary phylogenetic analyses of the major clades of *Calycopis* (including several previously recognized genera, such as *Calystryma* Field), the positions of *Calycopis caesaries* (H.H. Druce) and *C. cerata* (Hewitson) were "relatively primitive" and unstable (Duarte & Robbins, in prep.). To increase taxon sampling "density", we added to the analyses two undescribed species that share some unusual characters (detailed below) with *C. caesaries* and *C. cerata*. The purpose of this paper is to provide names for these two undescribed species before the phylogenetic results are published.

The two species described below belong to the *Eumaeini* because they have 10 forewing veins, greyhound shaped male genitalia lacking a juxta, and a male foretarsus that is fused, stubby tipped, and used for walking (Eliot 1973). They are members of the *Lamprospilus* Section of the Eumaeini because they lack

androconia, have the lateral edge of the female 8th abdominal tergum sclerotized and curved inwards, and have "fan-shaped" signa on the corpus bursae (Figs. 12 & 13) (Duarte & Robbins, in prep.). They are placed in *Calycopis* because they have an orange-red spot in ventral hindwing cell Cu2-2A distal of the postmedian line (Figs. 2,4,6,8) and piliform setae on the ventral surface of hindwing vein 2A (Fig. 9) (Duarte & Robbins, in prep.).

We describe the two new species by comparison with *Calycopis caesaries* and *C. cerata*. These are the only *Calycopis* species that share with the new species muted blue color on the dorsal surface of male wings (Figs. 1 & 5, the described species are figured in D'Abrera 1995). *Calycopis caesaries* and the two new species also have male genitalia in which the ductus ejaculatorius enters the penis ventrally (Figs. 10 & 11). This structure has not been previously reported in the Eumaeini (e.g., Eliot 1973), suggesting that these three form a monophyletic lineage. However, the ductus ejaculatorius enters laterally in *C. cerata* and some other *Calycopis*, and phylogenetic interpretation of this structure is yet uncertain.

Although associating the sexes of *Calycopis* species is often difficult, the newly described species have

distinctive ventral wing patterns and restricted known geographical ranges, factors that allow us to associate the sexes with a high degree of confidence.

MATERIALS AND METHODS

The results in this paper are based upon a comparison of adult morphology using 5,700+ *Calycopis* specimens in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, plus numerous specimens in other museums. Of particular relevance, we examined 340 specimens of *C. cerata* from 11 countries and 26 of *C. caesaries*—including three pairs *in copula*—from six countries. In addition to specimens of the new species in the USNM, we borrowed specimens from the Allyn Museum of Entomology (AME), Florida State Museum (via loan to J.B. Sullivan); Instituto Nacional de Biodiversidad (INBIO), Santo Domingo de Heredia, Costa Rica (via loan to J.B. Sullivan); and Robert Busby (RCB), Andover, MA, USA. Finally, specimens are being deposited in Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador.

We used standard entomological techniques (Robbins 1991) and state for each result below the number of specimens on which it is based. Genitalic terms follow those in Klots (1970), as illustrated in Robbins and Nicolay (2002), and wing vein terminology follows Nicolay (1971, 1977). Forewing lengths were measured with a vernier caliper and reported statistically as a mean and standard deviation (SD) with sample size.

Calycopis sullivanii Robbins & Duarte, New Species

Diagnosis. *Calycopis sullivanii* and *C. caesaries* differ in the shape of the ventral hindwing cubital spots (compare Figs. 2 & 4 with those of *C. caesaries* in D'Abbrera 1995, p. 1228 & in Draudt 1919-1920, plate 158) and the shape of the male genitalia labides in dorsal aspect (Fig. 10) (*C. caesaries* lacks a notch between the labides). *Calycopis sullivanii* differs from *C. cerata* by yellow ventral hindwing cubital spots (orange-red in *C. cerata*), a wider black border on the dorsal surface of male forewings than *C. cerata* (compare Fig. 1 with those of male *C. cerata* in D'Abbrera 1995, p. 1226 & in Draudt 1919-1920, plate 158), the shape of the male genitalia labides in dorsal aspect (Fig. 10) (*C. cerata* lacks a notch between the labides), gnathos without small teeth (Fig. 10)

(present in *C. cerata*), and presence of piliform setae on ventral hindwing vein 2A (Fig. 9) (lacking in *C. cerata*, presumably a homoplasy). Occasional individuals of *C. cerata* have aberrant yellow cubital spots that are similar to those of *C. sullivanii*, but they can be immediately distinguished by the lack of the piliform setae.

Description of male (N=6). Mean forewing length 11.0mm, SD=1.14.

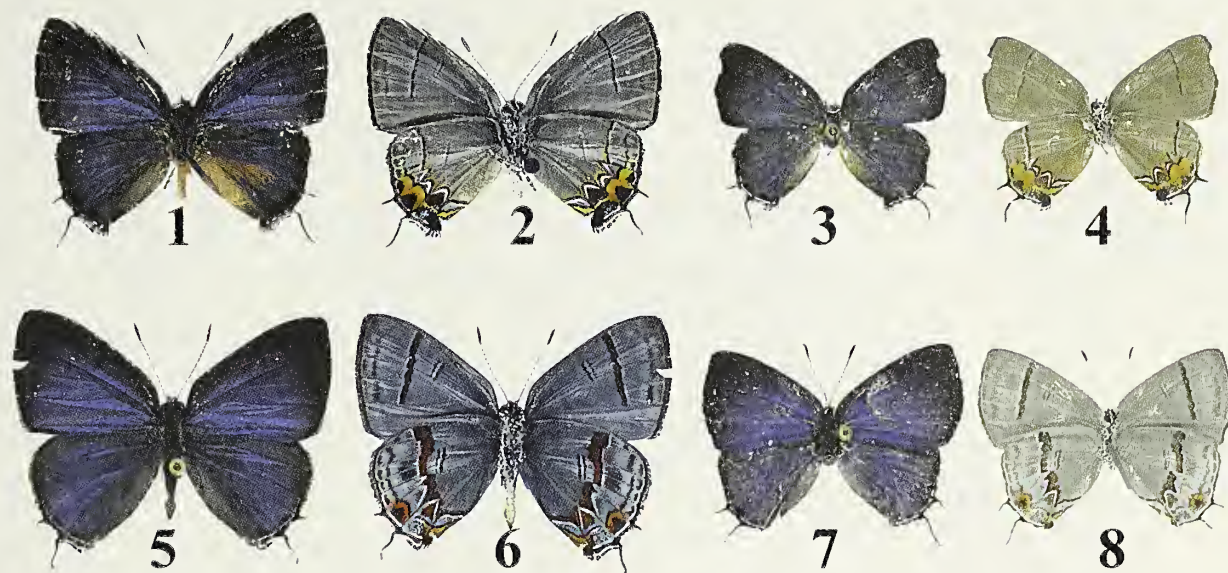
Dorsal wing pattern (Fig. 1). Forewing basal 65-80% muted blue. Border dark brown, basal edge is diffuse. Fringe brown. Hindwing basal 80-90% muted blue with basal edge of dark brown border diffuse. Submarginal black spots in cell Cu1-Cu2 and Cu2-2A. A marginal line, white basally and black distally, extends from Cu1 to the dark brown anal lobe. Fringe scales between Cu1 and anal lobe basally white and distally black except at the end of Cu2, where the scales are all white. Short (1-1.5mm) white-tipped tail at terminus of vein Cu1. A second white-tipped tail (3-3.5mm) at terminus of vein Cu2.

Ventral wing pattern (Fig. 2). Forewing ground color silver-gray. Dark brown postmedian line from vein R2 to Cu2 bordered distally with white scales and basally with occasional red scales. A similar line, but with less dark brown, at distal end of discal cell. Dark brown marginal line with fringe of dark brown scales that have some orange-red color basally. Hindwing ground color, postmedian line, and discal cell line similar in color to forewing except that the postmedian line is bordered basally with yellow scales. A conspicuous orange-red spot just distal of the postmedian line in cell Cu2-2A. Submarginal band complex. In cell 2A-3A, black anal lobe bordered basally with white, gray, yellow, and a black line. In cell Cu2-2A, a black submarginal spot with scattered white/blue scales bordered basally with yellow scales and a black line. In cells Cu1-Cu2 and M3-Cu2, a black pupilled yellow submarginal spot bordered distally with a black line. The other cells have vestigial components of the coloring in cell M3-Cu2. Vein 2A with regularly spaced piliform setae (Fig. 9).

Head. Antennae with 17-19 white-ringed segments on the stalk and 10-12 segments on the club. Nudum confined to the club. Eyes bordered with white scales. Frons brown. Third segment of labial palps brown with white scales only at the tip.

Description of female (N=1). Forewing length 8.7mm.

Dorsal wing pattern (Fig. 3). Same as male except blue scaling is more extensive and of a lighter hue.



Figs. 1-8. *Calycopis* adults, 1.75x actual size.

1. *C. sullivanii*, male, dorsal; 2. same, ventral; 3. *C. sullivanii*, female, dorsal; 4. same, ventral; 5. *C. cicero*, male, dorsal; 6. same, ventral; 7. *C. cicero*, female, dorsal; 8. same, ventral.

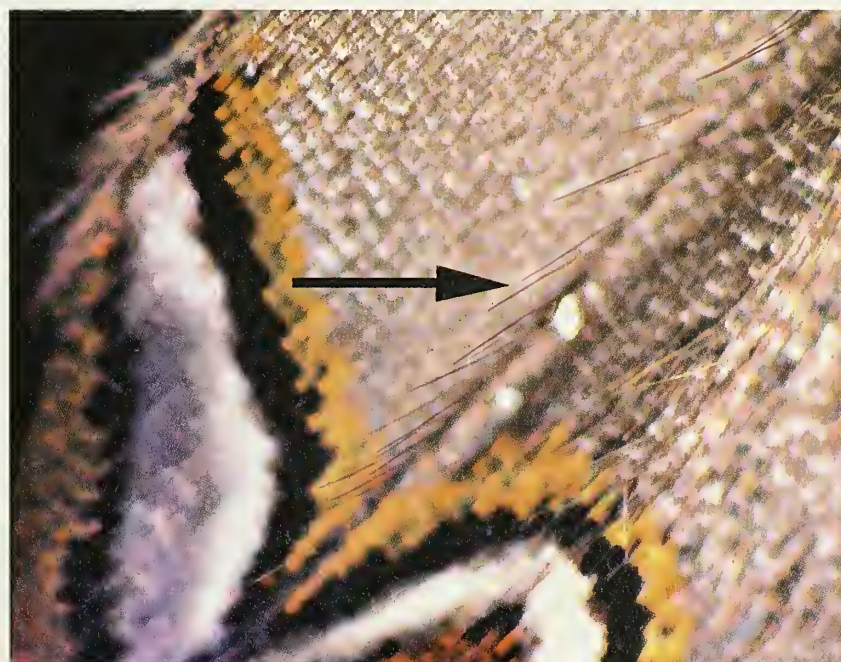
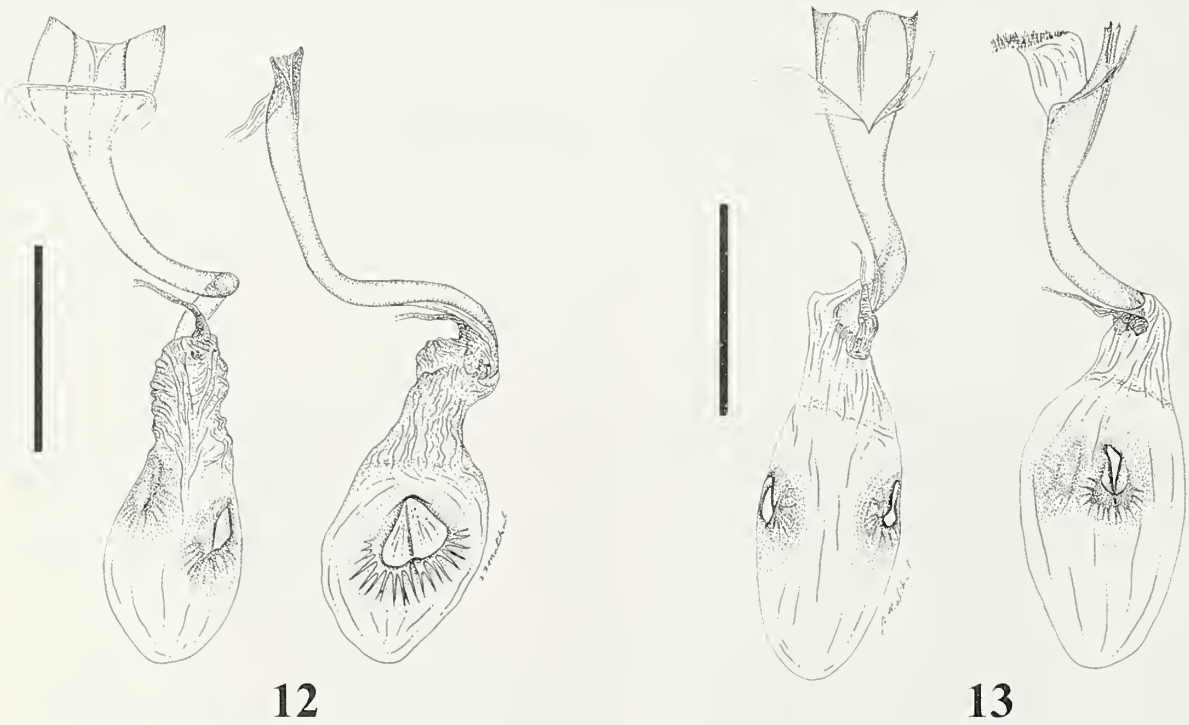
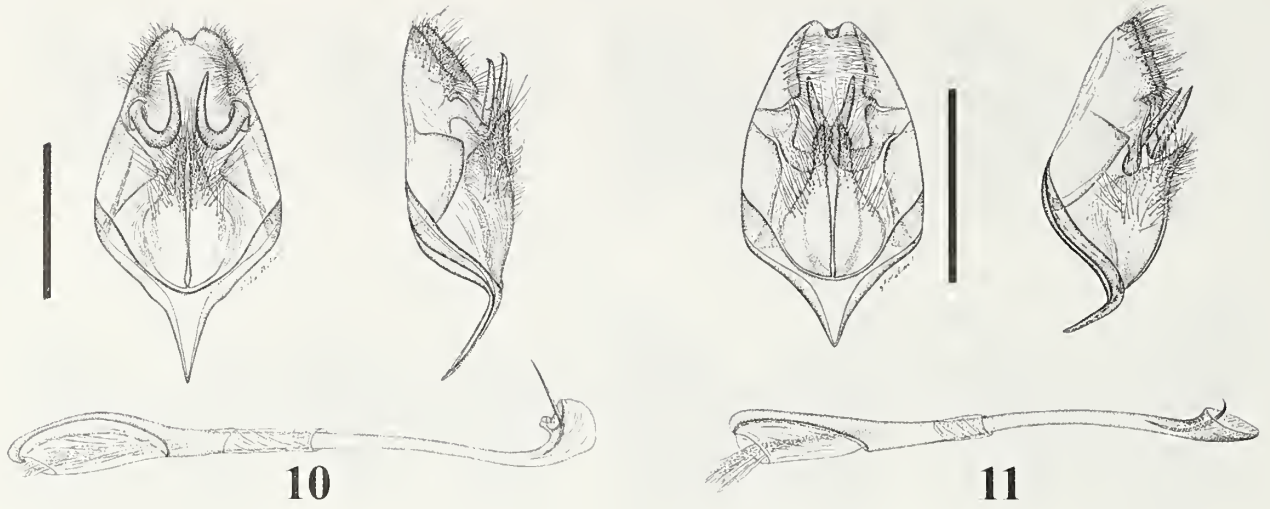


Fig. 9. Ventral hindwing *C. sullivanii* showing piliform setae on vein 2A (arrow).



Figs. 10-11. Male genitalia in ventral and lateral aspects, with penis in lateral aspect. Ductus ejaculatorius enters the penis ventrally. Scale 1mm. 10. *C. sullivani*; 11. *C. cicero*.

Figs. 12-13. Female genitalia (bursa copulatrix) in ventral and lateral aspects. Scale 1mm. 12. *C. sullivani*; 13. *C. cicero*.



Fig. 14. Distribution of *C. sullivanii* (circle), and *C. cicero* (triangle).

Ventral wing pattern (Fig. 4). Same as male.

Head. Same as male, but there are no antennae on the only known female.

Types. Holotype (Figs. 1 & 2). 'M' Panama, Canal Zone (now Canal Area), Gatún, 2 May 1970, Leg. G. B. Small. Deposited USNM.

*Paratypes** (5 'M' & 1 'F'). 3 'M' & 1 'F' USNM (Figs. 3 & 4), Costa Rica, Heredia, Finca La Selva, 3 km S Pto Viejo (10°46'N, 84°01'W), leg. H. Hespeneheide, 3 April 1985, 4 April 1985, 6 April 1989, 3 April 1985. 1 'M' INBIO, same data except Est. Biol. La Selva, 50-150m, leg. J. Bolling Sullivan, 29 August–2 September 2003 (ALAS # INB0003602140). 1 'M' AME, Panama, Canal Zone (now Canal Area), Piña, 20 April 1970.

Etymology. This species is named for J. Bolling Sullivan, who collected one of the paratypes and recognized it as an undescribed species.

Type locality. The type locality is in the Canal Zone (now Canal Area) of Panama to the south, south-west of Gatún (9°16'N, 79°55'W) in the vicinity of the road to Escobal (cf. map in Ridgely 1976). In the 1970s the Canal Zone's Achiotte Road began at Lake Gatún

and ended in the forest south of Piña (9°16'N, 80°02'W, the road has since been extended to Piña). Those specimens that Small collected along the road to Escobal and near the beginning of Achiotte Road were labeled "Gatún, Canal Zone", and those collected near the north end of Achiotte Road were labeled "Piña, Canal Zone" even though Piña is in Panama Province just west of the border with the Canal Area. Although the data label on the "Piña" paratype is Gordon Small's handwriting, the specimen apparently was given to AME by Vernon King (J.Y. Miller, pers. comm.). King and Small exchanged specimens extensively, and it is unclear who actually collected the specimen.

Habitat. The localities in the type series are in the wet Atlantic Coast lowlands. These areas receive 3 m or more annual precipitation and lack a significant dry season (Rand & Rand 1982, Coen 1983).

Distribution. *Calycopis sullivanii* is known from Gatún/Piña and La Selva (Fig. 14). It is sympatric with *C. caesaries* and *C. cerata* at both, but is rare in collections despite years of field work in Panama and Costa Rica. This rarity makes it difficult to predict whether it is more widespread than the Atlantic coast of Panama and Costa Rica.

* NOTE: in whole paper 'M' = male, 'F' = female

Discussion. We have seen no specimens in museum collections outside of the type series, although some might be misplaced under *C. cerata*. The conspicuous yellow cubital spots on the ventral surface of the hindwings should facilitate identification of additional specimens. As noted above, aberrant specimens of *C. cerata* may have cubital spots that are yellow or orange-yellow, but can be distinguished by genitalic structures and by the lack of piliform setae on hindwing vein 2A.

Calycopis cicero Robbins & Duarte, New Species

Diagnosis. *Calycopis cicero* differs from *C. caesaries*, *C. cerata*, and *C. sullivani* in the shape, number, and color of the ventral hindwing cubital spots (Figs. 6 & 8). More generally, the orange-red postmedian band on the ventral hindwing bordered with black scales basally and distally distinguishes it from all other *Calycopis* except *C. centoripa* (Hewitson), especially the females. Markings at the end of the ventral hindwing discal cell are basal of the orange-red band in *C. cicero* (Figs. 6 & 8) and are contained in the band in *C. centoripa*. We know of no other evidence to suggest a close relationship between *C. cicero* and *C. centoripa*. The shape of the male genitalia labides of *C. cicero* in dorsal aspect (Fig. 11) differs from those of *C. caesaries* and *C. cerata*, which lack a notch between the labides. The shape of the genital capsule in lateral aspect (Fig. 11) is less elongate than that of *C. caesaries*, *C. cerata*, and *C. sullivani* (Fig. 10). The ductus bursae, which is similar to that of *C. cerata*, is gently curved (Fig. 13), as opposed to the "sigmoid-shaped" ductus bursae of *C. caesaries* and *C. sullivani* (Fig. 12).

Description of male (N=12). Mean forewing length 11.5mm, SD=1.06.

Dorsal wing pattern (Fig. 5). Forewing muted blue with a narrow dark brown border (~1mm in width) on the costa and outer margin. The border has a diffuse basal edge. Fringe brown. Hindwing same blue color with dark brown border (~0.5mm in width). Submarginal black spots in cell Cu1-Cu2 and Cu2-2A. A marginal line, white basally and black distally, extends from Cu1 (sometime partially absent) to the dark brown and orange anal lobe. Fringe brown except at the end of Cu2, where the scales are all white. Short (1-1.5 mm) white-tipped tail at terminus of vein Cu1. A second white-tipped tail (~3mm) at terminus of vein Cu2.

Ventral wing pattern (Fig. 6). Forewing ground color

dark gray. Postmedian line from vein R2 to Cu2. Dark brown basally, a wide (~0.75 mm) orange-red band bordered distally with dark brown scales, in turn bordered with faint white scales. An off-white line at the end of the discal cell bordered basally and distally with dark brown scales. Two diffuse submarginal dark gray bands are variably developed. Fringe orange-red with scale tips brown. Hindwing ground color, postmedian line, and discal cell line same as forewing except that the postmedian line is wider (1-1.5mm), the white part of the postmedian line is more conspicuous, and there are orange-red scales bordering the discal cell in some individuals. Markings distal of the postmedian line are complex. In cell 2A-3A, the black anal lobe is bordered basally with white, orange-red, a black line, and gray. In cell Cu2-2A, there is a conspicuous orange-red spot just distal of the postmedian line, and there is a submarginal spot composed of black, white, and orange scales. In cell Cu1-Cu2 there is a black-pupilled orange-red submarginal spot bordered basally by a charcoal gray line. The other cells have various dark gray markings, perhaps the most conspicuous being dark gray patches just distal of the postmedian line in the medial cells. Vein 2A has regularly spaced piliform setae.

Head. Antennae with 16-18 white-ringed segments on the stalk and 10-12 segments on the club. Nudum confined to the club. Eyes bordered with white scales. Frons brown. Third segment of labial palps brown with white scales only at the tip.

Description of female (N=1). Forewing length 9.9mm.

Dorsal wing pattern (Fig. 7). Same as male.

Ventral wing pattern (Fig. 8). Same as male.

Head. Same as male.

Types. Holotype. 'M' Ecuador, Morona-Santiago, Río Abanico (02°15'S, 78°12'W), 1600-1800m, 12 September 1999, leg. Robbins & Aldas. Deposited USNM.

