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Differences in the Energetics and Behavior of Two Closely Related Gnawing Phyllophagous Insect Species at the Northern Boundary of Their Range

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Abstract—Two widespread geometrid species at the northern boundary of their ranges are ecologically similar in many respects. However, daily rhythms of feeding and the related temperature dependences of larval growth rate are different, which is explained by phenological differences in the feeding of caterpillars in the center of their range. The adaptiveness of their behavior in the southern Subarctic is discussed.

INTRODUCTION

Twenty-four-hour feeding activity is one of the main adaptations of insects in the southern Subarctic, a region with severe temperature conditions (Chernyshev, 1984; Bogacheva, 1995, 1998; Knapp and Casey, 1986). Such activity is also characteristic of leaf-gnawing insects. Among the latter, most lepidopterans and leaf beetles are remarkable in maintaining body temperature within the range of optimal (usually fairly high) values, and body heating by solar radiation is the main element of this process (Bogacheva, 1998). Together with continuous feeding (interrupted only by low temperatures at night), the maintenance of body temperature provides for a high growth rate of leaf-gnawing insect larvae. At the same time, in the forest tundra, at the northern limit of distribution of many widespread phyllophages, there are some species with mainly nocturnal feeding activity usually observed in many groups at more southern latitudes (Chernov and Rudenskaya, 1975; Chernyshev, 1984; Heinrich, 1979; Knapp and Casey, 1986). The question arises as to why their feeding activity has not become diurnal (or continuous) in the course of adaptation to low average daily temperatures.

Having found such a species, *Eulithis prunata* L., in the lower reaches of the Ob River, I studied the diurnal dynamics of its activity and the dependence of larval growth rate on temperature. For comparison, the same parameters were studied in *Epirrita autumnata* Bkh., a species largely similar to *E. prunata* but characterized by continuous feeding activity. The results were used for discussing the interdependence of these two parameters and revealing basic factors responsible for this phenomenon.

METHODS

Studies on *E. prunata* were performed in 1997 at the Ecological Research Station (Ural Division, Russian Academy of Sciences) in the town of Labytnangi (the lower reaches of the Ob River, forest tundra). Observations on *E. autumnata* activity during the day were conducted in the same place in 1982. The dependence of larval developmental rate on temperature in a Subarctic population was studied by Ayres and MacLean (1987) at the Kevo Station (Finnish Lapland, forest tundra).

Laboratory experiments on determining larval growth rate in *E. prunata* were performed by the standard method used previously (Bogacheva, 1995, 1998). Penultimate instar caterpillars collected in nature were kept in individual Petri dishes lined with moist filter paper. Every day and at the same time, they were weighed on a torsion balance with an accuracy of 1 mg. The caterpillars fed ad libitum on fresh leaves collected from many plants and replaced every day. All changes in the state and behavior of caterpillars were recorded. The relative growth rate was determined by the formula $RGR = (\ln P_T - \ln P_0)/T$, where P_0 and P_T are the initial and final values of caterpillar weight over the period of T days (Ayres and MacLean, 1987). Growth rate was calculated for caterpillars of the last instar since its onset to the moment when the caterpillar gained the maximal weight. Experiments were conducted at temperatures changing both during the day and from one day to another. To create contrasting thermal conditions, caterpillars were kept alternately in the laboratory and outdoors, in the shade. Temperature was recorded 24 hours a day using a thermographer. All the data on temperatures for this species are average values over the period of growth. Experiments on *E. autumnata* caterpillars were conducted at a constant temperature (Ayres and MacLean, 1987).

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In our experiments, caterpillars received leaves of their common food plants: *E. prunata was* fed on currant *Rubes hispidulum*, and *E. autumnata,* on birch *Betula pubescens* ssp. *tortuosa.*

To study diurnal activity, caterpillars were placed on plants in nature. The place where a caterpillar was found was marked with a piece of adhesive tape, and this label was transferred when the caterpillar moved to another place. When several caterpillars were near one another, they were also marked with a drop of water-soluble correcting fluid, which did not trouble the animal. Observations were performed on a 24-hour basis, with the location of a caterpillar, the type of its activity (feeding, locomotion, rest, or molting), weather, and illumination (direct or dispersed light, shadow) at the moment of observation recorded every hour. Twenty to thirty caterpillars were kept under observation simultaneously. A similar method for studying daily activity has also been used by other authors (Casey, 1976).

