LYCAENID BUTTERFLIES AND PLANTS: HOSTPLANT RELATIONSHIPS, TROPICAL VERSUS TEMPERATE

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ABSTRACT Hostplant range, scored as number of plant families utilized by the caterpillars, is reviewed for 168 species of the butterfly family Lycaenidae. The majority of species are oligophagous, being restricted to one plant family or genus. Polyphagous species account for a significantly larger proportion among tropical species than in temperate ones. This difference is independent of influence of myrmecophagy on hostplant relationships. A strong correlation between polyphagy and use of woody hostplants, as well as between oligophagy and connections with herbivorous butterflies, suggest that the more strongly developed chemical defense of herbaceous plants constrains the amplification of hostplant range of herbivor- ing Lycanidinae butterflies. Specialization on unpredictable ephemeral food resources (young leaves, inflorescences) in intermittent tropical environments, in contrast, may have favored the more frequent use of polyphagy. Accepted 16 May 1995.

Key words: Butterflies, herbs, hosts, polyphagous, tropical, species diversity

INTRODUCTION

The degree to which herbivorous insects are specific to certain hostplants has played a central role in estimat- ing tropical species richness, and hence global biodi- versity. For example, Erwin's (1982) estimates of insect species numbers are based on the assumption that a large portion of the beetle fauna is collected from any given tropical tree species is specific to that plant. However, more studies on tropical species communi- ties employ sampling techniques like canopy-fogging or light-trapping, from which hostplant ranges or host specificity of the animals sampled can at best be indi- rectly inferred. A notable exception is the study by Bus- ter (1992) of the herbivore fauna of an Australian Ster- culiaceae tree species, whose foliage sampling was subsequently supplemented by feeding trials and a sys- tematic evaluation of the available literature records on hostplant relationships.

Differences in host ranges have hitherto been dis- cerned between tropical and temperate members of various taxonomic groups (such as parasitoids or particu- larly phytophagous insects; see references in Buster 1992), but large taxa of herbivorous insects have ra- rely been analyzed in detail. One reason for this deficit is that for many herbivores, especially from tropical re- gions, information on hostplant relationships is still very scant. Hostplant relationships of caterpillars (su- perfamily Papilionoidea), however, are probably better known than those of any other insect taxon of compar- able diversity and distribution. Due to their conspicuousness and aesthetic appeal, butterflies have attract- ed the interest of numerous naturalists throughout the last 200 years. Accordingly, butterflies are relatively well known with respect to taxonomy, and life-history data are available for a considerable portion of the spe- cies, including myrmecophyt, Recent reviews of host- plant relationships cover the African and Australian butterfly fauna (Ackery 1991), or the world fauna of the largest butterfly family, Nymphalidae (Ackery 1988), but do not specifically address the comparison of tropical versus temperate hostplant ranges.

Here I investigate the hostplant relationships of the second largest butterfly family, the Lycaenidae. The ly- caenids comprise approximately 4500 described spe- cies worldwide (Bridges 1988), with life-history data available for more than 1200 of these (Fiedler 1991, 1995).

Tropical Lycaenidae, often assigned to the lyce- nids as a subfamily, are a separate family for the reasons given by DeVries (1991) and Robbins (1988, 1989). Portrait of the number of species within the Lycaenidae have been discussed by Harvey (1987) and DeVries et al. (1994). Following Scott & Wright (1990), the Lycae- ninae can be divided into four subfamilies (Pieroininae, Miletinae, Carininae, and Lycaeninae). Two subfami- lies of Lycaeninae have aberrant life-cycles. In- nine of Pteroininae mostly feed on lichens, fungi, algae or

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similar to species of Lycantera, which is a multistate family. The Lycantera complex consists of the single genus Lycantera with less than 20 species (Elliot 1998), whose larvae feed on plants of the order Fabales. The family includes species of Lycantera, and species of Lycantera are worldwide in distribution, except Antarctica. They occur in all terrestrial habitats from the subarctic to the hot tropical rainforests, where their diversity reaches a maximum.