Paratypes (12'M' & 1'F'). 1'M' USNM Ecuador, Sucumbíos, Rosa Florida, 1400m, December 2001, leg. I. Aldas, R.C. Busby. 6'M' (2'M' to be deposited in MECN) Ecuador, Napo, Km 49 Tena-Loreto Rd., 1350m, 18 March 2004, leg. J.P. Hall. 1'F' USNM (Figs. 7&8), Ecuador, Pastaza, Km 42 Puyo-Arajuno Road (1°18.4S, 77°42.4'W), 1000m, 8 September 2000, leg. R.C. Busby. 1'M' USNM, same data as holotype. 2'M' USNM, same data as holotype except 8 September 1999. 1'M' RCB Ecuador, Morona-Santiago, 20 km W of Macas, 1800m, 29 September 1998, leg. Robert C.

Busby (about 6 km west of the holotype locality). 1'M' USNM & 1'M' MECN & 2'M' RCB (Figs. 5 & 6), Ecuador, Zamora Chinchipe, Zamora (ridge W of town), 1450m, 20 May 2000, 18 September 2000, 22 September 2001, 22 September 2001, leg. Robert C. Busby. 1'M' USNM & 1'M' RCB, Ecuador, Zamora Chinchipe, 15 km Zamora/Romerillos Rd., La Pituca, 1500m, 23 September 2001, leg. Robert C. Busby. 1'M' RCB, Ecuador, Zamora Chinchipe, 10 km E of Namirez Bajo, 1800m, 20 May 2000, leg. Robert C. Busby.

Etymology. This name is meant to be associated with *C. caesaries*, the described species to which it appears to be most similar, because of the historical association of Caesar and Cicero in ancient Rome. The name is a noun in apposition.

Type locality. The Río Abanico type locality is along the only road currently going west from Macas. A logging path begins where the road crosses the river and rises steeply. The fauna at this locality is typical of cloud forest habitats.

Male behavior. In the middle afternoon, the senior author observed males perching on shrubs from 2-6 meters above the ground (specific records for four males range from 1358-1426 hours). As with most *Calycopis* and a few species of *Electrostrymon*, in which it is difficult to associate the sexes by behavior (Robbins unpubl.), males landed only briefly. According to notes from J.P. Hall, "Males perch in groups of 3-10 on ridge tops and in light gaps 4-5m above the ground from 1400 to 1530 hours, with the usual *Calycopis* flight and landing behavior. They flew in bright sun and in obscure conditions, even with a light drizzle when everything else had disappeared."

Distribution. Since *Calycopis cicero* was discovered in September 1998, it has been found at localities throughout eastern Ecuador from Sucumbíos to Zamora-Chinchipe at elevations from 900-1800m (Fig. 14), but is unknown from Colombia and Peru, where it probably also occurs. It is somewhat puzzling that this species was not discovered during the preceding decades, but once discovered, was found in many different widely scattered localities.

Discussion. *Calycopis* is a genus of primarily lowland species. Among the 62 previously described species, *C. vidulus* (H.H. Druce), *C. cyanus* (Draudt), *C. gizela* (Hewitson), *C. boliviensis* (K. Johnson), *C. suda* (Draudt), and *C. johnsoni* (Salazar) are unrecorded from the lowlands. All inhabit the eastern Andes and share an unusually wide red postmedian line on the ventral wings. *Calycopis cicero* is the sixth montane

species from the eastern Andes and also has a wide red postmedian line, but is distinguished by the postmedian line being basally bordered with black scales.

The ventral wing pattern of *C. cicero* superficially resembles that of *C. centoripa* (D'Abrera 1995 p. 1215 for an illustration of the male). It differs in that the distal end of the ventral hindwing discal cell is basal of the red line in *C. cicero*, as noted. It also occurs in montane habitats whereas *C. centoripa* occurs in lowland rain forest throughout the Amazon Region. The muted blue dorsal color of males and the ventral entrance of the ductus ejaculatorius in *C. cicero* suggest that it is more closely related to *C. caesaries* and *C. cerata* than to *C. centoripa*.

The ventral wing pattern of *C. cicero* also resembles that of some species in other genera, such as *Aubergina hesychia* (Godman & Salvin). However, the piliform setae on vein 2A and the red spot in cell Cu2-2A distinguish *C. cicero*, as should the late afternoon behavior already mentioned, from virtually any other hairstreak with which it might be confused.

ACKNOWLEDGMENTS

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Five new dry-area South American *Strymon* species (Lycaenidae: Theclinae) and their biogeographic significance

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Abstract: Five hairstreak species (Eumacini) are described that occur in dry areas of South America. They are *Strymon ahuenholzi* Nicolay & Robbins, *Strymon jacqueline* Nicolay & Robbins, *Strymon giffordi* Nicolay & Robbins, *Strymon michelle* Nicolay & Robbins, and *Strymon lamasi* Nicolay & Robbins. Three inhabit the Atacama/Tumbesian/Río Marañón areas of southwestern Ecuador and northwestern Peru, one the upper Río Apurímac in south-central Peru, and one the central plateau of Brazil. Evidence is presented concerning the closest relatives of each new taxon. The taxonomy of *Strymon*, which now contains 54 described species, is reviewed. To assess the biogeographic significance of the new taxa, the *Strymon* species with restricted distributions in various South American xeric regions are listed. The Atacama/Tumbesian/Río Marañón area is currently the richest for *Strymon* endemics. The closest relatives of the *Strymon* species in the Atacama/Tumbesian/Río Marañón region occur in variety of other biogeographic areas, suggesting a lack of diversification within this region. This pattern is similar to that of bird distributions, but not to those of lizards and amphibians.

Key words: Atacama, biogeography, Eumacini, hairstreaks, .

INTRODUCTION

The New World genus *Strymon* Hübner (Lycaenidae: Theclinae: Eumacini) contains 48 species (183 specific names) tentatively partitioned into nine species groups (Robbins & Nicolay 2002). It is characterized by a complex and conspicuous modification of the male genitalia in which setae on the dorsal surface of the valva have the flagellum reduced in size and the socket modified into an anteriorly pointing tooth (Figs. 1-8 in Robbins & Nicolay 2002). Although found in a great variety of habitats, most *Strymon* species inhabit xeric areas.

A variety of biogeographic zones have been proposed for the Andean dry areas (e.g., Lamas 1982, Morrone 2001), but the distributions of species endemic to these areas, as well as their phylogenetic relationships, are still being documented (Morrone 2001 and included references). As part of a project to inventory the

hairstreak butterfly fauna of the dry areas of Peru and Ecuador in collaboration with D. Ahrenholz, R. Busby, and G. Lamas, we discovered four new *Strymon* species. Additionally, we found another new species that inhabits the cerrado of Brazil (cf. Brown & Mielke 1967a,b for an overview of this habitat and its butterfly fauna). The purposes of this paper are (1) to describe the five new *Strymon* species, (2) to discuss the significance of these new taxa for the previously proposed "species group" taxonomy (Robbins & Nicolay 2002), and (3) to note the biogeography of the new *Strymon* species and the species that appear to be closely related to them.

MATERIALS AND METHODS

The results in this paper are based upon a comparison of adult morphology using 6,000+ *Strymon*

specimens in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, plus numerous specimens in other museums. We borrowed specimens of the newly described taxa from Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru; the Universidade Federal do Paraná (UFPR), Curitiba, Brazil; and the private collection of Robert Busby (RCB), Andover, MA, USA. Despite extensive searching, we found no other material of these taxa in other museum collections. One type is being deposited in Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador.

We used standard entomological techniques (Robbins 1991) and state for each observation below the number of specimens and dissections on which it is based. Genitalic terms follow those in Klots (1970), as illustrated in Robbins and Nicolay (2002), and wing vein terminology follows Nicolay (1971, 1977). Forewing lengths were measured with a vernier caliper and reported statistically as a mean and standard deviation (SD) with sample size.

All *Strymon* species discussed below have anteriorly pointing teeth on the dorsal surface of the valvae (as illustrated with SEM photomicrographs in Robbins & Nicolay 2002), but these teeth are omitted from the figures in this paper because they are too small to show clearly at the magnification used. All have brush organs (*sensu* Eliot 1973, morphologically characterized in Robbins 1991) on the dorsal vinculum, but are omitted from the figures for clarity. Finally, all these species possess the diagnostic characters of the Eumacini: 10 forewing veins, "greyhound shaped" male genitalia lacking a juxta, and a male foretarsus that is fused, used for walking, and stubby tipped (Eliot 1973).

STRYMON SERAPIO GROUP

This group of 13 described species is characterized by paired cornuti, larval food plants restricted to Bromeliaceae, and male perching on tree-trunks (Robbins & Nicolay 2002). Wing pattern and shape of the external penis and its cornuti are the primary sources of distinguishing characters; we have not found good distinguishing characters in the morphology of the female genitalia, antennae, androconia and legs. Three species belonging to the *S. serapio* group are newly described.

Strymon ahrenholzi Nicolay & Robbins, New Species

Diagnosis: *Strymon ahrenholzi* is the only member of the *S. serapio* species group with a penis tip that is straight or upturned and with terminal cornuti (Fig. 21). All others have a conspicuously down-turned penis tip (Figs. 22, 23, Fig. 16 in Robbins & Nicolay 2002) and cornuti that are subterminal or well within the shaft of the external penis (unless the vesica has been everted).

Description of male (N=4): Mean forewing length 13.5mm, SD=1.91.

Dorsal wing pattern (Fig. 1): Forewing dark gray-brown with rectangular black scent patch filling distal half of discal cell. Fore and hindwings slightly translucent, veins standing out rather sharply, and underside wing pattern showing faintly. On hindwing, a black cubital spot surrounded by orange scaling, with another black spot between Cu2 and 2A. Submarginal white line between Cu1 and anal lobe spot. Rudimentary black tail at Cu1. Long slender white-tipped black tail at Cu2. Fringes of both wings pale, almost white.

Ventral wing pattern (Fig. 2): Forewing pale gray with a dark, wide, straight, postmedian band from costa to Cu2. Distally edged with a white band of equal width, sullied with dark scaling. Scattering of white scaling submarginally. Fringes con-colorous. Hindwing pale gray, with a straight narrow, dark basal band from Sc+R1 to 2A. Curved postmedian band from Sc+R1 to inner margin. Double cell-end streak partially connected to postmedian band by brown scaling, giving appearance of being fused with this band. Postmedian band distally bordered with vague band of white scaling. A black cubital spot between Cu1 and Cu2. Dark line at margin fringed with pale gray scales.

Head: Frons with piliform scales, primarily white, with a few dark ones intermixed. Third segment of labial palps slightly longer than basal two and covered with closely appressed scales. Scales between the antennal bases gray. Antennae black with about 16 white-ringed segments and a club with about 14 segments. Nudum confined to club.

Description of female: Female unknown despite extensive collecting in past decade at type locality and other parts of Atacama Desert in northern Peru (often called Tumbesian region, Best & Kessler 1995).

Types: Holotype: Male. Ecuador, Loja, Loja-Catamayo Rd., Km 26, 1800 m, 15 May 1988, leg. S. S. Nicolay. Deposited in USNM.



Figs. 1-18. *Strymon* adults, 1.5x actual size. 1. *S. ahrenholzi*, male, dorsal; 2. same, ventral; 3. *S. jacqueline*, male, dorsal; 4. same, ventral; 5. *S. jacqueline*, female, dorsal; 6. same, ventral; 7. *S. giffordi*, male, dorsal; 8. same, ventral; 9. *S. giffordi*, female, dorsal; 10. same, ventral; 11. *S. michelle*, male, dorsal; 12. same, ventral; 13. *S. michelle*, female, dorsal; 14. same, ventral; 15. *S. lamasi*, male, dorsal; 16. same, ventral; 17. *S. lamasi*, female, dorsal; 18. same, ventral.



Fig. 19. Distribution of *S. ahrenholzi* (★), *S. jacqueline* (●), and *S. giffordi* (▲).

*Paratypes (2'M): 1'M USNM, same data as holotype. 1'M USNM, same data as holotype, except leg. D. H. Ahrenholz.

Etymology: This species is named for our good friend, Dr. David Ahrenholz, who collected one of the paratypes.

Wing pattern variation: The ventral wing pattern of the holotype (Figs. 1, 2) appears to be representative of fresh specimens. When worn, as are the two paratypes, the markings on the ventral wing surface become indistinct and blurred. A fourth male from Ancash, Peru (deposited in MUSM), has genitalia that are the same as those in the type series, but its ventral wings are markedly rubbed, and its pattern cannot be ascertained. For this reason, it was excluded from the type series. It differs from the type series in having 3 subterminal orange cubital spots on the dorsal surface of the hindwing.

Male genitalic variation (four dissections, Fig. 21): As noted, the cornuti are terminal except when the vesica is partially everted, as in Figure 21. The anterior edge of the vinculum is sinuate with a slight hump in all dissections.

Habitat and distribution (Fig. 19): Currently known from only two localities in the dry mountains (1800-2800 m) of southwestern Ecuador and northwestern Peru (Ancash). It appears to be an exceedingly rare species, having been collected on only two different days.

Relationships: We suggest that *Strymon eremica* (Hayward) and *S. ahrenholzi* are "closest relatives" because they share three wing pattern characters that are otherwise unique in the *S. serapio* group. The males are brown dorsally without any blue. The ventral wings may become markedly indistinct and blurred when worn. The number of orange cubital spots on the dorsal hindwing varies from one to three. *Strymon eremica* is a geographically variable species that occurs in dry habitats from the chaco of Bolivia,

* NOTE: in whole paper 'M' = male, 'F' = female

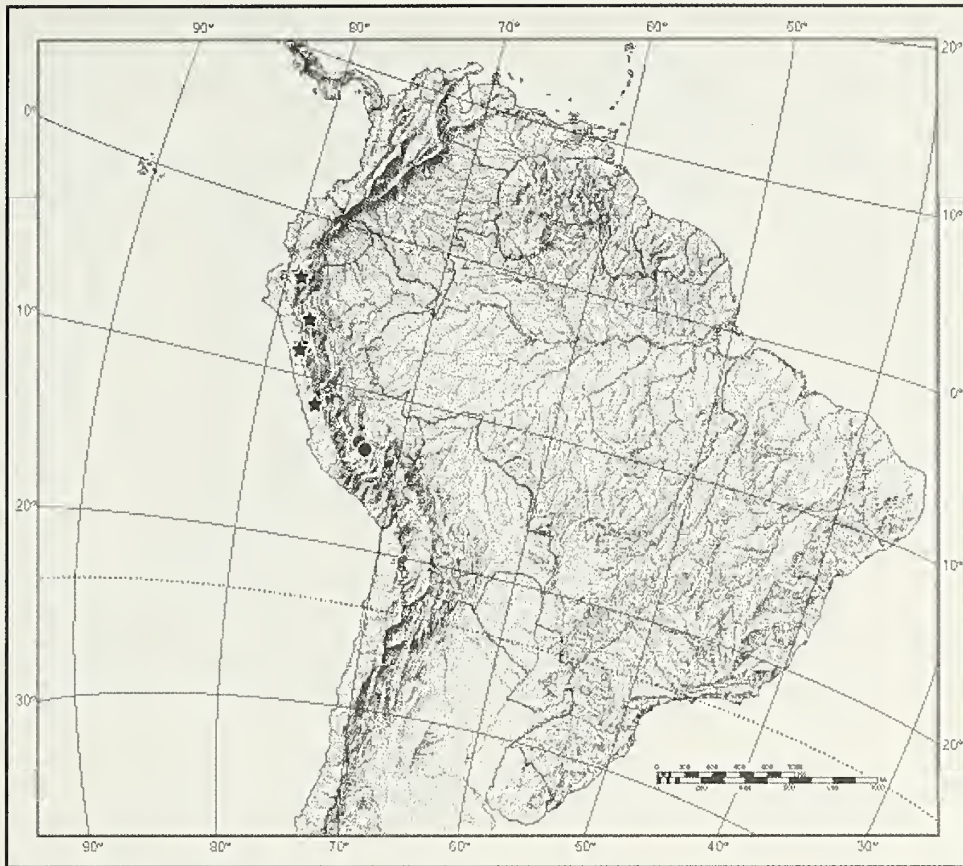


Fig. 20. Distribution of *S. michelle* (★) and *S. lamasi* (●).

Paraguay, and Argentina east to the cerrado of Brazil (MT, SP).

Strymon jacqueline Nicolay & Robbins, New Species

Diagnosis: The male and female dorsal wing patterns (Figs. 3, 5) are similar to those of *S. dindus* (F.), but the blue is a lighter hue and females often have orange spots on the forewing (Fig. 5). Also, *S. jacqueline* lacks the numerous ventral hindwing basal spots of *S. dindus* (Figs. 4, 6). The ventral wing pattern of *S. jacqueline* (Figs. 4, 6) is most similar to that of Central American *S. megarus* (Godart), but males of the latter have a brown "ray" along vein 2A on the dorsal forewing and females are brown dorsally without blue except for a few individuals from Mexico. The genitalia do not provide diagnostic characters, although penis length and shape of the male saccus and vinculum differentiate this species from some members of the *S. serapio* group, such as *S. serapio*.

Description of male (N=7): Mean forewing length 11.9mm, SD=0.87.

Dorsal wing pattern (Fig. 3): Forewing pale, chalky violet-blue with wide brown border along costa and outer margin, becoming narrow at tornus. Large, rectangular black scent patch fills distal three quarters of discal cell. Dark outer marginal line edged by pale fringes. Hindwing pale, chalky violet-blue with narrow brown border at the apex. Orange-red, black pupilled cubital spot between Cu1 and Cu2, trace of black spot between Cu1 and 2A with prominent black anal lobe spot, bordered basally in red. Black outer marginal line dusted basally with white scales, fringes white. Narrow white-tipped black tail at Cu2 and a short projection at Cu1. Abdominal fold pale gray.

Ventral wing pattern (Fig. 4): Forewing pale gray with single postmedian row of macular, orange linear spots faintly dusted distally in black. White scaling from Cu1 to Cu2. Outer marginal line dark brown, fringes paler. Hindwing pale gray with two small orange spots at wing base, the largest located just below the costa. Broken, postmedian line of orange linear spots follows wing contour from apex to inner margin

with breaks toward the base at M1 and M3, then sharply angled to inner margin at 2A. These spots dusted distally by scattered black, then more conspicuous white scaling, not heavily scaled and not very prominent. Orange-red, black pupilled cubital spot and black anal lobe spot edged with orange-red and white scaling. Ill-defined line of white submarginal scaling between vein terminals bordering a short submarginal dark line edged in orange-red beginning at Cu2 and terminating at inner margin. Dark outer marginal line; the fringes pale.

Head: Frons white, with a few dark piliform scales from center. Labial palps white ventrally. Third segment of labial palps slightly shorter than basal two and covered with closely appressed scales. Scales between the antennal bases gray. Antennae black with about 16 white-ringed segments and a club with about 14 segments. Nudum confined to club.

Description of female (N=9): Mean forewing length 15.6mm, SD=1.27.

Dorsal wing pattern (Fig. 5): Forewing pale violet-blue, with very wide brown border along costa, wider at apex and outer margin, tapering to a point on the inner margin near the tornus. Inner margin, widely solid pale violet-blue with no dark margin. A thin black outer marginal line from the apex to tornus. Fringes narrowly pale. Hindwing pale violet-blue with dark brown costal border ending just below apex. A narrow, dark submarginal line from apex to Cu1. An orange-red black-pupilled cubital spot between Cu1 and Cu2, a vague dark spot below Cu2, and a small black anal lobe spot lightly dusted with orange-red scales at inner margin. Prominent outer marginal line black with a prominent white inner margin. Fringes pale with a very short, white-tipped tail at Cu1, and a long, narrow black, white-tipped tail at Cu2. Abdominal fold pale gray.

Ventral wing pattern (Fig. 6): Forewing same as male. Hindwing same as male, but a thin, sharply etched black terminal line from apex to anal lobe. Line of pale scales on inner edge, and pale fringes on outer edge.

Head: Same as male.

Types: Holotype: Male. Peru, Cajamarca, Km 62 Pacasmayo to Cajamarca, 600m, CA., PERU, 4 March 1981, leg. G. Lamas. Deposited in MUSM.

Paratype (8'M', 9'F'): 3'M' MUSM, same data as holotype, but with an additional label on one saying that it was collected on a cactus. 1'M' MUSM, Peru, Cajamarca, Pucará (06°02'S, 79°08'W), 1000-1300m,

9 November 1975, leg. G. Lamas. 1'M' MUSM, Peru, Cajamarca, Km 59, Pacasmayo to Cajamarca, 550m, CA., PERU (07°14'S, 79°03'W), 19 November 1998, leg. J. Grados. 1'F' USNM, Peru, Cajamarca, Km 59, Pacasmayo to Cajamarca (07°14'S, 79°03'W), 550m, 15 September 1999, leg. Robbins, Lamas, Ahrenholz. 2'F' MUSM & 1'M' & 3'F' USNM, Peru, Cajamarca, Puente Chetilla (07°13'S, 78°45'W), 1050m, 17 September 1999, leg. Robbins, Lamas, Ahrenholz. 1'F' MUSM & 2'M' & 1'F' USNM, Peru, Cajamarca, La Capilla, 10 km W. Chilite (07°12'S, 78°57'W), 700m, 17 September 1999, leg. Robbins, Lamas, Ahrenholz. 1'F' MUSM, Peru, Cajamarca, cerca Tamborapa (05°26'S, 78°48'W), 460m, 19 June 1995, leg. G. Lamas.

