

# Similarity and Specialization of the Larval versus Adult Diet of European Butterflies and Moths

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**ABSTRACT:** Many herbivorous insects feed on plant tissues as larvae but use other resources as adults. Adult nectar feeding is an important component of the diet of many adult herbivores, but few studies have compared adult and larval feeding for broad groups of insects. We compiled a data set of larval host use and adult nectar sources for 995 butterfly and moth species (Lepidoptera) in central Europe. Using a phylogenetic generalized least squares approach, we found that those Lepidoptera that fed on a wide range of plant species as larvae were also nectar feeding on a wide range of plant species as adults. Lepidoptera that lack functional mouthparts as adults used more plant species as larval hosts, on average, than did Lepidoptera with adult mouthparts. We found that 54% of Lepidoptera include their larval host as a nectar source. By creating null models that described the similarity between larval and adult nectar sources, we furthermore showed that Lepidoptera nectar feed on their larval host more than would be expected if they fed at random on available nectar sources. Despite nutritional differences between plant tissue and nectar, we show that there are similarities between adult and larval feeding in Lepidoptera. This suggests that either behavioral or digestive constraints are retained throughout the life cycle of holometabolous herbivores, which affects host breadth and identity.

**Keywords:** herbivorous insects, nectar-producing plants, larval diet, Lepidoptera, food plants, plant-insect interactions.

## Introduction

Many adult insects feed on tissues that are dramatically different from those resources that they use as larvae. For example, many wood-boring beetles feed on plant stems as larvae but feed on leaves as adults (Hanks 1999). Mosquitoes filter-feed in aquatic environments as larvae, but they seek out nectar and (for females) blood meals as adults (Bentley and Day 1989). Most Lepidoptera (butterflies and moths) have leaf-chewing larvae, but utilize

floral resources as adults, and they may even be important pollinators (Boggs 1987). In Lepidoptera, the most commonly consumed floral resources are nectar sugars and amino acids, but such resources also include secondary metabolites that are sequestered by the plants for defense. The acquisition of these resources leads to greater longevity, larger quantity and quality of eggs, and greater fecundity for the adult lepidopterans (Mevi-Schütz and Erhardt 2005) and is thus an important aspect of the insect's diet. The specificity of larval lepidopterans to feed on particular host plants is well studied (Ehrlich and Raven 1964; Loder et al. 1998). In addition, emerging research has begun to show that nectar sources vary dramatically in their nutritional quality, which suggests that (to a lepidopteran) not all nectar is the same (Mevi-Schütz and Erhardt 2005; Kessler and Baldwin 2007). Nevertheless, the resources consumed by leaf-chewing herbivores and nectar-feeding pollinators are nutritionally very different, and trends in host specificity of larval lepidopterans have often been divorced from an understanding of their adult diet (Gilbert and Singer 1975). Recent research has focused on understanding the entire life cycle (and thus diet) of Lepidoptera (or other holometabolous insects that act as both traditional herbivores and as nectar feeders) in a few key species (Bopp and Gottsberger 2004; Wäckers et al. 2007).

Nectar is by far the most important resource for adult Lepidoptera (reviewed in Boggs 1987). Initial surveys of nectar sources for adult lepidopterans typically found that these insects nectar feed on only a few key flower species (Watt et al. 1974). Similarly, surveys of floral visitations by lepidopterans show that sympatric plant species (even if they are closely related) are visited by different moth species (Schemske 1976). Dietary specialization also occurs at an individual level (Bolnick et al. 2003), in which an individual's preference for certain nectar sources may differ from its conspecifics' preference, which is a trend that

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has been related to larval diet (Mevi-Schütz and Erhardt 2005).

There are two main adaptive mechanisms that may help to explain why lepidopterans use different numbers or types of nectar sources. First, larval host breadth may influence the realized number of nectar sources. Even in the absence of differences between floral resources, lepidopterans that interact with many plant species as larvae (and as ovipositing female adults) may simply encounter more flower species as adults, because the ovipositing females will be searching for a wider range of hosts than will the adults of monophagous species. There has been substantial evidence that suggests a correlation between oviposition sites and nectar-producing flowers visited. Floral resources in close proximity to a larval host are more often visited by butterflies than are flowers that are distant from a larval host plant (Ohsaki 1979; Wäckers et al. 2007). Likewise, suboptimal larval hosts may be selected by adults if they are in close proximity to a good nectar source. For example, a lycaenid butterfly oviposits on feral, introduced alfalfa in California and Nevada, despite alfalfa being a poor host for developing larvae (Forister et al. 2009). The suboptimal choice for oviposition is likely influenced by alfalfa being a good nectar source for the butterfly.

Alternatively, different qualities of nectars or floral adaptations may influence the host range of adult Lepidoptera. Different moth species appear to have different dietary requirements, and different flowering plants provide those resources. Amino acid content and composition have been shown to affect both lepidopteran preference and fitness for a few species (Mevi-Schütz and Erhardt 2005; Beck 2007). Hovering moths tend to require more carbohydrates to maintain flight, whereas nonhovering moths require a higher percentage of amino acids (Baker and Baker 1983). The plants that each group of moths frequently nectar feed on tend to contain the corresponding resource (Baker and Baker 1982). As another dietary constraint, some plants produce toxic nectars that dramatically limit the range of lepidopteran species that can visit the flowers (Rhoades and Bergdahl 1981; Adler 2000). Wild tobacco (*Nicotiana attenuata*) produces nectar that contains nicotine, which is a metabolite that is toxic to most insects (Kessler et al. 2008). Pyrrolizidine alkaloids in an artificial nectar (meant to mimic the nectar produced by many plants in the Asteraceae, Fabaceae, or Apocynaceae) limited the use of that nectar by a generalist nymphalid butterfly but were attractive to more specialized nymphalid species that sequester the toxins as defense against predators (Masters 1991). In addition to being constrained by diet, moths are constrained to nectar feeding on flowers whose morphology allows them access to nectar (Scoble 1995). Lepidopterans with a short proboscis cannot reach the nectar of flowers with deep corolla tubes (Alexan-

dersson and Johnson 2002), but lepidopterans with a long proboscis in relation to body size suffer an increase in handling time (Kunte 2007). Trade-offs between efficiently feeding on a few nectar sources and less efficiently feeding on many nectar sources may lead to differences in the number of plant species on which lepidopterans nectar feed.

