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Latitudinal trends in life strategy changes in the Macrolepidoptera of the Urals, Russia

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ABSTRACT

All main categories of food resources and their relation to hibernation stage and voltinism were studied in the Macrolepidoptera of the forest belt in the Urals, ranging from forested steppe to forested tundra. Food resources (leaves of deciduous woody plants, D, of dicotyledonous herbaceous plants, H, of evergreen plants, E, of 'graminoids', G; flowers and fruits, F; substrates of low nutritive value, LV) were divided into eight categories according to their ability to support a rapid growth of caterpillars and to their longevity. In the southern Urals, macrolepidopterans were shown to feed mainly on D (39.8%) and H (28.0%), and to hibernate as pupa (43.5%) or larva (41.8%).

In lepidopteran groups F – D – E – H, hibernation in the pupal stage dominates, falling to the end of this series from 71% to 47%. Many lepidopterans feeding on these resources (especially summer species on D and H) are bivoltine. In groups Pf ("polyphages"- species using more than two food categories) – LV – G, hibernation in the larval stage becomes increasingly essential. Lepidopterans feeding on spring foliage of D present a peculiar strategy of "early spring species", combining univoltinism enabled by an obligatory diapause with hibernation as egg or imago.

Northwards the food spectrum of lepidopterans fails to change much. The proportion of species feeding on E is slightly increased, but the percentages of species feeding either on the most valuable resource (F) or on the least one (LV) drop. Seasonality alterations are higher. Species hibernating as larva prevail at the northern tree line; species related to G and LV hibernate as larva, as a rule; the same is true for Pf species. The share of semivoltine species grows 6 times toward the Polar Urals;

two generations are not found there in any species, although potentially bivoltine species are numerous on the list.

Some lepidopteran taxa using a large set of trophic and seasonal strategies were also compared. In the southern Urals, Rhopalocera were shown to differ from Heterocera in their feeding habits and seasonality; the same is true for Geometridae and Noctuidae. The latter family considerably alters its feeding and seasonality toward the Polar Urals, noctuids there resembling geometrids in their food spectra. Differences between Rhopalocera and Heterocera continue to be significant.

Three Macrolepidoptera families, Nymphalidae, Geometridae and Noctuidae, dominate in the forest belt; the proportions of the former two families increase, however, to its northern border, whereas the share of noctuids falls abruptly. A group of Pf species with a two-year long development (two hibernations, usually as egg and then pupa) appeared within this family. Some nymphalids hibernate twice at the larval stage, this feature having allowed them to turn into truly arctic species. Geometrids come to the northern tree line virtually without changing their typical feeding and seasonality patterns, thriving there largely due to small sizes.

Key words: Macrolepidoptera, feeding, seasonality, latitudinal trends, Urals, Subarctic

INTRODUCTION

The species diversity of Lepidoptera, like that of most plant and other animal taxa, is known to usually drop from the tropics to the poles (Pianka, 1966; MacLean, 1975). This trend, however, differs from group to group. Thus, Nymphalidae, Geometridae and Noctuidae continue dominating among the macrolepidopterans in the forested tundra belt, but the proportions of the fiormer two families rise, whereas the share of noctuids falls abruptly. So the loopers form the richest family in the North while owlet moths are the first in the southern part of the forest zone.

Each of these three large families showing various feeding and phenological patterns, Bogacheva et al. (2003) have made an attempt to relate the capability of macrolepidopteran existence in the northern part of the forest zone to the quality of their food resources. First of all, we mean the differences between certain food categories (leaves of deciduous woody plants, of dicotyledonous herbs etc.) and their "palatability" (MacLean & Jensen, 1985; Chapin et al., 1986) for polyphages. In relation to these categories, some features of lepidopteran seasonality were analyzed, the hibernation stage in the first place.

A more detailed examination, however, shows that seasonal changes in food quality are essential for some food categories and that the quality of food used by caterpillars during the feeding period determines the seasonal strategy of any species. We have studied these strategies relating them to the main categories of food resources both for all Macrolepidoptera and for individual lepidopteran taxa. By detecting some features of feeding and phenology characteristic of the subarctic Macrolepidoptera, we can reveal some latitudinal patterns changing in some higher taxa from the southern to the northern boundary of the forest zone.

MATERIAL AND METHODS

In the Southern Urals (Ilmenky Nature Reserve, 55° N), material was collected in 1996-2003 (Olschwang et al., 2004). Material of Heterocera in the Middle Urals (56° 30' N) was obtained in 1997-2004 (Zamshina, unpublished data). Information concerning Rhopalocera was extracted from the monograph by Korshunov & Gorbunov (1995). In the Polar Urals (66-67° N), a total of 211 species were collected by different researchers in 1970-2007 (Olschwang, 1980; Gorbunov & Olschwang, 1993; several findings by K. Nupponen and T. Nupponen in 1998 and I.A. Bogacheva in 1970-2007). These lists served as the basis for two papers published earlier (Bogacheva et al., 2003; Bogacheva & Zamshina, 2006). Lepidopterans were caught by light traps, by butterfly nets in the daytime or reared in cages from caterpillars collected on their food plants.

In lepidopteran taxonomy, we followed the catalogue by Karsholt & Razowsky (1996). Information on food plants and lepidopteran phenology was taken from the literature (see bibliography in Bogacheva et al., 2003).

