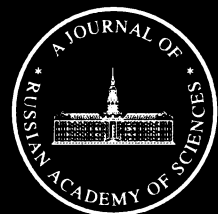


Volume 34, Number 6  
November–December 2003

ISSN: 1067-4136  
CODEN: RJOEIW



# RUSSIAN JOURNAL OF ECOLOGY

English Translation of *Ekologiya*

Editor-in-Chief  
Vladimir N. Bolshakov

<http://www.maik.ru>

A Journal of Original Papers and Reviews on Theoretical and Applied Ecology



Translated and Published by  
**MAIK "HAYKA/INTERPERIODICA" PUBLISHING**

Distributed worldwide by KLUWER ACADEMIC/PLENUM PUBLISHERS

# Latitudinal Gradients of Trophics in Ural Macrolepidoptera: The Role of Food Quality

I. A. Bogacheva, V. N. Olschwang, and G. A. Zamshina

*Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202,  
Yekaterinburg, 620144 Russia*

Received May 28, 2003

**Abstract**—The Macrolepidoptera fauna of the Urals, from the southern to the northern boundary of the forest zone (i.e., from the forest–steppe of the Southern Urals to the forest–tundra of the Polar Urals) has been analyzed. It has been demonstrated that the proportion of Lepidoptera feeding on woody plants, including evergreens, increases in this direction. Among the Heterocera, the proportion of species feeding on graminoids decreases; in the Polar Urals, none of these species is specialized. The food spectrum is particularly variable in noctuids and almost invariable in geometrids and Rhopalocera. It is assumed that foods with a low nutrient value (grasses, mosses, lichens, plant debris, wood, and roots of various plants) prevent Macrolepidoptera species from spreading in the Subarctic region. In the Polar Urals, multiyear developmental cycles and wintering at the larval stage are related to feeding on these types of food.

**Key words:** lepidopterans, northward spread, trophic changes, food resources, phenology, wintering stage.

It is known that the species diversity of plant and animal taxa usually decreases in the direction from the tropics to the poles (Pianka, 1966; Gaston, 2000), with the pattern of this decrease varying in different taxa. Regarding Arctic insects, the shift in the ratio between phytophagous and other (zoophagous and saprophagous) species towards a higher proportion of the latter has been repeatedly discussed (Chernov, 1973, 1992; Danks, 1986). However, there are phytophagous taxa that successfully spread to at least lower Arctic latitudes, e.g., some coleopterans (Chrysomelidae and Curculionidae), sawflies (mainly Tenthredinidae), and lepidopterans.

It could be supposed that the trophics of phytophagous insects changes as they spread northward. However, only a few studies addressed this problem (Scriber, 1973; Danks, 1986); they mainly dealt with the range of trophic links and feeding on different plant organs and tissues. To study latitudinal trends of insect trophics, we analyzed changes in the feeding of weevils (Olschwang and Bogacheva, 1990), leaf beetles (Bogacheva and Olschwang, 1998), and sawflies (Bogacheva, 1997b) with an increase in latitude from the southern to the northern borders of the forest zone (from the forest–steppe to the forest–tundra). In all studies, the northernmost region was the Polar Urals and the lower Ob' River basin, where insects had been collected since 1970. We demonstrated an extension of trophics only for leaf beetles; however, we unexpectedly discovered that the proportion of species feeding on woody plants increased in all groups of insects studied. Unfortunately, as the numbers of species in these

groups in the northern forest zone were small, we could regard many of the observed changes only as tendencies. This is not so with lepidopterans. The relatively large diversity of this group in the Arctic allows us not only to consider phenological and trophic trends of lepidopterans, but also to demonstrate taxonomic changes in the order Lepidoptera with an increase in latitude, relating them to the trophics of other taxa.

The Macrolepidoptera of the Urals were chosen as the object of this study, because sufficiently complete lists of their species living in the southern, middle, and polar Urals are available. Analysis of these species allowed us to demonstrate (Olschwang *et al.*, 2002) that, as we go from the southern to the northern borders of the forest zone, the species diversity of lepidopterans decreased in all taxa but not proportionally. For example, the proportion of nymphalids considerably increased (from 8.6 to 21.8%), the proportion of geometrids increased only slightly (from 27.0 to 34.1%), and the proportion of noctuids drastically decreased (from 36.9 to 17.5%). These three families were still dominant among Macrolepidoptera in the forest–tundra, as they are throughout Europe (Karsholt and Razowsky, 1996); however, in the northern Urals, geometrids were the largest family, whereas noctuids were the largest family in the south of the forest zone.