A special feature of Lycantera butterflies is their widespread association with ants, termed myrmecophily. The larvae of more than 50% of all Lycantera species are myrmecophiles, and certain species, the so-called obligate myrmecophiles, even depend on the presence of specific host ants for their survival (Fiedler 1991). Myrmecophily involves in various and complex ways with many life-histories traits of Lycantera butterflies. In many obligate myrmecophiles, for example, the female use the appropriate host ants as oviposition sites (Antaa 1981; Piere & Elgar 1985). As a consequence, the hostplant ranges of such obligate myrmecophiles tend to be broadened as compared to their facultative myrmecophiles or non-myrmecophiles relatives (Piere & Elgar 1985; Fiedler 1994). Piere (1985) also suggested that myrmecophily select for certain hostplant preferences among Lycantera butterflies, but this idea has recently been challenged (Fiedler 1995).

As in many other herbivorous taxa, hostplant relationships of Lycantera butterflies show distinct taxonomic patterns (Fiedler 1991), which are most likely governed by hostplant chemistry. Therefore, myrmecophily as well as taxonomic affinity is required to be taken into account as factors when comparing hostplant ranges of tropical and temperate Lycantera butterflies.

In this paper, I address the following questions:

1. Are there differences in the hostplant ranges between Lycantera butterflies living in tropical and temperate realms?
2. Are these latitudinal patterns independent of the myrmecophily relationships of the larvae?
3. Are the patterns consistent across the major taxonomic subgroups? (What is the significance of the hostplant growth form (woody versus herbaceous)?

DATA BASE AND ANALYTICAL PROCEDURE

Hostplant data were extracted from the literature for 1008 species of Lycantera butterflies. A provisional version of this database has been published (Fiedler 1991), and this has been extended using recent taxonomic recurrences, publications on the life-histories of individual species, and new fieldwork in Europe and Madagascar (a full list is available upon request). Only reliable hostplant records were accepted, whereas results of feeding experiments (e.g., Pratt & Balme 1995) were discarded.

As in a previous study (Fiedler 1994), hostplant ranges were essentially scored as number of plant families utilised. Meaningful number of the hostplant species are unattainable even for the well-studied European or North American Lycantera taxa as evidenced by the consistent distribution of the hostplant limits of butterflies in these taxa. Comparisons of genus level are obtained by the branchwise delineations of plant genera as used by different systematists when dealing with different regional floras. Family delineations, in contrast, are more widely accepted in a congruent manner, hence following the list of plant families in Groombridge (1992).

Butterflies are categorized in 5 groups with regard to hostplant range: (1) hostplant families, (2) hostplant families, (3) hostplant families, (4) hostplant families, (5) hostplant families and (6) hostplant families. In addition, butterflies known only from a single host genus within one plant family are scored as a separate category in a parallel analysis ("class analysis" below). As obligate myrmecophiles may have amplified hostplant ranges due to ant-dependent oviposition (Piere & Elgar 1985; Fiedler 1994), all comparisons are calculated twice (once considering all relevant species, once excluding the obligate myrmecophiles). To further investigate taxonomic patterns, I separately analyse the two most species groups "blue butterflies" (those Polyommatinae) and "butterflies" (those Theclinae and Eumaeinae). Data on hostplant families and (9) weight. It must be emphasised, however, that the monophyly of these bees requires thorough documentation employing clade-specific tests.

The scoring of a butterfly species as either tropical or temperate in distribution inevitably calls for some arbitrariness. Here, I adopt a categorisation which follows the well-established boundaries between the two biogeographical realms (e.g., Hepper 1991 for Lepidoptera). Hence, I score a Lycantera as "temperate" if its main dis-
tribution is in the Neotropical (North America north of Mexico) or Palaeartic zone (including the Himalaya), in New Zealand or in high-altitude Patagonia. As a corollary, a species is scored as “tropical” if its main distribution is in the Neotropics (Central and South America, including the Caribbean region, but except Paraguay), the Ethiopian region (Africa from the Sahara to the south west of Madagascar), the Oriental region (including the Indian subcontinent, but excluding the Himalayas), or Australia-Melanesia. Species which mainly occur in one region, but marginally extend into another (less than 10% of the range), are scored according to their main range. The very few species (n = 9) which have substantial portions of their range in tropical as well as temperate regions are omitted from all calculations.

