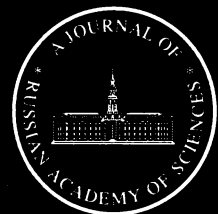


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Taxonomy, Phenology, and Trophics of the Urban Macrolepidoptera Feeding on Trees and Shrubs

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Abstract—A total of 107 macrolepidopteran species from 12 families have been recorded in 2006–2010 on trees and shrubs in the city of Yekaterinburg; in contrast to natural communities, no lasiocampids and few nymphalids have been found. The proportion of specialized species among the Macrolepidoptera living in the city is decreased, although the proportion of obligate dendrophagous species is increased. Differences in the phenology of lepidopterans living in urban greenery from those living in natural communities have been observed: a decreased proportion of autumn–spring species and an increased proportion of summer species. These differences can be explained both by relatively weak colonization of urban territory by facultative dendrophagous species with their specific seasonal strategies and by differences in methods used to collect the insects.

Keywords: macrolepidopterans, urban greenery, taxonomy, phenology, trophic range.

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In a previous study (Bogacheva, 2009), consideration was given to the connection between phenology and food specialization in macrolepidopterans living in natural communities of the forest zone. During the period from 2006 to 2010, a sufficient database on “urban” macrolepidopterans living in the greenery of a large city (Yekaterinburg) was accumulated (Bogacheva and Zamshina, 2009); a total of 107 species were found. The accumulated data made it possible to determine the lepidopteran families the members of which penetrate more easily into urban biotopes and find out whether any specific features of their phenology and/or trophics give some species an advantage in colonizing trees and shrubs of city parks, public gardens, courtyards, and streets. The database on the heteroceran macrolepidopterans of the Middle Urals (Bogacheva, Olschwang, and Zamshina, 2003; Bogacheva and Zamshina, 2006; Bogacheva, 2009) was used for comparison. The materials for that database were collected by G.A. Zamshina in 1997–2005 at the Biological Field Station of the Ural State University in Sysertsii district, Sverdlovsk oblast (56°36' N, 61°03' E), located in the southern taiga zone (*Flora i rastitel'nost'*..., 2003); data on the rhopaloceran lepidopterans of the Middle Urals were taken from the guidebook by Korshunov and Gorbunov (1995).

MATERIAL AND METHODS

Lepidopterans (at the larval stage), as well as other phytophagous species, were recorded while examining

trees and shrubs. For this purpose, several test plots were established in the city areas representing seven basic types of urban biotopes: from park forests (closely similar to natural forest communities) to tree planting along busy streets and highways. Ten plants were examined in each of the test plots. Censuses were taken for about 14 days four times a year: in late May to early June, in late June to early July, in late July to early August, and in late August to early September. All lepidopteran larvae found in lower parts of the crown in larger trees or throughout the crown in smaller trees and undergrowth were recorded. If the larvae could not be identified to species, they were kept in cages until the emergence of adults.

The number of researchers involved in this study was too small to allow a concurrent examination of all (or at least basic) kinds of trees and shrubs planted in the city. They were included in the study gradually, year by year. In 2006, six genera were examined: poplar, willow, birch, apple, maple, and lilac. In subsequent years they were supplemented by hawthorn, cotoneaster, mountain ash, and bird cherry (2007); aspen, pear, dog rose, raspberry, linden, elm, and ash (2008); and honeysuckle, viburnum, elder, currant, spruce, pine, and larch (2009). In 2010, the study continued with poplar, willow, birch and apple.

Macrolepidopterans collected at the field station were captured by various means, including light traps for nocturnal species, aerial insect net for diurnal spe-

Table 1. Taxonomic composition of macrolepidopterans found in urban and natural landscapes

Family	Urban species		Natural communities	
	number of species	%	number of species	%
Hesperiidae	0	0.00	1	0.38
Papilionidae	0	0.00	1	0.38
Pieridae	1	0.93	2	0.75
Lycaenidae	2	1.87	5	1.88
Nymphalidae	1	0.93	10	3.76
Psychidae	0	0.00	1	0.38
Lasiocampidae	0	0.00	10	3.76
Endromidae	0	0.00	1	0.38
Saturniidae	0	0.00	2	0.75
Sphingidae	5	4.67	6	2.26
Drepanidae	4	3.74	10	3.76
Geometridae	45	42.06	97	36.47
Notodontidae	8	6.99	21	7.89
Noctuidae	32	29.91	84	31.58
Pantheidae	1	0.93	1	0.38
Lymantriidae	5	4.67	8	3.00
Nolidae	2	1.87	2	0.75
Arctiidae	1	0.93	4	1.50
Total	107	100.00	266	100.00

cies, net sweeping, and collecting by hand from flowers and food plants.