Although there are numerous observational and manipulative studies that work with one or a few lepidopteran species to explore the host breadth of larvae or adults (e.g., Bopp and Gottsberger 2004; Mevi-Schütz and Erhardt 2005; Beck 2007; Forister et al. 2009), there are no large-scale summaries of what feeding strategies adult lepidopterans employ and how they relate to the larval food-plant spectrum. Large surveys that link larval feeding with adult nectar feeding are necessary, however, to assess how common different strategies of host specificity are in Lepidoptera and how linked the larval diet is to adult nectar feeding behavior. In this study, we compiled a large data set (Ebert 1991–2005) of larva–host plant and adult–nectar plant interactions for 995 lepidopteran species from central Europe, for which a molecular phylogeny for the higher classification of all species was also available (Regier et al. 2009; Zehner et al. 2011). We asked whether the host breadth of the adult (nectar feeding) lepidopterans is correlated with their larval diets. Because both lepidopterans and flowers differ in diurnal activity (flowers are mostly diurnal, whereas among the Lepidoptera, butterflies are diurnal, but most moths are nocturnal), we also ask whether diurnal lepidopterans are likely to nectar feed on more plant species than are nocturnal lepidopterans. Additionally, we consider the case of 82 species of moths that lack functional mouthparts as adults and thus cannot feed. We ask whether these species have a larval host breadth different from that of lepidopterans that can feed as adults.

One case of nectar feeding that deserves special attention is the degree to which an adult lepidopteran nectar feeds on its larval host plant (Wäckers et al. 2007). When an insect relies heavily on the same host plant during both stages of its life, the cost of herbivory to the plant may be balanced by the benefit of pollination (Thompson and Pellmyr 1991; Holland and Fleming 1999; Bronstein et al. 2009). In rare cases, such dynamics may result in an obligate mutualism, in which the plant relies on the insect for pollination, and the insect relies on the plant as a larval (and often as an adult) food source (Pellmyr et al. 1996; Sakai 2002). Alternatively, if the adult insect nectar feeds on different plants from its larval host, there may be associational costs for larval hosts that are in close proximity to nectar sources (Karban 1997). As such, the nectar-producing plant may benefit from the decreased fecundity of its neighbors. In reality, each of these scenarios are simply

the extremes of a gradient in which herbivores may rely to varying degrees on their larval host as a nectar source.

Wäckers et al. (2007) devised a conceptual scheme for describing the potential fitness outcomes for a nectar-producing plant that attracts nectar-feeding herbivores. In this scheme, the primary factors that determined whether a plant would be positively, negatively, or not affected by attracting a nectar-feeding herbivore were the degree to which the herbivore used the nectar-feeding host as a larval host and the degree of specificity to the plant-herbivore interaction (i.e., whether the larval insect is monophagous or polyphagous). In our study, we address how often lepidopterans use their larval host(s) as nectar resources. Furthermore, we used the data set to create a null model that describes how often these species would use their larval host as a nectar source if they include a random assemblage of the locally available nectar sources in their diet. By comparing the null model against the observed similarity between larval hosts and nectar sources, we asked whether larval host plants are overrepresented in the nectar feeding diets of adult lepidopterans.

## Material and Methods

### *Study Area*

Our study area is the German state of Baden-Württemberg in central Europe (center coordinates: 48°32'16"N, 9°2'28"E). Baden-Württemberg is in the southwestern part of Germany, to the east of the Upper Rhine, and has an area of 35,752 km<sup>2</sup>. The vertical extension of the study area ranges from 85 to 1,493 m above sea level.

### *Data on Lepidoptera*

Our study focuses on all Lepidoptera species traditionally classified as Macrolepidoptera that have been recorded in Baden-Württemberg (Ebert 1991–2005), including, based on traditional taxonomic classifications (Karsholt and Razowski 1996), the clades of Bombycoidea, Cossoidea, Drepanoidea, Geometroidea, Hepialoidea, Lasiocampoidea, Noctuoidea, Papilionoidea (including HesperIIDae), Psychoidea, Sesioidea, Thyridoidea, and Zygaenoidea. To control for phylogenetic nonindependence in our analyses, we compiled an up-to-date molecular phylogeny of all Lepidoptera included in our analyses based on published data for the higher classification of Lepidoptera (Regier et al. 2009; Zahiri et al. 2011). A molecular phylogeny (and sequence data) is not yet available for every species, and we thus restricted ourselves to a phylogeny for the higher taxonomic levels (traditionally described as superfamilies, families, and subfamilies) and added the species as polytomies within each subfamily. In appendix A in the on-