While the “temperate” species categorized in the above way only inhabitconsynums with a temperate or cold climate, the climatic conditions are more variable for the “tropical” group. Parts of South America (e.g., high Andes) and southern Australia (Tasmania) have a distinctly temperate climate. However, herbivore data of only two Penangian (Apodidea; Apodidae spp.) are available, and these are included in the temperate species. Only 4 Australian species (Nehockey 3 spp.; Pseudelephantopus) have their main distributions in the temperate zone of southern Australia. This small species number is negligible in view of the large database. In south-eastern Africa, the species-rich Cape fauna of Lycanid beetles does not indicate a long separate history (in contrast to the famous Cape flies), but is clearly derived from the ethological region (Cornell 1985). Hence, the use of the straightforward subdivision of ‘temperate’ and ‘tropical’ using zoogeographic boundaries with few alterations appears sufficiently robust for the following approach.

All quantitative analyses are conducted using Chi^2 contingency tables to test for homogeneity (Sachs 1992; for a similar approach see Fiedler 1994). Tests are carried out on absolute species numbers, and are restricted to groups with sufficiently large species numbers. Hence, in the taxonomic comparisons, the tribes Lycanini (herbivore information available for 46 spp.) and Aphelechini (76 spp.), were not analyzed separately.

RESULTS

The quantitative data are summarized in Table 1. On a subfamily level, there is a significant difference in the herbivore range distributions between tropical and temperate zone lycanid beetles (5-class analysis, excluding obligate myrmecophiles: Chi^2 = 12.851, P < 0.02; 6-class analysis, excluding obligate myrmecophiles: Chi^2 = 14.345, P < 0.025). This difference is caused by a greater proportion of highly polyphagous species (No. 1 herbivore families used) in the tropics (18.3% vs. 9%). The great majority of lycanid butterfly species, however, is restricted to one herbivore family (tropical: 74.7%; temperate: 84.4%), and more than half of the species even to one hostplant genus (tropical: 58.3% vs. temperate: 61.4%).

This same pattern is observed when the obligate myrmecophiles are included (5-class analysis: Chi^2 = 13.656, P < 0.02; 6-class analysis: Chi^2 = 16.194, P < 0.01). Neither the percentages of polyphages nor those of oligophages change distinctly. Hence, invertebrates of myrmecophily, there is a significant homogeneity in herbivore ranges of Lycanid beetles, with tropical species showing a greater proportion of polyphages than temperate-zone inhabitants.

A comparison of two subfamilies of Lycanini species exemplifies this difference (Fig. 1). The herbivorous fauna of the Malay Peninsula and the island of Borneo has been the subject of intensive taxonomic and evolutionary research (Seki et al. 1991; Ebih 1992), and herbivore data are available for 109 (28.6%) of the roughly 356 Lycanini species known from this region (Fiedler 1991, and unpublished). About 24% of the Malaysian Lycanini species for which herbivore information could be traced are known from at least two herbivore families. In contrast, among the 342 Holcistic Lycanini species with available herbivore information, only 11% are yet known to utilize two or more hostplant families.