The significance of changes in the proportions of species was estimated by the χ^2 test (Pesenko, 1982).

RESULTS

Taxonomic composition. A total of 266 species from 18 families of macrolepidopterans feeding on trees and shrubs were found in natural communities, and 107 species of 12 families were found in the city. The families Psychidae, Lasiocampidae, Endromidae, Saturniidae, Hesperiidae, and Papilionidae were absent in the city, while other families were represented approximately in their natural proportions (Table 1). The families Geometridae and Noctuidae were represented by the greatest numbers of species, with the former somewhat prevailing over the latter both in the city and in natural communities.

Phenology. The starting date and duration of larval feeding are the basic features of lepidopteran phenology. Both directly depend on the quality of food (tree and shrub leaves) consumed by the larva in the course of its development, with the duration of feeding being also dependent on individual body size. Thus, large summer species (e.g., Sphingidae) do not have enough time to produce more than one generation per year, while smaller species of Geometridae, Notodontidae,

and Drepanidae often produce two generations. Most species (Table 2) start feeding in summer (second half of June to July); a large proportion of species start feeding in spring (May to early June); and the smallest proportion of species start feeding in autumn (August to early September).

The starting date and duration of larval feeding largely determine the third important feature of the species phenology, the hibernation stage. The combination of food type, start of larval feeding, and hibernation stage determines what is termed "life strategy" here. In dendrophagous species, there are only four basic life strategies. Following Kryukov (2006), we divide these insects into four groups depending on the period of larval feeding: the early spring, spring–summer, summer, and autumn–spring groups.

(1) Early spring species. The larva feeds on growing springtime leaves, the most valuable food resource (in May to early June). This resource is extremely abundant and provides for a high growth rate, but the period of its existence is short. In order to hatch by the moment it emerges (for classic early spring species, by the opening of buds), these species overwinter at the egg stage (or, sometimes, at the adult stage). Feeding on young leaves is obligatory for larvae of earlier instars; at later instars, they can continue feeding on leaves that have stopped growing. About one-fourth of all species follow this strategy (Table 2).

Table 2. Comparison of proportions (%) of macrolepidopteran species with different types of phenology and food specialization living in natural habitats and in urban greenery

Group	Urban greenery			Natural habitats		
	geometridae (<i>n</i> = 45)	noctuidae (<i>n</i> = 32)	all macrolepi- dopterans (<i>n</i> = 107)	geometridae (<i>n</i> = 97)	noctuidae (<i>n</i> = 84)	all macrolepi- dopterans (<i>n</i> = 266)
Specialists	6.7 (3)	6.2 (2)	13.1 (14)	17.5 (17)	10.7 (9)	21.0 (56)
Dendrophages	82.2 (37)	59.4 (19)	77.6 (83)	74.2 (72)	41.7 (35)	63.5 (169)
Early spring	13.3 (6)	37.5 (12)	23.4 (25)	15.5 (15)	35.7 (30)	21.8 (58)
Spring–summer	20.0 (9)	18.7 (6)	14.0 (15)	14.4 (14)	11.9 (10)	10.9 (29)
Summer	48.9 (22)	34.4 (11)	49.5 (53)	38.1 (37)	22.6 (19)	36.1 (96)
Autumn–spring	13.3 (6)	9.4 (3)	10.3 (11)	19.6 (19)	26.2 (22)	23.3 (62)
Other strategies	4.4 (2)	0.0 (0)	2.8 (3)	12.4 (12)	3.6 (3)	7.9 (21)

Note: In Tables 2 and 3, figures in brackets indicate number of species.