All lepidopterans were divided into groups according to the categories of food resources. These groups were divided into subgroups corresponding to the beginning of larval feeding in the South of the forest zone (April-May, June-July, August-September). The subgroups were also subdivided according to hibernation stage.

The significance of the differences was estimated using Chi-squared test (Hudson, 1970).

RESULTS

Food resources of lepidopterans in accordance with their food value which is considered as the capability of supporting a rapid growth of caterpillars and with the period of their existence were divided into eight groups:

- Deciduous woody plants (D):
  - (a) Spring leaves of deciduous woody plants. A valuable food resource rich in proteins and water, existing only 3-4 weeks until the leaf reaches its final size. This resource provides a rapid growth of caterpillars, mainly owing to a high P/C coefficient. In the temperate zone, this resource is used by species that start feeding in April to early May, often with buds that are not broken yet into leaves (Feeny, 1970).
  - (b) Young leaves of woody plants appearing in the summer on auxiblasts. In some plant species they grow up to mid-August. A valuable food resource

rich in proteins; the water content is however lower than in spring leaves. This resource supports a rapid growth of caterpillars.

(c) Old leaves of woody plants, existing from the end of May to the end of the growing season. Both protein and water contents are lower while the percentages of carbohydrates, defensive substances (mainly tannins) and cellulose are increased. Caterpillar growth is retarded (Mattson, 1977).

- Dicotyledonous herbaceous plants (H). The seasonal alterations of their leaves are generally the same as in deciduous woody plants, but less significant and more gradual (Schweitzer, 1979; Scriber & Slansky, 1981 etc.). Most of the species of dicotyledonous herbs produce their shoots throughout the vegetation season, this also being favourable for phytophages. These plants ensure rapid larval growth owing both to a high P/C coefficient and high feeding intensity (Scriber & Slansky, 1981; Slansky & Scriber, 1982), but many of them defend their leaves against phytophages by means of specific chemical substances. So they are damaged by a restricted number of specialized phytophages (Mattson, 1977).
- Evergreen woody plants (E): coniferous trees and shrubs, Ericaceae, Empetraceae, partly Vacciniaceae and some others. Feeding on their leaves is impeded because of a dense cuticle, a high content of lignin (not only indigestible, but it also lowers protein digestibility) and resins. Larval growth is retarded.
- 'Graminoids' (G). In the literature, this term is accepted for Poaceae, Cyperaceae, Juncaceae and Typhaceae. They are nutritive enough only in the beginning of their growing; later on they do not support rapid larval growth. Silicon is known to be the only defensive substance (MacLean & Jensen, 1985).
- Food resources of low nutritive value (LV). Mosses, lichens, wood, debris and withering leaves on plants, plant roots and lower part of herb stem were to be assigned to this food category. Larval growth on them is slow throughout the vegetation season because of a low P/C coefficient and low feeding intensity (Slansky & Scriber, 1982). As a matter of fact, some species feeding on this resource are saprophagous.
- Generative parts of plants: flowers and fruits (F). They have to be considered as a very valuable but short-living food resource. Certain kinds of these resources appear in different periods of the growing season.

All macrolepidopteran species were attributed to the above categories of food resources. This was simple for species feeding on one resource category; the species feeding on two categories, however, were also attributed to one of them in accordance with their food preference. Lepidopterans using more than two resource categories were denoted as polyphages (Pf).

Lepidopteran species feeding on deciduous woody plants would be divided into three subgroups according to three different types of their leaves (a, b, c). Unfortunately, the literature usually fails to contain information as to which type of food, b or c, is used by caterpillars feeding in the summer on a deciduous woody plant. Therefore, instead of a-c leaf categories we have used a period when the caterpillar begins to feed: April-May, June-July, August-September. Species feeding on dicotyledonous herbaceous plants were also subdivided in Tables into these seasonal groups. So in Tables 1-6 all the species were divided into seven categories: D, H, E, G, LV, F and Pf; while D and H also show seasonal subcategories.

In the beginning, let us take the macrolepidopterans of the southern Urals (Table 1) and examine their food preferences. We can see that the proportion of species feeding, either exclusively or mainly, on H is the highest, about 40%, followed by those feeding on D (28%). Each of the remaining five food resources attracts no more than 10% of lepidopteran species, the least lepidopteran share feeding on E.

Hibernation as larva or pupa prevails among southern Urals Macrolepidoptera (Table 2). In lepidopteran groups F – D – E – H, the hibernation as pupa dominates, falling to the end of this series from 71 to 47%. In groups Pf – LV – G, hibernation in the larval stage becomes more and more essential. Hibernation in the stage of egg and, especially, imago is infrequent.

The fact is noteworthy (Table 2) that species which begin to feed in the spring hibernate in the stage of egg or imago (1); those which begin to feed in the summer hibernate in the pupal stage (2); those feeding in August and later hibernate as larvae completing

Table 1. Distribution of food resources among different macrolepidopteran taxa, %, Southern Urals

Food resources	Lepidopteran taxa				
	Rhopalocera	**Heterocera**	**Geometridae**	**Noctuidae**	**Total**
D, spring	6.1	10.0	9.7	11.7	9.2
D, summer	3.8	14.5	14.2	5.6	12.4
D, autumn	8.3	5.8	8.1	1.2	6.2
D, total	18.2	30.3	32.0	18.5	28.0
H, spring	6.8	3.7	2.5	6.4	4.3
H, summer	25.8	16.6	21.8	15.7	18.3
H, autumn	27.3	14.9	19.3	14.9	17.2
H, total	59.9	35.2	43.6	37.0	39.8
E	0	3.2	6.1	0.4	2.6
G	21.2	6.9	0.5	14.1	9.5
LV	0	9.8	0	12.8	8.0
Pf	0.7	6.9	5.6	8.8	5.7
F	0	7.9	12.2	8.4	6.4
Total species number	132	571	197	249	703

D – deciduous woody plants; H – dicotyledonous perennial herbs; E – evergreen woody plants; G – "graminoids"; LV – resources of low value; F – flowers and fruits; Pf – more than 2 resource categories are used.

