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ZOOLOGY

Features of the Life Cycles of *Pterostichus montanus* (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) (Coleoptera, Carabidae) in Conditions of the Mountain Taiga Belt in the Eastern Sayan

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Abstract—We studied the seasonal dynamics and demographic structure of abundant ground beetle species from the mountain taiga belt in the Eastern Sayan. Data on the dynamics of the sexual and age structure of the populations as well as on the reproductive capacity of females in the biotopes on the slopes with different exposure and height were obtained. Life cycles with one- and two-year development were revealed for the ground beetles typical for the mountain taiga belt. As an example, data on the life cycles of *Pterostichus montanus* (Motschulsky, 1844) with one-year spring development and *Carabus loschnikovi* (Fischer-Waldheim, 1822) with two-year polyvariant multiseasonal development are given for the first time. Two strategies were revealed in the life cycles of ground beetles under alpine conditions: an accelerated population development in spring one-year species and a two-year development with pronounced polyvariance in two intrapopulation groups of ground beetles of the *Carabus* genus. The seasonal dynamics of the activity and reproduction periods proved to vary for these species on the slopes along the height gradient.

Studies on ground beetle life cycles actively progress since the work of Larsson (1939). Numerous publications deal with this problem. Wallin (1987) entered a new stage of this research when he proposed to study seasonal dynamics of sexual and age structure of populations of ground beetle imagoes by the degree of gonad development. Application of this approach considerably changed our understanding of ground beetle life cycles. Russian carabidologists contributed to the life cycle theory by the notion of polyvariance as a variable development of intrapopulation groups of species (Makarov, 1990, 1994) and by the notion of synchronized development of preimaginal stages (Matalin, 1993). In addition, data on seasonal occurrence of all ontogenetic stages of individuals were used to interpret ground beetle life cycles. This made possible the generalization of our views on the life cycle of ground beetles as a combined development of intrapopulation groups associated with heterogeneous structure of species.

Recent studies indicate that seasonal activity and development timing of ground beetles vary with different range parts and landscape conditions (Lindroth, 1945; Paarmann, 1979; Sharova 1990; Sharova and Filippov, 2003).

Life cycles of Siberian ground beetles are poorly explored and there is no such data for alpine conditions. The first data on the biology of reproduction in widespread Siberian ground beetle species living in the Southern Baikal regions were collected by Shilenkov (1978). In addition, data on breeding and development of certain Siberian ground beetle species are available (Berlov and Berlov, 1984, 1989; etc.). For the first time we studied the seasonal dynamics of activity and population structure of abundant ground beetle species from the mountain taiga belt of the Eastern Sayan. Below we present data on development of two ground beetle species, *P. montanus* (Motschulsky, 1844) and *C. loschnikovi* (Fischer-Waldheim, 1822), that are most adapted to alpine conditions.

MATERIALS AND METHODS

This publication is based on the material stationary collected from May to September in 2000–2001 in the mountain taiga larch belt of the Okinskoe Plateau at the Eastern Sayan along the transverse profile of the Ekhe-Kheregte river basin in larch forests on slopes with northern and southern exposures at the height from 1500 to 2000 m above the sea.

The material was collected in the mountain taiga belt using the method of soil traps in 21 biotopes. Plastic 200 ml beakers 75 mm in diameter half-filled with 4% formalin were used as traps. Ten traps were set in each biotopes. The beetles were collected once in a decade. In total, 60000 trap-days were processed. The seasonal activity curves were plotted on the basis of the material collected in 2001.

Demographic structure of ground beetle populations was described on the basis of the generative status and age of the imagoes as proposed by Wallin (1987). He recognized four imaginal ages according to the degree of gonad development: juvenile (j), immature (im), generative (g), and postgenerative (pg).

Interpretation of the life cycle primarily relied on the general pattern of the seasonal dynamics, its duration, reproduction timing, activity peaks, and quantitative indices of egg production by females, which allowed us to reveal seasonal patterns of specific reproduction. The composition of age groups in a population was determined from the composition of wintered developmental stages. In addition, the sequence of occurrence of all developmental stages during a season was taken into account.

Our investigation of ground beetle life cycle was based on the following developmental notions (Matalin, 1998; Sharova and Filippov, 2003). Ontogenesis was considered as development of an individual from egg to its natural death. Ground beetle species vary by ontogenetic duration; they can live one, two, and more years. They are further divided into monocyclic species that reproduce once and recyclic ones that reproduce once or, less frequently, twice a season. Life cycle of a population is considered as a cyclic development of individuals in a population. Life cycles of ground beetles can be one-year, two-year, or one–two-year from hatching to the first reproduction. Seasonal cycle of a population was considered as development of individuals during the vegetation period after wintering until the next winter diapause. A phenological succession of ontogenetic stages of individuals is observed during the seasonal cycle and it differs in species with different life cycle.