line edition of the *American Naturalist*, we describe in detail how the molecular phylogeny was compiled and give the tree (fig. A1) used in the analyses. We used published data on insect-plant interactions of both larval and adult Lepidoptera (Ebert 1991–2005; Altermatt 2001). Interactions with larval Lepidoptera describe observations of food plants used by the larvae, whereas interactions with adult Lepidoptera describe plants used for nectar feeding. All data are based on observations made under natural, unmanipulated field situations. In total, the data set contains 11,923 species-specific insect-plant interactions (687 from Altermatt 2001 and 11,236 from Ebert 1991–2005). Of those, 5,541 comprise interactions with larval stages, and 6,382 comprise interactions with adult stages. Each specific insect-plant interaction may be based on one to many (>100) observations in the field, and information on the strength of the interaction is given on an ordinal scale from 1 to 5 (Ebert 1991–2005). Interaction strength (i.s.) 1 describes a single observation; i.s. 2 refers to a few isolated observations; i.s. 3 refers to several observations, and the plant may be locally or temporally of significance for the Lepidoptera species; i.s. 4 refers to many observations, and the plant may be locally or temporally of high significance for the Lepidoptera species; and i.s. 5 refers to very many observations, and the plant has a key role as a food source for the specific Lepidoptera species.

The insect-plant interactions refer to 995 Lepidoptera species (from 25 families), which are using a total of 1,184 plant species (from 103 families). One lepidopteran species can use one to many plants either as a larva or as an adult, and one plant species can be used by one to many lepidopteran species, in either their larval or their adult stage. Of all 995 Lepidoptera, 913 have a functional proboscis, and for 927 Lepidoptera species, larval food plant information is available in the data set. We restricted most of our analyses to the 845 Lepidoptera species that have a proboscis (and thus can potentially feed on flowers) and for which information on larval food plants is also available. To describe the diet of the larva, we used the number of plant species used by a lepidopteran species and also classified the diet breadth of the larval stages of the Lepidoptera as monophagous (feeding only one food plant species), strictly oligophagous (feeding on more than one food plant species but on only one food plant genus), oligophagous (feeding on more than one genus but on only one food plant family), or polyphagous (feeding on more than one food plant family). This classification was mostly based on the current data set; however, in the few cases where our classification of diet breadth deviated from that of Koch (1991), we used Koch's classification.

Furthermore, we calculated the median flight period of each of the Lepidoptera species, based on a data set of Lepidoptera from the Basel area, covering parts of south-

western Baden-Württemberg and northwestern Switzerland (Altermatt 2010a, 2010b; Altermatt et al. 2006). That area largely overlaps with Baden-Württemberg. The data set consisted of 182,665 records and covers the time period from the 1850s to 2007.

#### Data on Plants

Nomenclature of the plant species follows Oberdorfer (1983). Using published plant databases (Bundesamt für Naturschutz 2010), we determined whether each plant is insect- or wind-pollinated. Insect-pollinated plants usually produce nectar and can be used as a food source by adult Lepidoptera, whereas wind-pollinated plants generally do not produce nectar. For each plant, we extracted the main flowering phase during the year from the published database (Bundesamt für Naturschutz 2010) using the classification of Dierschke (1995). We complemented the flowering phases with Julian dates to align them with the flight periods of the Lepidoptera. We used the following flowering phases: prespring (phase 1, January 1–March 31), start of early spring (phase 2, April 1–15), end of early spring (phase 3, April 16–30), start of midspring (phase 4, May 1–15), end of midspring (phase 5, May 16–31), start of early summer (phase 6, June 1–15), end of early summer (phase 7, June 16–15), midsummer (phase 8, July 16–August 15), and early autumn (phase 9, August 16–September 15).

#### Statistical Analyses

We conducted all analyses in R 2.10.1 using the nlme-, ape, and vegan packages (Paradis et al. 2004; Oksanen et al. 2009; R Development Core Team 2009; Pinheiro et al. 2010). We assessed whether the number and range of adult nectar plants (square root transformed) used by a species is explained by the number of larval host plants (square root transformed) and the daily activity pattern of the species (diurnal or nocturnal) as well as their interactions. In a first analysis, we used the absolute number of plants used by the larvae of a species to describe the larval diet and fitted a generalized least squares model using the lepidopterans' phylogenetic relationships as the expected autocorrelation structure (Garland and Ives 2000). The generalized least squares were fitted by maximum likelihood, and model selection was based on the Akaike Information Criterion. In a second analysis, we used the diet breadth (monophagous, strictly oligophagous, oligophagous, and polyphagous) to describe the larval diet. We again fitted a generalized linear model and used the phylogenetic tree to describe the within-group correlation structure.

It is known that measures of host use can be sensitive to sampling efforts (e.g., different sampling efforts for lar-

val and adult stages or for diurnal vs. nocturnal species). Thus, the recorded diet breadth might increase with sample size within a species. Even though such a bias cannot be totally excluded, it seemed unlikely for the current data set because of two reasons. First, Ebert (1991–2005) specifically ensured that larval stages and nocturnal species were well recorded. Second, it is a very extensive data set with a total of 2,149,363 adult individuals and 2,342,415 larval individuals recorded for the 995 Lepidoptera species (excerpt of the database of Ebert 1991–2005). Nevertheless, we tested for possible systematic sampling effort bias in the data set to make sure that our main analyses were justified. We used the number of adult individuals and larval individuals for each species ever recorded in Baden-Württemberg (Ebert 1991–2005) to test for systematic differences in the data set. We did not see a systematic bias in the number of individuals recorded between diurnal and nocturnal species (fig. B1 in the online edition of the *American Naturalist*) nor was the number of adult individuals recorded positively correlated with the number of larval individuals recorded (fig. B2).