Table 2. Some features of phenology in species feeding on different food resources (% species in each group). Southern Urals

Food resources	Species number	Hibernation stages				Two or more hibernations	Two or more generations
		egg	larva	pupa	imago		
D, spring	65	52.3	0	30.7	17.0	0	6.2
D, summer	88	0	0	95.4	4.6	1.1	38.6
D, autumn	44	0	79.5	20.5	0	0	9.1
D, total	197	17.2	17.8	57.4	7.6	0.5	21.3
H, spring	30	70.0	0	23.3	6.7	0	20.0
H, summer	129	0	15.5	81.4	3.1	3.1	40.3
H, autumn	121	0	84.3	15.7	0	2.5	25.6
H, total	280	7.5	43.6	46.8	2.1	2.5	31.8
E	18	11.1	38.9	50.0	0	0	5.6
G	67	6.0	86.6	6.0	1.4	6.0	10.4
LV	56	8.9	82.2	8.9	0	8.9	1.8
Pf	40	5.0	60.0	30.0	5.0	0	25.0
F	45	22.2	4.4	71.2	2.2	0	24.4
The mean in the order	703	11.1	41.8	43.5	3.6	2.4	22.9

their development next spring (3). The situation looks quite natural. These three main seasonal strategies are used by 13.2, 32.4 and 36.4% of all lepidopterans, respectively, combined 82% of the total. The first strategy is basically related to D, the second to D, H and F, while the third to H, G and LV. In addition, there are further three strategies, each being used by about 5% species: (4) caterpillars begin to feed in the spring but hibernate as pupae. This strategy is mainly related to D. (5) caterpillars begin to feed in June-July, but hibernate without reaching a pupal stage. This strategy is usually related to H and G. (6) caterpillars begin to feed in August, accomplishing their development during the current growing season and hibernating as pupae. This strategy is mainly related to H and F. All these six strategies account for 97% macrolepidopteran species.

As already noted above, the range of seasonal strategies varies noticeably in species feeding on different resources. It also differs in various Macrolepidoptera taxa. Small Lepidoptera families often show only one prevailing strategy. Thus, species feeding in summer months on D and hibernating as pupae dominate in Notodontidae and Drepanidae. Some Sphingidae species can feed on D, the others on H, but caterpillars usually start feeding in the summer and hibernate at the pupal stage. The sets of strategies observed in larger families, where a certain strategy characterizes a subfamily or even genus, differ distinctly. Thus, the percentage of species feeding on valuable resources (D, H, F) is higher in geometrids than in noctuids (Table 1). In contrast, the latter family contains far greater proportions of broad polyphages (Pf), on the one hand, and species restricted to resources of low nutritive value (LV and G), on the other. Geometrids begin to feed in the summer (47.2% of all species) and hibernate as pupae (62.4%) more frequently than noctuids do, whose feeding in the end of the vegetation season (39.8%) and larval hibernation (39.0%) are more common than in geometrids. Rhopalocera which prefer to feed on herbaceous plants (H, G), begin to feed in the end of the season and therefore hibernate as larvae, thus differing in all these respects from Heterocera.

Another feature of lepidopteran biology is obviously related to the quality of food resources. Some species show two-year long generations. At the southern border of the forest zone such are rare (Table 2), mainly related to LV (Sesiidae and Cossidae feeding on wood) or G (some *Erebia* and *Oeneis* spp.). In contrast, the other species have two and even three (e.g., *Pieris*) generations per year. This is more characteristic of summer species feeding on D, H and F, as well as of autumnal species feeding on H and of Pf species. The percentage of species with more than one generation per year is 34.8 in Rhopalocera, as opposed to only 20.1% in Heterocera ($\chi^2 = 13.2$; $\upsilon = 1$; $p < 0.001$). Geometrids also differ of noctuids in this respect (26.9% vs. 15.3%; $\chi^2 = 9.1$; $\upsilon = 1$; $p < 0.01$).

Northwards, both macrolepidopteran food spectra (Tables 1, 3, 5) and seasonal strategies (Tables 2, 4, 6) tend to change. The share of species feeding on H drops, the same being true for LV and F species as well. On the contrary, the percentage of species feeding on D, E and of Pf species rises. Food spectra on the Southern and on the Polar Urals differ significantly ($\chi^2 = 21.4$; $\upsilon = 6$; $p < 0.01$). The alterations in noctuids ($\chi^2 = 54.8$; $\upsilon = 6$; $p < 0.001$) are more considerable than in geometrids ($\chi^2 = 9.2$; $\upsilon = 4$; $p < 0.1$; NS), whereas food spectrum changes in Rhopalocera are the least ($\chi^2 = 6.9$; $\upsilon = 4$; $p < 0.2$; NS). In all lepidopteran groups except for F feeders the shares of species hibernating in larval stage increase. As a result, this becomes a leading strategy of hibernation notably exceeding the hibernation in the pupal stage (Table 6).