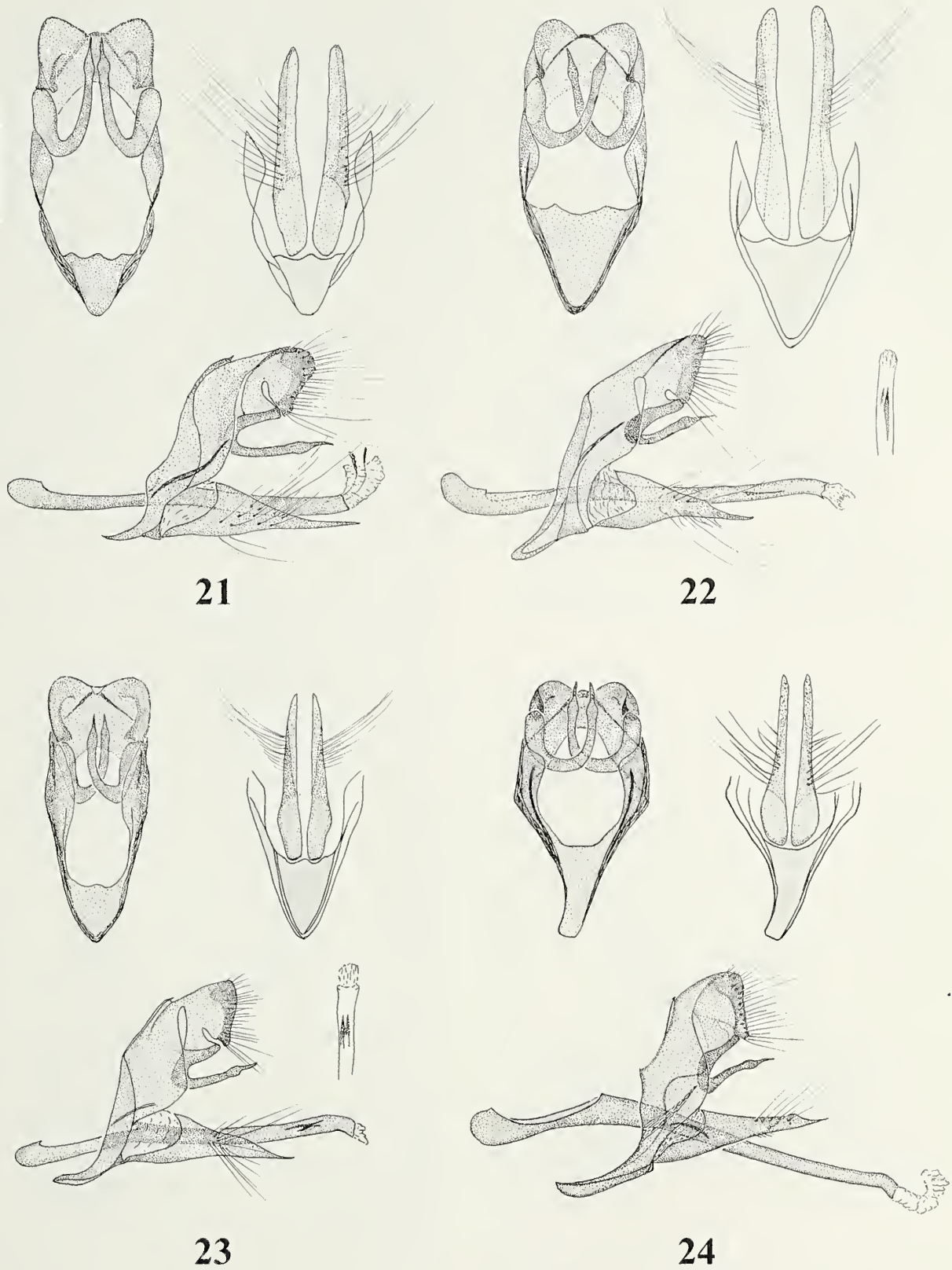
Etymology: This beautiful species is named as a noun in apposition for Jacqueline Nicolay, daughter of Stephen and Linda Nicolay and granddaughter of the senior author.

Wing pattern variation: The amount of orange on the dorsal forewings of females varies from absent to reasonably conspicuous (Fig. 5). The expression of orange scaling is positively correlated with elevation in the type series of nine females, but more specimens would be needed to verify this correlation. The two orange-red ventral hindwing basal spots vary in both sexes from well-developed to absent (Figs. 4, 6), which is highly unusual for the *S. serapio* species group. The ventral hindwing postmedian line varies slightly in width with those illustrated being relatively narrow (Figs. 4, 6).

Male genitalic variation (five dissections, Fig. 22): In some individuals, the dorsal cornutus, which is located to the left of the ventral one, is inconspicuous and may not be visible in lateral aspect (Fig. 22). Otherwise, the genitalia are indistinguishable from many species in the *S. serapio* group (Fig. 16 in Robbins & Nicolay 2002).

Female genitalic variation (four dissections, Fig. 26): The bursa copulatrix is typical of *Strymon* as described in Robbins & Nicolay (2002) with minor variation in the shape of the sclerotized loop of the ductus bursae.

Habitat and distribution: *Strymon jacqueline* occurs in dry scrub habitats in northwestern Peru (Cajamarca) at 460-1300m elevation in the Tumbesian Regions and the Río Marañón Valley. It has been collected in March, June, September, and November. Adults have been observed on vegetation along streams, on weedy roadside flowers, and on cactus plants in the "middle"



Figs. 21-24. Male genitalia in ventral aspect with valvae removed; saccus, vinculum, and valvae in ventral aspect, and male genitalia in lateral aspect (teeth on valvae and brush organs omitted). 21. *S. ahrenholzi*; 22. *S. jacqueline* with detail of penis tip in ventral aspect—the dorsal cornutus was not visible in lateral aspect; 23. *S. giffordi*; 24. male. Scale line 0.5 mm.

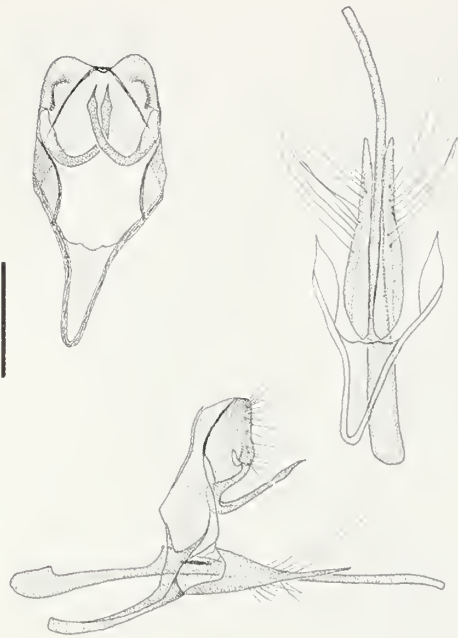


Fig. 25. *Strymon lamasi* male genitalia in ventral aspect with valvae removed; saccus, vinculum, and valvae in ventral aspect (cornutus omitted for clarity); and male genitalia in lateral aspect (teeth on valvae and brush organs omitted). Scale line 0.5 mm.

of the desert. It has not been found to date in similar habitats in southwestern Ecuador. Although this species appears to be exceedingly rare, ten individuals were found in one day at two localities.

Relationships: It is unclear which species within the *S. serapio* species group are the closest relatives of *S. jacqueline*. The dorsal wing pattern of *S. jacqueline* is shared with *S. dindus*, and the ventral wing pattern with *S. megarus*. The genitalia provide little definitive evidence.

Strymon giffordi Nicolay & Robbins, New Species

Diagnosis: Within the *S. serapio* group, the dorsal wing pattern of both sexes of *S. giffordi* is shared only with *S. veterator* (H.H. Druce) while the ventral wing pattern is shared only with *S. megarus*. The genitalia do not provide diagnostic characters, although penis length and shape of the male saccus and vinculum differentiate this species from some members of the *S. serapio* group, such as *S. serapio*.

Description of male (N=2): Mean forewing length 12.6mm, SD=0.14.

Dorsal wing pattern (Fig. 7): Forewing dark brown with pale fringes. Rectangular black scent patch

approximately 2mm in length that fills the distal end of the cell. Dusting of blue scales along the inner margin near wing base. Hindwing purple-blue with broad, brown costal margin tapering near veins M3 and M2 to a thin dark terminal line that continues to anal lobe. Anal lobe spot red with another small black spot between veins 2A and Cu2, and a small black cubital spot with basal red scaling between Cu2 and Cu1. A white-tipped black tail at Cu2 and a short one at Cu1. Abdominal fold gray, fringes pale.

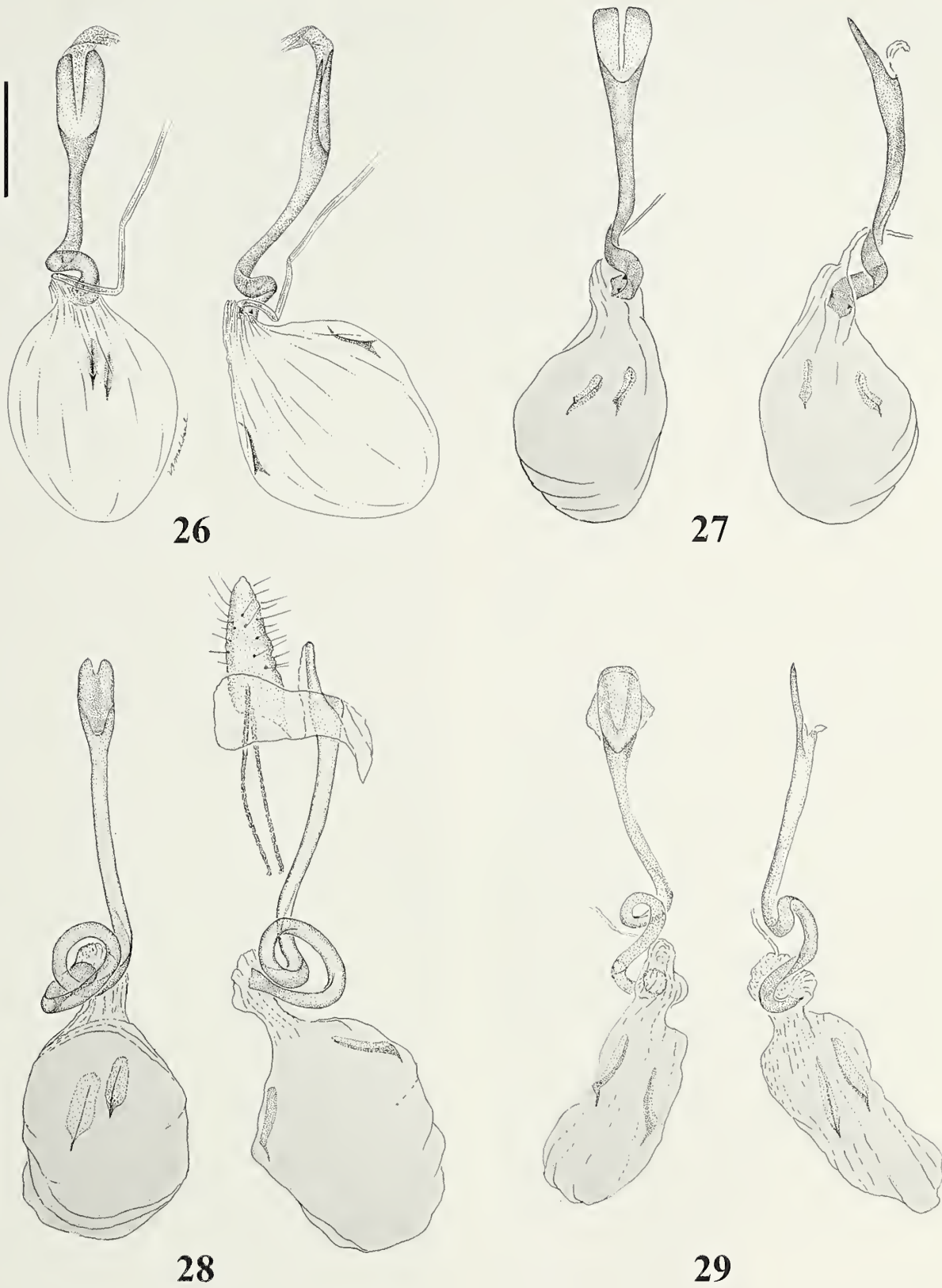
Ventral wing pattern (Fig. 8): Forewing gray, paler along inner margin. Postmedian line of red spots from costa to Cu2, distally edged in black then thinly in white. Narrow, obscure dark gray submarginal line with a dusting of white scales on both sides from costal margin to 2A. Margin a mixture of orange and black scales; fringes gray. Hindwing gray. Four postbasal black-edged red spots. Postmedian line from costa to inner margin consists of red spots distally edged in black, then white scales. Vague submarginal line of white scaling from costal margin to inner margin, distally bordered by thin line of gray crescents. Margin black with inner line of white scaling between Cu1 and anal lobe; fringes gray. Cubital spot red with small black spot below center; the anal lobe black with red inner half and a mixture of scattered red and black scales between veins 2A and Cu2.

Head: Frons white with dark piliform scales from center. Labial palps white ventrally. Third segment of labial palps slightly shorter than basal two and covered with closely appressed scales. Thin line of orange-red scales between antennal bases. Antennae black with about 18 white-ringed segments and a club with about 16 segments. Nudum confined to club.

Description of female (N=3): Mean forewing length 15.6mm, SD=1.27.

Dorsal wing pattern (Fig. 9): Forewing dark brown, fringes pale. Very sparse scattered blue scales along inner margin. Hindwing powder-blue with wide dark costal margin from costa to base of M2, thence distally to the outer margin. Narrow black marginal line. Small black spots between M2 and M3 and between M3 and Cu1. Cubital spot black with red inner margin. Black spot between Cu2 and 2A. Anal lobe spot red with a black outer margin. Long black white-tipped tail at Cu2, a short one at Cu1. Abdominal fold gray; fringes pale.

Ventral wing pattern (Fig. 10): Similar to male. Marginal line dark brown and fringes pale. Hindwing postbasal markings very sparse (two small spots



Figs. 26.-29. Female genitalia (bursa copulatrix) in ventral and lateral aspects. 26. *S. jacqueline*; 27. *S. giffordi*; 28. *michelle*; 29. *S. lamasi*. Scale line 1 mm.

instead of four) and the cubital spot more orange than red.

Head: Same as male.

Types: Holotype: Male. Brazil, Goiás, Serra Dourada (16.3°S, 50.6°W), 7 February 1980, leg. Gifford. Deposited in UFPR.

Paratype (1'M'&4'F'): 1'F' UFPR, same data as holotype. 1'F' USNM, same data as holotype except it was collected on 4 February 1980. 1'F' UFPR, Brazil, Goiás, Ilha do Bananal (this locality is now in the state of Tocantins), 28 June 1979, leg. Gifford. 1'F' USNM, Brazil, Minas Gerais, Serra do Cipó, 1300m, 2 May 1975, leg. C. J. Callaghan. 1'M' USNM, Brazil, Goiás, Pirenópolis (15°53'S, 48°59'W), 1200m, 2 May 1991, leg. Robbins & Becker.

Etymology: This species name is a patronym for the late David Gifford, who collected the holotype during his extensive field work in the cerrado of Brazil.

Wing pattern variation: Although the type series is limited, females are consistently and conspicuously larger than the males. The wing pattern of each sex shows almost no variability except that one female paratype, which is worn, has orange-yellow spots on the ventral wings instead of red-orange spots.

Male genitalic variation (two dissections, Fig. 23): The genitalia of the two known males are similar and are well-represented in the figure.

Female genitalic variation (three dissections, Fig. 27): The shape of the ductus bursae is variable. In each of the three dissections, the shape of the loop, the lamella postvaginalis, and the middle part is different. However, this intraspecific genitalic variation is typical of *Strymon*.

Habitat and distribution: This species is known only from Brazil's cerrado (cf. Brown & Mielke 1967a,b for an overview). Although recorded elevations are 1200-1300m, Serra Dourada and Ilha do Bananal are at lower elevations. The paratype collected by the junior author was found in a hilly, rocky, desert scrub area that is superficially similar to the desert-like caatinga habitat of eastern Brazil. As with most of the new species described in this paper, *S. giffordi* is rare in museum collections, but it is possible that additional specimens will be found misplaced in series of *S. megarus*.

Relationships: *Strymon giffordi* appears to be closely related to *S. veterator*, with which it shares a similar dorsal wing pattern, and to *S. megarus*, with which it shares a similar ventral wing pattern. It is sympatric with *S. megarus* and allopatric with *S. veterator*, which

occurs from Paraguay to the dry eastern foothills of the Argentinean Andes.

STRYMON MARTIALIS GROUP

This species group contains two Antillean species (*S. martialis* Herrich-Schäffer and *S. christophei* W.P. Comstock & Huntington) that have a single "wide" cornutus (0.05-0.1mm in dorsal aspect), and a lightly sclerotized plate on the dorsal posterior corpus bursae that is anterior of the ductus seminalis (Robbins & Nicolay 2002). The discovery of the following species was surprising because its range is widely disjunct from the Antilles and because it lacks the lightly sclerotized dorsal plate of the corpus bursae.

Strymon michelle Nicolay & Robbins, New Species

Diagnosis. The convoluted shape of the ductus bursae of *S. michelle* (Fig. 28) is shared in the Eumaeini only with *S. martialis* (Fig. 23 in Robbins & Nicolay 2002), and the ventral hindwing postmedian line of both species is similar (Figs. 12, 14, Fig. 40 in Robbins & Nicolay 2002). The lack of a lightly sclerotized dorsal plate of the corpus bursae and brown upperside wing color differentiates *S. michelle* from *S. martialis*.

Description of male (N=6): Forewing length 14.0mm, SD=0.95.

Dorsal wing pattern (Fig. 11): Forewing brown with a black rectangular (almost square), scent patch filling the distal end of the cell. Narrow, dark terminal line from the apex to the inner angle; the fringes pale. Hindwing brown with two submarginal black spots between veins Cu1 and 2A. Bordered basally by bluish-white scaling from M3 to 2A, and distally by white scaling from the apex to the anal lobe. Red anal lobe spot. Black marginal line from apex to anal lobe with a single narrow white-tipped, black tail at Cu2; fringes white.

Ventral wing pattern (Fig. 12): Forewing light brown, paler along the inner margin. A narrow white cell-end streak. Black postmedian line from costa to Cu2 with sparse orange-red scaling basally and white distally. Marginal black line with paler fringes. Hindwing light brown with black postmedian line, basally bordered in orange-red, distally in white. Nearly straight from costa to 2A, then curved rather sharply to inner margin. Faint white submarginal band from apex to prominent black, orange-margined

cubital spot. Faint dusting of pale blue scales between veins Cu2 and 2A. Anal lobe black, edged basally with orange-red and white scaling. Black marginal line basally edged with white from M2 to anal lobe. Fringes white with narrow dusting of orange-red scales along the posterior inner margin.

Head: Frons white with dark piliform scales intermixed. Labial palps white ventrally. Third segment of labial palps shorter than basal two and covered with closely appressed scales. Orange, black, and white scales between antennal bases. Antennae black with about 17 white-ringed segments and a club with about 14 segments. Nudum confined to club.

Description of female (N=4): Forewing length 13.0mm, SD=0.75.

Dorsal wing pattern (Fig. 13): Forewing brown with pale fringes. Hindwing brown except for pale, light blue on distal third of posterior wings. Black submarginal spots from M1 to 2A, largest spot between veins Cu1 and Cu2. Anal lobe spot red and black. Marginal line black; fringes white. Single white-tipped, narrow black tail at Cu2.

Ventral wing pattern (Fig. 14): As in male, but postmedian line more prominent.

Head: Same as male.

Etymology: This beautiful species is named as a noun in apposition for Michelle Dawn Nicolay, the daughter of Joe and Dawn Nicolay and the granddaughter of the senior author.

Types: Holotype: Male. Ecuador, Loja, Loja-Catamayo Rd., Km 28, 1700 m, 10 Sept. 1975, leg. S. S. Nicolay. Deposited in USNM.

Paratypes (5'M' & 5'F'): 3'F' USNM, same data as holotype. 1'M' MECN & 1'M' USNM, Ecuador, Loja, Vilcabamba, 1600m, May 1974, leg. R. de Lafebre. 1'F' RCB, Ecuador, Loja, 4 km E. of Catamayo, 1400m, May 2001, leg. I. Aldas, R. C. Busby. 1'M' MUSM, Peru, Amazonas, 3.5 km S Quebrada Mariposa (06°20'S, 77°56'W), 1700m, 23 August 1998, leg. J. Grados. 1'F' USNM, Peru, La Libertad, Casmiche (07°59'S, 78°39'W), 1950m, 27 September 1999, leg. Robbins, Lamas, Ahrenholz. 1'M' MUSM, Peru, La Libertad, alto Río Chicama, Coina, 8-9 May 1982, 1900-2000m, leg. G. Lamas & E. Pérez. 1'M' MUSM, Peru, Lima, Huinco, 1800 m, 20 September 1965, leg. P. Hocking.

Wing pattern variation: Wing pattern and wing size are remarkably similar among the 11 types. However, rounder wings and light blue color on the posterior half of the dorsal hindwings distinguishes females from males.

Male genitalic variation (four dissections, Fig. 24): In specimens with a non-everted vesica, as illustrated in the figure, the cornutus is at the anterior end of the external penis, but the vesica is often partially everted. The cornutus is not as wide (about 0.04mm in dorsal aspect) as that of *S. martialis* and *S. christophei*. A short process on the anterior vinculum is associated with the anterior base of the brush organs, and its occurrence is consistent in the four dissections. Otherwise, the male genitalia barely differ from those of *S. martialis* and *S. christophei*.

Female genitalic variation (three dissections, Fig. 28): There is slight variation in the exact shape of the loops of the ductus bursae among the three dissections.

Habitat and distribution: *Strymon michelle* is known from the dry mountains of southwestern Ecuador and western Peru in a narrow elevational band from 1400-2000m. Ten specimens are from the western slope of the Andes and one from the inter-Andean Río Marañón Valley (Amazonas). *Strymon michelle* inhabits desert with sparse, scrubby growth, including various species of cacti and small trees. It co-occurs with *S. daraba* (Hewitson) (= *S. tyleri*, Robbins & Lamas 2002) and *S. davara* (Hewitson), which are often abundant in contrast to *S. michelle*. Despite extensive searching during the past decade in suitable habitat in Ecuador and Peru, only three additional individuals of *S. michelle* have been found.

Relationships: *Strymon michelle* is most closely related to the Antillean *S. martialis* and *S. christophei*, but the relationship of these three species is unresolved. The convoluted ductus bursae and ventral hindwing postmedian line suggest that *S. michelle* and *S. martialis* are sisters while the lightly sclerotized posterior dorsal corpus bursae suggests that *S. martialis* and *S. christophei* are sisters. Although the straight postmedian line on the ventral hindwing of *S. michelle* superficially resembles those of sympatric *S. daraba* and *S. ahrenholzi*, these species are structurally different and are placed in different species groups (Robbins & Nicolay 2002).

STRYMON MELINUS GROUP

This species group is not delimited by clear-cut synapomorphies, but all included species lack a scent patch on the dorsal surface of the male forewing and have genitalia that are identical, or nearly so, to those

of *S. melinus* (cf. Figs. 9, 18 in Robbins & Nicolay 2002). Within the group, *S. rufofusca* (Hewitson) and *S. cyanofusca* Johnson, Eisele & MacPherson have more rounded wings, especially female hindwings, than those of the other species, and males set up mating territories on small shrubs rather than on hilltops (Robbins unpubl.). We have discovered a new "rounded wing" species of the *S. melinus* group.

***Strymon lamasi* Nicolay & Robbins, New Species**

Diagnosis: *Strymon lamasi* is distinguished from other *Strymon* species by (1) faint submarginal orange spots on the ventral surface of the forewing, especially in cell Cu1-Cu2 (Figs. 15, 17, the spots are very faint in the illustrated male), (2) a cornutus at the anterior end of the external penis (Fig. 25, this character is shared only with *S. michelle*, as discussed below), and (3) a long (~0.8mm) sclerotized segment of the ductus bursae between the corpus bursae and the most posterior loop (Fig. 29).

Description of male (N=41): Mean forewing length 13.5mm, SD=1.43.