(2) Spring–summer species. The larva also starts feeding on growing springtime leaves, but two to three weeks later than in early spring species. As the leaves grow older, their quality as food deteriorates; the development of the larvae slows down, so that they complete feeding by July to August and hibernate at the pupal stage. Only 11–14% of all species follow this strategy; apparently, the necessity to readjust the digestive system according to changes in food quality is not favorable for leaf-eating species.

(3) Summer species. The larva feeds on mature leaves, i.e., those that have stopped growing. In mid- and late summer this resource is abundant and the enzyme system of the larvae is adapted to it, so that not only do summer species complete their development before hibernation (at the pupal stage), but also many of them have enough time to produce two generations per year. It is interesting to compare this strategy with the previous one: spring–summer species have 1 to 1.5 months more of the warm season at their disposal, but only 10.3% of spring–summer species in natural communities and 13.3% in urban communities are capable of producing two generations per year. Among summer species, the proportions of those that produce two generations are almost three times as high: 31.2% and 30.8%, respectively. Summer species make up the largest proportion of the combined checklist and practically half of the urban checklist.

(4) Autumn–spring species. The larva starts feeding on mature leaves in late summer or early autumn (in August or September). Larval development is not completed the same year; the larva hibernates (usually at one of the early instars) and continues feeding on springtime leaves at the start of the next warm season. This is one more way to utilize the most valuable food resource of springtime leaves that makes the fourth type similar to the first one, although formally they are opposite: autumn–spring species feed on mature leaves at the beginning of their development and on

growing springtime foliage at later instars. This strategy is followed by 23.2% species in natural communities, but the proportion of such species in urban communities is only 10.3% (Table 2).

In some macrolepidopteran families, all or almost all species follow the same life strategy. Thus, Sphingidae, Drepanidae, and Notodontidae are summer species hibernating at the pupal stage. Members of two largest families, Geometridae and Noctuidae, use all life strategies mentioned above (Table 2). At the same time, these two families visibly differ in the set of strategies: among dendrophagous geometrids, summer species are the largest group, while the largest group among dendrophagous noctuids is that of early spring species. These differences are significant in natural biotopes ($\chi^2 = 16.200$; $p < 0.01$) but not significant in the city because of relatively small number of species ($\chi^2 = 7.278$; $p < 0.2$).

Among all macrolepidopterans feeding on tree and shrub leaves in nature, summer species are the largest group (36.1%; Table 2), and autumn–spring species are on the second place (23.3%). In the city, the proportion of summer species is even greater (49.5%), and the proportion of autumn–spring species is smaller, making early spring species the second largest group (23.4%). Therefore, the start of feeding in urban species is shifted closer to the start of the warm season. The set of strategies in urban species differs significantly from that in species of natural communities ($\chi^2 = 13.854$; $p < 0.01$); among the geometrids and noctuids living in the city, the proportion of summer species is also increased, and the proportion of autumn–spring species is decreased, although the differences are insignificant in this case.

Urban macrolepidopterans include a smaller proportion of specialized species (we use this term to denote species feeding on plants of the same family, as opposed to the “generalized” species feeding on plants of different families), but a higher proportion of obli-

gate dendrophagous species, i.e., those that feed exclusively on trees and shrubs; in natural habitats, more than one-third of macrolepidopteran species are facultative dendrophages, i.e., those that can feed not only on trees or shrubs but also on herbaceous plants, usually dicotyledons (Table 2). This is why generalized dendrophages account for 64.5% of the total checklist of macrolepidopterans collected in the city, while the proportion of such species in natural communities of the Middle Urals is only 42.5%. The narrowing of the food spectrum in urban macrolepidopterans, compared to that of macrolepidopterans living in natural communities, and the widening of the food spectrum in urban obligate dendrophages are opposite trends accounted for by different factors, which are discussed below.