Life cycles of ground beetles with synchronous individual development were considered as monovariant, while those with asynchronous development of intrapopulation groups were considered as polyvariant. In the case of a monovariant cycle, the seasonal sequence of developmental stages in a population corresponds to their ontogenetic sequence (from an egg to sexually mature individuals). Species with a polyvariant life cycle can simultaneously have early and late ontogenetic stages during the season, which is due to the presence of intrapopulation groups with different timings of development and reproduction.

Monovariant life cycles were divided into spring and autumn ones according to the system of Larsson (1939). The spring species feature spring reproduction, summer development of preimaginal stages, autumn hatching of imagoes, and their subsequent wintering. The autumn species feature summer–autumn reproduction, wintering of larvae, and completion of preimaginal development in mid-summer of the next season.

Presently, we know that a fraction of beetles after the first reproduction winter in postgenerative state in many spring and autumn species living for two and more years. Next season, they enter the generative state and reproduce together with the young beetle generation. In this case, groups of imagoes of different age take part in reproduction and give rise to a new generation of beetles with synchronous development. That is why, we considered the species living for one year (monocyclic) and those living for several years and reproducing annually together with their young generation (recyclic) as monovariant.

Species with one-year polyvariant life cycle differ from those with one-year monovariant cycle by the presence of different intrapopulation groups with different timing of reproduction during the same season.

The two-year life cycles are also polyvariant. In this case, the populations include two groups. The first group reproduces during the first season at the stage of imago and the hatched larvae winter, while the second one completes preimaginal development and winters at the stage of immature imagoes. Next season, the first group completes preimaginal development of the larvae, while the second one starts reproduction at the stage of imago. In the case of the two-year cycle, two intrapopulation groups demonstrate a synchronous reproduction; they reproduce every two years, thus, providing for annual reproduction of the species (Sharova and Filippov, 2003). All individuals in a population have one wintering at the stage of larva and another one at the stage of immature imago. The two-year cycles feature the presence of one reproduction period and one period of juvenile imago emergence during a season. At the same time, occurrence of the generative and juvenile individuals partially overlaps. The above-mentioned life cycle properties were used to identify the type of development in the studied ground beetle species.

RESULTS

The above-mentioned properties of seasonal development of ground beetles allowed us to identify life cycle types for two mountain taiga ground beetle species from the Eastern Sayan.

P. montanus is a Siberian mountain taiga species (Shilenkov, 1972, 2000). In conditions of Southern

Baikal Regions, it reproduced in June; juvenile imagoes emerged in July–August; the imagoes wintered (Shilenkov, 1978). However, no detailed investigation of this species development was carried out.

In order to describe the life cycle of *P. montanus*, we studied the seasonal dynamics of its demographic structure in the Ekhe-Kheregte river basin on slopes with northern and southern exposures at different heights from top to bottom. In total, eight larch forests were studied. In 2001 season, 699 individuals of *P. montanus* were collected.

The general curve of seasonal dynamics of imagoes at different ages (combined for all biotopes) is given in Fig. 1. The pattern of seasonal dynamics of *P. montanus* indicates a one-year spring type of development in this species. The maximum activity in the reproduction period was observed in the first half of the season (from the second decade of May to the second decade of July). In the second half of the season, an insignificant activity of the juvenile and immature imagoes was observed in the third decade of July. The larvae could be found in the traps in late June. The first major increase in the imago activity was due to the emergence of immature and postgenerative imagoes and their transition to the generative state and the subsequent reproduction. The proportion of beetles involved in repeated reproduction was no less than that of beetles reproducing for the first time. The young imago generation and postgenerative beetles after spring reproduction wintered. The young generation demonstrated a low activity and largely wintered in the pupal cells, which is an adaptation to severe climatic conditions in the mountain taiga belt with early frosts in August–September. Individuals developed synchronously in a population. During a season, developmental stages proceeded from imago to imago in the ontogenetic order, which points to a monovariant life cycle. The season cycle formula is as follows:

1st season	wintering
Iim–Ig–O–L–P–Ij–Iim	Iim
Ipg → Ipg	Ipg

The described seasonal development of *P. montanus* populations allowed us to assign its life cycle as a one-year monovariant with spring reproduction.