Dorsal wing pattern (Fig. 15): Forewing light reddish brown with a narrow marginal black line and paler fringes. No scent patch. Hindwing ground color same as the forewing with one or two submarginal cubital spots distally black pupilled. Faint dusting of orange scales between veins M3 and Cu1. Anal lobe spot, small, black and faintly outlined distally in white and pale orange scaling. A single narrow, black tail at Cu2.

Ventral wing pattern (Fig. 16): Forewing reddish-brown, paler along the inner margin. Narrow marginal black line, with paler fringes. Postmedian brown line curves unevenly from R3 to Cu2. Bordered basally with dull red scales and distally with white. Faint, pale submarginal crescents. Hindwing reddish-brown. Postmedian line from costa to inner margin. Same three colors as forewing. Two submarginal bands of pale crescents, separated by brown ground color. A small cubital black spot is basally pale orange with a faint dusting of pale orange scales in space Cu1-M3. Black anal spot tiny, faintly outlined in white and orange scales. Narrow marginal black line with white fringes.

Head: Frons white with dark piliform scales intermixed. Labial palps white ventrally. Third segment of labial palps shorter than basal two and covered with closely appressed scales. Orange, black, and white between antennal bases. Antennae black

with about 18 white-ringed segments and a club with about 15 segments. Nudum confined to club.

Description of female (N=16): Mean forewing length 12.7mm, SD=1.87.

Dorsal wing pattern (Fig. 17): Pale reddish-brown as in male with a scattering of orange overscaling within and beyond the cell. Black marginal line and white fringes. Hindwing same reddish brown. Black cubital spot at base of large orange spot with an additional small patch of orange scaling above the cubital spot between veins Cu1 and M3. Faint dusting of orange scales near black anal spot. Fringes white, with a black marginal line.

Ventral wing pattern (Fig. 18): Forewing similar to male, but with a paler inner margin. Postmedian line more boldly colored, the red scales less dense basally. Diffuse submarginal pale crescents dusted with red scaling. Black marginal line outlined sharply by the white fringes. Hindwing color and pattern the same as in the male, but postmedian line more heavily marked with somewhat brighter and more extensive colors.

Head: Same as male.

Types: Holotype: Male. Peru, Cuzco, 15 km SW Limatambo, 2000m, 10 October 1981, leg. G. Lamas. Deposited MUSM.

Paratypes (40'M' & 16'F', MUSM & USNM): 3'M' & 1'F' Peru, Apurímac, E. of Curahuasi (13°33.04'S, 72°36.85'W), 2200m, 21 June 2003, leg. R. Robbins. 21'M' & 11'F' Peru, Apurímac, Río Pachachaca, 2km S. Matará (13°46.57'S, 72°56.35'W), 2050m, 22 June 2003, leg. R. Robbins. 15'M' & 2'F' Peru, Cuzco, Quebrada Uraca, SW of Limatambo (13°30.04'S, 72°26.26'W), 2800m, leg. R. Robbins. 1'M' Peru, Cuzco, Limatambo, 29 October 1964 (MUSM). 1'F' same data as holotype. 1'F' Peru, Ayacucho, Ninabamba, 2300m, 5 April 1978, leg. P. Hocking. All 2003 specimens of *S. lamasi* were accidentally labeled "leg. R. Robbins", but some (we do not know which ones) were collected by G. Lamas and C. Peña.

Etymology: This species is named for Gerardo Lamas in recognition of his prodigious contribution to knowledge of the Peruvian butterfly fauna. In addition, he collected the holotype and part of the type series.

Wing pattern variation: Forewing length varies from 10.7-16.4mm in males and from 10.0-16.2mm in females, which means that the largest individuals have about twice the wing area of the smallest. Since larger

individuals tend to have more orange scaling on average than smaller ones, a small series of specimens could easily appear to be two species.

The dorsal forewing of both sexes varies from all brown to brown with orange patches over half the wing. The illustrated specimens (Figs. 15, 17) have some orange scales at the distal end of the discal cell. All specimens in the type series have a subterminal, black-pupilled orange spot in dorsal hindwing cell Cu1-Cu2. About half also have an orange spot in an adjoining wing cell (Figs. 15, 17). The illustrated ventral wing patterns (Figs. 16, 18) are fairly typical, but most specimens have less orange on the subterminal part of the hindwing than the illustrated female, sometimes reduced to a single cubital spot in wing cell Cu1-Cu2.

It is sometimes difficult to distinguish the sexes in the *S. melinus* species group because sexual dimorphism in wing pattern is minimal and because males lack androconia. However, females of *S. lamasi* can be routinely distinguished by their consistently more rounded wings, especially hindwings.

Male genitalic variation (four dissections, Fig. 25): There is substantial variation in the shape of the saccus, anterior vinculum, and length and curve of the penis, but this variation is equivalent to that in other eumaeine species (e.g., Robbins 1990).

Female genitalic variation (four dissections, Fig. 29): As with many *Strymon* species, the most variable part of the bursa copulatrix is the shape of the sclerotized loop in the ductus bursae. The anterior segment of the ductus bursae is "S"-shaped in three dissections (Fig. 29) and concave in the other.

Habitat, distribution, and behavior: All known specimens were collected in the dry upper Río Apurímac drainage at 2000-2300 m, mostly on weedy flowers, especially Milkweed (*Asclepias*). Additionally, seven males were observed occupying mating territories on low shrubs along paths between 1425 and 1525 hours. The behavior of the males was indistinguishable from that of male *S. rufofusca* (sometimes perching on the same shrubs at the same time), but individuals of *S. lamasi* were immediately recognizable in the field because they had a more robust body than *S. rufofusca*. *Strymon lamasi* is the only member of the *S. melinus* group that is restricted to habitats above 2000 m elevation.

Relationships: We place *S. lamasi* in the *S. melinus* species group because it lacks a scent patch and because it shares its underside wing pattern and

"rounded" wings with *S. rufofusca* and *S. cyanofusca*. It differs from these two species by its male genitalia, female genitalia, and wing pattern, as noted in the diagnosis above, and by its larger average size.

Although some individuals of *S. rufofusca* from the southern part of its distribution have a wingspan as wide as *S. lamasi*, they have a less robust thorax and abdomen. The phylogenetic relationships among *S. lamasi*, *S. rufofusca*, and *S. cyanofusca* are unresolved. The widespread *S. rufofusca* is sympatric with the other two, whose distributions are allopatric.

The only *Strymon* species in which the cornutus occurs at the very anterior end of the exterior penis are *S. lamasi* and *S. michelle*. However, other evidence does not support a close relationship between these two. *Strymon lamasi* lacks androconia and has relatively rounded wings, in contrast to *S. michelle*. The loop of the ductus bursae is quite complex in both—which may be correlated with a long vesica and a relatively anterior cornutus—but the shape is considerably different (Figs. 28, 29).

DISCUSSION

Strymon Systematics

Strymon now contains 54 described species. Robbins and Nicolay (2002) listed 48, but on the basis of new information, Robbins (2004) removed four names from synonymy, synonymized two others, and transferred one to another genus. We describe *S. ahrenholzii*, *S. giffordi*, *S. jacqueline*, *S. lamasi*, and *S. michelle* in this paper. There appear to be another 2-3 undescribed *Strymon* species, but sufficient material to assess variation is not yet available.

The five newly described species slightly alter characterization of the species groups previously proposed (Robbins & Nicolay 2002). *Strymon ahrenholzii* is the first species in the *Strymon serapio* species group with a straight or upturned penis tip, but is otherwise quite similar to *S. eremica*. *Strymon michelle* is the first species in the *S. martialis* group without a sclerotized "plate" on the posterior corpus bursae, but the shape of its ductus bursae is otherwise the same as that of *S. martialis*. The genitalia of the *S. melinus* group are homogenous except for those of *S. lamasi*, which are different from those of all other *Strymon*. We place *S. lamasi* in the *S. melinus* group because it and *S. rufofusca* share a similar wing pattern, wing shape, lack of androconia, and male behavior.

Endemism of *Strymon* Taxa in the Dry Areas of South America

Although some *Strymon* species, such as *S. sylea* (Hewitson) and *S. gabatha* (Hewitson), occur in wet lowland forest, most species are restricted to, or are most common in, xeric areas (Robbins & Nicolay 2002).

Many are widely distributed, but a few have restricted ranges in South America, such as the five species described in this paper. As an overview of the *Strymon* that have restricted ranges in the xeric regions in South America, (1) *S. ahvenholzi*, *S. jacqueline*, *S. michelle*, and *S. daraba* are endemic to the Atacama Desert of western Peru north to the Loja region of southern Ecuador, with the latter three also occurring in the inter-Andean Río Marañón Valley; (2) *Strymon lamasi* is endemic to Peru's Río Apurímac Valley; (3) *S. sabinus* (C. Felder & R. Felder) and a dark phenotype of *S. rufofusca*—probably a distinct species—are endemic to the llanos of Colombia, Venezuela, and the Guianas; (4) *S. ohausi* (Spitz) and *S. giffordi* are endemic to Brazil's cerrado; and (5) *S. veterator* appears to be endemic to the chaco in Argentina. Others, such as *S. tegaea* (Hewitson) and *S. evenica*, occur in more than one of these areas.

The dry inter-Andean valleys of Peru are arguably the most poorly collected of the South American xeric regions and are most likely to contain undiscovered *Strymon* species. For example, we found *S. lamasi* commonly at two localities in the upper Río Apurímac Valley, yet it was previously not represented in any North American or European museum.

Besides the endemic species listed in the previous paragraphs, a number of geographical variants of *Strymon* have restricted ranges in South America. Three distinctive geographical phenotypes of *S. bubastus* (Stoll) occur in Peru; one is endemic to the Atacama Region (to which the name *sapota* Hewitson refers), another to the Río Apurímac Valley, and a third to the Río Mantaro Valley. A slightly differentiated form of *S. yojoa* (Reakirt) inhabits the Atacama Region with another phenotype in the Río Marañón Valley. Finally, a slightly differentiated phenotype—the ground color of the ventral wings is darker on average—of *S. ziba* (Hewitson) occurs in the chaco of Argentina, to which the name *diaguíta* Hayward refers.

Strymon Biogeography and the Atacama Desert of Ecuador and Peru

Amphibian and lizard species that are endemic to the Atacama Desert and Río Marañón of northern Peru and southern Ecuador are usually reported to be related to other species in this region (Cadle 1991, Duellman & Wild 1993). In striking contrast, the closest relatives of birds in a variety of other regions (Best & Kessler 1995), as appears to be the case with *Strymon*. The evidence is reasonably strong that *Strymon michelle* is most closely related to two species that inhabit the Greater Antilles. There are no close relatives in suitable habitat in the intervening areas, and extinction is a possible explanation for this disjunct distribution. *Strymon ahvenholzi* appears to be the sister of *S. evenica*, a species that occurs in chaco and cerrado habitats east of the Andes. Although the wing pattern of *S. daraba* superficially resembles that of *S. yojoa*, it is closely related to *S. melinus* (Nicolay & Robbins 2002, unpubl.), a North and Central American species that ranges south to the llanos. Analysis of the entire Tumbesian butterfly fauna should provide a clearer picture of butterfly biogeography in this region.

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Biology, distribution, and extinction of *Colias myrmidone* (Lepidoptera, Pieridae) in Bavaria and its situation in other European countries

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Abstract: *C. myrmidone*, the Danube Clouded Yellow, one of the most endangered butterfly species in Germany and listed as threatened with extinction, is very likely to be currently extinct. For *C. myrmidone* and several other pontic south-east European species (i.e. of the genus *Cytisus*) the slopes along the river Danube served as an immigration route to Bavaria. The paper describes how a period of decline followed a period of suspected dispersal. In Germany, *C. myrmidone* was last reported in the year 2000 although great efforts were undertaken to find the species in 2001 and 2003. A combination of factors were likely to be responsible for the decline and extinction of *C. myrmidone* in Bavaria and Germany. Firstly, unfavourable grassland management led to a drastic deterioration of habitat quality over the last 10 years. Furthermore, larval habitats like sun-exposed xeric hillsides constantly decreased. Lastly, heavy summer rainfalls and mild, wet winters over more recent years were probably disadvantageous. The present study and recommendations developed were too late to prevent any apparent extinction across Germany.

The aim of this paper is to summarise the conservation biology of *C. myrmidone*, to discuss factors influencing its extinction in Bavaria and to provide insight into its conservation status in other European countries. Conclusions are given regarding the future conservation of the butterfly.

Key words: butterflies, *Colias myrmidone*, conservation, distribution, habitat-use.

INTRODUCTION

Colias myrmidone (Esper 1780), the Danube clouded yellow, is one of the most endangered butterfly species in Germany, if not globally. The species is listed as being threatened with extinction in both the Red Data Book of Germany (Pretschner 1998) and in the Red Data Book of Bavaria (Geyer & Bückner 1992). *C. myrmidone* is rapidly declining in neighbouring countries, e.g. the Czech Republic and Slovak Republic, Austria, and Hungary (Beneš et al. 2002, Kudrna & Mayer 1990). In Europe *C. myrmidone* was already classified as "vulnerable" in the 1980's and again recently (Heath 1981, van Swaay & Warren 1999).

Populations of *C. myrmidone* in southern Germany were restricted to Bavaria and at the end of the 20th century, the species completely disappeared from southern Bavaria. Its center ranges around Regensburg have been reduced to a few populations. Prior to 2000 the butterfly occurred north of Regensburg, near to Kallmünz in the Naab valley. Some authors (Weidemann 1989, Kudrna & Mayer 1990) pointed out a serious decrease in population sizes combined with a decline in habitat quality over the past 25 years and they predicted an imminent extinction of the species.

Although conservation efforts started in the late 1980's (Kudrna & Mayer 1990), it is very probable that *C. myrmidone* is now extinct in Bavaria and the species was last seen in the year 2000 (two males, Geyer et. al 2001).

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In this paper we discuss the reasons for this particular extinction and the situation in other countries.

THE BIOLOGY AND ECOLOGY OF *COLIAS*

MYRMIDONE

Understanding the distribution and extinction of *C. myrmidone* in Bavaria (Germany) requires knowledge of its biology and ecology. The Western European range of *C. myrmidone* should be referred to as *C. myrmidone myrmidone* (Esper, 1781). Populations found east of Southern Ukraine belong to the distinct subspecies *C. myrmidone ermak* (Grum Grshimailo, 1890). *C. myrmidone* occurs in Central Europe and eastwards in Poland, Hungary, the former Northern Yugoslavia, Bulgaria and across Southern Russia as far as Western Asia. The most western edge of the *C. myrmidone* distribution range is Bavaria, with the northern edge of the range not well-known (Menhofer 1938, Schneider 1936, Settele et al. 1999, Kudrna & Mayer 1990, Weidemann 1989, 1995). Single records from western and eastern Prussia date from the early 20th century (Menhofer 1938, Warnecke 1929). Generally, *C. myrmidone* is very locally distributed.

The butterfly is associated with continental biotopes (Kudrna & Mayer 1990). Suitable habitats at the edge of the western distribution range are calcareous and dolomitic grasslands with a southern slope exposure, primary heath-steppes, open heath-forests, secondary xeric grassland communities of grazed flat slopes, xeric valleys with oligotrophic grassland communities and clearings in pine-forests (Gauckler 1962, Settele et al. 1999, Weidemann 1995). *C. myrmidone* is confined to the occurrence of its host-plants, which, in Bavaria are several and complex. Thus Weidemann (1989, 1995) observed egg-laying on *Cytisus ratisbonensis* in the field, whereas eggs were also laid on *Cytisus nigricans* and *Cytisus purpurascens* in cages (plant nomenclature: Oberdorfer 1990). However, larvae did not feed on these broom species. By contrast, Metschl & Sälzel (1925) noted that females preferred *C. ratisbonensis* to *C. nigricans*, and Kudrna & Mayer (1990) found that larvae fed on both *C. ratisbonensis* and *Cytisus supinus*. There is also a different host-plant use in different geographical regions (Warnecke 1929). Nevertheless, *C. myrmidone* is monophagous on the genus *Cytisus*.

In Bavaria the Danube Clouded Yellow is usually bivoltine, but during long, hot summers a partial third generation may occur (Gauckler 1962, Metschl & Sälzel 1925). Adults of the first generation emerge in late May or in early June and fly until mid to late June. The second generation flies from mid July to early September (Metschl & Sälzel 1925, Kudrna & Mayer 1990, Settele et al. 1999).

Kudrna & Mayer (1990) stated that *C. myrmidone* requires large expanses of biotopes with a characteristic set of resources, i.e. flowery patches, rocks with food-plants, and shelter. Gauckler (1962) and Weidemann (1995) emphasised that eggs are always laid on the upper side of leaves near the top of a sprout. Furthermore only sun-exposed sprouts at microclimatically-favoured, warm sites were chosen for egg-laying. This observation was confirmed by Romstöck-Völkl et al. (1999) who additionally found that oviposition depended on the size and position of food-plant patches. There was a significant accumulation of oviposition on patches with over 30 sprouts present and in patches close to rocks (< 1m distance). A study in the White Carpathians and adjacent sites (Czech Republic and Slovakia) revealed similar results (Geyer et al. 2001, Dolek et al. in prep.). The Carpathian yellows used *Cytisus austriacus* as a food-plant with eggs laid at the top of young, exposed shoots as well. *C. myrmidone* is clearly largely thermophilous.

Young larvae feed on leaves near the top of a sprout and when resting, they firmly attached themselves to the upper side of the leaves by a small mat of silk (Geyer et al. 2001, Kudrna & Mayer 1990). In the laboratory caterpillars never move far from their resting position during early instars and although adult larvae become increasingly mobile, they remain on the top of the plant (Geyer et al. 2001). In the field, larvae of the first generation pupate on stems near the ground (Metschl & Sälzel 1925, Kudrna & Mayer 1990, Weidemann 1995, Settele et al. 1999), while in the lab pupation never took place near the ground, but at the end of the sprouts (Geyer et al. 2001). Furthermore, information on hibernation is contradictory. Weidemann (1995) stated that third instar larvae hibernate in the litter on the ground. By contrast, Metschl (1923, cited in Gauckler 1962) described that larvae hibernate on the stems of their host-plant.

The Danube Clouded Yellow is a specialized species with regard to microclimatic conditions and

larval food requirements. At the immature stages they are extremely vulnerable since they do not hide.

DISTRIBUTION AND EXTINCTION OF *C. MYRMIDONE* IN BAVARIA

C. myrmidone was first found in Bavaria in 1849. Speyer & Speyer (1858) wrote that *C. myrmidone* regularly appeared after 1849 at a well collected location near Regensburg, although it had never been seen before this. A possible hypothesis for this pattern follows: For several pontic southeastern European species (e.g. the plant genus *Cytisus*), slopes of the Danube served as a migration corridor (Gauckler 1962, Gößmann 1962, Weidemann 1995). These species are adapted to dry and hot summers as well as cold winters. Such conditions only occur in the most

continental parts of Germany, such as the Regensburg area. In the middle of the 19th Century the "Little Ice Age" ended bringing cold winters and wet summers to Europe for several centuries causing bad harvests and famines (e.g. www.aurocontrol.at/cgi-bin/lexikon.cgi?Kleine_Eiszeit). The wet summers in particular were certainly not very favorable for *C. myrmidone* thus preventing its expansion to Central Europe. At the end of the Little Ice Age and the once again changing climate an expansion to the west became possible.

During the second half of the 1800's, the butterfly's range expanded and many new sites were colonized (or discovered, if the above assumption is incorrect). At the beginning of the 1900's, *C. myrmidone* was known to have two main distribution centers, one in the Munich area and one in the Greater Regensburg area (Fig. 1). Most known



Figure 1: Distribution and decline of *C. myrmidone* in Bavaria. Literature used: Gauckler 1962, Knörzer 1914, 1917, Kraemer 1911, Kudrna & Mayer 1990, Menhofer 1959, Metschl & Sälzel 1925, Osthelder 1925, Romstöck-Völkl & Völkl 1996, Segerer et al. 1987, Warnecke 1929, Weidemann 1989, Wolfsberger 1950.

Munich area colonies were situated close to or south of Munich. *C. myrmidone* was also found across scattered sites in Upper Bavaria (Kudrna & Mayer 1990, Krämer 1911, LfU 2001, Osthelder 1925, Warnecke 1929, Wolfsberger 1950). Both Regensburg and Franconian Jura sites were on the slopes of the rivers Danube, Anlauter (a tributary to the Altmühl), Naab and Regen (Gauckler 1962, Knörzer 1914, 1917, Metschl & Sälzel 1925, Osthelder 1925). The village Emsing, near Eichstätt, was the western-most site of the butterfly (Krämer 1911).

However, *C. myrmidone* became extinct in all areas close to Munich before 1960, with a slower decline in the Jura. Gauckler (1962) enumerated over 20 sites with populations of the species. However, this meant a decline of about 50% from the maximum distribution. Between 1980 and 1989 only five sites near Kallmünz and Regensburg were left (Kudrna & Mayer 1990; Segerer et al. 1987). By 1996 Romstöck-Völkl et al. (1999) mentioned only three remaining sites. During an intensive investigation in 2000 Geyer et al. (2001) only found two males on a hillside near Kallmünz. In both 2001 and 2003 no individuals were found. The species appears to have become extinct in Bavaria since 2001.

EXPLANATIONS FOR THE EXTINCTION OF *C. MYRMIDONE* IN BAVARIA

Metschl & Sälzel noted decreasing numbers of *C. myrmidone* at the sites near Regensburg from about 1925. At that time people kept sheep and goats in stables in the villages and *Cytisus ratisbonensis* was gathered in large amounts as fodder. Osthelder (1925) wrote that populations of butterfly were declining because of increased cultivation of heathland that negatively impacted *C. ratisbonensis*.

By the end of the 1980's both Kudrna & Mayer (1990) and Weidemann (1989) warned of decreasing population sizes of *C. myrmidone* in the remaining colonies near Kallmünz. They attributed the steep decline to a massive deterioration of habitat quality. Weidemann (1989) specifically criticized the lack of grazing. The slopes near Kallmünz had been extensively grazed by sheep for a long period, with grazing being abandoned around 1960 (Kudrna & Mayer 1990). Weidemann (1989) pointed out that the lack of grazing resulted in the spreading of shrubs. Furthermore, increased nutrient (nitrogen)

input from air pollution and the surrounding agricultural practices resulted in a selective increase in grass growth (for nitrogen emission by air see e.g. Ellenberg 1985). All of these factors changed the microclimatic conditions especially those close to the ground. This would have prevented females of *C. myrmidone* from detecting suitable host plants for oviposition under the required microclimatic conditions. Moreover, the loss of a mosaic of habitat patches, resulting in a loss of diversity of the required resources was to the butterfly's disadvantage (Kudrna & Mayer 1990, Weidemann 1989). Kudrna & Mayer (1990) showed from mark and recapture studies that recaptures were only made within sites. This was the only mark and recapture study carried out, with the number of marked individuals being so low that the usually small number of individuals assumed to be moving between sites could not be assessed. Consequently, one might reconsider the interpretation that non-suitable, "butterfly-hostile" habitats between sites prevented adults from passing from one site to another. Clearly, the small population size itself makes movements between habitat patches extremely unlikely. Many former nutrient-poor meadows and open pine stands with rich herb-layers disappeared following fertilization, afforestation, or agricultural intensification. Kudrna & Mayer (1990) regarded the small remaining populations as intrinsically threatened, with increasing vulnerability from stochastic variations in the environment and population size.