RESULTS AND DISCUSSION

As noted above, the geometrids under study are ecologically similar: both are widespread species for which the southern Subarctic is at the northern boundary of their ranges. Insects overwinter at the egg stage, and emerging caterpillars feed in spring on early leaves of arboreal plants. However, *E. autumnata* may be classified as an early spring species, as its caterpillars begin feeding as soon as the buds open, whereas *E. prunata* is rather a spring–summer species: in the temperate zone of Europe, *Eulithis* larvae actively feed in May and June, compared to April and early May in *Epirrita* (Koch, 1961). Both species are polyphagous, i.e., they feed on plants belonging to different families, although *Epirrita* has a broader food spectrum: in addition to many foliate species, it includes larch, a conifer (Koch, 1961). In both species, caterpillars have cryptic coloration and are similar in size: the maximal body weight of a caterpillar is about 150 mg. Nevertheless, they significantly differ in the dependence of growth rate on temperature and in the pattern of daily activity.

According to the results of experiments performed at temperatures ranging from 6 to 24°C (Ayres and MacLean, 1987), *Epirrita* can feed at even lower temperatures (Fig. 1). This was confirmed by direct observations on the nighttime feeding of caterpillars in nature at 3–5°C during the perpetual day (when the sun does not descend below the horizon). These caterpillars were in the lower part of the crown, in the shadow, and could not increase their body temperature by basking in the sun (Fig. 2a). The calculated critical temperature of growth for *Eulithis* was about 9°C. During field observations conducted in July 1997, the temperature did not decrease below 11.5°C, and caterpillars continued feeding at this temperature (Fig. 2b); however, some caterpillars kept in cages ceased to feed between 4 and 8 a.m., whereas no such pauses were observed at higher

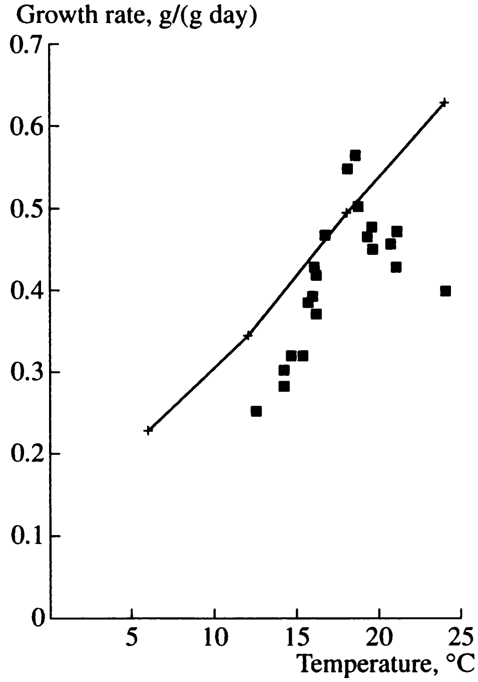

Fig. 1. Growth rate as a function of temperature in the last instar larvae of *E. autumnata* (Ayres and MacLean, 1987, solid line) and *E. prunata.*

night temperatures. Apparently, this temperature actually approaches the lower critical value.

The dependence of growth on temperature in *Epirrita* was almost linear up to 24°C. Suppressed feeding activity and, hence, growth were observed in captive caterpillars only at temperatures approaching 30°C. During the period of *Epirrita* development in nature, and not only in the lower Ob region, but also in the southern taiga, such temperatures are rarely observed even at midday. Much lower temperatures are typical, and this is reflected in a low temperature threshold of growth. Basking in the sun allows caterpillars to increase their body temperature. The corresponding behavior in morning hours is especially typical: a nonfeeding caterpillar "sits still" on a leaf along the midrib and perpendicular to the sunlight shining on it or "stands" on the auxiblast near the apical leaf at the top of a young tree. Such behavior is typical of this and many other species with similar dates of feeding in temperate latitudes.

The temperature optimal for *Eulithis* caterpillars is fairly low, about 18°C (Fig. 1), and they do not bask in the sun. On the contrary, caterpillars exposed to sunlight try to escape it and hide in the shadow inside a bush. Moreover, most of the caterpillars leave their food plants during the daytime and hide in the shadowed part the of grass near the ground. It is apparent that the daily rhythm of activity typical of this species in the temperate zone is retained in the Subarctic, and this fact is reflected in the Russian name of the genus