FIG. 1. Comparison of herbivore ranges of Holcistic (n = 342 spp.) versus Malaysian (Pseudelephantopus Malaysia and Borneo, n = 109) Lycanini species. The Holcistic fauna comprises a very high proportion of herbivore specialists, whereas in South East Asia almost a quarter of the species utilize two or more hostplant families.
A comparative summary of the larger tribes reveals important differences. Among the "hauaiatoki butterflies" (tribes Theliini and Eumaeini), no disparity in host-range distributions between tropical and temperate species can be found in the 5-class analyses, with all obligate mycophagous: *Ch. meadi* = 0.793, *P* = 0.13; including obligate mycophagous: *Ch. meadi* = 0.681, *P* = 0.003), while the difference becomes significant in the 6-class analysis (without obligate mycophagous: *Ch. meadi* = 1.51, *P* = 0.05. Among the Polyommatini, in contrast, a highly significant heterogeneity emerges throughout the 5-class analysis without obligate mycophagous: *Ch. meadi* = 20.820, *P* < 0.001, (6-class analysis: *Ch. meadi* = 25.00, *P* < 0.001), and this pattern remains unchanged when obligate mycophagous are included (5-class analysis: *Ch. meadi* = 15.906, *P* < 0.005; 6-class analysis: *Ch. meadi* = 18.877, *P* < 0.001). Only 8.2% of temperate-zone Polyommatini feed on 3 or more co-occurring species, whereas among tropical Polyommatini the respective proportion is 15.4%. Previous studies (Pierce & Elgar 1988, Feistner 1991, 1994) have shown that, in general, hairstreak butterflies tend to be more polyphagous than Polyommatini species. The present analysis only partly confirms this result. When the obligate mycophagous are excluded, the host-range distributions of *Theli- ti* + *Eumaeini* and Polyommatini (tropical plus tem-
petiole species combined) are homogeneous (5-classe analysis. Chi² = 5.86, P = 0.29) or marginally heterogeneous (6-classe analysis. Chi² = 11.08, P = 0.05). Species known from more than 5 hostplant families are disproportionately more common among the hair-strand butterflies, but overall differences are small. The pattern becomes more distinct when obligate myrmecophiles are included (5-classe analysis. Chi² = 5.99, P = 0.03; 6-classe analysis Chi² = 15.25, P = 0.01). Between compare zone Polymeniota and (The- lissi + Eumastrii), no differences in hostplant ranges can be observed with (or without obligate myrmecophiles, Chi² = 5.38, P = 0.20, for 5-classe analysis, Chi² = 8.4, P = 0.3, for 6-classe analysis). Tropical (Thelissi + Eumastrii), in contrast, comprise a significantly larger proportion of polyphagous species than tropical Polyommiinae (P = 0.01 in all 5- and 6-classe analyses, irrespective of the inclusion of obligate myrmecophiles). Hence, the greater "tropicalistic" tendency towards amplified hostplant ranges of hairstrut butterflies is more pronounced in the tropical faunas.

**DISCUSSION**

Like other herbivores (Jaenike 1996), and particularly like other families of butterflies (Meier 1987, Ackery 1988, Schecke et al. 1995), the Lycaeninae embrace a high proportion of oligophages which are specialized on one hostplant genus (e. 60% of all species) or family (c. 70%). This high degree of host specialization in herbivores is most certainly governed by phylogenetic barriers (Jaenike 1996, Berroba 1990), although studies on the chemical evolution of hostplant relationships in lycaenid butterflies are still scant (Fiedler et al. 1993, Wiemken et al. 1994). Superimposed on the preponderance of hostplant specialization is the well-documented, contrasting effect of obligate mutualistic relationships towards ants. Due to ant-dependent species, such species tend to utilize amplified hostplant ranges (Petres & Edgar 1985, Fiedler 1996). Furthermore, as shown above, a greater proportion of tropical lycaenids has polyphagous larvae as compared to temperate-zone species. This difference is pronounced among the Polyommiinae, but absent in the (Thelissi + Eumastrii).

This study raises three questions: (a) Is the pattern real? (b) What might be the causal factors responsible for this tropical- versus-temperate difference in hostplant specialization? (c) Why is this difference not universal among lycaenid butterflies?

The reliability of the pattern observed can be assessed for five reasons. First, the number of species in the analysis is high. Minor inconsistencies in the life-history data of individual species, or forthcoming additions of a few species, therefore, are unlikely to cause severe changes. Second, the analysis was restricted to a single, specific, cosmopolitan subfamily. Third, it would reduce possible effects of taxonomic heterogeneity or of highly uneven geographical distributions of the taxa under investigation. Third, although less than 30% of the examined species diversity is represented in the database, all major subordinated taxa of the subfamily Ly- caeninae are covered to a roughly equal extent. Fourth, with only a single exception the outcome of the statistical calculation was identical in the 5- and 6-classe analyses, which shows that the method of scoring of host ranges did not flaw the results. Fifth, the hostplant relationships of tropical species are less well recorded than are the hostplant ranges of temperate-zone lycaenid butterflies. As a consequence, the documented hostplant ranges of tropical lycaenids will probably become larger, but certainly not smaller, when the tropical fauna becomes better known. Hence, further additions to the database are likely to corroborate or even strengthen, instead of diluting, the pattern.

Therefore, it must be taken as valid that tropical Ly- caeninae species comprise a larger proportion of polyphagous than their temperate-zone counterparts. What reasons can be responsible for this trend? It will be discussed three potentially important factors: (a) myrmecophily, (b) the preference of lycaenid caterpillars for young growth and inferences of their hostplants, and (c) the "ant's" growth forms. (a) Myrmecophily is clearly not the major selective force behind the higher proportion of polyphages among tropical lycaenid butterflies. Although obligate myrmecophiles tend to utilize a larger range of hostplants (Fiedler 1994), all results in the analyses presented above remain unchanged when obligate myrmecophiles are excluded.