Thus, the ability to spread northward varies in different taxa. The purpose of this study was to determine the possible role of food resources of lepidopterans in this process.

## MATERIALS AND METHODS

In the southern Urals (SU; the Il'men Reserve, 55° N), the material was collected in 1996–2001. The total number of species was 767. Data on the Heterocera living in the middle Urals (MU; 56° 30' N) were obtained in 1997–2001 (Zamshina, unpublished data). Data on the Rhopalocera were taken from the study by Korshunov and Gorbunov (1995). In total, 574 species of the Macrolepidoptera were found in the MU. In the polar Urals (PU; 66°–67° N), a total of 211 species were collected by different researchers in different years (Olschwang, 1980; Gorbunov and Olschwang, 1993; personal collections performed by V.N. Olschwang in 1970–1996; and several findings by K. Nupponen and T. Nupponen in 1998 and I.A. Bogacheva in 1970–2001).

In our study, lepidopterans were classified according to the catalogue by Karsholt and Razowsky (1996). Plant taxonomy was checked in the *Opredelitel' sosudistykh rastenii Srednego Urala* (1994). We used published data on the phenology of lepidopterans and their food plants (Gofman, 1897; Lampert, 1913; Kozhanchikov, 1950; Zolotarenko, 1970; Merzheevskaya *et al.*, 1976; Henriksen and Kreutzer, 1982; Koch, 1984; Derzhavets *et al.*, 1986).

Most collections of Heterocera in the MU and SU were performed by means of light traps. In the daytime, representatives of this group were caught with a butterfly net. We also reared adult insects from caterpillars. The latter two methods were mainly used in the PU, where attraction of lepidopterans by light was ineffective; these methods were also used for collecting Rhopalocera at all the three spots.

All food resources were divided into groups according to their qualities as insect food. We proceeded from the notions of researchers who earlier studied the acceptability of tundra plants for polyphagous animals (MacLean and Jensen, 1985; Chapin *et al.*, 1986). The leaves of deciduous woody plants, including trees, bushes, and vines (group 1), have a high nutrient value (primarily, high water and nitrogen contents) and maintain a high growth rate of phytophagous insects only in the beginning of the growing season. Their protective substances are common for many plant taxa. The leaves of dicotyledonous herbaceous plants (group 2) have a high food value during the most part of summer (Scriber and Slansky, 1981; Slansky and Scriber, 1982); however, different families of these plants (Futuyama, 1976) and even different genera within families (Maiorana, 1978) considerably differ in chemical composition. A few representatives of Liliaceae and ferns were also included into this group. The only substance specific for the leaves of grasses, sedges, and rushes is silicon, which is common for these groups. The nutrient value of these plants drastically decreases by the end of summer. In the literature, they are often collectively called graminoids (group 3). Leaves of evergreens (group 4), with their thick cuticle, contain lignin and

often, in addition, some specific protective substances; therefore, they are almost useless as food for phytophagous insects. The last two groups were mosses and lichens (group 5) and some substrates of low nutrition value, such as wood, plant roots, and debris (group 6).

All lepidopteran species from groups 1–4 were divided into specialists and generalists. A species was considered a specialist if it only fed on plants belonging to one family. If it fed on plants from more than one family somewhere within its geographic range, we considered this species a generalist (Scriber, 1973). The only exception was made for species feeding on graminoids, because of the lack of accurate data on the particular plants on which they fed, as well as considerable similarity between the three families of this group of plants with respect to chemical composition. Therefore, we regarded the species that fed only on grasses, sedges, and rushes as specialists; and the species that had additional food resources other than graminoids, as generalists.

The significance of differences found in this study was estimated using Student's *t*-test, after calculating the percentage error for the groups compared (Mitropol'skii, 1961).