In the studied region, the seasonal dynamics of the activity and age structure of *P. montanus* population varied between biotopes on the slopes with different exposure and height (Fig. 2). In total, we studied eight biotopes on two slopes with northern and southern exposures. Three biotopes were selected on the northern and southern slopes at the same height (Figs. 2a, 2c) as well as on the northern slope at different heights

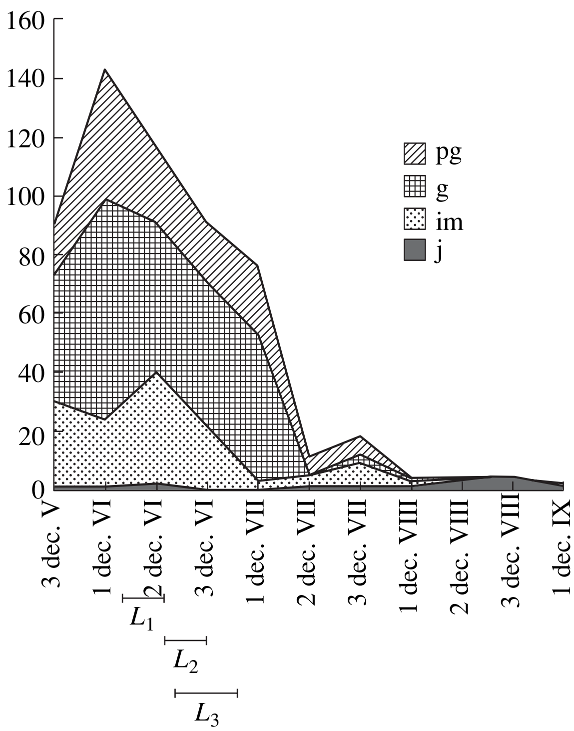
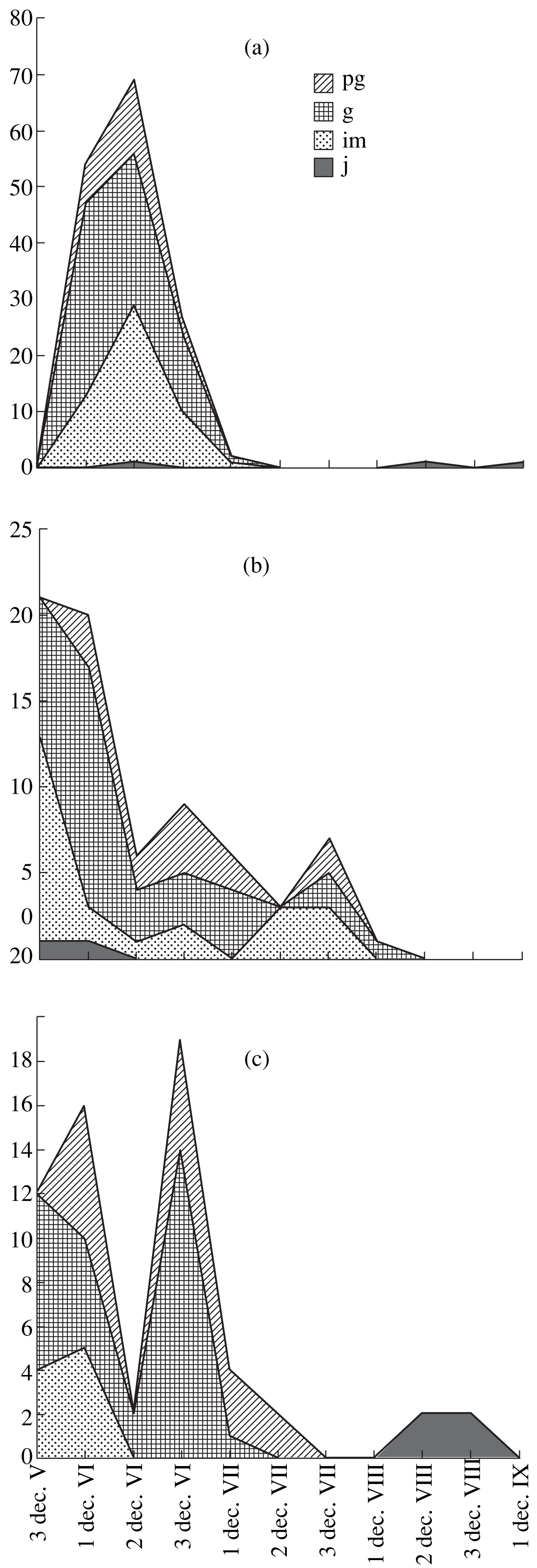


Fig. 1. General curve of *P. montanus* seasonal activity in larch forest on the slopes with northern and southern exposures in the Ekhe-Kheregte river basin; stages of imago (I) development: j, juvenile; im, immature; g, generative; pg, postgenerative; larval (L) stages: L_1, first stage; L_2, second stage; L_3, third stage; ordinate: absolute abundance of imagoes; abscissa: occurrence of larvae (for Figs. 1, 2, 4, 5).

(Figs. 2a, 2b) in order to reveal individual effects of two factors, height and slope exposure, on *P. montanus* population.

For instance, only a spring activity associated with reproduction within just four decades peaking in the second decade of June was pronounced in the larch shrub forest on the slope with northern exposure at the height of 1850 m (Fig. 2a). No activity of the young generation was observed. This biotope demonstrated the highest abundance of this beetle species, which maintained its successful reproduction under alpine conditions.