Table 3. Distribution of food resources among different lepidopteran taxa, %, Middle Urals

Food resources	Lepidopteran taxa				
	Rhopalocera	Heterocera	Geometridae	Noctuidae	Total
D, spring	4.5	13.1	14.2	13.9	11.6
D, summer	1.8	17.2	16.9	7.5	14.4
D, autumn	7.3	5.1	7.7	1.5	5.5
D, total	13.6	35.4	38.8	22.9	31.5
H, spring	13.6	3.1	3.8	4.0	5.0
H, summer	25.5	12.3	16.9	10.4	14.7
H, autumn	20.0	13.6	15.8	15.4	14.7
H, total	59.1	29.0	36.6	29.8	34.4
E	0.9	3.7	6.6	1.0	3.2
G	19.1	6.6	1.1	13.9	8.9
LV	0.0	10.3	0.5	13.9	8.4
Pf	3.6	8.0	6.0	11.0	7.2
F	3.6	7.0	10.4	7.5	6.4
Total species number	110	487	183	201	597

Very high, 6-fold, is a percentage increase in macrolepidopterans capable of hibernating twice (Tables 2 and 6). At present this is known not only for species feeding on LV and G, although in these two groups such a situation is indeed more evident, but also

Table 4. Some features of phenology in species feeding on different food resources (% species in each group). Middle Urals

Food resources	Species number	Hibernation stages				Two or more hibernations	Two or more generations
		egg	larva	pupa	imago		
D, spring	69	55.1	1.5	33.3	10.1	0.0	10.1
D, summer	86	0.0	2.3	94.2	3.5	0.0	35.9
D, autumn	33	0.0	81.8	18.2	0.0	0.0	6.1
D, total	188	20.2	16.0	58.5	5.3	0.0	20.7
H, spring	30	66.7	0.0	26.6	6.7	3.3	36.7
H, summer	88	0.0	18.2	79.5	2.3	0.0	42.0
H, autumn	88	0.0	87.5	12.5	0.0	2.3	25.0
H, total	206	9.7	45.1	43.2	2.0	1.5	34.0
E	19	5.3	57.9	36.8	0.0	0.0	5.3
G	53	5.7	84.9	9.4	0.0	3.8	15.1
LV	50	8.0	82.0	10.0	0.0	10.0	2.0
Pf	43	7.0	62.8	27.9	2.3	0.0	27.9
F	38	13.2	18.4	65.8	2.6	0.0	26.3
The mean in the order	597	12.4	42.9	41.9	2.8	1.7	23.6

Table 5. Distribution of food resources among different lepidopteran taxa, %, Polar Urals

Food resources	Lepidopteran taxa				
	Rhopalocera	Heterocera	Geometridae	Noctuidae	Total
D, spring	5.8	10.7	10.8	11.8	8.9
D, summer	2.9	19.7	21.5	5.9	13.6
D, autumn	10.1	9.8	7.7	17.6	10.0
D, total	18.8	40.2	40.0	35.3	32.5
H, spring	5.8	3.3	4.6	2.9	4.2
H, summer	26.1	13.1	10.8	11.8	17.8
H, autumn	17.4	12.3	18.5	2.9	14.1
H, total	49.3	28.7	33.9	17.6	36.1
E	2.9	8.2	4.6	20.6	6.3
G	23.2	2.4	0	8.8	10.0
LV	0	3.3	1.5	0	2.1
Pf	5.8	11.5	10.8	14.8	9.4
F	0	5.7	9.2	2.9	3.6
Total species number	69	122	65	34	191

Table 6. Some features of phenology in species feeding on different food resources (% species in each group). Polar Urals

Food resources	Species number	Hibernation stages				Two or more hibernations	Two or more generations
		egg	larva	pupa	imago		
D, spring	17	64.6	0	17.7	17.7	11.8	23.5
D, summer	26	0	7.7	88.5	3.8	0	34.6
D, autumn	19	0	94.7	5.3	0	21.0	0
D, total	62	17.7	32.3	43.5	6.5	9.7	21.0
H, spring	8	50.0	0	37.5	12.5	0	37.5
H, summer	34	0	29.4	64.7	5.9	8.8	55.9
H, autumn	27	0	96.3	3.7	0	3.7	40.7
H, total	69	5.8	52.2	37.7	4.3	5.8	47.8
E	12	25.0	58.3	16.7	0	33.3	8.3
G	19	0	94.7	5.3	0	42.1	10.5
LV	4	0	100.0	0	0	50.0	25.0
Pf	18	0	83.3	16.7	0	22.2	11.1
F	7	14.3	0	85.7	0	14.3	0
The mean in the order	191	10.0	52.4	34.0	3.6	15.2	27.2

for any of the remaining categories. Later on this will be discussed in further details. The percentage of lepidopterans that can have more than one generation in the southern Urals does not fall northwards (Table 6). On the contrary, it is slightly increased, although in the North such species certainly support only a single generation per year.