To improve the habitat quality of suitable slopes, all authors agreed that the appropriate measures should have been taken to remove bushes. Furthermore, grazing, the traditional form of land-use in the Franconian Jura, was generally recognized as the most effective form of management for long-term conservation (Dolek 1994, 1995, Harnischmacher 1988). Kudrna & Mayer (1990) however noted that grazing could imply hidden dangers as sheep feed on *Cytisus* sp. In spite of this insight, sheep grazing was reintroduced as a form of conservation in the 1990's, without being monitored for its effectiveness. Ironically, now all measures are too late.

A combination of factors are likely to have driven the extinction of *C. myrmidone* in Bavaria. 1) There was a constant decrease in suitable habitats as slopes were converted when grazing ceased. 2) Unfavourable management practices were introduced on the

remaining grasslands in the 1990's. Some parts of the land lay fallow while other parts were used as fenced pastures with high grazing pressure. 3) Romstöck-Völkl & Völkl (1996) argued the loss of nectar plants due to an increased growth in grasses (annual herbs being suppressed) over large expanses of the sites and even in spite of the reintroduced sheep grazing. 4) There was no integrated management of grazing practice, since the behavior of caterpillars was not considered. Caterpillars feed and rest at the ends of sprouts that sheep feed upon and it is most likely that pupae as well as hibernating larvae remain on the plant, therefore a time period for harmless grazing was lacking (Dolek et al., in prep.). In order to avoid high mortality of *C. myrmidone*, only parts of each site should be grazed per year. Thus, a mosaic of differently grazed areas would be created. This policy would not only reduce the negative side-effects, but is also likely to increase total biodiversity. Unfortunately, grazing continued without a management plan and without sufficient instructions to farmers.

As part of a management plan shrubs were removed in 1993 and 1994 across part of the populated hillsides which anticipated an increase in the population size of *C. myrmidone* with an increase in habitat quality. Unfortunately, the butterfly became locally extinct at this comparably well, but formerly sparsely occupied hillside site. Romstöck-Völkl & Völkl (1996) assumed that this local extinction resulted from unknown ecological factors combined with a reduced population size. In any case, the outcome was not prevented by short-term conservation management.

Finally, high summer precipitation with wet, mild winters over the last few years presumably also contributed to the butterfly's decline. These unsuitable weather conditions are an example of stochastic ecological disasters that Kudrna & Mayer (1990) feared led to the extinction of many small populations in the past. Detailed information on the influence of a wet summer is available for *Parnassius apollo*: Large numbers of caterpillars were counted on a well studied site in the Northern Franconian Jura, but a long rainy period at the beginning of the flight period reduced butterfly numbers to a mere fraction of the expected number (Geyer & Dolek, unpubl. data).

Parnassius apollo went extinct locally in the mid 1990s on the hillsides near Kallmünz. Larvae of

Apollo are associated with sunny, warm, rocky places with abundant larval foodplant, *Sedum album* (Geyer & Dolek 1995). *C. myrmidone* requires similar microclimatic conditions for its larval development. It therefore seems likely that the strictly rock-loving *Parnassius apollo* died out first and was followed by *C. myrmidone* which is presumably less restricted to open rocks.

THE SITUATION IN OTHER EUROPEAN COUNTRIES

Kudrna & Mayer (1990) reported deteriorating conditions across the former Czechoslovakia. The Danube Clouded Yellow has been extinct in Bohemia since the 1970s. The local extinction of the last Bohemian populations coincided with the extinction from adjacent Austrian localities. Similarly, the butterfly has disappeared from most of its Moravian localities. Its current distribution in the Czech republic is now limited to the White Carpathians (Beneš et al. 2002), whereas in the Slovak Republic the last published finding was in 1950 (Kudrna & Mayer 1990). By contrast, van Swaay & Warren (1999) mentioned recent records in the Slovak Republic in their review of the European status of this species. Geyer et al. (2001) showed that *C. myrmidone* still occurs in the White Carpathians and adjacent areas on both sides of the border between the Czech Republic and the Slovak Republic. Although the meta-population there has higher numbers than in many other countries, there is no doubt of a significant decline. For example, at one site where *C. myrmidone* had a high density in 1999 and 2000 (Kopecek, pers. comm.), no butterfly was detected in 2001. Vegetation cover was laid fallow in the preceding two years, which presumably resulted in changes in habitat quality and the consequent disappearance of *C. myrmidone*. Populated sites appear to require small-scale, diversified land use: patchiness created by small scale grazing and mowing. However, such practices are currently diminishing throughout Central Europe. Without a change in current practices in the near future, this land use practice will be the key threat to the Danube Clouded Yellow and many other plant and animal species dependent on this dynamic habitat type.

For Austria, distribution data are available from an atlas based on the zoogeographical data bank "ZODAT" (Reichl 1992). Kudrna & Mayer (1990)

cited this resource that reported 11 quadrants inhabited by *C. myrmidone* after 1970, but only 4 quadrants after 1980. A 2000 survey revealed 7 more recent reports in ZOODAT. However, none of these occurrences has been confirmed (various informants, pers. comm., Geyer et al. 2001). Yet again, the most frequently cited cause of extinction was the change in habitat, e.g. at a site near Klagenfurt (Kärnten) patchy, mowed meadows were replaced by intensively cultivated meadows and cattle pastures (Dolek et al., unpublished). In the Red Data Book of Lower Austria (Höttinger & Pennerstorfer 1999) it is stated that there are new records (after 1980) from only a few sites (6 quadrants).

In Romania several colonies existed until recently (Mihut, pers. comm.). In the course of a visit in 2001, no individuals of *C. myrmidone* could be found in spite of an intensive search during the emergence time of both generations. Possible reasons for the rapid decline were the warm and humid weather during the previous winter and the extremely long dry period in the following summer (Mihut, pers. comm.). In contrast to the sites in most other western countries, such as Austria, habitat conditions still appear to be suitable.

The population sizes of *C. myrmidone* in Hungary are also in decline. Varga (pers. comm.) described the situation in terms of the most dramatic decline of any butterfly population observed in recent years.

In summary, *C. myrmidone* is decreasing in most parts of its geographical range (see Table 1). Although both proximate and ultimate causes of the declines and extinctions remain unknown, they appear to involve interacting factors as a result of changes in land use practices and changing weather patterns.

CODA

Although *C. myrmidone* would appear to be extinct on the last populated sites near Kallmünz, these hillsides still provide valuable habitat for other highly endangered insect species as butterflies (e.g. *Maculinea rebebi*, *Pseudophilotes baton*), bees (e.g. *Andrena ratisbonensis*) and grasshoppers (e.g. *Colliptamus italicus*). For some species the region is one of their last bastions in Germany. Hence the correct forms of conservation management should be implemented to maintain and improve habitat conditions. With

Table 1: Overview of present distribution and threat of *C. myrmidone* in other European countries.

country	references	region	situation and treath
Europe	van Swaay & Warren (1999)	whole	vulnerable, 20-50% SPEC 2: global distribution concentrated in Europe and considered threatened in Europe
Germany	Geyer et. al (2001), this study	Greater Regensburg area	extinct, changes in land use; declining area, unfavourable weather?
Austria	ZOODAT, Tschinder (pers. comm.)	Kärnten	probably extinct, changes in land use
Austria	ZOODAT, Zöchne (pers. comm.)	Greater Wien and Linz area	probably extinct, changes in land use
Hungary	Varga (pers. comm.)	whole	great decline, uncertain reasons
Czech Republic, Slovak Republic	Kopecek, Vitaz (pers. com.)	White Carpathians	decline, changes in land use
Romania	Mihut (pers. cmm.)	Greater Cluj Napoca area	unknown, no observaion in 2001, unfavourable weather?

such steps the habitat requirements of the Danube Clouded Yellow could be created and under such a scenario, possible existing populations might still occur and survive since it is always difficult to come up with concrete evidence for the extinction of any species. Should an overlooked population have survived, such management would obviously benefit the colony. Finally, reintroduction would be a further option following the restoration of habitat quality (for examples of other butterflies, see Wynhoff 1998).

As outlined above, the overall European situation of *C. myrmidone* is not promising. In most countries relative declines seem well underway and therefore conservation efforts in these places should start immediately. An international co-operation would be particularly useful for the Moravian and Slovakian White Carpathian colonies. The recent inclusion of *C. myrmidone* in the supplement of the FFH directive of the European Union will hopefully encourage immediate conservation efforts for the species.

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Territorial behavior of *Favonius taxila* (Lycaenidae): territory size and persistency

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Abstract: Territorial behavior of the hairstreak, *Favonius taxila* Bremer 1861, was investigated in Aomori Prefecture, Japan. Males were active in the morning hours, during which they showed territorial behavior. Territorial males persistently perched on almost the same leaf or a shoot and occasionally flew around a limited area, here referred to as inspection area. When another male intruded into this area, the resident and the intruder engaged in a circling flight. The flight occasionally strayed to outside of the inspection area, where it was terminated. The resident returned to his territory in most cases, but in a few cases, exchange of the territory owner occurred. In one case, a single butterfly occupied his territory throughout the observation period of 5 days, whereas in another, several times of exchanges occurred.

Key words: circling flight, intra-specific competition, residency, territory.

INTRODUCTION

For male mate-locating behavior of butterflies, Scott (1974) proposed three types: perching, patrolling and using pheromones. He stated that territoriality was absent or rare in butterflies. Recent investigations, however, revealed territorial behavior in many species, that perform perching behavior belonging to the families Nymphalidae (Watanabe 1977, 2002; Bitzer & Shaw 1980, 1983; Alcock 1985; Benson et al. 1989; Rosenberg & Enquist 1991; Lederhouse et al. 1992; Rutowski 1992; Kemp 2001), Papilionidae (Lederhouse 1982), Satyridae (Davies 1978; Knapton 1985), and Lycaenidae (Alcock 1983; Cordero & Soberón 1990; Fischer & Fiedler 2001). Rutowski (1991) cautioned that researchers should not confuse perching behavior with territoriality. Perching simply indicates staying in a specific area, whereas territorial behavior indicates a defense of a specific area.

According to anecdotal notes in a butterfly encyclopedia (Fukuda et al. 1984), some hairstreak species belonging to the tribe Theclini (Family Lycaenidae) show territorial behavior, occasionally comprising co-rotating flights between a resident and an intruder (Sibatani 1989). Such flights may last for more than 20 minutes in *Chrysozephyrus smaragdinus* Bremer 1861 (Fujii 1982). While other hairstreak species belonging to Theclini do not show territorial behavior, but show patrolling behavior for mating (Fukuda et al. 1984). Another characteristic feature of Theclini is that

some species show conspicuous sexual dichromatism on their wings, whereas others do not. Therefore, they are ideal subject to study intra- and inter- sexual selection. However, few systematic investigations have been made on behavior of butterflies of this group (but see Sibatani 1992). Their arboreal habits and relatively short activity period as adults (about a month) render field observations and experiments difficult.

To obtain systematic knowledge of their behaviour, we performed an observational study of a Thecline species, *Favonius taxila* Bremer 1861, at the foothills of Mt. Iwaki in Aomori Prefecture, where butterflies can be observed in close proximity to observers. Sibatani (1989) described males of *F. taxila* as showing the most conspicuous territorial behavior among species of *Favonius*. This paper reports activity time, territory size, occurrence of circling flights, and persistency of territory occupancy in this species.

STUDY SPECIES, STUDY SITE AND METHODS

Males of *Favonius taxila* have brilliant green dorsal wing surfaces due to interference of light. By contrast females are mostly black or dark brown. Forewing length is approximately 20 mm. This species inhabits deciduous forests in Hokkaido and Honshu, Japan, and is also distributed in northeastern China, the Amur region and Sakhalin in Russia, and the Korean peninsula

(Fukuda et al. 1984, Gorbunov 2001). Adults emerge once a year, mainly in July.

The field study was carried out near Dake Spa at the southern foothills of Mt. Iwaki in Aomori Prefecture (140° 20'E, 40° 40'N) from 13 to 19 July 1998 and from 18 to 23 July 2000. The study area was along a narrow path in deciduous forest. The main observation site was in grass and bushland (ca. 15 m x 30 m, Fig. 1) comprised of lower plants such as *Weigela hortensis* and ferns of 2 m height or less. The site was surrounded by forest containing *Quercus mongolica* trees 10 to 15 m tall (Fig. 1), the larval food plant of *E. taxila*. Butterflies appeared at the observation site, flying down to the grass and bushland and to the edge of the forests during a particular time of a day. We refer to this time period as activity time.

To obtain data of activity time, the main observation site was surveyed for flying or perching butterflies by slowly walking along the path every 5 to 60 min from

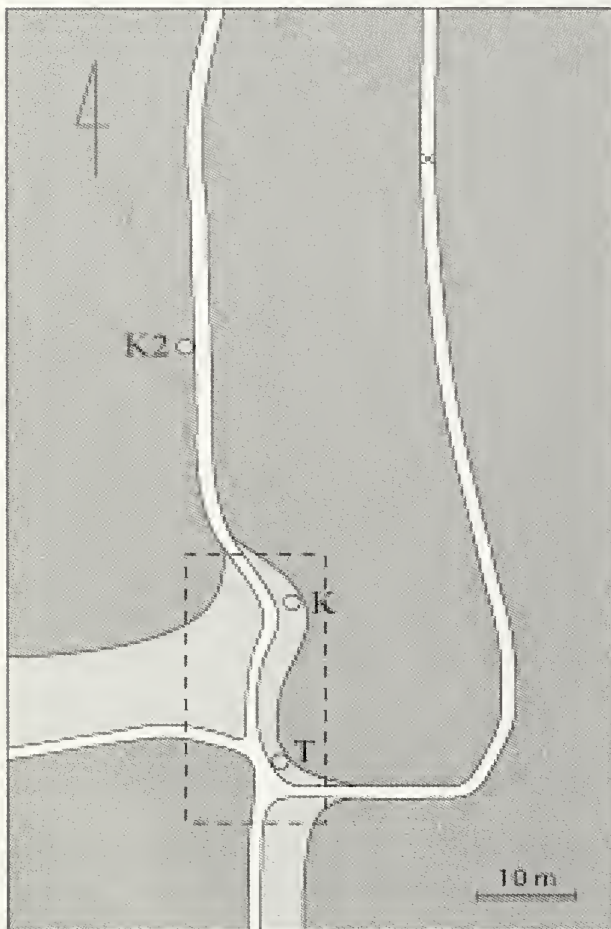


Fig. 1. A map of the study area. Dark gray: tall trees, Light gray: lower plants, White: bare ground (path) The dashed lined square is the main observation site. K, K2, and T are locations of the mainly observed territories.

6:00 to 18:00 on days with sunny weather. Air temperature was measured with a thermometer hung in the shade on a tree at 1 m height.

For the investigation of territorial behavior, males were captured and marked with a black or pink felt-tip pen (Mitsubishi™) along the edges of the ventral surface of the fore- and/or hind-wings of both left and right sides (Fig. 2). A total of 29 and 22 individuals were marked in 1998 and 2000, respectively.

During the activity time, a male who had occupied a territory as 'resident' typically perched on a fixed point, such as the tip of a shoot or twig of a tree, and occasionally and spontaneously flew around the perch point without being approached by other individuals. These spontaneous flights covered a limited range, which is referred to hereafter as the 'inspection area'. Inspection areas of resident males were recorded when they were most active during a day.

Residents reacted to approaching conspecific males with a particular flight: both individuals commenced with a rotation flight, which is traditionally called "manjidomoe" flight in Japanese (Fukuda et al. 1984). Other authors have termed this type of interaction spiral flight (Davies 1978), co-rotating flight (Sibatani 1989) or circling flight (Kemp 2001). Here we refer to it as circling flight. In *E. taxila*, two butterflies in circling flight circle in vertically separated planes (Fujii 1982).

The points where the circling flight was initiated and terminated, respectively, were plotted in a map. Initiation points were those at which the intruder was located when the resident started to rush towards him. These data were recorded when the butterflies were most active. To determine duration of territory occupation, residents of a territory were recorded every 15 minutes during activity time. This recording was made for 5 and 4 days respectively during 1998 and 2000.

RESULTS

Activity time and behavior

The number of *E. taxila* males counted at the main observation site is shown in Fig. 3. The activity time ranged from 7:30 to 11:30 in 1998. In 2000, butterflies were already active at 7:00 and became inactive by 11:00. Thus, the activity time was slightly earlier in 2000 than in 1998. Air temperature was also different

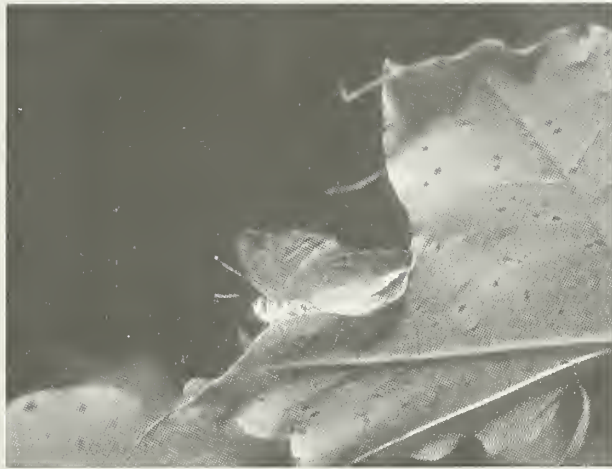
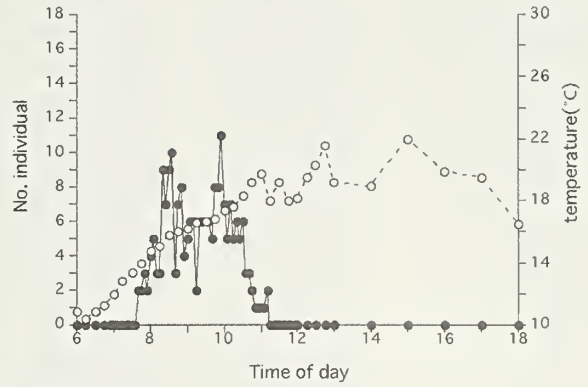
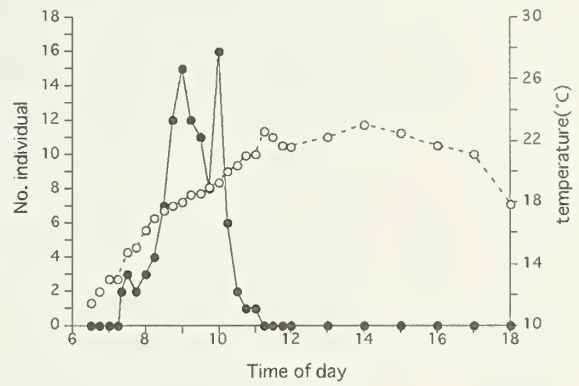


Fig.2a . A marked male exhibiting territorial activity, b: two males perching on the same leaf at the end of activity time.

a: 1998 July 14



b: 1998 July 15



c: 2000 July 19

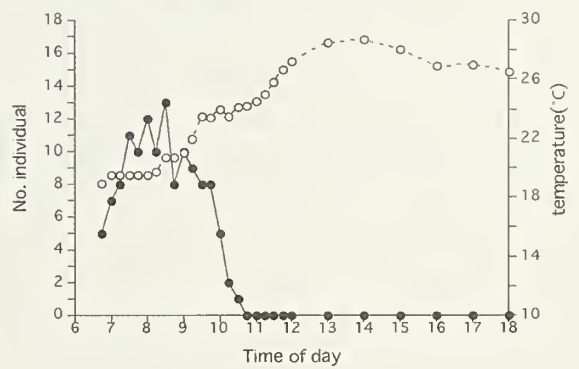


Fig. 3. Daily activity of *Favonius taxila*. The number of male *F. taxila* observed in the main observation site (solid circles) and air temperature (open circles) are shown.

between the two years: the air temperature at 7:00 was 12°C in 1998 and 20°C in 2000.

Prior to territorial activity, several butterflies were observed flying weakly around the canopy at approximately 10 m height and then coming down to lower places such as on the grass or bush surface where they basked with their wings opened. Thereafter, they initiated territorial activity. At the beginning, they seemed relatively insensitive to intruders, and occasionally disappeared from their territory for a while. Soon, they became responsive to intruders and persisted to their territory. During their territorial activity, they perched, with their wings opened, on a shoot or a twig extending from the bush (Fig. 2a). As the end of activity time approached, males became relatively less active again; they frequently perched with their wings closed and became insensitive to intrusion of other males. On a few occasions, two butterflies were found simultaneously perching on the same single leaf within the territory of one of them (Fig. 2b). At the end of activity time, butterflies were observed to fly up to high places, or could be found imbibing water on the ground.

Females were rarely seen during activity time, but near the end of the activity time, a few females were observed on the grass near or in a male's territory. However, mating behavior was not observed. At the main observation site, a closely related species, *Favonius jezoensis* Matsumura 1915, was found active and showed territorial behavior in the afternoon.

Inspection area

In 2000 the vegetation around the main observation site had largely been changed by bush cutting, and grasses were shorter than in 1998. The inspection area was approximately 33 m² for territory T by male No.8 in 1998, and approximately 60 m² by male No.9 and 32 m² by male J for territory K in 1998 and 2000, respectively (Fig. 4).

Circling flight

During activity time, the territory resident frequently interacted with intruding insects. In almost every case, the intruding insect was a conspecific male. The locations of the intruder when the resident started to rush toward him are shown in Fig. 4. Almost all points were located within the

inspection area. After the encounter, the two individuals performed a circling flight in a small circle for a period of a few seconds to several minutes. In a circling flight, the pair strayed apart, and occasionally moved out of the inspection area.

After almost every circling flight, the resident was confirmed to have returned to his territory, and the intruder flew away. The male returning after the interaction was defined as the winner of this interaction. There were so many circling flights that we were unable to record all of them. Therefore, we recorded the number of circling flight during specific periods. During the most active time from 9:02 to 9:49 on 14 July 1998, the resident of territory K (male No.9) engaged in 70 circling flights and "won" all of them. The resident in territory T (male No.8) also "won" all 36 circling flights observed from 9:00 to 9:30 on 16 July 1998.

Maintenance of territory

The residents of territories T and K on consecutive days are shown in Fig. 5. Territory T was occupied by a single individual, No.8, throughout the observation period from 15 to 19 July 1998. On the other hand, in territory K in 1998, the owner changed at least from No.9 through No.2 to No.3 in 5 days. Individual No.9 disappeared from territory K on July 15, but was later found to hold a new territory in another site approximately 30 m north from the original territory (K2 in Fig.1) on 16 July. In 2000, 5 individuals alternately occupied territory K.