The period of seasonal activity of this beetle species was much longer (eight decades) and their reproduction lasted five rather than four decades on the same slope in the cowberry–green moss–lichen larch forest (Fig. 2b). The changes in the seasonal dynamics of this species on the slope with southern exposure at a height of 1850 m in lichen–cowberry–green moss larch forest with a warmer microclimate (Fig. 2c) were similar to those in the biotope on a lower slope with northern exposure. The first peak of activity of these beetles was bimodal in these two biotopes; it was extended to six decades with two activity peaks (in the first decade of June and



in the third decade of July). The second peak of activity of the young generation was observed later (in August) and represented juvenile individuals. Apparently, maturation of beetles to the immature state took place in the soil during prewintering.

The indices of reproductive potential of females of this species differed for different slopes and heights (Fig. 3). The maximum egg production was observed on the slope with northern exposure at the height of 1850 m (Fig. 3a) within three decade of June. Reproduction took place in June in "warm" biotopes with southern exposure and on lower region of the slope with northern exposure (Figs. 3b, 3c) as well. Generative females occurred here for a longer period (6–7 decades rather than 3 decades as observed on the top of the northern slope) and reproduction started earlier in these biotopes (in May rather than June).

The optimal sex ratio (OSR) of –0.01 was observed in the population in the upper slope with northern exposure. Males predominated in the warm biotopes. According to the ecological valence of *P. montanus*, Alpine taiga conditions of slopes with northern exposure were the most favorable for this species. Its abundance was considerably higher and the demographic structure of populations was optimal there. Its adaptation to development in cold conditions of mountain taiga as compared to the warm biotopes was manifested as accelerated population development and earlier timing of spring reproduction, which underlay sooner completion of the seasonal cycle. Typically, the young generation demonstrated no activity at the end of the season due to early frosts. Accomplishing development of juvenile imagoes in the pupal cells was another adaptation to alpine conditions.

C. loschnikovi is a Siberian mountain forest species inhabiting forests as well as alpine meadows and tundra. It occurs in forest–tundra in the Northeastern European Russia, Western and Central Urals, and mountains in the Southern Siberia and Northern Mongolia (Shilenkov, 1996; Khobrakova, 2000; Chernov *et al.*, 2000, 2001). No published data on the development of this species were available.

The life cycle of *C. loschnikovi* was studied in the same biotopes and using the same methods as for *P. montanus*. We collected 250 beetles and a few tens of larvae of *C. loschnikovi* in eight studied biotopes in the mountain taiga belt of the Eastern Sayan in 2001.

Fig. 2. Seasonal dynamics of the age structure in *P. montanus* populations on the slopes with northern and southern exposures in the Ekhe-Kheregte river basin; (a) larch shrub forest, northern exposure, h = 1850 m; (b) cowberry–green moss–lichen larch forest, northern exposure, h = 1500 m; (c) lichen–cowberry–green moss larch forest, southern exposure, h = 1850 m (for Figs. 2, 3).

The general curve of seasonal dynamics of imagoes at different ages (combined for eight biotopes) is given in Fig. 4 together with the time of larva occurrence. The pattern of seasonal dynamics of *C. loschnikovi* activity indicates its multiseasonal development. Two activity peaks were observed. The first extended peak (from late May to August; eight decades) corresponded to reproduction of imagoes that wintered in immature and postgenerative states; the second one was observed at the end of the season (from late July to September; five decades) and corresponded to the emergence of young generation of beetles that wintered as larvae. These peaks had an overlapping zone within three decades. Analysis of the dynamics of population age structure allows us to conclude that *C. loschnikovi* has a polyvariant two-year life cycle. A complex population structure and polyvariant development of intrapopulation groups of this species is indicated by simultaneous occurrence of larvae and imagoes of various ages during the season. According to the age distribution of the population at the beginning of the season, one group of individuals, that wintered at the stage of imago, immediately starts reproduction; while another one, that wintered at the stage of larvae, continues preimaginal development. In the second half of the season, the first group completes reproduction and gives rise to a new generation of young larvae that will winter. At the same time, the second group completes preimaginal development by emergence of juvenile imagoes from the pupae and their subsequent transformation to the immature state.

Thus, the wintering stages include postgenerative imagoes and emerged larvae from the first group and immature imagoes from the second one.