DISCUSSION

Relationship between food resources and seasonal strategies

The proportion of species with two hibernations during one generation and that of species with two generations during one growing season are two ways to characterize the mean growth rate of specimens in any group, taxonomic or ecological. As the feeding stage takes the main period of development from egg to imago (besides hibernation), it appears natural that growth rate is related to food quality. Table 2 demonstrates that the valuable food resources (D, H) ensure rapid larval growth allowing any species for having 2-3 generations per season (a lower percentage of such species on the most valuable resource, F, is caused by its short-term existence). So the seasonal strategies of lepidopterans are also related to food quality.

On deciduous trees and shrubs (D), the strategy of early spring species is distinguished (Feeny, 1970; Schweitzer, 1979). These species feed only on this valuable but short-term resource; larvae of these species develop no longer than 2-3 weeks. Feeding on young leaves is quite necessary at least for young caterpillars of this group (Aide & Londono, 1989), and the congruence between host plant (spring bud burst) and lepidopteran (larval eclosion) phenologies becomes a leading factor of population dynamics (Hunter, 1991). Therefore, the hibernation at the egg or, more rarely, imago stage, that are the closest to the feeding one, is optimal for these species. They are simply not capable of producing more than one generation per year, as there is no food for them in the summer and autumn. So feeding is followed by an obligate diapause (usually at the pupal stage) which lasts to the end of summer or until autumn (Saulich, 1999), followed by imago eclosion and, in most species, egg-laying and winter egg diapause.

Not all of the species that start feeding in the spring show the same strategy. Some of them manage to have two generations per growing season. This means that larvae of these two generations use food resources of differing quality. This strategy is believed to offer some difficulties to phyllophages, because only few spring species have two generations, in contrast to summer ones. Finally, large lepidopterans can have only one generation toward the end of the season, the food quality for larvae constantly decreasing. All these lepidopterans hibernate in the pupal stage unlike the real early spring species.

Lepidopterans that begin their development on trees and shrubs in the summer are adopted to feed on old leaves. This is a long-existing food resource, so many species using it can have 2 generation within the same growing season (Table 2). The majority of summer species hibernate as pupae.

There are D lepidopterans that start feeding in the last summer month. In some species, caterpillars accomplish their development to the end of the growing season to hibernate as pupae. In fact these species do not differ considerably from summer ones, but have only one generation. The majority of autumnal species hibernate, however, as larvae that continue their feeding next spring. In this case, young caterpillars feed on old leaves while older instars on young leaves demonstrating a distinct feeding strategy contrasting to early spring species. This is, however, the second way to use spring foliage, a valuable food resource (Hunter, 1991). Such a strategy provides caterpillars with a chance to be "at table" just in time, and plant phenology does not limit it. In addition, caterpillars grow then intensely on young leaves in the instars when an increase in body mass is the highest.

Let us analyze now the feeding on dicotyledonous herbs (H). The season of feeding on H is shifted notably to autumn while the hibernation stage to larvae. When discussing the reasons for this, the opinion was advanced (Niemelä et al., 1982) that it is more difficult to occupy herbaceous plants because of their absence in the autumn: the imago cannot lay eggs on a herb plant as easily as on trees or shrubs. Nonetheless, some Lepidoptera are known to do this, but a developed strategy of early spring phyllophages is absent on H. Larger lepidopterans and slowly developing species, since not all H ensure rapid larval growth, begin to feed in spring. Many species, especially summer ones, have 2 or even 3 generation using H. The proportion of such species is higher on H than on D (Table 2), because larval growth is more rapid here.

In the next four lepidopteran categories (E, G, LV and Pf), the share of species that begin their feeding at the end of the season, and hibernate in the larval stage, exceeds the other seasonal strategies. Why so? We believe this is caused by different reasons.

Lepidopterans feeding on G have several reasons to begin their feeding closer to the end of summer. Firstly, females cannot lay eggs on their food plants in the end of the season, same as H group fails to do this. Secondly, hibernating caterpillars can begin their feeding as soon as a host plant appears using the period of high quality very short in G plants. In this connection, feeding on G is quite similar to that on old D leaves. Finally, the low-quality G resource retards larval development, so larval hibernation would seem useful when feeding cessation is not so precisely fixed temporally. Some species of the G group hibernate twice already at the southern border of the forest belt.

Species feeding on evergreen plants (E) are not so numerous. Larval growth is retarded on these plants; no early spring strategy of feeding is observed either. Almost all of the species have only one generation per year. Larvae start feeding in the summer or autumn, hibernating at the pupal stage or as larvae, respectively. These two strategies prevail in the E lepidopteran group.

Feeding on LV also demonstrates a strong shift to autumn. Because of a low growth rate these species have only one generation per year. Even more, individual development can take sometimes more than a year. This is one of the reasons for hibernation as larvae. Some of the LV lepidopterans hibernate twice even in the steppe (Anikin, 1997). Species feeding on stems and roots of herbaceous plants or on dry leaves are forced to begin their feeding in the end of the growing season, therefore mostly hibernation in the larval stage. At this stage the most LV species hibernate however, even those feeding on mosses, lichens and wood that are anytime available.

The last category of lepidopteran food resources is formed by flowers and fruits (F). These appear in different periods of the season, the onset of feeding neatly coinciding with their appearance. In early spring, lepidopterans begin to feed on poplar and willow catkins; like early spring phyllophages, they have only one generation and hibernate at the egg stage. Some species, especially those feeding in the summer on flowers and then on fruits of herbs, have enough time for two generations. Naturally, the autumnal species have only one generation per year, but, this being the only exception among all lepidopteran groups, these also succeed to accomplish larval development and to pupate. So hibernation as pupae prevails in this group like amongst D lepidopterans.