(b) Among the Lycaenidae, there is a widespread preference to utilize inflorescences, immature seeds, or young tender foliage as larval food (Petres 1985, Fiedler 1991). This preference has been related to the possibility of more frequent "oviposition mistakes", eventually followed by successful colonizations of novel hostplants (Chow & Robbins 1984). Furthermore, especially in unusual tropical rain forests, the spatial or temporal availability of inflorescences or young foliage is often unpredictable. For example, subsequent generations of a green leafcutter butterfly population at 5

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the same locality can be forced to switch between a set of hostplant species (Seifers & Fiedler, unpublised).

The Heliothine butterflies also prefer plant species (Fiedler, 1991), but do so on the basis of presence or absence of larval food plants. Intraspecific variation in hostplant selection has not been studied. The Heliothine butterflies appear to be more specialized or exclusive on hostplants than are the Bombyx butterflies (Seifers & Elgar 1985, Fiedler 1994). More frequent shifts towards utilising herbaceous hostplants may have led to a higher degree of specialization in the Bombyx butterflies. Furthermore, the role of plant growth form fits well into the concept of "species apparen-
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woody species tend to produce "quantitive" algal and herbivores has been suggested that hospitak butterflies (Seifers & Elgar 1985, Fiedler 1994). More frequent shifts towards utilising herbaceous hostplants may have led to a higher degree of specialization in the Bombyx butterflies. Furthermore, the role of plant growth form fits well into the concept of "species apparen-
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woody species tend to produce "quantitive" algal and
butterflies? Any generalizations should be made with great caution, since, like seaweeds, or even butterflies as a whole, may be a priori and conclusions could be drawn hasty misleading. Nevertheless, the study of host ranges of butterflies provides us with an almost unique opportunity for large-scale comparisons, since butterflies are one of the few taxa, if not the only larger inselberg group with a worldwide distribution, whose host-plant relationships are sufficiently well known to furnish a database for such considerations. With all caveats in mind, two conclusions emerge: (a) It is premature to assume that butterflies in tropical regions generally exhibit a similar or even higher degree of hostplant specialization than their temperate-zone counterparts. As far among lycaenid butterflies, a family of moderate species diversify, the opposite is true. Tropical swallowtail butterflies (family Papilionidae), on the other hand, tend to be more specialized feeders than their temperate zone relatives (Scherber et al. 1995). Hence, even among butter- flies latitudinal hostplant-range patterns differ between families. (b) As a corollary, a lower degree of specialization among tropical lycaenid butterflies is accompanied by a higher incidence of overlap in hostplant relationships between species. This overlap is further enhanced since only a fraction of the extant tropical floral diversity actually serves as hostplants for butterflies. Hence, floral diversity is often a poor predictor of butterfly species diversity (Van-Wright 1978). The departure- ter butterfly fauna of the Cape Province in South Afri- ca (Correll 1985), or of Australia (Common & Wu- rthuser 1981; Ackery 1991), which contrast sharply with the highly diverse regional flora, are excellent ca- ses in point. On the other hand, many taxonomic groups of butterflies, including speciose chases, “clus- ter” on specific hostplant taxa (families, orders) with frequent inter-specific overlap (Feather 1999 and 1995 for examples among the Lycaenidae). Hence, although extreme hostplant specialization do occur among tropical lycaenid butterflies, such special- ists interactions cannot sufficiently explain their high species diversity in tropical regions. Additional mechanisms, such as partitioning of the plant parasitism, specific interactions with ants in the case of oblig- atorily myrmecophytophagous Lycaenis (Patrick 1984; Feak- ler 1991; Steffen & Fielder, in prep.), or synchronic colonisation events in the temporarily and spatially un- predictable mosaic of potentially available hostplants, must play important roles in shaping the outcome of butterfly-hostplant interactions.

ACKNOWLEDGMENTS
I thank P. Siefert and an anonymous reviewer for crit- ical comments on the manuscript. This work was funded from grants F I 5471/1-1 and 1-2 by the Deut- sche Forschungsgemeinschaft (DFG ‘Mechanismen der Aufrechterhaltung tropischer Diversität’).

REFERENCES