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ECOLOGY AND NUTRITIONAL ENERGETICS OF THE  
LEAF BEETLE *Gonioctena pallida* L. IN THE  
SIBERIAN TAIGA AND FOREST TUNDRA

I. A. Bogacheva and L. N. Dubeshko

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In this paper we compare the biology, ecology, and nutritional energetics of the leaf beetle *Gonioctena pallida* L., which was observed in various regions differing considerably in their physical geography and climate: in the southern part of Primorskii Range, on the northwest shore of Baikal, in 1965-1969 (L. N. Dubeshko), and at the "Kharp" station in the forest tundra of the Lower Ob region in 1970-1972 (I. A. Bogacheva).

On Primorskii Range *G. pallida* is closely associated with the ravines, where it lives on shrubs of various species of willow and bird-cherry. In the ravines, sheltered from the winds by the slopes, the air temperature and humidity are appreciably higher than on the open shore of Baikal. Floodplain shrubs are abundant on the ravine bottoms, and are dominant along the sides of brooks. Their height does not exceed 3.5 m. The herbage consists mainly of brookside groups of plants with an admixture of boggrasses.

As distinct from the typical taiga vegetation of Pribaikal'e, the landscape of the "Kharp" station is dominated by various types of tundra composed of sparse larch wood, bogs, meadows, and shrub, which forms a narrow strip along the banks of rivers and numerous lakes. The shrub thickets, which occupy about 5% of the total area of this region, consist of dwarf birch (*Betula nana*), the tea-leaved willow (*Salix phylicifolia*), the woolly willow (*S. lanata*), *S. pulchra*, the gray-leaved willow (*S. glauca*), etc., and an occasional alder (*Alnus fruticosa*).

TABLE 1. Nutritional Energetics of *Gonioctena pallida* L.

Age of larva	Body weight, mg		Increment		Food consumption			Excrement		Energy consumption on metabolism	
	in- ital	final	mg	% of amount of food	wet weight, g	cal	% of total amount	mg	% of amount of food	mg	% of amount of food
Pribaikal'e											
1-й	0,4	3,5	3,1	56,3	5,5	9,3	5,7	0,9	16,7	1,5	27,0
2-й	3,5	9,7	6,2	49,5	12,5	21,2	13,1	3,6	28,8	2,7	21,7
3-й	9,7	17,8	8,1	27,0	29,5	50,0	30,7	15,0	50,0	6,4	23,0
4-й	17,8	18,8	1,0	2,0	48,6	82,4	50,5	18,7	38,7	28,9	59,3
Total	0,4	18,8	18,4	18,9	96,1	162,9	100,0	38,2	39,7	39,5	52,0
Priobskaya forest tundra											
1-й	0,2	1,1	0,9	32,2	2,8	4,7	4,0				
2-й	1,1	4,0	2,9	33,3	8,7	14,7	12,4				
3-й	4,0	8,7	4,7	30,3	15,5	26,2	22,1				
4-й	8,7	18,7	10,0	23,1	43,2	72,9	61,5				
Total	0,2	18,7	18,5	24,9	70,2	118,5	100,0				

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In the investigated region of forest tundra G. pallida is the only abundant species of leaf beetle, whereas in Pribaikal'e it occurs along with other, equally abundant, species (G. sibirica, G. ogloblini, G. viminalis, and G. rufipes).

In the European part of the USSR G. pallida feeds almost exclusively on shrubs of the family rosaceae: bird-cherry, rowan, hawthorne, etc. In Pribaikal'e this species attacks various species of willow and bird-cherry, whereas in the southern tundra it feeds only on willow, preferably the tea-leaved willow, and does not spread to the rowan, which is associated with the willow in the hills of the polar Urals.

In Pribaikal'e the leaf beetle is found in large concentrations on individual willow and bird-cherry bushes, frequently with as many as several hundred insects per bush; the grazing down of the foliage in this case is very considerable. In the forest tundra the leaf beetle is confined to shrub thickets on the banks of rivers and lakes, where it does considerable damage to the foliage in some places, and does not spread onto the open areas of the tundra, where the vegetation contains the same willow species, but in the form of scattered decumbent shrubs 10-20 cm high.