Intrapopulation groups develop asynchronously and reproduce alternately once in two years. The polyvariant two-year life cycle of this species can be logically presented as follows: season; 4. gr. 1; 5. group 2

1st season	winter	2nd season	winter
1 гр. Iim–Ig–O–L	L	1 гр. L–P–Ij–Iim	Iim
Ipg Ipg	Ipg	Ipg Ipg	Ipg
2 гр. L–P–Ij–Iim	Iim	2 гр. Iim–Ig–O–L	L

This formula corresponds to the properties of a two-year development:

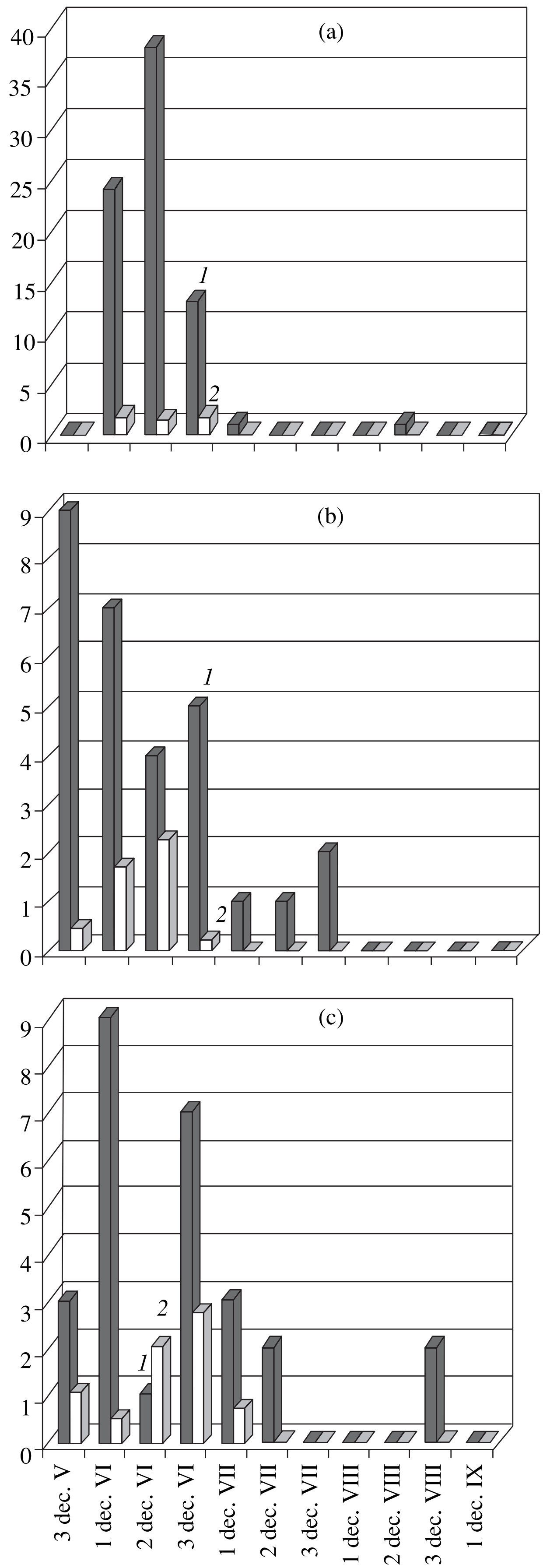


Fig. 3. Dynamics of reproduction potential of *P. montanus* females (the proportion of female numbers (*1*) to the mean number of eggs per female (*2*)); (a) OSR = –0.01; (b) OSR = –0.20; (c) OSR = –0.08.

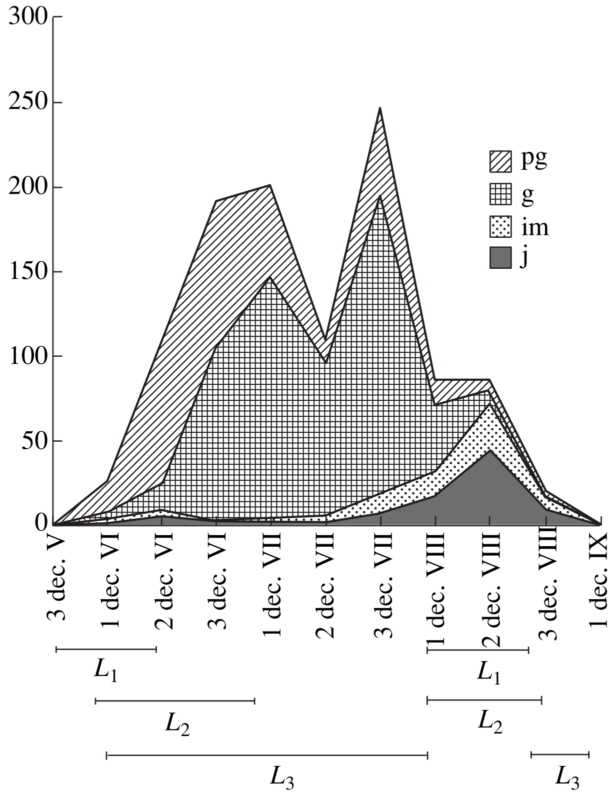


Fig. 4. General curve of *C. loschnikovi* seasonal activity in larch forest on the slopes with northern and southern exposures in the Ekhe-Kheregte river basin.