The number of consecutive days that a resident was observed in a territory is defined as his residence duration (here, a resident is defined as the male that occupied the territories for more than two consecutive observation times). Mean residence duration was 1.6 days \pm 1.3 days (N=10). It should be noted that during an early hours of the activity time on a day, a foreign individual occasionally occupied the territory, but was soon expelled by the habitual resident who came to the territory later (Fig. 6).

On 16 July in 1998, the resident of the territory T (No.8) was found imbibing water on the ground approximately 70 m from his territory beyond the canopy (cross in Fig.1) after the activity time. On the subsequent day, this individual was again found in the same territory as the previous day, suggesting that butterflies have some kind of spatial memory about the location of their territories within a limited area.

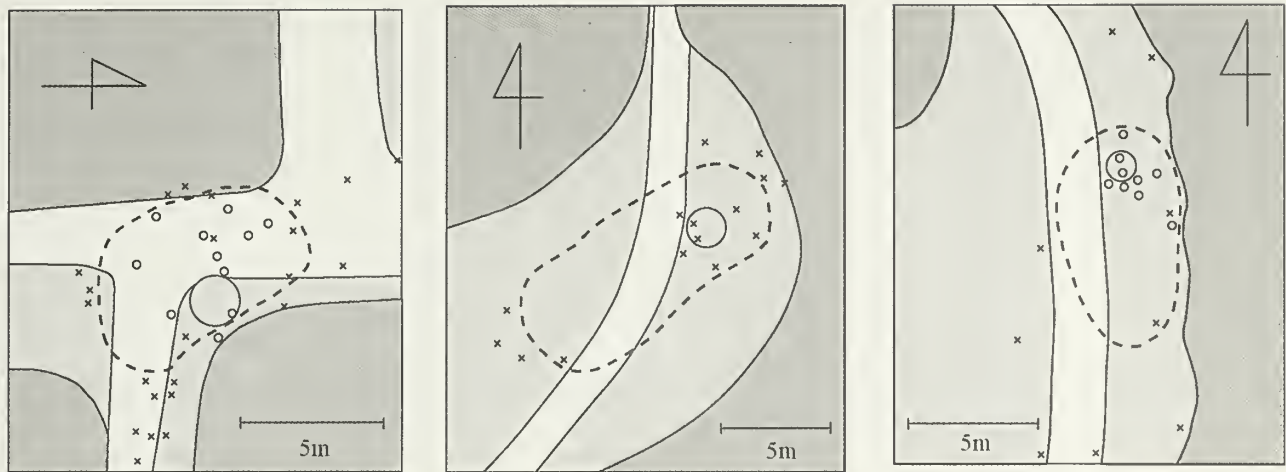


Fig.4 Map of territory structure of *Favonius taxila*. Dark gray: tall trees, Light gray: lower plants, White: bare ground (path), dashed lines: inspection area, circles: initiation points of circling flight, crosses: termination points of circling flight, Large circles: the plant in a territory where resident often perched. a; the territory T in 1998, b; the territory K in 1998, c; the territory K in 2000. The locations of territories (K and T) are shown in Fig.1. Fig.4b lacks circles because we did not recorded the initiation points.

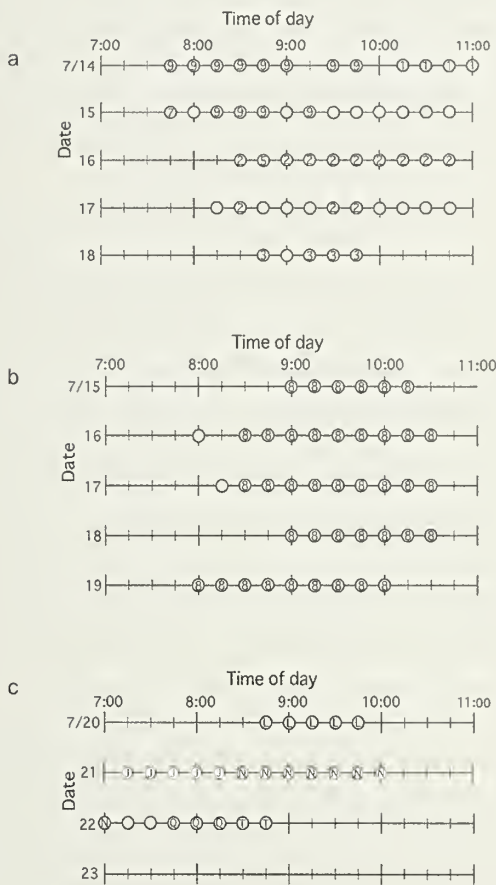


Fig.5 The resident of the territory T in 1998 (b), and of the territory K in 1998 (a) and in 2000 (c) on consequent days. The individual that occupied the territory at each time is indicated by the identification character. Open circles represent unmarked individuals or individuals we could not identify. In the territory K on 23 July 2000, no males were observed because of rain.

DISCUSSION

The activity time of *F. taxila* was limited to morning hours. This result coincides well with previous observations (Fukuda et al. 1984). One possible proximal factor that determines the activity time is air temperature, as suggested by later appearance in 1998, a cooler year, than in 2000. However, the morning activity may not be simply determined by air temperature because butterflies were not active in the afternoon even though temperatures in the evening did not largely differ from those during most of the active time in the morning. It appears likely that gross activity time is determined by some internal timing mechanism, e.g. a “physiological clock” (e.g. Sørensen & Loeschke 2002).

What are ultimate causes of the limited morning activity? At the present field site, a closely related species, *Favonius jezoensis* also occurs. This species, which is very similar in appearance to *F. taxila*, appeared and showed territorial activity in the afternoon. Thus, temporal segregation of the same space may be achieved between these species. Sibatani (1992) described that males of sympatric species of *Favonius* are partitioned with respect to their flying time during their territorial activity. He hypothesized that temporal segregation of flying time would exist in this genus. To test this assumption, it is necessary to examine the activity time of both species in the habitats where only one of them exists.

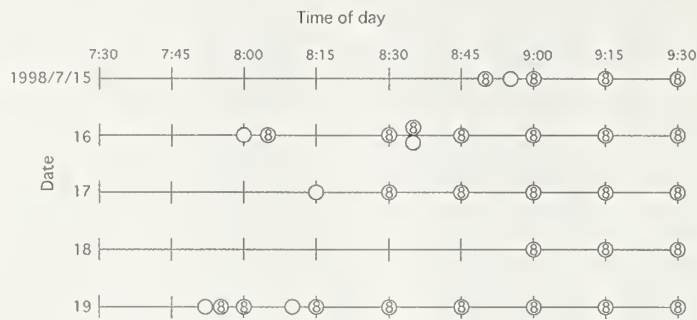


Fig. 6 Details of the shift of individuals that occupied the territory T in 1998 at the beginning of the activity time. Open circles indicate unmarked individuals. Two circles at 8:35 on 16 July indicate that the two individuals competed seriously for the territory.

It has been generally claimed that the resident of a given space is superior to an intruder in a territorial contest, a phenomenon called “effect of prior residence” (Ito et al. 1992). In butterflies, the “effect” has been observed in many species (reviewed in Kemp & Wiklund 2001). So, why do residents successfully defend their territories? According to the arbitrary asymmetry hypothesis, residents defeat intruders because competitors adopt a rule to fight seriously when one is the resident and to retreat when he is the intruder (Bourgeois strategy; Maynard Smith 1976). Davies (1978) showed that this strategy appears adopted in the speckled wood butterfly, *Pararge aegeria* Linnaeus 1758. However, Van Dyck et al. (1997) showed that wing color patterns, which correlate with thermal condition, play an important role in adult behavior. Recent work showed that in *Pararge aegeria*, the male whose body temperature was artificially controlled at 33.8°C won the territorial contest with the male whose body temperature was controlled at 26.7°C (Stutt & Willmer 1998). These body temperatures correspond to those of butterflies whose ecological status were a sunspot resident (33.8 °C) and a patroller in the wood (26.7 °C). Is it true that resident win also in nature because he can regulate his body temperature in the territory? In *F. taxila*, this seems unlikely. At the beginning of the activity time of *F. taxila*, a foreign individual that came into the space earlier than habitual resident and temporary occupied the territory, was later expelled by the habitual resident who came to the place later (Fig. 6). If resident wins because he can regulate his body temperature in his territory, the foreign individual (temporary resident) would defeat the habitual resident in that situation because he could regulate his body temperature in the territory while habitual resident could not. Thus residents win many

contests one after another. If thermal conditioning plays a crucial role in conflict, residents could not win so frequently in a short period (70 fights in 49 min or 36 fights in 30 min) because residents would lose body temperature by convective cooling during flight. This suggests that habitual residents have higher resource-holding potential (RHP; Parker 1974) for combat or else give higher value for the territory than intruders (Leimar & Enquist 1984). Note that RHP in butterflies’ combat has not been yet clarified (Kemp & Wiklund 2001).

Territory residents showed spontaneous flight within a limited area. This behavior seems to provide inspection of the territory. Therefore we named this space inspection area. Similar behavior has been observed also in *Oeneis chryxus* (Knapton 1985) and in *Lycaena hippothoe* (Fischer & Fiedler 2001). We define territory as a range of the inspection area. Ideally, the territory range should be determined by connecting the outermost points at which circling or fighting flights occurred. However our observations were too limited to provide this more precise data.

In the present study, the locations of the onset of circling flight were limited within the inspection area, whereas termination of these interactions frequently occurred outside this area. The situation also occurs with other butterfly species as *Oeneis chryxus* (Knapton 1985), *Lycaena hippothoe* (Fischer & Fiedler 2001), and *Polygonia c-aureum* (Watanabe 2002). The situation also appears different from observations with other animals: in mammals and birds aggressiveness frequently declines near the boundary of the territory (e.g. Matsubara 2003). In the case of butterflies, it appears usual that territories are not adjacent to each other, but neutral spaces are maintained among them (Knapton 1985). Chase or attack seem to continue into such neutral spaces.

Males of *F. taxila* showed territorial behavior and apparently do not use alternative strategies such as patrolling as has been observed in other butterflies (Davies 1978; Kemp 2001). Patrolling is a male mate-locating strategy for finding females while in flight without specific site fidelity. Our evidence leaves unclear whether territorial strategy is better for *F. taxila* than patrolling to acquire mates. We found few females that entered the territory. In a related territorial Theclinae species, *Chrysozephyrus smaragdinus*, females were observed to enter a male's territory accompanying a chase flight or mating attempt by males, and, though rarely, to copulate with the territory male (Fukuda et al. 1984). Similar phenomena have been observed in other butterflies (Lederhouse 1982; Wickman 1985; Alcock 1985). In *Pararge aegeria*, females appeared in territories of males more frequently than at other sites (Davies 1978), and all four virgin females released and successfully observed copulated with territorial males, but not with non-territorial males (Wickman & Wiklund 1983). Further close observations of *F. taxila* are needed to clarify females' appearance and behavior in males' territories.

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Effects of patch type and food specializations on fine spatial scale community patterns of nocturnal forest associated Lepidoptera

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Abstract. Species groups at different sites may build a meta-community that owns characteristic patterns of species distribution. Local differences, species interactions, random effects and dispersal characteristics can influence the diversity of local insect communities. We measured the diversity of nocturnal Lepidoptera at 12 sites of a temperate mixed forest that represented different patch types. To analyze causes of community structures, we tested for nestedness, checkerboards, clementsian, gleasonian, or evenly spaced gradients, and for random distribution as hypothetical patterns of a meta-community. The most diverse sites were patches at outer and inner edges of the forest. Lowest diversity was observed at a clearance inside the forest, and at three of four grove patches outside the forest. A cluster analysis of the similarity of Lepidoptera communities at different sites showed that the patch type and location, inside the forest (clearings, inner edge) or outside the forest (groves, outer edge), influenced the community structure. With increasing similarity of plant species growing at two sites, the faunal similarity of those two sites increased not significantly, indicating that differences of local plant communities caused a minor part of the faunal variation. The Lepidoptera communities were clearly nested, and different forms of gradients were detected in various subgroups of the Lepidoptera communities. Whereas nestedness indicated that patches were statistically depauperate subsets of the regional fauna, gradients showed that environmental changes between patches were responsible for different communities at that patches. Checkerboards and random distribution were not observed at all. This showed that interspecific competitions, as well as purely stochastic factors were not the driving forces in community regulation.

Key words: Communities, community patterns, food specialization, forest, gradient, nestedness, patch type, spatial distribution.

INTRODUCTION

The recognition of patterns in communities and of the causes of distribution and abundance of species as the most important determinant of natural community structure and composition is a central goal in community ecology. Ecological communities at different sites may build a meta-community that owns characteristic patterns of species distribution. Local and regional differences may transfer into the diversity of local communities, and the determinants of species richness of local communities are of large interest in research of the recent years (Zobel 1997; Hillebrand & Blenckner 2002).

Patterns that were observed in communities are at

least six that describe in an idealized way the distribution of species among sites, when species are ordered into a site by species matrix (Leibold & Mikkelsen 2002). Nested distributions occur, when species compositions on less rich sites are proper subsets of those on richer sites. Patterson & Atmar (1986) proposed to count the number of naturally occurring gaps, defined as species absences where species should have occurred in larger subsets, and used the number of gaps as a test statistics. So, a nested pattern occurs whenever the species observed in depauperate habitat patches are a subset of those found in more species-rich patches. A checkerboard distribution arises when certain species always competitively exclude each other. Species pairs then

have mutually exclusive distributions, but such pairs occur independently of other pairs (Diamond 1975). Clementsian gradients result in discrete communities that replace each other as a group (Clements 1916). Gleasonian gradients result in species turnover, but the arrangement of species ranges along the gradient is random (Gleason 1926). No discrete communities result in evenly spaced gradients but species ranges are arranged more evenly than expected by random chance (Tilman 1982). At random distributions there are no gradients or other patterns in species distributions among sites (Simberloff 1983). Each species may then be distributed independently of other species, causing a continuum, and all species have identical extinction probabilities at a site.

Community patterns represent idealized characteristics and result from diverse biogeographical and ecological processes. The diversity in local assemblages can be regulated by regional factors such as history of climate, evolution and migration and by local factors such as competition, predation, disturbance, or abiotic conditions (reviewed by, e. g., Hillebrand & Blenckner 2002). Differences in ecological specializations may influence the relative abundance of closely related butterfly species (Thomas 1995; Pullin 1995; Hughes 2000). Yet, for communities of Lepidoptera and Tenthredinoidea, Futuyma & Gould (1979) observed that few plant species in a deciduous forest had a highly distinct, specialized fauna. Various additional factors like patch isolation, temporal environmental stochasticity and dispersal limitations due to spatial constraints influence the colonization and abundance of Lepidoptera (e. g., Cappuccino & Martin 1997; Sutcliffe et al. 1997; Gutiérrez et al. 1999; Kitahara et al. 2000; Steffan-Dewenter & Tschardtke 2000; Petit et al. 2001; Nekola & Kraft 2002; Wahlberg et al. 2002).

Nestedness as a result from a wide array of such factors was observed in several butterfly communities (Fleishman & Murphy 1999; Summerville *et al.* 2002) and occurs also at fine spatial scales (Summerville *et al.* 2002). Other community patterns may occur as a result from species interactions as well as from spatial habitat changes. Furthermore, most investigations so far focused on species of grassland habitats. We therefore measured the patterns that occurred in Lepidoptera communities of different patches inside and nearby a forest in Luxembourg, Western Europe. We used different statistical tests developed by Leibold & Mikkelsen (2002) as well as by Atmar &

Patterson (1993, 1995) to detect nestedness, random and clumped distributions, or gradients. Effects of the degree and kind of host specializations of caterpillars of the observed Lepidoptera, as well as of taxonomical relations of species, on the type of community patterns were analyzed. To evaluate the importance of host specializations of caterpillars in determining the observed community patterns we also measured correlations of faunal and floral community similarities. We analyzed species occurrences at different patch types (clearances, inner and outer edge of forest, and groves nearby the forest) to determine effects of habitat changes on community patterns. Existing theory and our empirical data are discussed concerning which mechanisms are influential for the regulation of Lepidoptera communities in general and for the study system in particular.

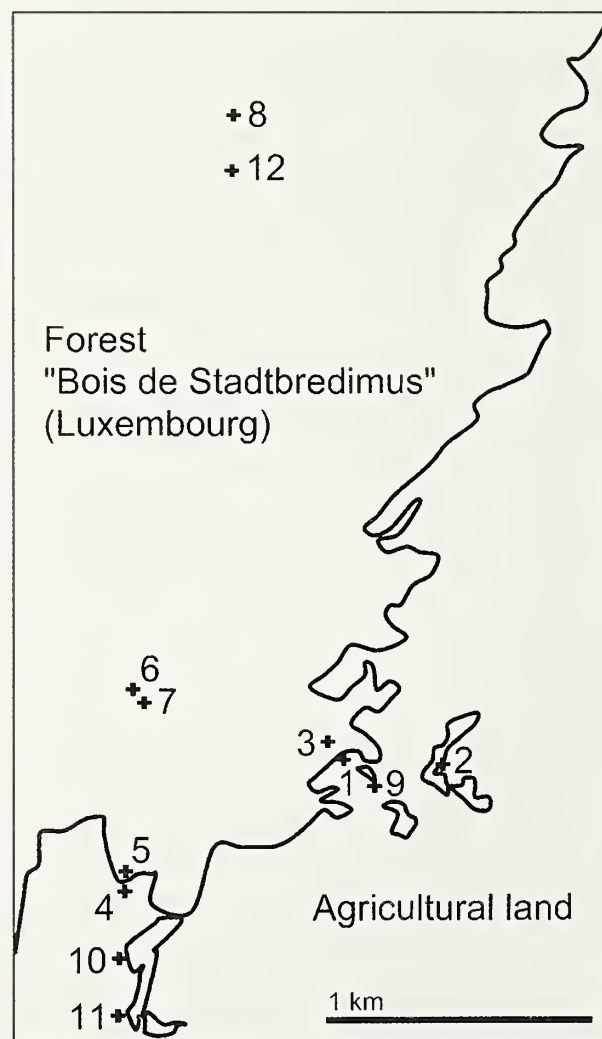


Fig. 1. Positions of sites at the forest "Bois de Stadtbredimus" (Luxembourg), where Lepidoptera species and the vegetation were investigated.

METHODS

Study area

Lepidoptera species and the vegetation were studied at 12 sites (Fig. 1) at the forest „Bois de Stadtbredimus“ in the south east of Luxembourg, Western Europe. Six of the 12 sites in each case represented one transect, reaching from clearances inside the forest (sites 6, 7, 8, 12) to the inner (3, 5) and outer edge of the forest (1, 4) and to groves lying outside the forest nearby (9, 10), or in larger distance (2, 11).

At sites 1 and 3 the forest is dominated by *Fagus sylvatica*, with *Hedera helix* covering large areas of the understory. At the forest edges *Prunus spinosa*, *Cornus sanguinea*, *Crataegus monogyna* grew outside, with *Quercus robur* and *Acer campestre* inside the edges. Outside the forest grassland covered most of the area, with *Arrhenatherum elatius*, *Anthoxanthum odoratum*, *Avenella flexuosa*, *Avenula pubescens*, *Lolium perenne* and *Poa trivialis* as the dominating grass species, and *Achillea millefolium*, *Lotus corniculatus*, *Medicago lupulina*, *Myosotis ramosissima*, *Veronica arvensis* as common herbs. At site 9 the edge of the grove was build by apple trees (*Malus sylvestris*), riddled with *Rosa* species, *Prunus spinosa* and *Sambucus ebulus*.

Fagus sylvatica and *Quercus robur* grew at sites 4 and 5 of the forest, with low numbers of flowering plants. The outer edge of the forest was build here by *Prunus spinosa* and *Carpinus betulus*. A pasture was located outside this site of the forest, with *Arrhenatherum elatior*, *Holcus lanatus*, *Lolium perenne*, *Poa trivialis* as grasses, and herb species like at sites 1 and 3. *Robinia pseudo-acacia* with *Rosa* sp. and *Prunus spinosa* grew at the groves of sites 10 and 11.

At sites 6 and 7 the tree species *Carpinus betulus* and *Quercus petraea* dominated the forest. Besides several grass species, *Sarothamnus scoparius*, *Populus tremula*, *Salix caprea*, *Rubus idaeus* and many *Rubus fruticosus* grew on the clearance area, where the two sampling sites were located.

Carpinus betulus, *Quercus petraea*, *Q. robur*, *Alnus glutinosa* and *Picea abies* were present at sites 8 and 12, as well as the bushes *Rubus fruticosus* and *Corylus avellana*. Among many grass species, herbs like *Leucanthemum vulgare*, *Galium mollugo*, *Rumex sanguineus*, *Anemone nemorosa* and *Geranium robertianum* grew on this clearance.

Sampling

Lepidoptera species were sampled seven times in the year 2001, simultaneously at all 12 sites once per month from April to October. The insects were captured during the nights by light trapping. These light traps with a fluorescent tube of 15 W power and a light emission spectrum of 320-480 nm wave length (super-actinic lights) were fixed in 1 m height above ground. Attracted insects fell into funnel pitfalls where they were killed by chloroform. To get early as well as late flying species the traps sampled from sundown to dawn. Macrolepidoptera were determined to species, using genital preparations where necessary (e. g. , in the genera *Mesopamea* and *Oligia*). The Lepidoptera species list was deposited by Goedert et al. (2003). Species were ordered in caterpillar host plant guilds and in groups of different degrees of food specializations (monophag, one host plant species; oligophag, 2 to 5 host species; polyphag, >5 host species) according to Ebert (1994-2001), Koch (1991) and Fajcik & Slamka (1996).

Plants were determined two times at each sampling site, in May and July. Vegetation cover was determined according to Braun-Blanquet (1964).

Diversity measures

The relative abundance of species was calculated as the abundance of one species in relation to the total individual number of all species of the investigated community. The “frequency of species” is given as the relative number of sites, where a species was present. Similarity of communities was calculated by the Sorensen-index S , with

$$S = \frac{2C}{A + B}$$

where C is the number of species present in both of two compared communities, and A , B are the number of species present in community A , or B .

The α -diversity was determined by the Shannon-Index H_s , with

$$H_s = -\sum \left(\frac{n_i}{N} \right) \ln \left(\frac{n_i}{N} \right)$$

where n_i is the abundance of species i , and N is the total number of individuals in the community.

The Evenness-index, or Shannon's equitability, is given by

$$E_s = \frac{H_s}{H_{\max}}$$

where S is the total number of species of a community; $H_{\max} = \ln S$.

A cluster analysis of similarity of Lepidoptera communities was done for presence absence data and the Euclidean distances on the basis of the list of species that occurred at the different patches. Ward's method was used for group linkage.