DISCUSSION

The large number of macrolepidopteran species recorded in the city during this study deserves attention by itself. For comparison, general censuses of all groups of insects feeding on trees and shrubs in the cities of Moscow and Krasnoyarsk revealed only 30 macrolepidopteran species in each case (Belova and Belov, 1999; Tarasova et al., 2004). Initially we considered that the situation was due to the inclusion of park forests in the range of urban biotopes, although they are not actually so despite being located within city limits. It turned out, however, that only six species—*Falcaria lacertinaria* (L.), *Plagodis pulveraria* (L.), *Jodis lactearia* (L.), *Hydrelia sylvata* (Den. & Schiff.), *Cerura erminea* (Esp.), and *Colocasia coryli* (L.)—were found exclusively or mainly in park forests; therefore, their contribution could not have any significant effect on the size of the checklist. It appears that the size of checklists for any particular taxon obtained in studies of similar kind simply reflect how carefully the researchers have worked.

Taxonomic composition. As mentioned above, members of six families have not been found in Yekaterinburg in the course of this study. Several of these families comprise large, rare species, and their absence in the checklists is understandable, but the situation with Lasiocampidae is unclear. Members of this family are mentioned in checklists of phyllophagous species found in urban greenery. Thus, *Malacosoma neustria* (L.) has been recorded in Moscow (Belova and Belov, 1999), in cities of Belarus (Gorlenko and Pan'ko, 1972), and in Krasnoyarsk (Tarasova et al., 2004); it is even listed among dangerous pest species (Kulagin, 1934; Losinskaya, 1960), which means that it can reach high abundance under urban conditions. Other lasiocampids found in urban green spaces include *Poecilocampa populi* (L.) and *Dendrolimus pini* (L.) (Gorlenko and Pan'ko, 1972). These three lasiocampid species have also been recorded in natural forest communities of the Middle Urals (although the former two species are rare in this region); after all, a total of ten

species of this family are on “natural” checklists for the region, but none of them has been found in Yekaterinburg.

The situation with Nymphalidae is also somewhat unclear. We have found in Yekaterinburg only one species of this family, *Polygonia c-album* (L.), whereas as many as ten nymphalid species have been recorded in natural biotopes around the city, and three species of the genus *Nymphalis* are common in some years (Olschwang et al., 2004). The nymphalid mentioned in the literature as a member of urban faunas more often than others is the western European *Nymphalis polychloros* (L.), which is usually found in European Russia (Gorlenko and Pan'ko, 1972; Belova and Belov, 1999; Bol'shakov, 2003) but also occurs in Krasnoyarsk (Tarasova et al., 2004). Another nymphalid recorded in cities is *Limenitis populi* (L.) (Baranik and Glotov, 1984; Tarasova et al., 2004). We found larvae of *Nymphalis antiopa* (L.) on birch in the town of Labytnangi at the Arctic Circle. In Yekaterinburg, we repeatedly observed flying *Hemaris fuciformis* butterflies during the study period but never found any larvae of this species.

On the other hand, we found in the city seven macrolepidopteran species not recorded at the field station: three geometrids, three noctuids, and the sphingid *Hemaris fuciformis* (L.). The last species even turned out to be common in the city: during one season, we recorded larvae of this species on honeysuckle in almost all types of biotopes studied, including a public garden on the central street of Yekaterinburg. This sphingid species was even abundant in the 1930s to 1960s, when honeysuckle occupied a much more prominent place among trees and shrubs planted in the urban territory (Pentin, 1939).

Phenology. We have found that the proportion of summer species in the city is higher, while the proportion of autumn–spring species is visibly lower. Two factors that have no direct relationship to lepidopteran phenology had to be tested first as possible causes of this difference in the sets of life strategies between urban and natural species communities.

The first possible cause concerns differences in penetration to the city among species differing in the level of abundance in nature. G.A. Zamshina estimated the abundance of macrolepidopterans she found at the field station on the six-grade scale previously used for the lepidopterans of the Il'menskii Nature Reserve (Olschwang et al., 2004). In this study, we have simplified that scale: all frequently occurring and common species (categories 1–4) are hereinafter termed “common” and all species of lower abundance (categories 5 and 6) are termed “rare.” We consider that common species penetrate to the city more easily due simply to their higher abundance in natural communities (although their relative abundance in the city should not necessarily remain at the same level as in nature). If common and rare species follow different life strategies, this may account for changes in the set