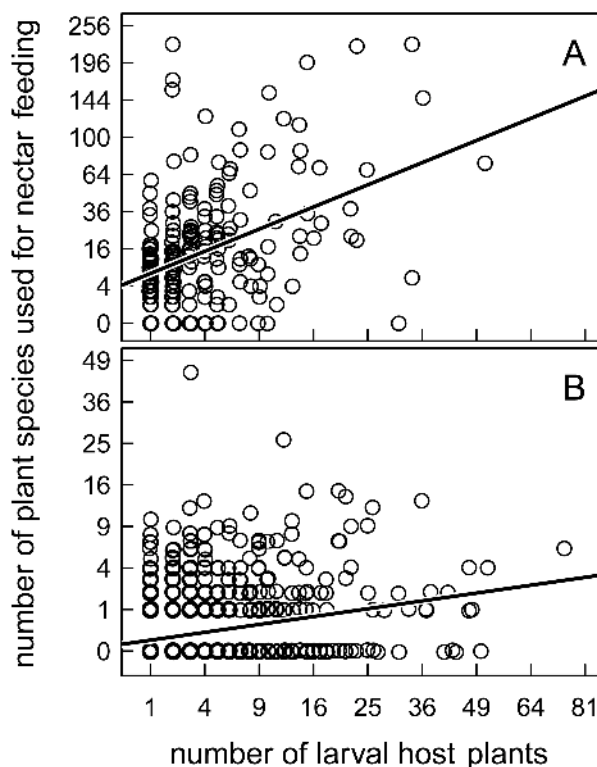
To assess whether the larval host plants are over-represented in the adult diet of lepidopterans, we further narrowed our data set to 459 Lepidoptera species and removed all records for which we had no information on adult hosts (including both adults lacking functional mouthparts and adults that could probably feed but have never been observed nectar feeding). We calculated four similarity indices that described the similarity between adult and larval diet for each butterfly and moth species. Indices fell into two categories: (1) Sørensen's index (SOI):  $1 - [(N_{\text{larval host}} + N_{\text{adult host}} - 2 \times N_{\text{shared hosts}}) / (N_{\text{larval host}} + N_{\text{adult host}})]$  and (2) a larval-weighted index that normalizes scores only to larval host data (LI; which is likely to be more accurate for our data set):  $1 - [(N_{\text{larval host}} - N_{\text{shared hosts}}) / N_{\text{larval host}}]$ . Each type of index was calculated using either only the presence or absence of an observed interaction or a quadratic function of Ebert's (1991–2005) interaction strength term. In the latter case, we weighted more commonly observed interactions more heavily on a quadratic scale. We then averaged the similarity score for each index across all Lepidoptera species, only diurnal species, or only nocturnal species. We then created a null distribution for each index based on permutations of the data set in which the larval-host interaction was retained and the adult-host interaction was permuted, such that the number of adult hosts that a butterfly or moth used was retained, but the identity of each host was randomized throughout the data set. For each comparison, we did 1,000 independent permutations and plotted the frequency distribution of the permuted similarity indices. To assess whether similarity between larval and adult hosts (compared with the null distribution)

could be explained by phenological matching (i.e., that adult lepidopteran could only utilize plants that matched their own phenology), we created an additional null distribution for each similarity index, in which the randomized adult host plants were constrained to plants that were in flower during the same time of year as the adult stage of the lepidopteran based on our phenological data sets for both plants and Lepidoptera. Ideally, we would have incorporated phenological changes in the flight period of Lepidoptera and phenological changes in the use of food plants (especially for nectar feeding) over time, because climate change has altered the phenology of both moth flight periods and flowering times to some degree (Altermatt 2010a). The data set on the use of host plants by larvae and adults, however, does not contain information on the date of the record, making such an approach currently impossible. For each comparison, we assessed the probability that the real similarity between larval and adult hosts fell within the null distribution.

### Results

The number of plant species used by the adult lepidopterans for nectar feeding was significantly positively correlated with the number of plant species used by the larval lepidopterans (fig. 1; table 1, pt. A). Diurnal Lepidoptera used more plant species for nectar feeding than did nocturnal Lepidoptera, but this difference was not significant. Furthermore, there was a significant interaction between the number of larval food plants and the daily activity pattern of the adults (diurnal vs. nocturnal) on the number of plants used for nectar feeding (table 1, pt. A; a detailed list on the number of plants used by Lepidoptera, grouped by families and subfamilies, as well as all other data are available in Dryad: doi:10.5061/dryad.cb6pk). Similarly, the number of plant species used by the adult Lepidoptera for nectar feeding was also significantly higher for oligophagous and polyphagous species than for monophagous and strictly oligophagous species (fig. 2; table 1, pt. B), and there was a significant effect of the daily activity pattern and a significant interaction of phagie and daily activity pattern (table 1, pt. B).

Of all plant species in our study, 440 were used by both larval and adult Lepidoptera, 423 are only used by larval Lepidoptera, and 321 are only used by adult Lepidoptera. In their larval stage, Lepidoptera species used 1–74 different food plants, and in their adult stage, they used 0–225 different plant species for nectar feeding. The larval diet breadth of Lepidoptera that do not have a functional proboscis was significantly larger (i.e., more plant species are included) than the larval diet breadth of Lepidoptera that have a functional proboscis (Wilcoxon test,  $W = 41,464.5$ ,  $P = .0028$ ; fig. 3).