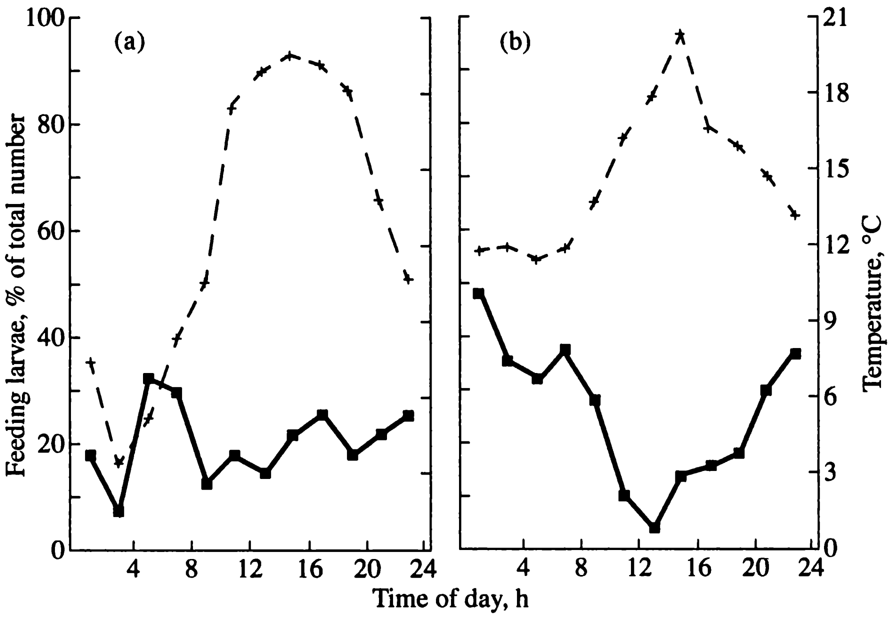

Fig. 2. Daily dynamics of feeding activity in (a) *E. autumnata* and (b) *E. prunata* larvae. The broken line shows temperature on the day of observation.

Eulithis Hb. (*Lygris* Hb.), which is translated as "nocturnal moth" (Lampert, 1913).

Differences in temperature dependence of larval growth rate in both species are obviously related to daily rhythms of activity typical of them. In *Epirrita* caterpillars, feeding activity is continuous and reaches a peak in the morning, after a decrease during the cool nighttime. In *Eulithis*, the peak of activity falls in the night hours, and feeding caterpillars are almost absent in the warmest time of the day (Fig. 2). Differences in energetics associated with daily rhythms of activity in closely related species were described previously (Knapp and Casey, 1986; Casey and Knapp, 1987). However, the temperature dependence of growth rate in the species analyzed by these authors had a different form: Gypsy moth larvae, which feed at night, had an almost constant growth rate and metabolic expenditures in a wide range of temperatures, whereas in *Malacosoma americanum* larvae, which live in silky nests and actively use sunlight for heating, these parameters proved to depend strongly on temperature.

If differences in temperature dependence of the growth rate between the two geometrid species are explained by differences in daily rhythms of their feeding activity, a related problem arises: what factors were responsible for the appearance of differences in daily rhythms? The nocturnal mode of life is more typical of species suffering from predation, which are protected by cryptic coloration combined with immobility during the daytime (Heinrich, 1979). In our case, however, both species are similar in this respect, and their divergence is apparently explained by phenological differences in the feeding of their larvae in the temperate belt of Europe, the center of their range. *Epirrita* larvae feed in the very beginning of the season, in April–May (Koch, 1961), when periods of cold weather are still possible in the forest zone, and night frosts are common. Under such conditions, caterpillars acquired the ability to feed and grow at low temperatures owing to feeding in the daytime (and, possibly, 24 hours a day) and basking in the sun. Conditions ensuring the rapid growth of caterpillars during the short period of leaf growth in food plants are especially important for this early spring species. In *Eulithis*, caterpillars feed in late May and June, when temperatures are significantly higher and remain above the lower threshold level even at night. However, these temperatures usually do not exceed 20°C. Hence, optimal feeding conditions for caterpillars of this species, with their nocturnal activity, are at fairly low temperatures. A feeding caterpillar may be easily detected on a food plant because it makes leaves move, and a shift to the nocturnal mode of feeding may help to minimize the risk of predation. During the daytime, nonfeeding caterpillars hide in shelters that are often located beyond the food plant.

In the southern Subarctic, the phenological dates of larval development in the two species converge, although the development of *Eulithis* in this region is still accomplished a week or two later. The feeding strategy of *Epirrita,* formed in the temperate belt, is adaptive under these conditions as well, providing a good example of preadaptation to northern conditions (Lantsov and Chernov, 1987). The nocturnal feeding of *Eulithis* is nonadaptive in the Subarctic, where low temperatures at night are quite common, because the development of caterpillars is retarded under such conditions; moreover, rapid changes in the quality of leaves reduce their nutritional value, which also leads to growth retardation. Nevertheless, the nocturnal feeding activity of *Eulithis* larvae has not become diurnal or continuous. Such a conservativeness of behavior, a fairly labile parameter, is especially remarkable because average daily temperatures in the first half of July in the forest tundra of the Ob region are approximately within the range optimal for the growth of caterpillars. Such adaptations could have developed with further northward expansion of this species, but this expansion is prevented by the absence of food plants in northern regions.

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