## RESULTS

**Different food resources.** The spectra of food resources of the Lepidoptera living at different latitudes from the northern to the southern borders of the Ural forest zone differed insignificantly (Table 1). The proportion of lepidopterans feeding on grassy plants did not vary; herbaceous dicotyledons (group 2) were the main food of lepidopterans throughout the forest zone. We found a slight latitudinal trend towards an increased proportion of lepidopterans feeding on woody plants, both deciduous (group 1) and evergreen (group 4) in northern regions. The latter trend was statistically significant (9.6 and 18.2% in the SU and PU, respectively;  $p < 0.01$ ). This trend was observed even in the Nymphalidae and Geometridae, although their food spectra changed insignificantly, and the increase in the proportion of species feeding on evergreens was also statistically nonsignificant.

The data on noctuids were entirely different. In this family, the spectrum of food considerably changed when going from the SU to the PU: the proportion of species feeding on woody plants increased (almost five-fold in the case of evergreens), and the proportion of species feeding on herbs, especially graminoids, decreased. Species feeding on mosses and lichens (group 5) and on roots and debris (group 6) entirely disappeared from lepidopteran food in the northern regions, whereas the latter feeding strategy was common in the SU (Table 1). All of these differences were statistically significant when we compared lepidopterans from the PU and SU; and most of them, when comparing lepidopterans from the PU and MU.

**Table 1.** Trophic links of Macrolepidoptera with various food resources

Study region	Taxon	Number of species	Proportion of species in different trophic groups					
			1	2	3	4	5	6
Polar Urals	Rhopalocera	72	38.9	66.7	25.0	12.5	0.0	0.0
	Nymphalidae	41	36.6	53.6	39.0	14.6	0.0	0.0
	Heterocera	115	62.6	49.6	5.2	21.7	1.7	4.3
	Geometridae	57	59.6	57.9	1.7	21.0	1.8	1.8
	Noctuidae	35	71.4	48.6	8.6	31.4	0.0	0.0
	All species	187	53.5	56.1	12.8	18.2	1.1	2.7
Middle Urals	Rhopalocera	120	35.8	69.2	22.5	3.3	0.0	0.0
	Nymphalidae	59	33.9	61.0	35.3	3.4	0.0	0.0
	Heterocera	451	53.9	50.6	10.0	14.0	3.1	9.7
	Geometridae	175	57.0	58.0	2.9	18.3	0.6	1.0
	Noctuidae	179	47.0	59.0	21.0	10.6	0.6	17.0
	All species	571	50.1	54.5	12.6	11.7	2.5	7.7
Southern Urals	Rhopalocera	142	34.5	70.4	21.1	3.5	0.0	0.0
	Nymphalidae	65	35.4	56.9	36.9	4.6	0.0	0.0
	Heterocera	595	49.6	56.0	14.4	11.1	2.9	7.6
	Geometridae	198	55.1	60.6	3.5	12.6	0.0	0.5
	Noctuidae	266	38.0	66.2	25.9	6.4	1.1	11.7
	All species	737	46.7	58.8	15.7	9.6	2.3	6.1

**Table 2.** Proportions of polyphagous species in different trophic groups of Macrolepidoptera

Taxon	Trophic group	Polar Urals	Middle Urals	Southern Urals
Rhopalocera	1	82.1	69.8	70.8
	2	72.3	63.8	59.2
	3	10.5	14.3	9.7
	4	88.9	100.0	100.0
Heterocera	1	75.7	81.6	82.4
	2	73.7	69.2	66.1
	3	100.0	77.8	59.3
	4	88.0	88.9	83.3
All Lepidoptera	1	77.6	79.7	80.8
	2	73.1	67.8	64.4
	3	32.0	54.2	46.6
	4	88.2	89.6	84.5

**The ratio between polyphagous and specialized species.** Families of lepidopterans considerably differed from one another in this parameter. The trend towards an increased proportion of polyphagous species was found in the entire order Lepidoptera (59.3 and 64.1% in the SU and PU, respectively) and in many individual families, e.g., in noctuids (61.6 and 71.4% in

the SU and PU, respectively); however, the differences were nonsignificant. We also did not find changes in the proportion of polyphagous species in lepidopteran trophic groups (Table 2) except for the species feeding on graminoids: in the PU, only a few lepidopteran species fed on graminoids along with plants from other groups.