Table 3. Comparison of proportions (%) of species with different life strategies in different categories of macrolepidopterans living in natural communities

Life strategy	Category			
	common	rare	obligate dendrophages	facultative dendrophages
Early spring	9.92 (12)	31.72 (46)	23.08 (39)	19.59 (19)
Spring–summer	12.40 (15)	9.66 (14)	11.83 (20)	9.28 (9)
Summer	44.63 (54)	28.97 (42)	44.97 (76)	20.62 (20)
Autumn–spring	25.62 (31)	21.38 (31)	14.79 (25)	38.14 (37)
Other strategies	7.44 (9)	8.28 (12)	5.32 (9)	12.37 (12)
Total	100 (121)	100 (145)	100 (169)	100 (97)

of life strategies in urban species, compared to those in natural communities.

The groups of common and rare dendrophagous macrolepidopterans found in natural landscapes proved to be similar in size: 121 and 145 species, respectively (Table 3). Among the species common in nature, 63 (52.1%) have penetrated to the city, compared to only 26 (24.8%) among rare species. These two groups significantly differ in their sets of life strategies ($\chi^2 = 19.761$; $p < 0.001$), but in different way than do the groups of all urban and natural macrolepidopteran species. The proportion of summer species among the species common in nature is indeed higher, but the proportion of autumn–spring species is no lower. Importantly, the proportion of early spring species among the species common in nature is very small, whereas it is not so among common urban species. These facts do not confirm the hypothesis that the composition of urban species differs from that in natural communities because, above all, it is mostly species common in natural communities (with their characteristic set of life strategies) that penetrate in the city.

The second possible cause of differences in the sets of strategies between the group of urban macrolepidopterans and the group of macrolepidopterans from natural habitats is the aforementioned relatively low proportion of species with the mixed feeding type (facultative dendrophagous species) in the former group. The question was whether obligate dendrophagous species and those with wider food spectra differ in their sets of life strategies. With this purpose, we divided all species of the combined checklist into these two groups and compared the sets of strategies in each.

Table 3 shows that facultative dendrophagous species (i.e., those that have wider food spectra) are significantly different from obligate ones: they include a smaller proportion of summer species, but a larger proportion of autumn–spring species ($\chi^2 = 29.151$; $p \leq 0.001$). But comparison of obligate dendrophagous species found in nature with those found in the city, i.e., those that make up the core of the tree-damaging species assemblage, reveals no significant differences in their sets of strategies ($\chi^2 = 3.230$; $p < 0.6$).

Therefore, the different set of strategies found in urban species is determined by macrolepidopterans of the mixed feeding type, which are less represented in the material collected in the city. These species actually have a different set of strategies, which is closer to that of the lepidopterans that feed on herbaceous plants (Bogacheva, 2009).

The expression “material collected in the city” is used here on purpose. It should be reminded that in natural communities we used various sampling methods, including light traps, which allowed us to catch large amounts of insects nonselectively of their feeding mode. In the city, we only collected larvae from trees and shrubs, which reduced the chance to find species of the mixed feeding type. At the same time, facultative dendrophagous species can actually be underrepresented in a city, depending on the food supply it provides for phyllophages. Bol’shakov (2003) also found that in an urban landscape (namely, in the city of Tula), the lepidopterans of the regional fauna that feed on trees and shrubs were much more fully represented than those feeding on herbaceous plants. He explains this difference by the fact that trees and shrubs in the city are preserved and cultivated, and therefore can be used as shelter by lepidopterans at different developmental stages. The trend he revealed has nothing to do with methods of sampling. As for Yekaterinburg, it remains unclear whether urban macrolepidopteran communities (compared to natural ones) actually include fewer species capable of feeding on both trees or shrubs and herbaceous plants, or the observed difference is an artifact of sampling methods used in this study.

A supposed cause of the reduced proportion of specialized species in the city (and, thus, an increased proportion of generalized species) is in some specific features of urban greenery. The wide spectrum of trees and shrubs used in city landscaping and, at the same time, the mosaic structure of their distribution within city limits leave few possibilities for monoculture and, therefore, give generalized Macrolepidoptera species an advantage over specialized species.

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