To summarize, the value of each food category and the period of its availability determine the seasonal strategies of lepidopterans, including the period of larval feeding and hibernation stage.

Latitudinal trends in lepidopteran feeding

As shown earlier (Bogacheva & Zamshina, 2006), the nutritional base of lepidopterans expressed as the number of food plant species is decreased significantly from the forested steppe to the forested tundra. The number of lepidopteran species drops even more rapidly. The proportion of certain food categories in the lepidopteran nutritional base is increased, however, while that of the other categories falls. Some changes in food spectra (Tables 1, 3, 5) are not very high, but quite distinct. We intend to discuss these changes in order to understand whether they are related to the distribution of certain lepidopteran taxa in the Subarctic.

Evergreen plants are well represented in the Polar Urals flora. Now E plants are represented by Ericaceae, Empetraceae, *Vaccinium vitis-idaea*, *Dryas* and *Diapensia* rather then by conifers (*Picea obovata* and *Juniperus* spp., which remain virtually undamaged by macrolepidopterans, while *Larix* is considered as a D resource). E plants are consumed by many geometrids and noctuids, usually together with other food resources, especially D, in spite of low "palatability" of E in cages (MacLean & Jensen, 1985; Chapin et al., 1986). They do not support a rapid larval growth, a small proportion of species hibernating in the pupal stage and a high percentage of species hibernating twice serving to prove this statement. Nonetheless, in the Polar Urals a higher share of lepidopterans feed on evergreen plants (Table 6) than in the South Urals (χ^2= 6.3; υ = 1; p < 0.02).

LV is a food resource that induces a many-year long development already in the South of the forest zone (Danks, 1992; Anikin, 1997). In the forested tundra, LV's use is more poor (χ^2= 8.2; υ = 1; p < 0.01) than in the South Urals. Four species only, i.e. *Pharmacis fusconebulosus* (DeGeer) (Hepialidae) feeding on roots of herbaceous plants, the only species caught more or less regularly, two Sesiidae (one species in willow stems, the other in stems of birch and alder) and *Idaea seriata* (Schrk.) eating mosses, lichens and dry leaves, have been found in the near-Ob forested tundra and over the Polar Urals. But such groups very considerably represented in the South of the forest belt as noctuids, which feed either on lichens or on G stems and roots, or on withering leaves of many other plants, and Lithosiinae are completely absent from the northern border of forests. Why so? Almost all Lithosiinae hibernate as pupae, being possibly unable to reach this hibernation stage before the end of the growing season or to alter it on the North. However, most of LV noctuids (23 of 32) hibernate as larvae already in the South of the forest zone, failing however to switch to a many-year seasonal strategy on the North and therefore disappearing from the fauna.

On the contrary, flowers and fruits (F) are the most valuable food resource, but the share of lepidopterans feeding mainly on this resource also falls northwards, though insignificantly. Only seven species largely consuming plant flowers, fruits or seeds have been registered here: six geometrids from the genera *Perizoma*, *Eupithecia* and *Epirrhoe*, and one noctuid, *Parastichtis suspecta* (Hb.), which starts its development on willow catkins. The majority of lepidopterans using this resource in the South of the forest belt are specialized on one plant species or genus, more rarely a single family. This specialization might present some difficulties in the North, as all species penetrating there continue to be specialists.

This resource is well known to fluctuate widely from year to year, decreasing the number of its consumers specialized on F. If the F resource is available, however, it is used by usual phyllophagous species together with leaves. Thus, we have observed repeatedly that *Eulithis prunata* (L.) caterpillars eat not only leaves, but also green berries of *Ribes glabrum* while *Itame brunneata* (Thunb.) consume unripe berries of *Vaccinium uliginosum*. Observations of *Aglais urticae* (L.) caterpillars for 24 hours showed that nettle inflorescences, the plant then in full bloom, were consumed even more readily than leaves.

Caterpillars of *Hyles galii* (Rott.) rising on a new stem of *Chamaenerion angustifolium* eat its flowers in the first place, only later switching to leaves. In general, Lepidoptera larvae do not neglect the valuable F resource, but they are not specialized exclusively on it.

The most valuable food categories could ensure a rapid growth of tundra phytophagous insects, thus giving a chance to accomplish their development during one growing season. An analysis of the food spectrum shows, however, that the proportion of early spring species is not increased in the North, the share of F species even dropping. This means it is in the North that some features of these food resources pose significant difficulties to phytophages feeding on them there. For F consumers, the constraints seem to lie both in the need in narrow specializations of phytophages and wide yearly fluctuations of the nutritional base, for early spring species in the lack of a congruence between lepidopteran and plant phenologies in the very beginning of the season (Hunter, 1991) and the danger of an open egg hibernation on the host plant (Niemelä et al., 1982). So the growing leaves are better exploited by hibernated larvae rather than by freshly eclosed ones, whereas the flowers and fruits are consumed by numerous phyllophagous lepidopterans in addition to plant foliage. The use of LV resources is declined to zero at the northern border of the forest zone, although already in the South of the forest belt it is LV that induce another hibernation in the larval stage so typical of tundra insects.