**Table 3.** Proportions of wintering stages in different trophic groups of Macrolepidoptera

Region of study	Trophic group	Number of species	Proportions of species wintering at the stages of:			
			egg	larva	pupa	imago
Polar Urals	1	95	11.4	47.9	39.6	6.2
	2	99	6.2	55.7	37.1	6.2
	3	19	5.0	100.0	8.8	0.0
	4	33	6.1	72.7	39.4	0.0
	5	1	0.0	100.0	0.0	0.0
	6	5	0.0	100.0	0.0	0.0
Middle Urals	1	272	17.3	31.6	48.9	4.8
	2	277	8.7	49.1	43.3	3.6
	3	63	6.3	82.5	15.9	1.6
	4	71	14.1	62.0	28.2	1.4
	5	14	0.0	92.9	7.1	0.0
	6	44	13.6	77.3	6.8	0.0
Southern Urals	1	344	15.7	32.3	48.0	6.4
	2	433	8.8	49.0	42.5	4.2
	3	116	7.8	78.4	12.1	1.7
	4	71	12.7	46.5	40.8	1.4
	5	17	0.0	82.4	17.6	0.0
	6	45	13.3	73.3	11.1	2.2

**Wintering stage.** The Macrolepidoptera usually spent winter at the larval or pupal stage (in the SU, 45.6 and 43.0%, respectively). In some families, wintering at a particular stage was dominant; e.g., pupa was the main wintering stage in the Sphingidae and Notodontidae. Other families were characterized by a more or less complete set of wintering stages. Wintering at any developmental stage was possible in regions as far north as the lower Arctic latitudes. The ratio between wintering stages in the Nymphalidae and Geometridae did not exhibit a distinct latitudinal trend; in lepidopterans as a whole, the proportion of species wintering at the larval stage was somewhat increased in northern regions (to 54.6% in the PU).

The relationship between trophic groups and wintering strategies in Macrolepidoptera was more interesting (Table 3). Wintering at the larval stage was prevalent even in the SU in all trophic groups of Macrolepidoptera except for species feeding on deciduous woody plants, in which the pupa was the main wintering stage (44.8%). The domination of the strategy of larval wintering increased northward. In the PU, the species that fed on poorly digestible food resources (groups 5 and 6) wintered only at the larval stage. All lepidopterans feeding on graminoids also wintered at the larval stage; many species from this group wintered again at the pupal stage. Wintering at the larval stage became the

leading strategy in the PU even in species feeding on deciduous trees and bushes, although its frequency in these insects did not exceed 50%.

## DISCUSSION

An increase in the proportions of the Nymphalidae (and Rhopalocera in general) and Geometridae and a decrease in the proportion of the Noctuidae northward was the main trend in the taxonomic composition of the Macrolepidoptera (Olschwang *et al.*, 2002). To determine the cause of these changes, we analyzed the quality of food resources of the Macrolepidoptera.

Regarding the "acceptability" of leaves of different plants, our results, at first glance, do not completely agree with this theory. It was earlier demonstrated (MacLean and Jensen, 1985; Chapin *et al.*, 1986) that the leaves of deciduous woody and dicotyledonous herbaceous plants were the most acceptable; however, the proportion of lepidopterans feeding on these plants in the PU was almost the same as in southern regions. Conversely, the most significant trend is the northward increase in the proportion of species feeding on evergreens, although their acceptability was the lowest, even lower than that of mosses and lichens. However, only species found in the PU fed exclusively on evergreens (*Eupitecia abietaria*, *Sympistis nigrita*, and *Xes-*

*tia quieta* fed only on *Picea*, *Dryas*, and *Empetrum*, respectively); most species that fed on these plants consumed other plants also, especially deciduous bushes. They were polyphagous, lived in tundra plots, and fed on various plants, such as *Vaccinium uliginosum*, *V. vitis-idaea*, some Ericaceae, *Empetrum* spp., and willows. We think that this type of polyphagy, rather than feeding on evergreens per se, is widely spread at lower Arctic latitudes.

The proportion of species feeding on mosses and lichens (group 5) and on wood, roots, and debris (group 6) somewhat decreased northward. In the PU, the subfamily Lithosiinae specialized for feeding on lichens disappeared from the family Arctiidae. However, some species living in the PU fed on these food resources. These are representatives of the Hepialidae and Sesiidae, as well as *Lypusa maurella* (Psychidae) and *Idaea seriata* (Geometridae). However, the mixed type of feeding (on both green leaves and debris or both roots of grassy plants and their green stems) that was common in noctuids living in the SU was entirely absent in the PU.