Testing for community patterns

We first tested for a nested distribution of all species by the nestedness temperature calculator (Atmar & Patterson 1995). We then tested for nestedness as well as for five further hypothetical patterns of species' distribution among sites (checkerboards, clementsian, gleasonian, evenly spaced gradients and random distribution) according to Leibold & Mikkelsen (2002). Coherence, turnover and boundaries refer to three aspects of an incidence matrix that characterize each pattern. Coherence was calculated by the occurrence of embedded absences in ordinated matrices. Species turnover was indicated by the number of times one species replaces another between two sites ("Replacements"). Boundary clumping was indicated by Morisita's Index. The statistical tests of coherence, species turnover and boundary clumping are explained in detail by Leibold & Mikkelsen (2002). Occurrence of patterns was tested for all Lepidoptera species, for different taxonomical groups, for groups of differential degrees of food specializations of caterpillars (polyphagous, oligophagous, monophagous), and for different types of host plant specializations. A software program based in Excel to conduct these tests was kindly supplied by M.A. Leibold, Dept. of Ecology and Evolution, University of Chicago. Mantel tests were done with the help of the software PopTools (version 2.5.9; Hood, G. M. 2003; <http://www.cse.csiro.au/poptools>).

RESULTS

Diversity at different patches

We observed 325 Lepidoptera species, with a total of 5893 individuals, as well as 247 plant species at the

12 sites of the investigated forest region. Calculation of nestedness temperature showed that the distribution of Lepidoptera species among the 12 sites was clearly nested ($p [T < 41.36^\circ] = 1.24^{30}$, run count=100, average temperature=65.78°, std. dev.=2.08°). Island reorganization vectors gave a row position of study sites as it is given in Table 1, where site 1 is the most species rich. Most diverse sites were patches at outer and inner edges of the forest, as well as patch 2 at a grove's edge. Diversity was lowest at a clearance inside the forest, and at three of the four grove patches outside the forest. The Lepidoptera species number at individual patches varied from 176 to 73, with total abundances being 804 respectively 166. Plant species number varied from 71 at patch 1 and 74 at patch 12, to 37 at patch 3. Obviously a correlation of Lepidoptera species number and plant species number or vegetation cover did not occur (Table 1; pearson correlation: $p=0.7420$).

Patch location and caterpillar host plants

A cluster analysis of the similarity of Lepidoptera communities at the different patches showed that communities at similar patches were grouped together (Fig. 2). All four patches at clearances as well as two patches at inner edges of the forest built one of two main groups; outer edges and grove patches built the second group. This indicated that the general patch type or location, inside or outside the forest, determined the communities. Whether the plant species growing at the different sites influenced the presence of Lepidoptera species, was analyzed by a comparison of floral and faunal similarities of communities (Fig. 3). With increasing similarity of plant species growing at two sites, the faunal similarity of those two sites increased slowly, explaining at best a minor part of the faunal variation only. A Mantel test revealed, that the dissimilarities of fauna and flora at two sites were not significantly correlated ($p=0.08$ for a positive correlation of faunal and floral dissimilarities). The extent of floral differences as well as of faunal differences of two sites also did not significantly depend on the geographical distance of that sites (Mantel test: $p=0.0775$ for a positive correlation of floral dissimilarity and geographical distance; $p=0.115$ for a positive correlation of faunal and geographical distance).

The relative number of Lepidoptera species that are specialized to different caterpillar host plants, did

Table 1. Patch types and characteristics of vegetation and Lepidoptera communities. Patches are arranged according to the island reorganization vectors of a nestedness calculation of all determined 327 Lepidoptera species. No. 1 is the most species rich patch, whereas least species inhabit patch no 12. Abundance values are numbers of individuals at a patch registered during seven catches between end of April and October of 2001. (ld, large distance to forest = 0.8-1.0 km; sd, short distance to forest = 0.2-0.3 km; H_s , Shannon-Index; E_s , Evenness-index; RA, Relative abundance of species; F, frequency of species at patches; $H_{max} = \ln S$)

No	Patch Type	Vegetation cover							Lepidoptera species				
		Plant sp. number	Tress %	Bushes %	Herbs %	Number	Abundance	Diversity H_s	Evenness E_s	H_{max}	Most abundant species	RA %	F %
1	Outer edge of forest	71	40	16	44	176	804	4.46	0.86	5.17	<i>Noctua pronuba</i>	8	100
											<i>Cyclophora linearia</i>	6	100
											<i>Campaea margaritata</i>	6	100
2	Edge of grove, ld	52	10	15	75	156	687	4.28	0.85	5.05	<i>Xestia c-nigrum</i>	7	100
											<i>Ochropleura plecta</i>	5	100
											<i>Epirrhoe alternata</i>	4	100
3	Inner edge of forest	37	50	20	30	147	847	4.23	0.85	5.00	<i>Cyclophora linearia</i>	8	100
											<i>Noctua pronuba</i>	6	100
											<i>Cyclophora annularia</i>	5	67
4	Outer edge of forest	87	44	15	41	138	484	4.28	0.87	4.93	<i>Xestia c-nigrum</i>	7	100
											<i>Cyclophora linearia</i>	7	100
											<i>Noctua pronuba</i>	5	100
5	Inner edge of forest	44	42	22	36	135	599	4.17	0.85	4.91	<i>Cyclophora linearia</i>	14	100
											<i>Cyclophora annularia</i>	5	67
											<i>Noctua pronuba</i>	5	100
6	Edge of clearing	65	42	20	38	129	381	4.36	0.90	4.86	<i>Noctua pronuba</i>	6	100
											<i>Calliteara pudibunda</i>	6	92
											<i>Mythimna impura</i>	6	83
7	Clearing, mean part	51	0	40	60	125	421	4.05	0.84	4.83	<i>Mythimna impure</i>	17	83
											<i>Noctua pronuba</i>	6	100
											<i>Deltote deceptoraria</i>	5	42
8	Edge of clearing	74	46	15	39	101	454	3.96	0.86	4.62	<i>Hypomecis roboraria</i>	6	75
											<i>Asteroscopus sphinx</i>	6	83
											<i>Campaea margaritata</i>	6	100
9	Edge of grove, sd	51	21	15	64	112	404	4.09	0.87	4.72	<i>Xestia c-nigrum</i>	10	100
											<i>Agrotis exclamationis</i>	6	92
											<i>Ochropleura plecta</i>	5	100
10	Edge of grove, sd	55	11	16	73	98	351	3.80	0.83	4.58	<i>Xestia c-nigrum</i>	16	100
											<i>Ochropleura plecta</i>	8	100
											<i>Mythimna impura</i>	6	83
11	Edge of grove, ld	53	19	10	71	83	295	3.77	0.85	4.42	<i>Xestia c-nigrum</i>	13	100
											<i>Ochropleura plecta</i>	12	100
											<i>Xestia xanthographa</i>	6	92
12	Clearing, mean part	74	0	45	55	73	166	3.95	0.92	4.29	<i>Calliteara pudibunda</i>	6	92
											<i>Habrosyne pyritoides</i>	6	92
											<i>Ochropleura plecta</i>	5	100

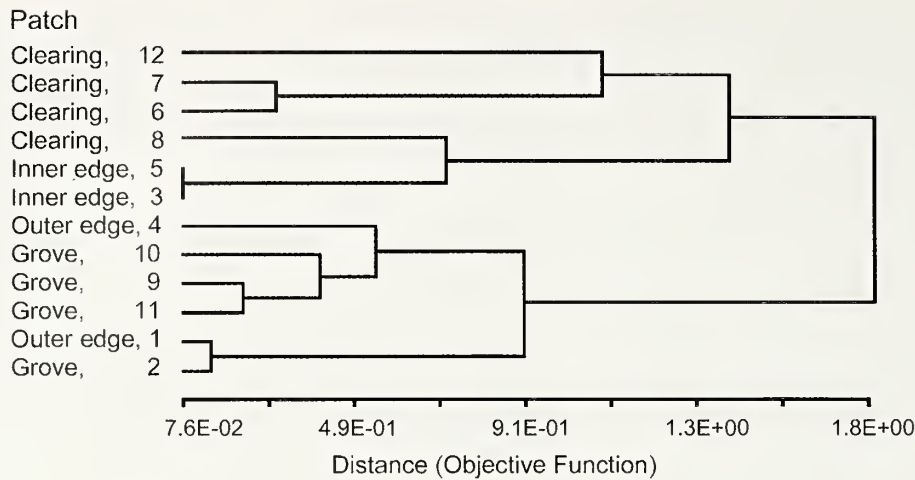


Fig. 2. Cluster analysis of similarity of Lepidoptera communities at different sites.

not vary significantly among sites of different diversity and location, whereas the absolute species number decreased with the diversity (Fig. 4; Table 2). Yet, at the sites 9, 10, and 11 outside the investigated forest, species that are specialized to conifers or deciduous trees only were more seldom, than at other sites. Consistently, species specialized to herbs as caterpillar food were more abundant at these sites.

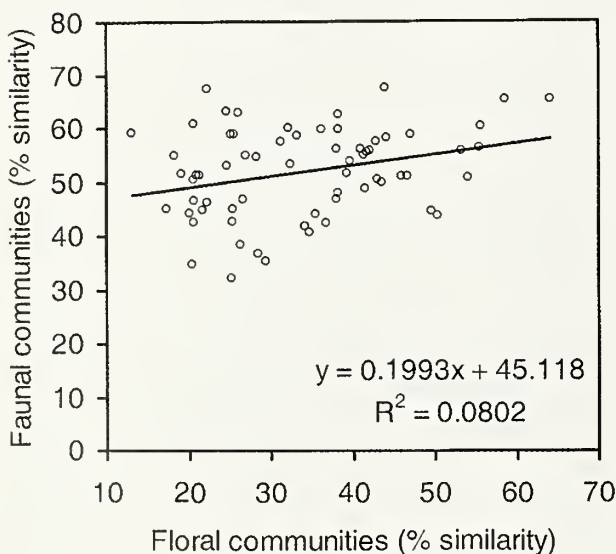


Fig. 3. Similarity of the Lepidoptera fauna at two sites, in dependency of the similarity of the flora at the same sites, respectively.

Community patterns

To find out which factors substantially regulate the occurrence of certain species at different patches, we analyzed the presence of different community patterns in the observed Lepidoptera species and in subgroups of those species. Subgroups consisted of different families, of species with different degrees of caterpillar specializations, or of species with different type of caterpillar host plants. Whereas nestedness temperature calculation identified a nested distribution in the observed 325 species of Lepidoptera, nested distributions and different forms of gradients (evenly spaced, Gleasonian, or Clementsian) were detected in the various subgroups of the Lepidoptera communities (Table 3). Checkerboards and random distributions were not observed at all. This showed that interspecific competitions, as well as purely stochastic factors were not the driving forces in community regulation. No patterns were detected in Lepidoptera species of group A, representing Hepialidae (3 species), Limacodidae (1), Zygaenidae (1), Lasiocampidae (6), Sphingidae (5), Drepanidae (10), and Geometridae (125) (Table 3). Lepidoptera species of group B, representing Notodontidae (16 species), Noctuidae (131), Pantheidae (1), Lymantriidae (4), Nolidae (5), and Arctiidae (17) showed a Clementsian distribution among patches. Different families showed different patterns, as well as did groups with different specializations of caterpillars (Table 3).

Polyphagous species were most frequent (247

Table 2. Linear regression analysis of changes in species numbers within groups with special caterpillar food resources and among patches. Patches were ordered according to decreasing total species number as obtained from nestedness calculation (as in Table 1 and in Figure 4). So, the independent variable was the species richness of the site, and the dependent variable was the proportion of Lepidoptera species which are specialized to a given group of food plants. The coefficient gives the slope of the respective regression line. Relative numbers of species within groups of food specializations are given in Figure 4.

Food specializations	Coefficient	SE	p
Regression of absolute species-numbers			
Deciduous trees	-2.6434	0.4981	0.0003
Coniferes	-0.3392	0.1136	0.0137
Herbs	-2.4895	0.6760	0.0042
Trees & bushes and/or herbs	-1.1049	0.2538	0.0014
Bushes and herbs	-1.0245	0.1500	<0.0001
Gramineae	-0.4441	0.2015	0.0521
Lichens	-0.3252	0.1377	0.0399
Others	0.0490	0.1304	0.7153
Regression of relative species-numbers			
Deciduous trees	-0.3738	0.5182	0.4872
Coniferes	-0.1419	0.0786	0.1011
Herbs	0.4216	0.6432	0.5269
Trees & bushes and/or herbs	-0.0507	0.2599	0.8493
Bushes and herbs	-0.2028	0.1270	0.1415
Gramineae	0.2816	0.1608	0.1105
Lichens	-0.0726	0.1204	0.5600
Others	0.1384	0.1106	0.2394

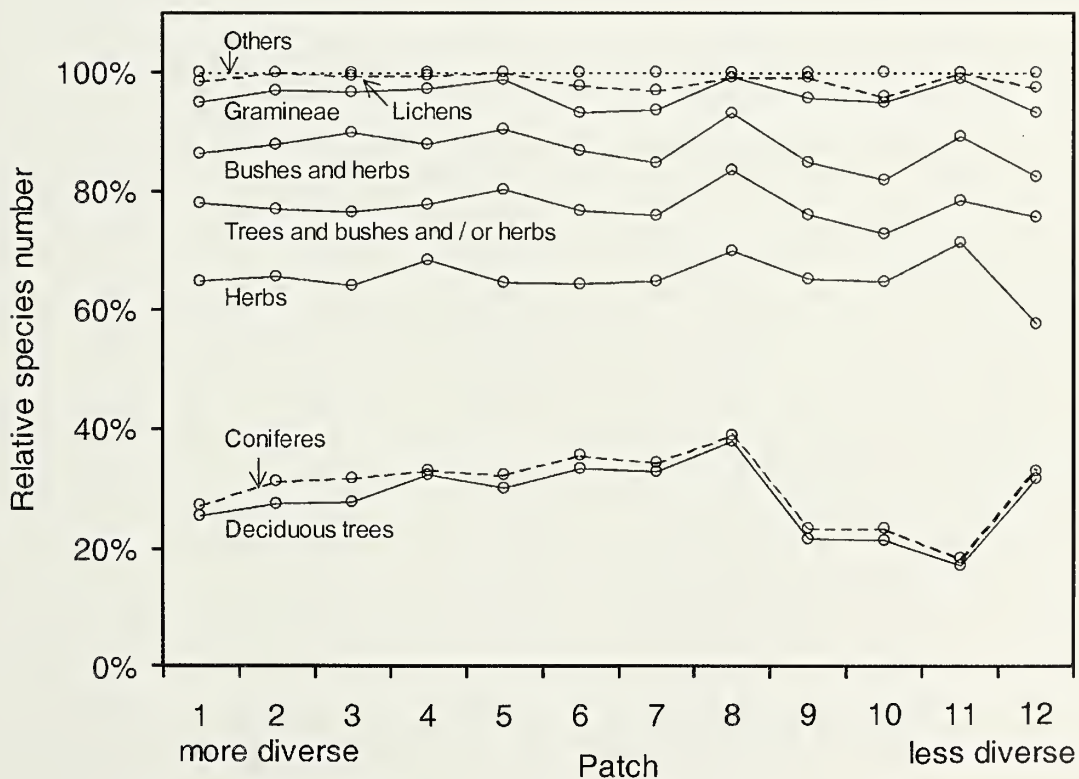


Fig. 4. Relative numbers of Lepidoptera species within groups with special caterpillar host plants (given in the figure) and at different patches. Patches are arranged from left to right according to their diversity as calculated from nestedness temperature calculator (left side, highest diversity; right side, lowest diversity).

Table 3. Community patterns of Lepidoptera species at different forest patches. Patterns were calculated according to Leibold and Mikkelson (2002). P-levels give the significance of differences between observed and simulated patterns. (N, number of species; DF, Degree of freedom; Lepidoptera A, B, see text; *Hepialidae ++; Hepialidae ++; Lasiocampidae, Limacodidae, Sphingidae, Zygaenidae; **Others: Furze, Ferns, Foliage, Clematis spec.; ***Gradient: Clementisian, Gleasonian, or Evenly spaced gradients could not be distinguished in these cases)

Community	N	Embedded absences			Replacements				Community boundaries				Overall community pattern***		
		ob-served	simulated (mean + SD)	p-level	coherence	ob-served	simulated (mean + SD)	p-level	turn-over mode-rate	Morita's index	Chi square	DF		p-level	Clumped or over-dispersed
Taxonomical groups															
Lepidoptera A	151	674	900.4 + 28.6	<0.0001	yes	19158	17468.7 + 8297.9	0.3189	mode-rate	0.000	128.00	149	0.8925	no	not detected
Lepidoptera B	174	963	1042.2 + 28.0	<0.0001	yes	12907	7268.0 + 3467.2	<0.0001	high	2.996	213.91	172	0.0164	clumped	Clementisian
Arctiidae	17	43	63.9 + 6.8	<0.0001	yes	357	610.7 + 177.2	<0.0001	low	1.753	29.82	14	0.0080	clumped	Nested
Drepanidae	10	16	25.3 + 4.9	<0.0001	yes	93	208.3 + 59.0	<0.0001	low	1.905	28.33	7	0.0002	clumped	Nested
Geometridae	125	488	718.4 + 21.7	<0.0001	yes	16636	13278.4 + 5026.1	0.0027	high	0.532	112.18	122	0.7268	no	Gradient
Noctuidae	131	648	760.1 + 16.2	<0.0001	yes	13565	9962.8 + 3356.4	<0.0001	high	0.000	107.00	128	0.9115	no	Gradient
Notodontidae	16	46	54.9 + 7.8	<0.0001	yes	548	391.5 + 135.8	<0.0001	high	1.333	19.67	13	0.1038	no	Gleasonian
Geometridae + Noctuidae	253	1432	1541.0 + 26.5	<0.0001	yes	32178	16082.1 + 5587.5	<0.0001	high	0.000	229.00	250	0.8256	no	Gradient
Hepialidae ++	12	41	53.4 + 6.7	<0.0001	yes	354	648.2 + 188.6	<0.0001	low	1.576	25.09	13	0.0225	clumped	Nested
Food specialisations of caterpillars															
A. Degree															
Polyphagous	247	1310	1489.1 + 32.9	<0.0001	yes	24537	14468.6 + 6742.1	<0.0001	high	1.065	246.36	245	0.4635	no	Gradient
Oligophagous	34	139	162.2 + 12.1	<0.0001	yes	3183	2014.7 + 806.4	<0.0001	high	0.943	30.86	32	0.5243	no	Gradient
Monophagous	44	198	205.8 + 11.5	0.0026	yes	2791	2608.4 + 872.6	0.3058	mode-rate	1.065	41.36	40	0.4109	no	not detected
B. Type															
Deciduous trees	93	420	516.3 + 19.5	<0.0001	yes	11561	5880.8 + 2327.6	<0.0001	high	1.970	110.36	90	0.0714	no	Gleasonian
Conifers	9	14	18.0 + 5.0	0.0006	yes	186	158.72 + 41.1	0.0029	high	1.637	17.47	6	0.0077	clumped	Clementisian
Herbs	105	448	577.1 + 25.9	<0.0001	yes	11785	6716.4 + 3091.9	<0.0001	high	1.338	109.09	102	0.2974	no	Gleasonian
Trees & bushes, herbs	41	148	200.2 + 14.7	<0.0001	yes	3285	2585.3 + 1038.5	0.0025	high	0.844	34.73	38	0.6216	no	Gradient
Bushes & herbs	32	79	146.8 + 9.3	<0.0001	yes	1374	2065.6 + 735.5	<0.0001	low	1.558	40.73	29	0.0727	no	Nested
Gramineae	27	89	117.2 + 10.7	<0.0001	yes	1047	1084.1 + 393.2	0.6419	mode-rate	0.714	18.29	24	0.7889	no	not detected
Lichens	11	14	27.0 + 5.9	<0.0001	yes	193	290.0 + 83.1	<0.0001	low	2.455	41.73	8	0.0000	clumped	Nested
Others**	9	1	6.2 + 3.0	<0.0001	yes	109	145.0 + 16.4	<0.0001	low	1.029	16.00	6	0.0138	clumped	Nested

species), compared to 34 oligophagous species and 44 monophagous ones. Polyphagous and oligophagous species showed gradients, whereas no patterns were detected in Lepidoptera species with monophagous caterpillars. Whereas nestedness indicated that patches were statistically depauperate subsets of the regional fauna, gradients showed that environmental changes between patches were responsible for different communities at that patches. Since nestedness and gradients were observed within taxonomical groups also, the related community regulating factors may act on taxonomically related species. So, species turnover should concern related species, and species loss of communities due to low patch quality may affect taxonomical subgroups of communities as well as the entity of the regional fauna.

DISCUSSION

Patch type and location

The nested distribution of 325 Lepidoptera species at 12 patches of a temperate mixed forest showed that communities at single patches represent a statistical subset of communities present at more species rich patches. Low quality patches, e.g. those of small size or unfavourable location often have small communities (Connor & McCoy 1979; Patterson & Atmar 1986; Boecklen 1997). Patch quality therefore should have been a major force regulating the community size of Lepidoptera at the studied forest patches. In the present study, forest edges showed the most species rich communities, island habitats like clearings inside the forest and groves surrounded by agricultural land had smaller communities. The diversity of butterflies on calcareous grasslands was positively correlated with habitat area, as was plant diversity, but not with habitat isolation (Steffan-Dewenter & Tscharrntke 2000). Effects of spatial structure on communities depend on the mobility and dispersal strategies of the considered species. Immigration and emigration rates declined in butterfly populations with increasing patch area, while the resident fraction increased (Sutcliffe et al. 1997, Johst et al. 2002, Wahlberg et al. 2002). At fine spatial scale, Summerville et al. (2002) observed nestedness in butterflies, generated by variation in patch use by species. High flying, habitat restricted species avoided small patches, low flying and less

discriminating "ubiquitous" species were distributed more evenly. Therefore, the size of patches, as well as patch isolation, are determinants of its quality, with different significance for Lepidoptera species that differ in mobility and dispersal strategy.

Ecological adaptations

Cluster analysis revealed that the general patch type or location, inside or outside the forest, determined the present communities, with similar species composition at similar patches. Species' adaptations to environmental factors should influence the community compositions at different patches (Hutchinson 1953). Ecological adaptations and species interactions cause clumped distributions or result in gradients for communities at different patches (Clements 1916, Gleason 1926, Tilmann 1982, Leibold & Mikkelsen 2002). Food specialization groups that developed by coevolution of butterflies and their larval host plants (e.g., Benson et al. 1975), represent environmental adaptations that may regulate butterfly communities (Futuyma 1976). We observed types of gradients in groups of different food specializations, indicating that the kind of food specialization influenced the distribution of the observed Lepidoptera species among patches associated to forests. Yet, with increasing similarity of plant species growing at two sites, the faunal similarity of those two sites did not increase significantly. Also, the relative number of Lepidoptera species at different sites that are specialized to different caterpillar host plants, did not vary significantly among sites of different diversity and location. Futuyma & Gould (1979) already observed that the correspondence between faunal similarity and plant affinity is not strong. The complexity of distribution of insects over plants indicated that insects responded to many factors that differentiated plant species in a deciduous forest. Ecological adaptations, and a low quality of spatial habitat characteristics possibly may lead to an overlay of nestedness and gradients in local communities. The similarity of flora and fauna at a patch may then be limited despite the ecological adaptations, e.g. of caterpillars to host plants.