**Figure 1:** Number of plant species used by adult Lepidoptera for nectar feeding predicted by the number of host plant species used by a larval Lepidoptera species, where the activity pattern of the adult is either (A) diurnal or (B) nocturnal. There is a significant positive relationship between the diet breadth of the larva and the diet breadth of the adult. The axes are on a square root scale. The lines give the values predicted by the generalized least squares. The records are slightly jittered around the X-axis to increase readability.

In analogy to the postulated table by Wäckers et al. (2007), we classified the 845 Lepidoptera species by their shared use of plants as both larva and adults, their activity pattern, and their larval diet breadth (table 2). Of the 845 Lepidoptera with functional mouthparts, 459 used at least one of their larval food plants for nectar feeding.

We created a null model that described the expected similarity between larval and adult hosts. Specifically, it predicted how often adult Lepidoptera would include their larval host plants in their adult diet when nectar-producing plants were sampled randomly from the assemblage of plants used by nectar-feeding Lepidoptera in Baden-Württemberg. Comparison of the observed similarity between larval hosts and adult nectar sources for 845 Lepidoptera with the null model revealed that lepidopterans tend to include nectar resources from their larval host in their adult diet more often than would be expected by chance (fig. 4; all panels, permutation tests  $P < .001$ ). This pattern

**Table 1:** Influence of the larval diet and the activity pattern of the adult on the number of plants used by the adults for nectar feeding

Covariate	Value	SE	<i>t</i> value	<i>P</i>
A. No. plants used:				
Intercept	1.54	1.06	1.45	.15
No. larval hosts (square root)	1.02	.10	10.63	<.00001
Daily activity pattern	-.36	.37	-.98	.33
No. larval hosts and daily activity pattern	-.82	.11	-7.81	<.00001
B. Diet breadth categories:				
Intercept	3.14	1.12	2.80	.005
Phagie narrow oligophagous	.16	.31	.53	.59
Phagie oligophagous	.79	.29	2.70	.01
Phagie polyphagous	1.07	.31	3.45	.0006
Daily activity pattern	-1.94	.38	-5.06	<.00001
Phagie narrow oligophagous and daily activity pattern	-.01	.37	-.04	.97
Phagie oligophagous and daily activity pattern	-.55	.35	-1.56	.12
Phagie polyphagous and daily activity pattern	-.67	.35	-1.91	.057

Note: We did generalized least squares fits by maximum likelihood and used a molecular phylogeny to control for phylogenetic nonindependence. In the first model (A), the number of plants used by a species was used to describe the larval diet. In the second model (B), four categories (monophagous, strictly oligophagous, oligophagous, and polyphagous) were used to describe the breadth of the larval diet.

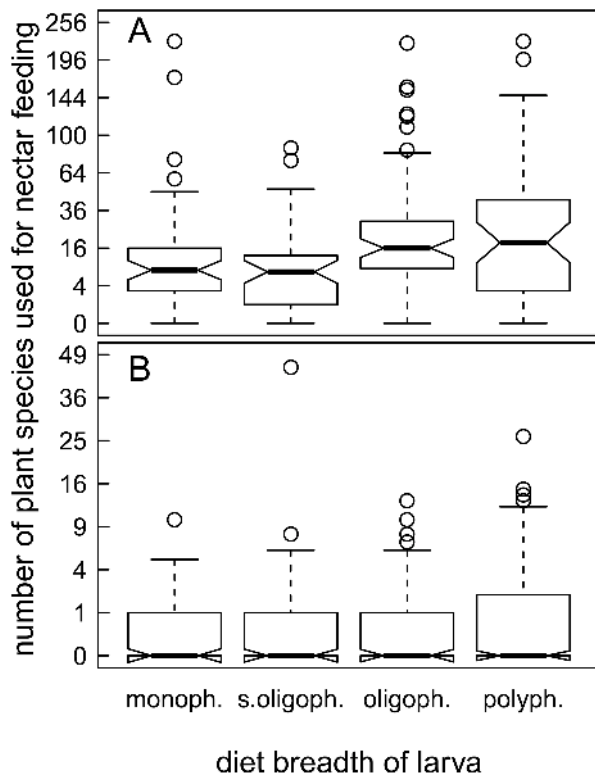
held true for four different measures of similarity of larval and adult host use (SOI and LI, both with presence and absence data as well as strength of interaction data) and across both nocturnally and diurnally active lepidopteran species (fig. 4). When the phenology of the nectar plants was taken into account, the results were qualitatively and quantitatively very similar and are therefore not shown.

### Discussion

Insects, especially holometabolous insects, are key organisms in many ecosystems. They are not only very diverse and often abundant but also affect the ecosystems by being important pollinators, herbivores, parasites, or detritivores (Gullan and Cranston 1994). Holometabolous insects have two different life stages in which they can feed (larval and adult stages), and the types of interaction between the insect and its food sources can be manifold, both between species and between the two life stages. Understanding the relationship between larval and adult food sources is especially important in times of great biodiversity losses and dislocations of species, because trophic interactions and food networks may get disrupted. For example, introduced or invasive plant species are commonly used as nectar sources by adult butterflies, but only a relatively small proportion of these plant species can be used by larvae (Graves and Shapiro 2003). Thus, to understand how changes in vegetation affect herbivorous insects, all life stages have to be considered. Recently a conceptual comparison of larval and adult food-foraging patterns has re-

ceived some interest (Wäckers et al. 2007), but data for a species-rich group of insects have been lacking.