The situation with graminoids is very interesting. As noted above, the proportion of Rhopalocera species feeding on graminoids in the northern regions was the same as in southern ones, whereas the proportion of these species among the Heterocera considerably decreased, mainly due to noctuids (Table 1). In addition, the trophic relationships of species feeding on graminoids were entirely different in the Rhopalocera and Heterocera (Table 2). While many Rhopalocera (mainly, Satyrinae) could feed on graminoids alone, the proportion of graminoid specialists among Heteroptera was only 40% (mainly, noctuids) in the SU, and there were no such species at all in the forest-tundra. All of the six Heterocera species that fed on graminoids in the forest-tundra were generalists.

The phenology of lepidopterans was connected with both the duration of the growing season and the phenology of plants on which they feed. In the SU, many species (8.7% of their total number) had two or even three generations per year, whereas species whose development lasted for more than a year were rare (eight species, about 1% of their total number); these were species that fed on low-quality food resources. In the PU, none of Macrolepidoptera had more than one generation per year. Conversely, 39 species (22.7% of all species for which the wintering stage is known) developed for more than a year in this region. The proportion of species with long life cycles among lepidopterans with a high growth rate (those feeding on the leaves of deciduous woody plants or dicotyledonous herbs) was as low as 9–12%; among the species that fed on evergreens and graminoids, these proportions were 27 and 42%, respectively.

The data on the wintering stage (Table 3) agree with the data on generation lengths: in the species whose food resources did not ensure high growth rates, winter-

ing at the larval stage was more common. This relationship could be expected, because a food resource of low nutritive value cannot guarantee the completion of larval development before the cold autumn weather begins; moreover, the development duration is often longer than a year. Insects can have long developmental cycles only if wintering at the larval stage is possible. However, wintering at the larval stage was more characteristic of the species feeding on dicotyledonous herbs than of those feeding on deciduous trees and bushes (Table 3). This phenomenon may be explained by the late start of the feeding season in species feeding on herbs (Niemelä *et al.*, 1982); as a result, species with larger body sizes do not have enough time to complete their development.

Do the relationship between phytophagous insects and their food plants prevent the insects from spreading to high latitudes? Most published studies give a negative answer to this question, because it is well known that the ratio between the numbers of the species of phytophagous insects and plants decreases northward (Downes, 1964; Danks, 1986). In other words, as MacLean (1983) noted, food plants go farther north than their characteristic phytophages. It may be assumed that the spread of phytophagous insects in the Arctic is limited by factors unrelated to food plants (Downes, 1964). However, the spread of phytophagous insects to low-latitude Arctic zones (the lower Ob basin) may be limited by the absence of their respective food plants or the low density of these plants in suitable biotopes (Bogacheva, 1997a). In our study, the tortoiseshell (*Nymphalis*) and the cabbage butterfly (*Pieris*) were such phytophages exemplifying the former and latter situations, respectively. Apparently, the northward spread of lepidopterans is also limited by the low quality of their food resources, although the species that feed on them winter at the larval stage even in the southern forest zone. The unexpected fact that the species feeding on the poorly digestible evergreens successfully spread into the Subarctic may be explained by the facultative type of this trophic link. The high density of evergreen plants in tundra spots may also play a role.

Regarding the aforementioned latitudinal taxonomic changes in groups of Macrolepidoptera, we may assume that the relatively low proportion of noctuids in Arctic communities is partly determined by their trophic characteristics: the species of this family that feed on low-quality food (graminoids, plant roots, and debris) are absent in the northern regions. However, it is likely that the main reason is the behavioral characteristics of their caterpillars: in the southern forest zone, caterpillars of many Noctuidae live in soil and only come onto the surface to feed at night, and others live in grass stems (e.g., in *Phragmites*). All of these species are absent in the Subarctic.

Conversely, geometrids successfully spread to the Subarctic, because the species of this family that feed on deciduous woody plants and dicotyledonous grassy

plants, which ensure high growth rates, are dominant even in the southern forest zone. In addition, the small body sizes of geometrids, in contrast to noctuids, favor the completion of their development even in a cold summer.