(1) only one out of two intrapopulation groups reproduces each season;

(2) reproduction of one of groups partially overlaps in time with the emergence of juvenile imago from the pupae of another group;

(3) each group winters twice during ontogenesis: at the stage of larva and later at the stage of immature imago;

(4) involvement of postgenerative imagoes of one group in the first reproduction of beetles maintains genetic unity of the species and prevents group isolation.

Thus, *C. loschnikovi* has a two-year life cycle with polyvariant development. This species has two main groups that alternately reproduce once in two years and winter either at the stage of imago or at the stage of larva. Imagoes of this species live for several years and the postgenerative individuals are repeatedly involved in reproduction. The polyvariant life cycle and recyclic reproduction provides for annual multiseasonal reproduction of *C. loschnikovi*.

The seasonal dynamics of *C. loschnikovi* activity changed on the slopes with different exposure and height (Fig. 5). The highest abundance of this species was observed on the upper slope with northern exposure at the height of 2000 m in fescue–lichen larch forest. Despite severe climatic conditions, the seasonal activity of the species was observed for 10 decades in this biotope, while reproducing beetles (Ig) could be observed for 6 decades (from the second decade of June to the first decade of August). The most active reproduction was observed in the third decade of July. The young generation of beetles appeared in early July and remained active until the end of the season. Maximum activity of the young generation was observed in the second decade of August (Fig. 5a). Activity of the beetles insignificantly changed in the fescue–moss–cereal larch forest on the same slope but at the height of 1650 m. High spring activity of beetles started by one decade earlier as compared to the first biotope (Fig. 5b), while the duration of reproduction was by one decade longer (seven decades); the young generation also remained active for a longer period (Fig. 5b). On the slope with southern exposure in cider–lichen–moss larch forest (Fig. 5c), the abundance of the species was twice lower as compared to the upper slope with northern exposure (Fig. 5a); the activity curves were also different. For instance, the species became active in spring by one decade earlier in the cider–lichen–moss larch forest at the height of 2000 m (Fig. 5c) as compared to that on the northern exposure slope at the same height (Fig. 5a). The peak of reproduction was observed by two decades earlier on the southern slope as compared to the northern one; activity of the young generation was lower here as compared to the northern slope. This confirms the positive preference of the species for colder conditions of the slope with northern exposure. The data on reproduction in *C. loschnikovi* populations (Fig. 6) confirm more optimal conditions on the slope with northern exposure. The females with eggs were observed for 6–7 decades starting from the second decade of June; egg production peaked on July 11 (Figs. 6a, 6b). On the southern slope (Fig. 6c), high occurrence of females with eggs was observed only for three decade of June. The sex ratio was more optimal on the northern slope than on the southern one.

The life cycle of *C. loschnikovi* in mountain taiga conditions of the Eastern Sayan is two-year polyvariant with multiseasonal reproduction and recyclic repeated reproduction of the beetles. Analysis of the data on seasonal dynamics of the species activity as well as on the dynamics of reproductive potential of females on the slopes with different exposure demonstrated optimal ecological conditions for *C. loschnikovi* at the upper boundaries of mountain taiga and tundra on the slopes with northern exposure. The following population properties of *C. loschnikovi* living in mountain taiga confirm that it is a mountain forest–tundra species: maximum abundance, dynamic density, and optimal age and sex structure on the slopes with northern exposure at the height of 2000 m.

Adaptations to the life cycle under pessimal alpine conditions include the duration of development of the species similar to other representatives of the genus *Carabus* under boreal and alpine conditions in Europe. In addition, the peak of reproduction under alpine conditions is shifted to the warmest period of the season (July), while it occurs earlier on the slopes with southern exposure. Two-year development of *C. loschnikovi*, which is the most abundant species in the mountain taiga forest of the Eastern Sayan, is one of trends in adaptive evolution of alpine carabid fauna.

DISCUSSION

Investigation of the population structure and dynamics of the most abundant ground beetle species in the mountain taiga belt of the Eastern Sayan allowed us to demonstrate that *P. montanus* has a one-year monovariant life cycle with spring reproduction, while *C. loschnikovi* has a two-year polyvariant life cycle with multiseasonal reproduction.

We used a set of tests (including original ones) in the study of the life cycles of these species.

For instance, we propose to consider the phenological sequence of occurrence of the developmental stages to identify polyvariant or monovariant development of ground beetle populations. Occurrence of the ontogenetic sequence of beetle developmental stages is indicative of a monovariant development, e.g., for *P. montanus*. Simultaneous occurrence of early and late ontogenetic stages during the season suggests a polyvariant development of the species including different intrapopulation groups, as was observed for *C. loschnikovi*.