We studied how the composition and spectrum of the larval and adult diet of 995 European Lepidoptera species are related. All of these species are herbivores as larvae, and most of them use plants for nectar feeding as adults. Using phylogenetically explicit comparisons, we found that species that consumed a larger number of host plants as larvae also used a larger number of plants for nectar feeding (figs. 1, 2; table 1). This suggests that being a generalist is at least partially conserved throughout the life cycle of a Lepidoptera species. Possible functional explanations for this pattern could be behavioral or physiological constraints. Specialist Lepidoptera with a narrow larval diet breadth often have a local spatial distribution, because they are restricted to the localities of their larval host plant. The adults often do not disperse beyond the habitat in which the larval host plants are occurring. Therefore, only plants flowering within that area will be used for nectar feeding. Likewise, species with more generalist larvae are less restricted to a specific habitat, and the adults may roam more freely and encounter and use a larger array of plants for nectar feeding. Alternatively, a species' digestive ability (especially its ability to metabolize secondary plant compounds) may be conserved throughout its life stages. Many plants protect their tissue from herbivores by specific secondary compounds, and only larvae of coevolved herbivores can feed on these plants. Similarly, but less well known, the nectar of many plants contains secondary compounds (Rhoades and Bergdahl 1981; Masters 1991; Adler 2000; Kessler and Baldwin 2007). Thus, nectar is not, as

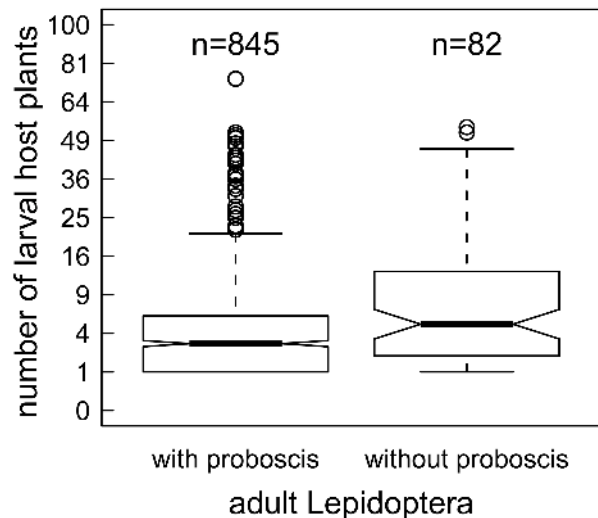


**Figure 2:** Box plots showing the number of plants used by Lepidoptera species for nectar feeding, depending on their diet breadth as larvae (*monoph.* = monophagous, *s. oligoph.* = strictly oligophagous, *oligoph.* = oligophagous, and *polyph.* = polyphagous) and the activity pattern of the adults, which are either diurnal (A) or nocturnal (B). The thick horizontal line in each box plot shows the median value, the box shows the twenty-fifth and seventy-fifth percentile, and the whiskers are 1.5 times the interquartile range. The Y-axis is on a square root scale.

is often assumed, only a solution of sugar and amino acids but contains secondary plant compounds, such as nicotine, and its quality can affect the foraging preference (Kessler and Baldwin 2007; Kessler et al. 2008) as well as the fitness (Masters 1991; Mevi-Schütz and Erhardt 2005) of nectar-feeding insects. Consequently, a lepidopteran species that can use and digest many different plant species as a larva may also be able to use a wide array of nectar as an adult. On the other hand, a species with a restricted larval diet may be able to metabolize some specific plant compounds, such as nicotine or pyrrolidizine alkaloids, and consequently can also (potentially exclusively) use the nectar of the same plant as an adult (Kessler and Baldwin 2007). These two processes are not mutually exclusive. The specific use of plants by larval and adult Lepidoptera may reflect constraints as well as monopolizations, because being a generalist often comes with the cost of not being

able to exploit a given resource as efficiently as would a specialist of that resource (Masters 1991; Kunte 2007). A quantification of how commonly the secondary compounds between larval and adult food plants match would be a possible test for the second hypothesis.

Although the use of more plant species for nectar feeding by Lepidoptera with a wide diet breadth as larvae was a significant pattern in our data set overall, it was much less pronounced for nocturnal species than for diurnal species (fig. 1; table 1). Furthermore, nocturnal species use, on average, fewer plant species for nectar feeding than do diurnal Lepidoptera (fig. 1). This difference, however, was only significant in the comparison that included four larval diet breadth classes (table 1, pt. B) and not the total number of larval host plants (table 1, pt. A). Many flowers have a diurnal pattern of activity, in which they open their corollas or emit scents only at particular times of day. Consequently, flower-visiting insects can choose from a large number of species. During dusk and during the night, a much smaller number of plant species actively display flowers. Nocturnal Lepidoptera thus have many fewer options of flowers to choose from, which could be reflected in the small number of plants species used for nectar feeding. As an evolutionary consequence of the more restricted



**Figure 3:** Box plots showing the number of larval host plant species used by Lepidoptera, which either have or do not have a functional proboscis as adults. Lepidoptera species without a functional proboscis as adults use, on average, significantly more plant species as larva than do Lepidoptera species with a functional proboscis ( $W = 41,464.5$ ,  $P = .0028$ ). The number of Lepidoptera species ( $n$ ) is given for each group. The thick horizontal line in each box plot shows the median value, each box shows the twenty-fifth and seventy-fifth percentiles, and the whiskers are 1.5 times the interquartile range. The Y-axis is on a square root scale.