Generalists and specialists

Differences in the ecological specialization may influence the relative abundance of closely related

species (Brown 1984). Generalists will be abundant where they occur, and will occupy a large geographic range, because they can tolerate a broad environmental spectrum. Specialists, which are more restricted in the resources and microhabitats they can use, should be locally rare and narrowly distributed. A few studies provide support for the ecological specialization hypothesis (e.g. Gaston 1988, Inkinen 1994, Jonsen & Fahrig 1997), whereas others do not (e.g., Hanski et al. 1993). Monophagous, oligophagous and polyphagous butterfly species showed differential responses to the area of grassland habitats with respect to species richness. The slope of species-area relationships increased with food plant specialization (Steffan-Dewenter & Tscharnke 2000). Along a gradient of human disturbance in grassland habitats, butterfly species richness was more strongly correlated with the number of specialist species than with that of generalists, and generalists were more widely distributed over communities than were the specialists (Kitahara et al. 2000). Consideration of the scale of a species' resource specialization (within or among habitats) appears to be key to understanding the relationships between resource specialization, resource availability, and a species' abundance and distribution (Hughes 2000). In our fine spatial scale investigation gradients were present among communities of polyphagous as well as of oligophagous species, but not in monophagous Lepidoptera caterpillars. The kind of food specialization, but not its degree may therefore significantly contribute to community regulation in Lepidoptera, when different kinds of habitats, forest, edges and groves are compared. The extent of differences of compared habitats should then decide, whether the kind and extent of food specialization contributes to community changes among habitats.

We conclude that in the studied forest system the patch location (isolated or at habitat edges) had most influence on the habitat quality, and resulted in nested distributions of Lepidoptera species among habitats, with species loss at low quality patches. Ecological adaptations of caterpillars to host plants produced gradients in communities among different patch types, with the scale of resource specialization being less important as a regulator. Interspecific competition, resulting in checkerboard patterns, was not observed to influence significantly the community structure. Stochastic effects, e.g., due to dispersal by wind, habitat size, and spatial barriers between island

habitats, should cause random patterns, which also were not observed in the present investigation. Similarly, in acid peatland butterflies of the Lake Superior drainage basin of Wisconsin communities deviated from random at small (<50 km) habitat extents (Nekola & Kraft 2002).

ACKNOWLEDGEMENTS

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Nectar host plant selection and floral probing by the Indian butterfly *Danaus genutia* (Nymphalidae)

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Abstract: Visitation frequency of the butterfly (*Danaus genutia*) to four species of nectar host plant species: *Nerium oleander* (L.) Blanco, *Barleria cristata rosea* L., *Crotalaria juncea* L., and *Bauhinia purpurea* L. was determined throughout the day light period of flight over 48 days during a time of maximum population density. The observations showed that the highest number of butterfly visits per hour occurred during 11.00 – 12.00 a.m. period, with the next highest number occurred during 10.00 – 11.00 a.m. period. Among the four plant species studied, *C. juncea* flowers were preferred by the butterfly as mean number of visits were significantly highest across all the time intervals recorded. Lastly, it was also found that the time spent during single visit by the butterfly was greater on unopened flowers than on open flowers of *C. juncea*. However, the maximum time, spent on unopened (41.0 seconds) and opened (20.1 seconds) *C. juncea* flower was found to be the highest of all other tested nectar host plants.

Key words: *Bauhinia purpurea*, *Barleria cristata rosea*, *Crotalaria juncea*, *Danaus genutia*, meal size, nectar host plant, *Nerium oleander*, probing behaviour.

INTRODUCTION

Adult butterflies are considered opportunistic foragers that visit a wide variety of available flowers (Courtney 1986). However, in studies conducted to date, observed species have shown distinct flower preferences that can differ between them (Erhardt & Thomas 1991). Under any circumstances nectar resources for adults are likely important limiting factors (Gilbert & Singer 1975) and may shape community patterns (Gilbert 1984). In the present investigation, the preference of nectar host plants and probing behavior of the common tiger butterfly, *Danaus genutia* (Cra.m.er), were studied in a florally rich area of Northeast India. The example is of interest since this is an area of high biodiversity in contrast to most temperate sites.

MATERIALS AND METHODS

Site of observation and species

Our study site was located in the Kaziranga National Sanctuary. The reserve covers 430 sq. km. in Golaghat district, Assam, India (longitude 90°5′W to 90°4′E and latitude 26°30′S to 25°45′N). The site encompassed 500 sq m located 8 km South East of Bokakhat, the nearest town and bordered by Dhansiri river in the east. The site has high diversity and exhibits an especially rich flora with both abundant nectar and larval food plants. The common tiger butterfly, *Danaus genutia*, flies in abundance.

We designed our study to determine if there is a preferred nectar host plant among four flowering plant species that are known rich nectar sources: *Nerium oleander*, *Barleria cristata rosea*, *Crotalaria juncea*, and *Bauhinia purpurea*. Four patches of the flowering plants,

*corresponding author

each in close proximity were delimited to facilitate efficient observations (map, Fig. 1).

Field observations

The study was performed in two stages. The first was to determine whether the four frequently used nectar sources were selected at random. If the null hypothesis is rejected, a pattern of preference should be quantitatively revealed.

For this first stage, a total of 30 individual flowers were marked on 10 randomly distributed plants of each species. Therefore, a total 120 flowers were sampled each day for each of the four species of plants. Observations were taken on the number of butterfly visits to each marked flower hourly from 6 a.m. to 5 p.m. throughout the day. The observations were made at 4 day intervals for the period, November 10 to December 26, 2000. The period includes the flowering time for these plant species. A total of 12 observation days were completed. Prior to each day sampling a fresh set of flowers were marked. Data thus obtained on visitation frequency on the different plant species was analysed using the fractional split plot design with 30 replications each. The plant species showing the significantly highest mean

number of butterfly visit per defined the favored host plant.

A second set of observations was restricted to *Crotalaria juncea*, which was shown by the initial study to be the preferred nectar source. For this study, 10 flowers each of open bloom and unopened bloom (one day ahead of bloom) were marked at random. The duration of time spent by the butterfly in a single trip on open or closed flowers individually was recorded. The work was done on hourly basis from 6 a.m. to 5 p.m. at the same periodicity as above.

Statistical analysis

Significance amongst the species with respect to number of butterflies visits to flowers and visiting time on the four nectar host was evaluated by F-test as outlined by Bhattacharyya (Bhattacharyya 1999). Accordingly, standard error differences (SEd \pm) were calculated using:

$$\text{SEd } (\pm) = \frac{\sqrt{(\text{error MS } X^2 / \text{pool number of replication})}}{2}$$

Critical differences (CD at 5%) were calculated to test the differences amongst the nectar hosts and visiting times of the butterflies as,

$$\text{CD } (5\%) = \text{SEd } (\pm) \times t$$

where t is 5% tabulated value of 't' at error degree of freedom.

RESULTS

Table 1 presents both frequency and total number of butterfly visits to each of the four nectar host plant species during different times of day. The highest frequency of visits to *C. juncea*, *N. oleander*, *B. cristata rosea*, and *B. purpurea* were observed to be 33.8, 13.6, 13.0, and 11.6 during the 11–12 a.m. interval followed by 31.9, 13.2, 11.6, and 9.2 during the 10–11 a.m. interval respectively. The total number of butterfly visits corresponded to frequency and was also higher during these periods of observation. Table 1 clearly shows that the frequency of butterfly visits to all plant species increased from morning to midday (11–12 a.m.), then decreased with the resulting lowest numbers during 4–5 p.m. interval. The frequency of

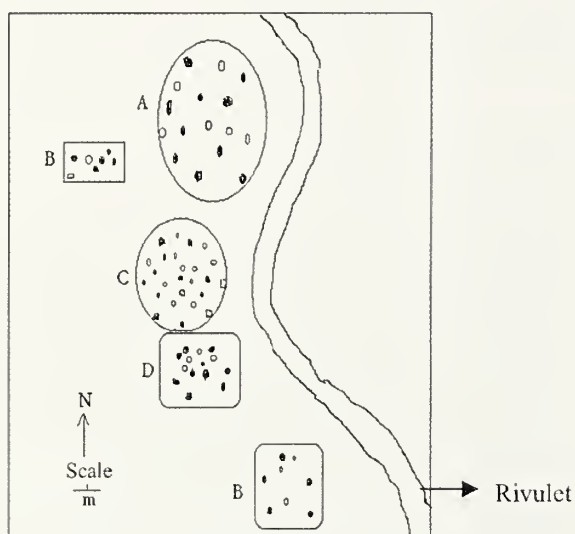


Fig. 1. Map showing distribution of the plant species in the study area giving number of individuals of those sampled. A - *Bauhinia purpurea*, B - *Crotalaria juncea*, C - *Barleria crista rosea*, D - *Nerium oleander*. (opaque dots indicate individuals with flowers sampled)

Table 1. Mean and total number of visits (total of all observations) of *Danaus genutia* on the four different nectar host plants at different times of the day.

Time period	Plant species				Total
	<i>Crotalaria juncea</i>	<i>Nerium oleander</i>	<i>Barleria cristata rosea</i>	<i>Bauhinia purpurea</i>	
6-7 am	4.36 53	2.93 35	2.13 26	2.53 30	11.95 144
7-8 am	5.50 66	3.83 46	2.47 30	2.97 36	14.77 178
8-9 am	6.47 78	3.60 43	3.07 37	3.93 47	17.07 205
9-10 am	13.40 160	8.77 105	6.33 76	5.93 71	34.43 412
10-11 am	31.87 382	23.20 278	11.63 140	9.23 111	75.93 911
11-12 am	33.87 406	13.60 164	13.03 156	11.60 139	72.10 865
12-1 pm	9.97 120	7.90 95	7.00 84	6.60 79	31.47 378
1-2 pm	6.03 72	5.03 60	4.40 52	3.57 43	19.03 227
2-3 pm	10.83 130	4.07 49	3.97 48	4.10 49	22.97 276
3-4 pm	8.00 96	2.80 34	3.17 37	2.40 29	16.37 196
4-5 pm	4.13 50	2.53 30	2.67 32	2.35 28	11.68 140
Total	134.43 1613	78.26 939	59.87 718	55.21 662	327.77 3932

* Bold numbers signify the frequency of visit of butterfly/day of respective hour

** Normal letter signify the total number of visits of butterfly in respective hour during the observation period.

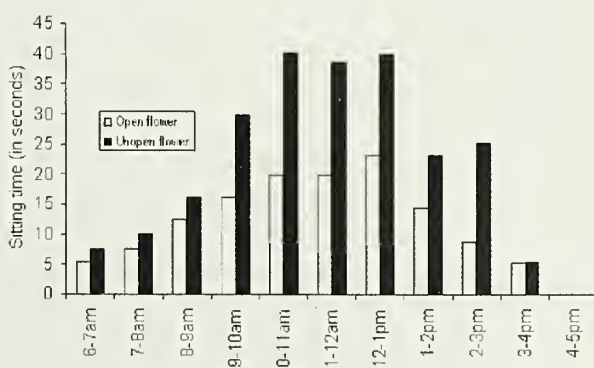


Fig. 2. Duration of visitation times of *D. genutia* at hourly intervals comparing visits to both open and unopened flowers of *Crotalaria juncea*.

visits was highest for *C. juncea* (33.9 and 31.9), followed by *N. oleander* (13.6 and 13.2), and lowest for *B. purpurea* (11.6 and 09.2) during 11 – 12 a.m. and 10 – 11 a.m. intervals respectively.

Studies on time spent on single trip

In respect of time spent by butterfly in a single visit to a flower of the favored nectar host plant, *C. juncea*, it was observed that duration of a single visit increased to mid-day and gradually decreased later in the day (Fig. 2).

It is clear from Fig. 2 that *D. genutia* spends more time on unopened flowers, by comparison to open flowers, at any time of the day. The highest visit

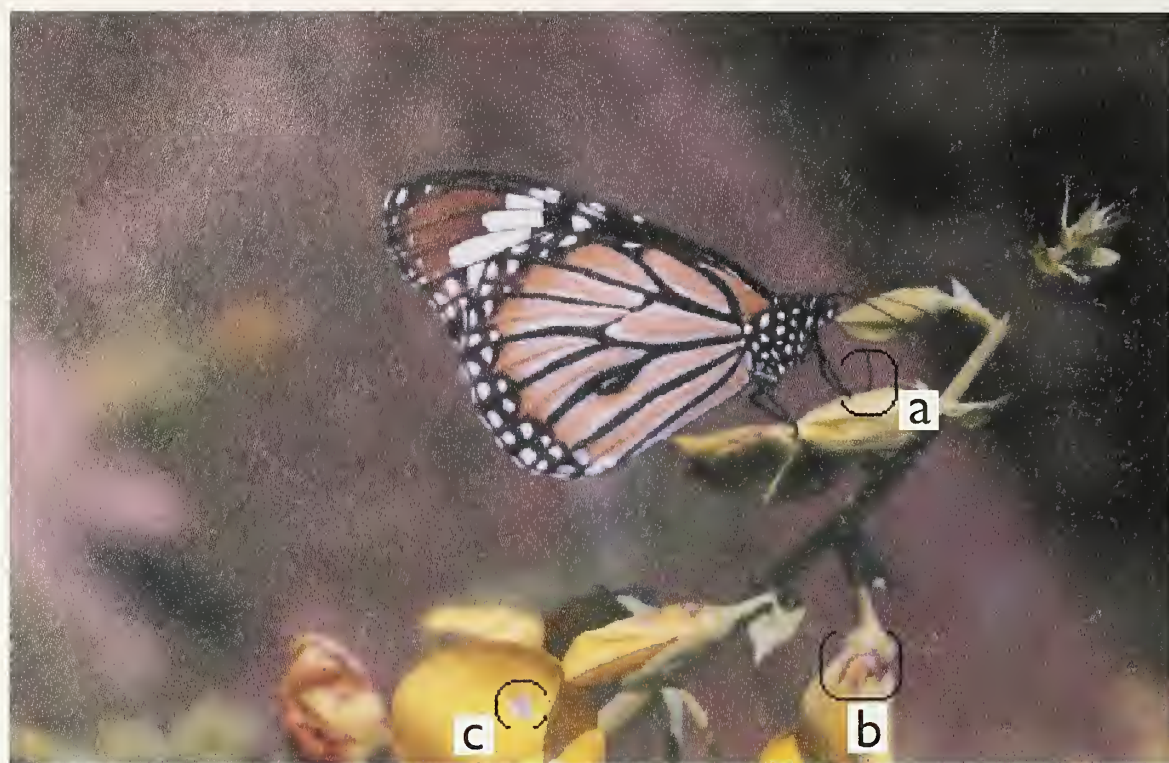


Fig. 3. Image showing *D. genutia* collecting nectar from unopened flower bud of *Crotalaria juncea*. a – butterfly probing by proboscis on unopened flower; b – piercing site on unopened flower; c – peircing hole on unopened corolla observed after complete bloom.

duration for a single trip to an open or unopened flower was found respectively to be 20.1 and 41.0 seconds during the 10–11 a.m. interval and 21.6 and 40.5 seconds during the 12–01 p.m. interval. After visiting an unopened flower, most butterflies immediately proceeded to probe with their proboscis and penetrate the sealed corolla to imbibe nectar (Fig. 3)

DISCUSSION

As diurnal animals, butterfly foraging activity largely depends on temperature and intensity of light. The favored time period found in the present experiment likely is the result of an optimum temperature and intensity of incident light required for highest activity of the butterflies.

The flowers of most of the plant species are believed to be adapted to attract restricted groups of pollinators. For a large pollinator as a butterfly, a flower must offer a reasonable reward, yet may physically restrict access to the reward. Access may be limited by complex flower structure demanding

particular foraging skill (Slater & Neill 1986). This character of the flowers of *Crotalaria juncea* might be adapted to provide ease in perching for collection of nectar by the butterfly.

In respect to time spent by a butterfly during a single visit to a flower of the favoured nectar host plant (*C. juncea*), it was observed that duration of the visit increases from early morning to mid day followed by a gradual decrease visitation duration (Fig. 1). This effect might be due the nectar intake rate increases as the viscosity of nectar decreases with rising temperature as the day progresses as shown in another species by Pivnick & Neil (1985).

We also show that *D. genutia* spends more time on unopened compared with completely open flowers during all time periods. The cause of differences of sitting time during a single trip of the butterfly might be due the unopened flower providing a larger and fresher resource of nectar for the butterfly. Unopened flowers would be more attractive and justify the added energy required to access such nectar. The sitting time on unopened flower would be consequently be of longer duration because of added time needed to puncture the corolla.

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Book review

BUTTERFLIES OF OREGON: THEIR TAXONOMY, DISTRIBUTION, AND BIOLOGY BY ANDREW D. WARREN. 2005.

Published as part of the "Contributions of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University." Fort Collins. 405 pages, 2 maps, soft-cover, perfect-bound. Projected Publication date: 15 March, 2005. Pre-publication cost (payment received before March 15): US \$30.00. Post-publication cost (payment received after March 15): US \$34.50 Order from Dr. Paul A. Opler, Department of Bioagricultural Sciences, Colorado State University, Fort Collins, CO 80523 U.S.A.

As the pre-publication announcement states, this is a monograph, which is defined by Cambridge as "a long article or a short book on a particular subject." As either, it is a revival of an old tradition for dealing with the butterfly fauna of a particular region. The same announcement states that this monograph is intended as a companion to Dornfeld, 1980, Hinchliff, 1994, Guppy and Shepard, 2001, and Pyle, 2002, but it is this reviewer's experience that Hinchliff's maps are essential to appreciate the depth of information provided.

This monograph is arranged as a scientific paper, with an Introduction, "Methods and Procedures" and "Results" prefatory portion. The species accounts follow. Each account begins with the specific name, author and date of publication. The distribution by counties follows, accompanied by a subspecies name when it is clear that such a name can be applied. Otherwise, the distribution is arranged by counties, but not assigned to a subspecies. Each entry includes a section of "Taxonomic notes", where geographic variation is detailed along with a discussion of the application of subspecies, and "Biological notes" where details of habitat, flight period and food-plant are discussed. The depth of the detail is astonishing, based on a diligent investigation of the literature, comprehensive examinations of many collections, both public and private, and the author's own considerable experience, as elaborated in "Methods and Procedures". No species is given short shrift. Common butterflies like *Vanessa cardui* and *Pieris rapae* are given complete and thorough evaluation. Conversely, genera like *Euphilotes* (15 1/2 pages), *Callophrys* (green 11 pages; gryneus group over 8 pages) and *Colias occidentalis* group (5 1/2 pages) receive special attention as befits the complexity that they present in Oregon.

The coverage is the state of Oregon, but the relationship of this butterfly fauna to that of California, northern Nevada, Washington and Idaho is obvious. The systematic coverage is current, and the author clearly states the reasons for his arrangements. There are some novel interpretations, clearly noted, e.g. in the status of *Callophrys barryi*. Otherwise, though it is not a revision, it gives a structurally sound basis for future evaluation of Oregon butterflies.

The culmination is a bibliography that includes over 1300 references and indices of larval food-plant and butterfly names. The bibliography is, for this reviewer, worth the price of the book. The bibliography is cited throughout the text and any reading of a species account draws one to the "back" pages.

I mentioned that this book is a revival of traditional regional works. It is not hyperbole to say that it may be an innovation with all that has transpired since the last such monograph. Among the best examples are Field, 1940, on the butterflies of Kansas and Forbes, 1960, on New York and neighboring states. The value of these documents remains to this day; they continue to be cited in bibliographies of their regions. This document on Oregon's butterflies is so thorough and in depth that it will take a while to process it in a satisfactory way. It will be cited in innumerable papers and be on the shelf of anyone interested in western butterflies, or butterflies in general. It is going to be a constant source of reference, a place to go to refresh one's memory of certain facts or, for one as I, as pleasure reading to soak in.

My only complaint is that updated maps *a la* Hinchliff could not be included. Such a task is onerous and beyond the means and time allotment of a Graduate student. It remains to be done.

The authors opening statement in the introduction “The purpose of this document is to provide an update on the taxonomy, distribution and biology of Oregon’s 171 naturally occurring butterfly species.” is rather modest considering the sheer volume of the “update”. Anyone interested in western butterflies will require it and the affordable price makes that easy.

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Book review

BUTTERFLIES OF THE CZECH REPUBLIC: DISTRIBUTION AND CONSERVATION, PARTS I AND II (2 VOLUMES).
J. BENES & M. KONVICKA, EDS. WITH J.H. DVORAK, Z. FRIC, Z. HAVELDA, A. PAVLICKO, V. VRABEC, AND Z. WEIDENHOFFER.

Published by Společnost pro ochranu motýlu, (Czech Butterfly Conservation Society) Prague. 857 pp (2 volumes). In Czech and English. Publication cost: 990 CZK. You can order by email: vit@kabourek.cz

Another “Butterflies of...” work. Ho hum? But this one stands out above almost all of them. The editor’s clear intentions were to provide a baseline database for conservation purposes. The work mirrors a massive and well coordinated team effort. Thus the substance of the two-volume work is the species accounts, which of course defines every faunal list. The conservation information is primarily given in distribution maps that included both past and present data. The map formats are familiar in recent European, especially U.K., literature.

The editors manage the bilingual problem with an exhaustive text in Czech, with English used to summarize each species account in the detail terms of conservation parameters. A sort of translation index provides enough to let the non-Czech reader at least get bearings. Basic biology cites (in Czech): global range, habitats, ecology and host plants, voltinism and flight periods, behavior and population biology, Czech distribution, threats and conservation, references. The maps are grids following the “Central European grid” with cells of about 11.1 x 12.0 km. There are 675 cells for the country with records covering four periods. A total of 176 volunteers provided data with over 165,000 individual records from 4177 localities. The editors provide a detailed discussion of the data, especially its limitations and interpretation that is well worth reading. They strongly emphasize that this is a work in progress.

Without dwelling on the volumes further, which would necessitate paraphrasing everything, I can only recommend anyone in conservation to buy the set (they are limited – and very reasonably priced). The only problem would be with the Czech parts, but the editors clearly referenced these background sections. Congratulations.

Rudi Mattoni

INSTRUCTIONS TO AUTHORS

Submission of Manuscripts. Papers must be written in English. Your initial manuscript must be submitted as an electronic version by e-mail to the editor, preferably as a WORD document, 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 genus and species. Do not use boldface or vary type size (12 point preferred) 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-high quality JPEG format. Do not send original artwork at this stage. Please read preferences for tables and illustrations (figures) below.

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