In order to distinguish a one-year monovariant life cycle (*P. montanus*) from a two-year polyvariant one (*C. loschnikovi*), we considered two properties at the same time: the number of intrapopulation groups and the timing of reproduction and emergence of juvenile imagoes. In the case of a one-year monovariant cycle (such as that of *P. montanus*), development of a group is accompanied by one (spring) reproduction period followed by the period of emergence of juvenile imago that completed preimaginal larval development. Only imagoes of this species winter. In the case of a two-their polyvariant development (such as that of *C. loschnikovi*), only one out of two population groups

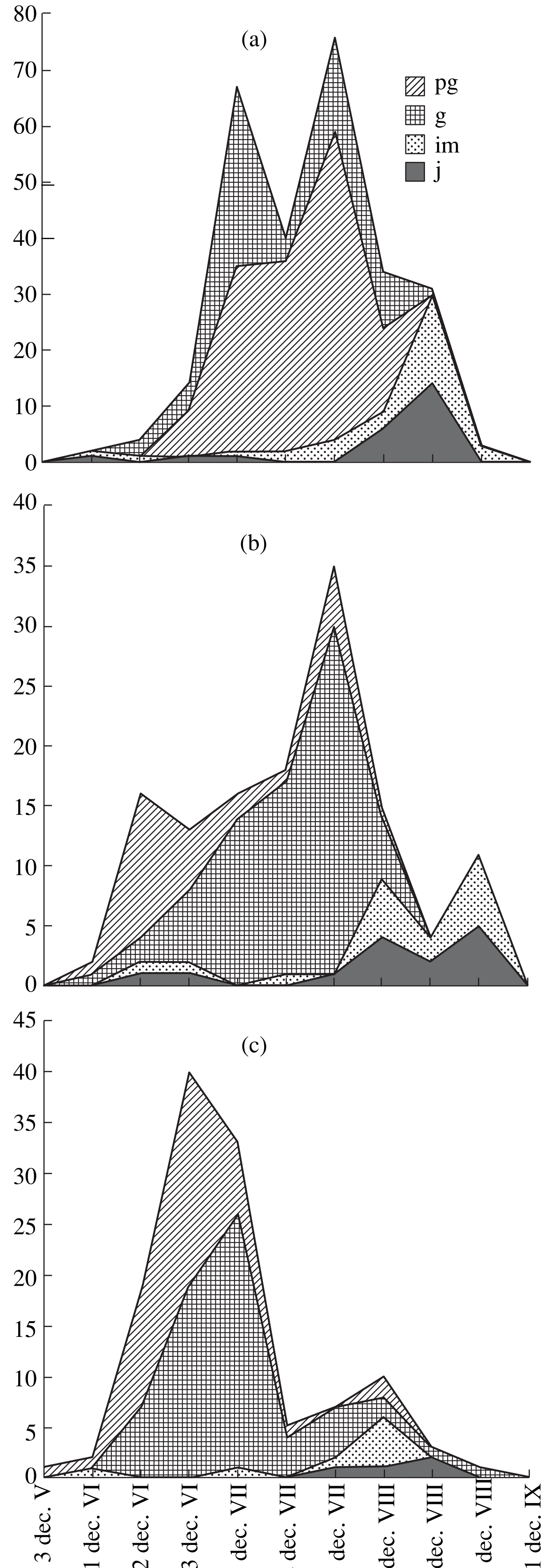
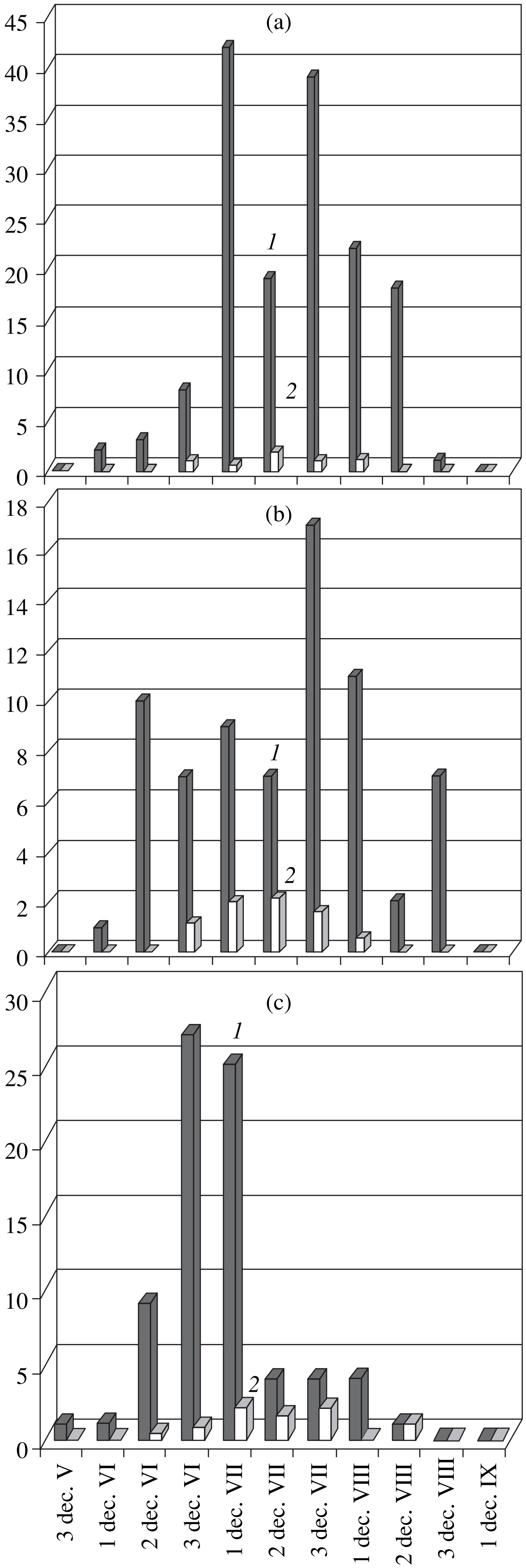