Latitudinal trends in seasonality

Let us consider now the hibernating stages and the general duration of development.

As noted above and elsewhere (Niemelä et al., 1982), hibernation in larval stages prevails among the boreal Macrolepidoptera. Hibernation as larvae is the necessary condition to develop a many-year long strategy (see below).

Species with rapidly growing larvae can have two, sometimes even three, generations per year in the southern parts of the forest zone. At the northern tree line we observe no completed second generation in any species. If the number of generations in the southern taiga zone is controlled by photoperiod, the question arises as to which factors are decisive in the North, where photoperiodic keys are known to be week (Downes, 1965; MacLean, 1975; Danks et al., 1994). There is evidence that the northern populations of widespread species become monovoltinuous, with an obligate diapause (Saulich, 1999; Scriber, 2001), or the cessation of their development is regulated merely by temperature (Saulich, 1999).

Certain attempts at starting a second generation sometimes do occur, however, among macrolepidopterans on the North. In 2005, when the vegetation season was early and warm, a colony of young caterpillars of *Aglais urticae* (L.) undoubtedly belonging to a second generation was found at Labytnangi in mid-August (Bogacheva, 2007). In 2007, in the same weather situation, final instar larvae of *Drepana lacertinaria* (L.) were collected there on July 18th, versus usually the middle of August. Some moths eclosed in cages in the very beginning of August, without freezing, which was apparently an attempt to begin a second generation since this species hibernates strictly only as larvae. Just as expected, attempts at a second generation were observed in summer species feeding on D or H. Early spring species have no second generation at all, F being a short-term food resource while E, G and LV ensuring no rapid growth of larvae.

A biannual generation implies two hibernations. Strictly speaking, quite different phenomena underlie the figures in the penultimate columns in Tables 2, 4, 6. Several species with normal one-year generations, but with two pupal hibernations in some specimens were placed in this column. Double hibernating in some specimens is typical of insects living in unpredictable conditions to ensure their survival when the next growing season appears to be unfavorable (Danks, 1992). Two or more hibernations at a resting stage are very usual in sawflies, and we believe that in lepidopterans this is not rare either. Such species have been registered even in the South of the forest zone (Anikin, 1997).

Some noctuids, mainly *Sympistis* and *Xestia,* pass to hibernation at two different stages, the first as eggs or young larvae, the second as pupae. The whole life cycle lasts two years, larvae feeding throughout the vegetation season or also in the end of the preceding one. This seasonal strategy goes with feeding on typical tundra vegetation: *Betula nana*, some *Salix* species, *Vaccinium uliginosum, Empetrum,* Ericaceae, *Dryas, Polygonum viviparum, Astragalus* spp., with caterpillars usually using several types of resources, including evergreen plants. This is already the strategy of truly tundra phytophagous insects, even though the need in completing larval development before the autumn might limit such species. One species, *Xestia alpicola* (Zett.), is capable of passing its second hibernation also as larvae.

The most flexible strategy, with two hibernations as larvae, is characteristic of many Rhopalocera species in the Polar Urals, not only of numerous *Erebia* and *Oeneis*, but also of *Boloria* which are also very common there, of *Colias hyale* (L.), *C. tyche* Böber and *Euphydrias iduna* (Dalm.). The former two genera are associated with Poaceae and Cyperaceae, the remaining feed on 2-3 types of resources using D, H, E and, more rarely, G in various combinations. Again their host plants (willows, *Vaccinium, Dryas, Cassiope, Viola, Rubus chamaemorus, Polygonum*) are usual inhabitants of tundra biotopes.

Another feature of the seasonal strategy that adds certain flexibility is variation in hibernating stages. Some species can hibernate in any two adjacent stages: egg/young larva or full-grown larva/pupa. This is almost indifferent from a trophic viewpoint, but helpful for the species facing an early onset of the autumn.

The same six main seasonal strategies distinguished earlier among southern lepidopterans dominate also this animal group in the forested tundra. The proportion of species beginning to feed in summer months and hibernating as pupae is somewhat decreased insignificantly (27.7% vs. 32.4%; $\chi^2 = 1.5$; $\upsilon = 1$; $p < 0.3$) but larger lepidopterans using this strategy are either eliminated from the forested tundra or sporadic, disappearing after a cold summer and then reappearing through migrants (Bogacheva, 1995). Smaller species with rapidly growing larvae (mainly Geometridae) show a normal life there. On the contrary, the percentage of summer species hibernating in larval stages increases considerably (from 5.4 to 12.6%; $\chi^2 = 12.1$; $\upsilon = 1$; $p < 0.001$). Such species are plentiful among Rhopalocera.

Active and passive adaptations to the Arctic in forested tundra macrolepidopterans

On the one hand, some forested tundra species grow rapidly using valuable food resources (D, H, F) to fully develop during one year. On the other hand, as many as 15% species have two-year generations there. The prolonged development of such species is related to food resources of low value (E, G, LV).