**Table 2:** Host plant use of 845 Lepidoptera species (as larvae and adults)

	Nectar plants used by adult Lepidoptera includes larval food plants, no. (%) species ( $n = 845$ )	
	Yes	No
Overall	459 (54.3)	386 (45.7)
Activity pattern of adult Lepidoptera, diet breadth of larvae:		
Diurnal	183 (21.6)	23 (2.7)
Monophagous	48 (5.68)	5 (.59)
Strictly oligophagous	34 (4.02)	10 (1.18)
Oligophagous	61 (7.22)	2 (.24)
Polyphagous	40 (4.73)	6 (.71)
Nocturnal	276 (32.7)	363 (43.0)
Monophagous	35 (4.14)	67 (7.93)
Strictly oligophagous	33 (3.91)	72 (8.52)
Oligophagous	43 (5.09)	60 (7.1)
Polyphagous	165 (19.53)	164 (19.41)

Note: The host plant use is given as the number and percentage of Lepidoptera species that fall into the different categories. All of these Lepidoptera species have a functional proboscis.

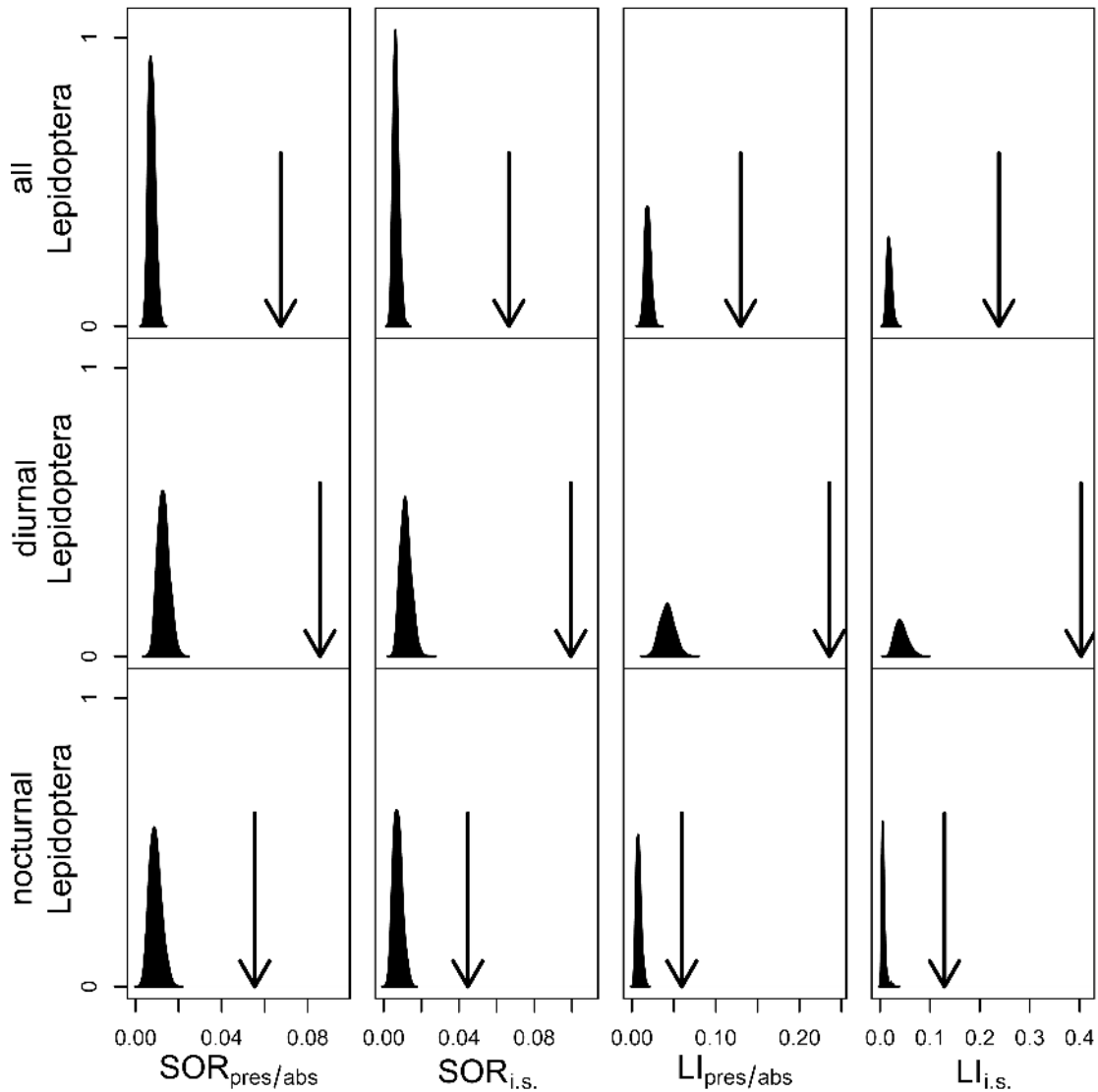
availability of flowers during the night, moths may either specialize on few flowers (e.g., sphingid moths and co-evolved flowers) or give up their nectar feeding behavior overall. This trend may help to explain why several groups of nocturnal species have reduced mouthparts and have totally lost their ability to feed as adults, whereas diurnal species across families are usually strong nectar feeders. We note that, with a comparative data set, such as ours, we cannot exclude the possibility that fewer observations of nectar-feeding moths were made during the night, because it is more difficult to observe insect behavior during the night. However, we think that this is an unlikely explanation, because nocturnal species were not systematically underrepresented in the current data set (Ebert 1991–2005), compared with diurnal species (fig. B1). We therefore conclude that the difference between diurnal and nocturnal lepidopteran host breadth is a biological pattern and not a sampling artifact.