Fig. 5. Seasonal dynamics of the age structure in *C. loschnikovi* population on the slopes with northern and southern exposures in the Ekhe-Kheregte river basin; (a) fescue–lichen larch forest, northern exposure, h = 2000 m; (b) fescue–moss–cereal larch forest, northern exposure, h = 1600 m; (c) lichen–moss larch forest, southern exposure, h = 2000 m (for Figs. 5, 6).



reproduces. The reproduction period of this group is multiseasonal and partially overlaps with the periods of emergence of juvenile imagoes of the second group that wintered at the stage of larva. In the case of this species, ontogenesis of individuals of each group completes in two seasons. Asynchronous alternate reproduction of the groups provides for annual reproduction of the species.

We propose the formulas of seasonal development describing the phenological sequence of ontogenetic stages for one or two intrapopulation groups in order to characterize the types of ground beetle life cycles.

We have obtained the first data on changed phenology in two model species (*P. montanus* and *C. loschnikovi*) under alpine conditions as a function of the height and exposure of the slopes.

P. montanus demonstrated different timing of activity and reproduction in the biotopes on the slopes with different exposure and height. Seasonal activity of the species and its reproduction period are longer on the slope with southern exposure and on the lower parts of the slope with a warmer microclimate as compared to the higher slope with northern exposure. The abundance of this species is considerably higher in the alpine part of the belt. Its adaptation to successful reproduction and development under alpine conditions is manifested as accelerated and synchronized development of the population, which allows it to complete the seasonal cycle within a short vegetation season. A similar adaptation to accelerated seasonal development was observed in spring ground beetle species living in conditions of northern taiga in the European Russia as compared to the southern regions of the forest belt (Sharova and Filippov, 2000).

Seasonal activity of *C. loschnikovi* in the studied region considerably differed on the slopes with northern and southern exposures. The peak of its reproduction on the southern slope starts by two decade earlier as compared to the northern slope. *C. loschnikovi* demonstrates better demographic indices and high activity of the young generation on the slope with northern exposure. This indicates adaptation of the species to alpine conditions. The two-year development, polyvariant population structure, and recyclic reproduction are among the most important adaptations of this species to the mountain taiga conditions. One of its intrapopulation groups actively reproduces during the whole season together with repeatedly reproducing beetles, while the other group completes the preimaginal develop-

Fig. 6. Dynamics of reproduction potential of *C. loschnikovi* females (the proportion of female numbers (*1*) to the mean number of eggs per female (*2*)); (a) OSR = 0.14; (b) OSR = 0.17; (c) OSR = 0.27.

ment. Their alternate reproduction every two years maintains annual reproduction of the species.

Published data agree with a two-year development of species of the genus *Carabus* under conditions of the Northern Europe (Larsson, 1939; Sharova and Dushenkov, 1974; Houston, 1981; Korobeinikov, 1991; Sharova and Filippov, 2002) and under alpine conditions (Forsskål, 1972; De Zordo, 1979; Refseth, 1980, 1984; Schatz, 1994). At the same time, most species of this genus demonstrate a one-year development under conditions of lowland temperate climate. Apparently, the two-year development of *C. loschnikovi* can be considered as an evolutionary advanced life cycle extending the range of possible life conditions. This species is widespread in South Siberian mountains and valleys and maintains its typical two-year development. Apparently, the life cycle of *C. loschnikovi* is an example of evolutionary completed transition from a one-year to two-year development, while this transition can be observed in European species of the genus *Carabus* with geographic variability from a one-year cycle in warm latitudes to a two-year one under boreal alpine conditions. It is also possible that the two-year development of *C. loschnikovi* appeared in its lowland ancestors, which allowed this species to colonize alpine habitats.

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