When analyzing lepidopteran feeding and seasonality, we face the problem of active and passive ways of adaptation as advanced and thoroughly discussed for insects by Yu. I. Chernov (Chernov, 1974, 1978; Lantsov & Chernov, 1987). Rapid development as a result of intense feeding and growth, the life cycle's precise timing, the hibernation in strictly determined developmental stage – all of these are elements of an active way of adaptation. On the contrary, feeding of low intensity on different food resources resulting in an extended development, coupled with the lack of temporally precise stages of development characterize a passive way of adaptation. Ju.I. Chernov emphasizes that the active adaptations mainly used by boreal species reaching the low-latitude Arctic are restricted. We believe that exhaustion of active adaptive strategies in lepidopterans starts already in the Subarctic, because the use of some valuable resources (strategy of early spring phyllophages, specialization on F resources) becomes less varied. To rapidly grow, larvae consume there the spring foliage of D in their older instars (after hibernation) or leaves of dicotyledonous perennials.

Already in the Subarctic, lepidopteran species with one-year long life cycles feeding on H and, especially, D can fail in the shortest and coldest growing seasons. Further to the North, species with many-year generations begin to prevail among Macrolepidoptera. Some truly arctic lepidopterans tend to consume increasingly larger proportions of valuable food resources; this allowing them for growth, if not due to enhanced consumption intensity, which mainly depends on temperature, then at least owing to higher feeding efficiency. This trophic feature is an element of active adaptations to Arctic conditions in species that generally are passive adaptive strategists (Chernov, 1978).

Among the truly arctic species, the proportion of active elements is rather high. Thus, *Gynaephora groenlandica* is a species well-studied at present (Kukal & Dawson, 1989; Kevan & Kukal, 1993; Kukal, 1997). During one vegetation season it passes through the stages of pupa, imago (including the search and insemination of the female) and egg, the first larval instar (the larvae feed on old willow leaves) and molting between the first and the second instars. In this stage, the first hibernation takes place. Later caterpillars need to feed on growing willow leaves otherwise even the minimum weight increments would be impossible. So they feed only for 2-3 weeks and start preparing themselves for hibernation still before the period of the highest environmental temperatures.

This seasonality pattern is easily recognized as a typical lymantriid strategy, with young larvae feeding on old leaves, hibernation in the second larval instar and rapid growth of older caterpillars on spring foliage. Poor if any flight capacities in females, egg-laying off host plants and polyphagy are also usual in Lymantriidae. In the temperate belt, higher temperatures and slower changes in leaf quality allow lepidopterans to accomplish a complete development within one year. Low temperatures and rapidly growing leaves in the high-latitude Arctic break the situation by extending species development to 14 years or even more, so every instar lasts 3-4 years. A number of highly interesting adaptations observed in this moth have virtually nothing to do with either feeding or seasonality, being related to weight gain conservation, to maintaining a high body temperature during feeding and to an increased cold-hardinss.

Let us analyze now the feeding and seasonality patterns observed in three largest macrolepidopteran families in the Urals. Satyrinae occupy a particular position among the nymphalids – as, according to Karsholt & Razowski (1996), Satyridae are a subfamily belonging to Nymphalidae. Having possibly originated in cold tundra-steppe landscapes, they became specialists of "graminoids" hibernating as larvae. Numerous species of *Erebia* and *Oeneis* in the tundra conditions show two-year life cycles. In the southern Urals, they are rather relicts restricted to delimited bog and mountain tundra biotopes (Olschwang et al., 2004), preserving the feeding patterns inherent to Satyrinae and, sometimes, also two-year life cycles. Heliconiinae species feeding on H in the South of the forest belt obtain in the tundra the features of polyphages and, based on larval hibernation, the capability of hibernating twice. Some Nymphalini species are spread up to the low-latitude Arctic with their usual food spectra of D, H or DH, and with hibernation as imago or pupa inherent to them.

As regards geometrids, at the northern tree line they are virtually the same as in the southern taiga zone. Their food spectrum is somewhat shifted to deciduous woody plants, although dicotyledon herbs are still abundant in the diet; specialized consumers are not rare; the main hibernation stage is still pupa; species with extended life cycles are absent. Many species common in the temperate belt show two generations per year, this meaning that one generation takes only part of the summer. This is enough for species to accomplish their development in the Subarctic during one year, this time certainly with only one generation annually, and to take their place in tundra ecosystems. Small sizes of most of the species undoubtedly play some roles in their successful penetration into the North. About a dozen geometrids with different feeding habits and seasonal strategies were registered in the Polar Urals in the warm period of 2000-2007 for the first time (Bogacheva, 2007).

On the contrary, noctuids common in the temperate belt go northwards rather reluctantly. It still remains to question whether any feature of their feeding or seasonality could account for this situation. However, both appear to be quite different in the North. Instead of species feeding on herbaceous plants, those consuming deciduous woody plants take an important position there; the same is true for Pf species with hibernation at two different stages so unusual in southern Urals noctuids. The latter are truly tundra species. Only a few species new to the Polar Urals fauna appeared also in the Low Ob region in the warm period of 2001-2007. We have registered only *Melanchra pisi* (L.) and *Papestra biren* (Goeze), both common forest species.

Summarizing, at the northern tree line the Macrolepidoptera more or less clearly show two strategies. The first is the strategy of rapid development based on D, H and F resources. It is mainly used by common boreal species thriving there at the northern limit of their distribution. They hibernate as imago, egg or pupa. Small body sizes favour them, since large specimens might not accomplish their development in unusually cold summer seasons. The second one is the strategy of many-year development. Species using it are either polyphages or specialists of food categories that support no rapid larval growth, especially so on "graminoids"; they hibernate at the larval stage, as a rule. They fail to dominate the Urals fauna of Macrolepidoptera yet, but they do compose its considerable share.

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