In the Priobskaya forest tundra the adult beetles appear on willows in early July, just when the leaves open. The leaf beetle is viviparous. Its fecundity is low — an average of 22-24 larvae per female. The first young larvae appear on the leaves on July 10-12. In some parts of willow groves the density of the larvae in mid-July reaches 130 per m<sup>2</sup>, and their biomass reaches 1.2 g/m<sup>2</sup>. The larva takes about three weeks to develop, during which it passes through four instars, and by the end of development it attains a weight of 17-25 mg (the females are heavier, on the average, than the males). In early August the larvae move into the litter, where they pupate in approximately ten days. The pupal stage lasts 10-12 days. The first young beetles appear in the litter in mid-August, and all the individuals complete metamorphosis by the end of August. The beetle winters in the imaginal stage in the litter, and does not leave it to feed even in favorable weather conditions.

In Pribaikal'e the beetles also leave their wintering sites when the leaves open, which is usually in the last ten days of May. The larvae are born four or five days after the beetles emerge from their wintering sites; each female produces about 40 larvae. The larval stage lasts 18-21 days when the mean ten-day temperature is 12.3°; at lower temperatures the larval stage lasts longer (up to 35-36 days in some cases). Pupation usually takes place in the top layer of soil in the first ten days of August. The beetles feed for seven to 20 days, after which they hide in the litter and remain there for the winter. In some years the beetles do not leave the soil after emergence from the pupae. This is obviously due to the later time of emergence from the pupae.

The development of the leaf beetles in the forest tundra begins approximately a month later than on Baikal, but the periods of development of all stages are practically the same, and the slight differences in biology are a direct consequence of climatic factors. In both the taiga and forest tundra the leaf beetles abound in willow groves, where they select parts sheltered from the wind. A special feature of this species at both sites of observation, in comparison with the central belt of the European USSR, is their viviparity, which is characteristic, however, of many species of Gonioctena and other genera. Viviparity in the leaf beetle can be regarded as an adaptation to extreme living conditions and is usually manifested in beetles living at high latitudes and high altitudes. It allows more rapid development, since no time is spent in the egg stage. It is of interest to note that the fecundity of beetles from Pribaikal'e is almost twice that of the Yamal beetles (40 and 22-24 larvae, respectively).

Leaf beetles in the forest tundra and on Baikal constitute a considerable proportion of the insect associations of some plant communities and usually comprise 10 to 30-40% of the total number of phytophages in floodplain shrubland. One of the main ways of determining the role of leaf-eating insects in a biogeocenose is an investigation of the nutritional energetics. If the density of the leaf beetles and the lengths of their feeding periods are known, the volume of foliage consumed can be determined.

The nutritional process is represented by the equation  $C = P + R + F$ , from which it follows that the consumed food (C) is expended on production (P), and on metabolism (R), and some is lost with excrement (F). Leaf beetles collected in the field were kept in vivaria in the laboratory. The age and the amount of food consumed in the period of development of the leaf beetles from the time of emergence of the beetles from their wintering sites to their return to these sites were determined. Table 1 gives the averaged data.

The experiments on Baikal were carried out in 1968-1970. As Table 1 shows, the absolute increment was higher in larvae of the 2nd and 3rd instars, particularly the latter, but the relative growth was greatest in 1st-instar larvae. Metabolism was most rapid in the beetles and 4th-instar larvae. In the

whole period of its development the larva consumed 96.1 mg of leaves. The imago consumed even more during its spring and autumn supplementary feeding (131.5 and 102.5 mg, respectively). Thus, during the whole period of development one G. pallida consumed 350.1 mg of leaves.

The nutritional energetics of the leaf beetle in the forest tundra (see Table 1) was investigated in 1971-1972. The leaf beetle larva during the whole period of development consumed about 70 mg of leaves, which is equivalent, in the case of an average leaf weight of 20 mg/cm<sup>2</sup>, to only 3.5 cm<sup>2</sup>, i.e., an average-sized tea-leaved ivy leaf.

As Table 1 shows, the nutritional energetics of this leaf beetle in the different zones is generally of the same type, although there are definite differences in a few details. For instance, the larvae of the tundra beetles are appreciably smaller than the Baikal larvae, right up to the last instar, and it is not until just before pupation that this difference is leveled out, thus ensuring the normal course of the pupal stage. The relative increment of Pribaikal'e larvae decreases rapidly during development, whereas in northern larvae it is constant. Finally the northern leaf beetles consume less food.

These differences in the northern individuals are obviously due to adaptation to the extreme conditions of existence in high latitudes (short growing season, low mean diurnal temperatures), as is indicated by the intensive feeding of the late-instar larvae, which occurs in the warmest period, the higher degree of assimilation of the food, and the tendency towards size reduction, at least at certain stages of development.