The success of the Rhopalocera (especially the Nymphalidae) in the Arctic is unlikely to be related to their trophic characteristics. In general, the proportion of polyphagous species in diurnal lepidopteran families (33–50%) is considerably lower than in the Heterocera. In diurnal lepidopterans, the proportion of species feeding on deciduous woody plants is lower, and that of species feeding on graminoids is higher, than in the Heteroptera. All these characteristics are generally believed to be unfavorable for spreading in the Arctic. The ratio between specialists and generalists and the food spectrum in the Rhopalocera do not display latitudinal gradients. We assume that, in the case of Rhopalocera, the wintering at the larval stage is an important preadaptation to the appearance of multiyear life cycles. Probably, many species (first of all, the Satyrinae) are also preadapted to the low temperatures of the Arctic region, because they inhabit biotopes with similar temperature conditions (bogs, tundra, etc.) even in the southern forest zone.

## ACKNOWLEDGMENTS

We are grateful to the Finnish entomologists K. Nupponen and T. Nupponen for the information on the biology of some lepidopteran species and identification of part of the material.

## REFERENCES

- Bogacheva, L.A., Factors Limiting Northward Expansion of Phyllophagous Insects: The Example of *Pieris napi* L. and *Pieris brassicae* L., *Ekologiya*, 1997a, vol. 28, no. 4, pp. 293–296.
- Bogacheva, I.A., Some Latitudinal Changes in Trophic Characteristics of Phyllophagous Insects Revealed by Analyzing Faunistic Lists, in *Uspekhi entomologii na Urale* (Advances in Entomology in the Urals), Yekaterinburg, 1997b, pp. 125–128.
- Bogacheva, I.A. and Olschwang, V.N., Leaf Beetles (Coleoptera, Chrysomelidae) in the Northern Part of the Ob Region, *Entomol. Obozr.*, 1998, vol. 77, no. 4, pp. 775–786.
- Chapin, F.S., McKendrick, J.D., and Johnson, D.A., Seasonal Changes in Carbon Fractions in Alaskan Tundra Plants of Different Growth Forms: Implication for Herbivory, *J. Ecol.*, 1986, vol. 74, no. 3, pp. 707–731.
- Chernov, Yu.I., Synopsis of Trophic Groups of Invertebrates in the Typical Tundra Subzone of the Western Taimyr Peninsula, in *Biogeotsenozы Taimyrskoi tundry i ikh produktivnost'* (Biogeocenoses of the Taimyr Tundra and Their Productivity), Leningrad: Nauka, 1973, no. 2, pp. 166–179.
- Chernov, Yu.I., Whom Is Tundra Dominated by: Predators or Phytophagans? in *Tsenoticheskie vzaimodeistviya v tundrovyykh ekosistemakh* (Cenotic Interactions in Tundra Ecosystems), Moscow: Nauka, 1992, pp. 111–127.
- Danks, H.V., Insect–Plant Interactions in Arctic Regions, *Rev. Entomol. Quebec*, 1986, vol. 31, pp. 52–75.
- Derzhavets, Yu.A., Ivanov, A.I., Mironov, V.G., *et al.*, The List of Lepidopterans (Macrolepidoptera) of Leningrad Oblast, in *Fauna cheshuekrylykh (Lepidoptera) SSSR* [The Fauna of Lepidopterans (Lepidoptera) of the Soviet Union], Leningrad: Nauka, 1986, vol. 67, pp. 186–271.
- Downes, I.A., Arctic Insects and Their Environment, *Can. Entomol.*, 1964, vol. 96, pp. 276–307.
- Futuyma, D.J., Food Plant Specialization and Environment Unpredictability in Lepidoptera, *Am. Nat.*, 1976, vol. 110, pp. 285–292.
- Gaston, K.J., Global Patterns in Biodiversity, *Nature* (London), 2000, vol. 405, no. 6783, pp. 220–227.
- Gofman, E., *Atlas babochek Evropy* (Atlas of European Butterflies), St. Petersburg: A.F. Devrien, 1897.
- Gorbunov, P.Yu. and Olschwang, V.N., Fauna of Diurnal Butterflies in the Arctic Urals, in *Fauna i ekologiya nasekomykh Urala* (The Fauna and Ecology of Ural Insects), Perm, 1993, pp. 19–34.
- Henriksen, H.J. and Kreutzer, I., *The Butterflies of Scandinavia in Nature*, Odense: Scandinavian Bogforlag, 1982.
- Koch, M., *Wir bestimmen Schmetterlinge*, Leipzig: Neuman Verlag, 1984.
- Korshunov, Yu.P. and Gorbunov, P.Yu., *Dnevnye babochki Aziatskoi chasti Rossii* (Diurnal Butterflies of the Asian part of Russia), Yekaterinburg: Ural. Gos. Univ., 1995.
- Kozhanchikov, I.V., *Volnyanki* (Vaporer Moths), vol. 12 of *Fauna SSSR: Nasekomye cheshuekrylye* (Fauna of the Soviet Union: Insects, Lepidopterans), Leningrad: Akad. Nauk SSSR, 1950.
- Lampert, K., *Atlas babochek i gusenits Evropy i otchasti Russko-Aziatskikh vladenii* (Atlas of Butterflies and Caterpillars of Europe and, in Part, Asian Territories of Russia), St. Petersburg: A.F. Devrien, 1913.
- MacLean, S.F., Life Cycles and the Distribution of Psyllids (Homoptera) in Arctic and Subarctic Alaska, *Oikos*, 1983, vol. 40, pp. 445–451.
- MacLean, S.F. and Jensen, T.S., Food Plant Selection by Insect Herbivores in Alaskan Arctic Tundra: The Role of Plant Life Form, *Oikos*, 1985, vol. 44, no. 1, pp. 211–221.
- Maiorana, V.C., What Kind of Plants Do Herbivores Really Prefer? *Am. Nat.*, 1978, vol. 122, pp. 631–635.
- Merzheevskaya, O.I., Litvinova, A.N., and Molchanova, R.V., *Cheshuekrylye (Lepidoptera) Belorussii* [Lepidopterous Insects (Lepidoptera) of Byelorussia], Minsk: Nauka i Tekhnika, 1976.
- Mitropol'skii, A.K., *Tekhnika statisticheskikh vychislenii* (The Technique of Statistical Calculations), Moscow: Fizmatgiz, 1961.
- Niemela, P., Tahvanainen, J., Sorjonen, J., Hokkanen, T., and Neuvonen, S., The Influence of Host Plant Growth Form and Phenology on the Life Strategies of Finnish Macrolepidopteran Larvae, *Oikos*, 1982, vol. 39, pp. 164–170.
- Olschwang, V.N., Insects of the Polar Urals and Forest–Tundra of the Ob Region, in *Fauna i ekologiya nasekomykh Priobskogo Severa* (Fauna and Ecology of Insects in the Northern Ob Region), Sverdlovsk, 1980, pp. 3–37.
- Olschwang, V.N. and Bogacheva, I.A., Weevils (Coleoptera, Curculionidae) of the Northern Ob Region, *Entomol. Obozr.*, 1990, no. 2, pp. 332–341.