Approximately 10% of the considered Lepidoptera species do not have a functional proboscis. We found that the larval diet breadth of these species is, on average, significantly larger than the 90% of considered Lepidoptera species with a proboscis (fig. 3). The latter can at least partially compensate for larval nutrient deficiencies (e.g., amino acids deficiencies) by feeding on nectar (Mevius-Schütz and Erhardt 2005) or even on nonplant resources, such as puddles, carcasses, dung, or rotting vegetation, in search of nutrients not available in nectar (Adler and Pearson 1982; Scoble 1995). Specifically, the energy gained by nectar feeding is often needed for flying and directly prolongs the life span of lepidopterans. Species that can feed in both their larval and adult stages may therefore have fewer constraints in acquiring all of the resources needed in their life (e.g., for growing, mobility, defense, and

production). This is not possible for those species without proboscis. Consequently, we expect them to have the ability to balance their diet in the larval stage, which may mean larvae of these species have a more flexible digestive physiology. A complementary scenario could be that many of the species without functional mouthparts are short-lived as adults (often only living one to a few days; see Ebert 1991–2005), possibly as a consequence of their inability to uptake nectar. Because they must lay their eggs in a short time and may not be able to search intensely for specific larval host plants (because they are constrained in either time or energy for dispersal), they could have evolved to have a broader larval diet, which increases their options for egg laying (Bernays and Janzen 1988).

Our data strongly suggest that adult Lepidoptera often use their larval food plant for nectar feeding (table 2; fig. 4). Such a pattern has been predicted (Wäckers et al. 2007), but to our knowledge, this is the first time that it has been found in a large comparative data set. More than half of the lepidopterans included their larval food plant(s) for nectar feeding (table 2). This percentage is even higher (63%) when the 120 Lepidoptera species that fed as larvae exclusively on wind-pollinated plants were removed from the data set (table 2; because these plants do not produce nectar, they were never used as nectar sources by any Lepidoptera). The overproportionate use of the larval food plants for nectar feeding is also independently demonstrated with our permutation analyses (fig. 4). Both diurnal and nocturnal Lepidoptera species tend to include their larval food plants in their adult diet (for nectar feeding) much more than one would expect if they choose their nectar plants by chance. This finding was consistent and robust, and it was affected by neither the exact definition





**Figure 4:** Similarity of larval and adult hosts. Distribution plots comparing the observed similarity of larval and adult host plants (observed averaged score for each panel shown with an arrow) with a null data set (filled distribution curve). In the null data set, the larval-host interaction was held constant, but the adult-host interaction was permuted. Similarity scores ( $X$ -axis) were computed using either a Sørensen's similarity index (SOI) or a larval weighted index (LI) and either relied only on the presence or absence of an interaction (pres/abs) or took into account observed interaction strengths (i.s.) between adult lepidopterans and plants. In all cases, the observed similarity score between larval and adult hosts fell above the null distribution, meaning that adult lepidopterans include their larval food plant within their range of nectaring plants more often than would be expected if determined by chance.

of the food-plant similarity index (SOI or LI) nor the restriction to seasonally available nectar plant species.

We identify three mutually nonexclusive explanations as to why Lepidoptera (and perhaps holometabolous insects in general) tend to use the same plants both as larvae and as adults, two of which refer to the pattern caused by a “probability” effect caused by behavioral constraints. First, if species occur in and show strong fidelity to very

different habitats containing different plant communities, they are only exposed to a subset of possible plants that can be used for feeding both as larvae and adults. Many Lepidoptera are known to live in specific habitats, and species living in forests or marshes will mostly encounter the respective plants throughout their lives (Ebert 1991–2005). However, our understanding of the spatial use of different habitats is only at its beginning in Lepidoptera

(e.g., Saastamoinen and Hanski 2008). Although a few species are restricted in their use of habitats, we cannot say how general this is and whether spatial constraints are reflected in the food plants used both by the larvae and the adults. Second, the behavioral constraint could occur on a more restricted scale. For many Lepidoptera, the adults are not only looking for nectar but also for mates and (for females) larval host plants for egg-laying within the same habitat. When feeding behavior is not independent in space and time from reproductive behavior, this could result in an over-proportionate use of the same plants for both activities. For a few Lepidoptera species, such a correlation has been found (Graves and Shapiro 2003; Forister et al. 2009). Wäckers et al. (2007) reviewed different specific insect-host interactions and reported that adult insects indeed often aggregate around specific nectar sources, just because they also “plan” to lay their eggs on these plants. Ultimately, the “probability” effect could also translate into selection to optimally use a secure nectar source. Selection could act both on finding the plant and on digesting its nectar optimally. However, the use of the same plant as a nectar source may not always be a consequence of looking for a specific egg-laying substrate (Wäckers et al. 2007), and further mechanisms may apply. The third possibility is that Lepidoptera have digestive constraints that are retained throughout their life cycle and are functionally restricted to a specific set of plants both as larvae and adults. We cannot tell these different mechanisms apart with our data set. However, this would be an important direction of future research.

Although the degree of similarity between larval and adult diets definitely alters our understanding of what selection pressures have shaped the evolution of herbivore-plant relationships, the more immediate application of comparing larval and adult diets lies in conservation. For example, herbivores that feed on similar plants across life stages may be restricted to certain habitats (Beck and Kitching 2007) and be more susceptible to changes therein. However, the identification of those plants that are used by both larvae and adults may also improve conservation success, because both life stages profit from the protection of one or few plant species. It has already been recognized that some plant species are an especially important resource for many insects in their larval stages. Incorporating information about nectar-producing hosts may help to identify which plant species are most important for a large number of insects and thus deserve special attention in conservation.

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