Olschwang, V.N., Bogacheva, I.A., and Zamshina, G.A., Latitudinal Trends of Taxonomy, Phenology and Trophics in Urals Macrolepidoptera, *Abstr. XIII European Congress of Lepidopterology. KORSOR (Denmark), June 1–6, 2002*, pp 48–49.

*Opredelitel' sosudistyykh rastenii Srednego Urala* (A Key to Vascular Plants of the Middle Urals), Moscow: Nauka, 1994.

Pianka, E.R., Latitudinal Gradients in Species Diversity: a Review of Concepts, *Am. Nat.*, 1966, vol. 100, pp. 33–46.

Scriber, J.M., Latitudinal Gradients in Larval Feeding Specialization of the World Papilionidae (Lepidoptera), *Psyche*, 1973, vol. 80, pp. 355–373.

Scriber, J.M. and Slansky, F., The Nutritional Ecology of Immature Insects, *Annu. Rev. Entomol.*, 1981, vol. 26, pp. 183–211.

Slansky, F. and Scriber, J.M., Selected Bibliography and Summary of Quantitative Food Utilization by Immature Insects, *Entomol. Soc. Am. Bull.*, 1982, vol. 28, no. 1, pp. 43–55.

*The Lepidoptera of Europe. A Distributional Checklist* Karsholt, O. and Razowski, J., Eds., Stenstrup: Apollo Books, 1996.

Zolotarev, G.S., *Podgryzayushchie sovki Zapadnoi Sibiri* (Owlet Moths of Western Siberia), Novosibirsk: Nauka, 1970.