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ZOOLOGY

Life Cycles of Ground Beetles (Coleoptera, Carabidae) from the Mountain Taiga and Mountain Forest–Steppe in the Eastern Sayan

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Abstract—Seasonal dynamics and demographic structure was studied in 15 dominant ground beetle species in the mountain taiga and mountain forest–steppe belts of the Eastern Sayan (Okinskoe Plateau). Life cycles of the dominant ground beetle species were classified by developmental time, seasonal dynamics, and intrapopulation groups with different reproduction timing. The strategies of carabid life cycles adapted to severe mountain conditions of the Eastern Sayan were revealed.

Studies of life cycles of ground beetles, an abundant group of soil-forming insects, are among topical problems of ecology, since specific development of these beetles reflect many environmental parameters and can serve as their markers. Studies of this problem were primed by Danish entomologist Larsson (1939) and numerous publications since then reflect the data and approaches to interpretation of the life cycle typology (Thiele, 1969; Sharova and Dushenkov, 1979; Houston, 1981; Makarov, 1991; Andersen, 1984; Refseth, 1984, 1988; Sota, 1985, 1986; Brandmayr and Zetto Brandmayr, 1986; Butterfield, 1986; Paarmann, 1986; Wallin, 1987; Makarov and Chernyakhovskaya, 1989, 1990; Schats, 1994; Sharova and Denisova, 1995, 1996, 1997; Matalin, 1997, 1998; Cárdenas and Hidalgo, 2000; Khobrakova, 2002; Sharova and Khobrakova, 2002, 2005; Sharova and Filippov, 2003).

MATERIALS AND METHODS

In this work, original data on life cycles of ground beetles from the mountain taiga and mountain forest–steppe belts in the Eastern Sayan were analyzed.

The material was collected in 2000–2001 on the Okinskoe Plateau in the Oka River basin and its tributary Ekhe-Kheregte covering 37 biotopes. During the whole investigation period, 19 446 ground beetle imagoes of 15 dominant species were collected. The beetles and larvae were collected by soil traps with 4% formalin. Ten traps were monitored in each biotope. Beetles were collected once in a decade. The demographic structure of dominant species populations was analyzed on the basis of the generative status and age of the imagoes of both sexes using the method of Wallin (1987).

Life cycles of 15 dominant species were determined from the seasonal dynamics of imago activity. The typology of life cycles of ground beetles was adopted from published materials (Makarov and Chernyakhovskaya, 1989, 1990; Makarov, 1991; Sharova and Denisova, 1996, 1997; Matalin, 1997, 1998; Sharova and Filippov, 2003; Sharova and Khorakova, 2005).

RESULTS

All studied dominant ground beetle species were long-lived (two and more years) with repeated (recyclic) reproduction each season. This was indicated by postgenerative imagoes as the wintering stage for all species, which allows repeated reproduction next season.

The individual developmental time from egg to reproducing generative imago allowed us to recognize

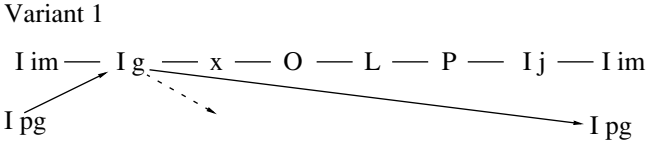

Fig. 1. ISpM, one-year spring monovariant development; stages of beetle development: E, egg; L, larva; P, pupa; I, imago; j, juvenile; im, immature; g, generative; pg, postgenerative; - - →, death; x, reproduction (for Figs. 1, 3, 5, 7).

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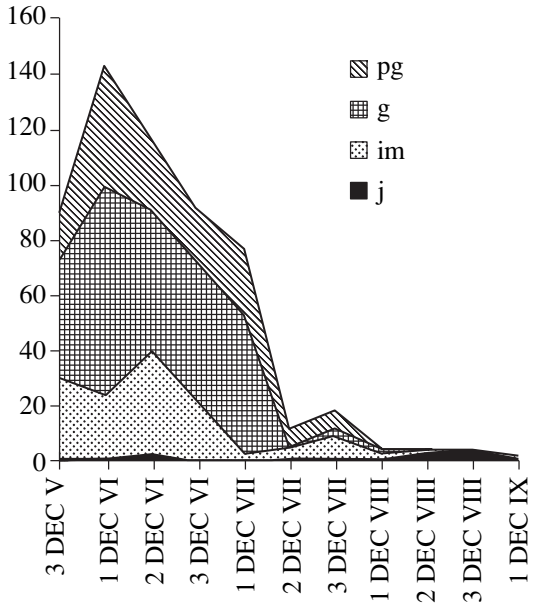

Fig. 2. *Pt. montanus* seasonal activity in larch forest of the Okinskoe Plateau; imago (I) ages: j, juvenile; im, immature; g, generative; pg, postgenerative; ordinate: absolute abundance of imagoes; abscissa: account time, decades (for Figs. 2, 4, 6, 8).

species with one-year (I), two-year (II), and one/two-year (I/II) life cycles.

I. One-year life cycles of studied ground beetle species can be divided into two developmental types by the timing of reproduction, wintering stages, and intrapopulation patterns:

(1) ISpM, one-year spring monovariant development was revealed in ground beetles of the genus *Pterostichus: Pt. montanus* (Motschulsky 1844), *Pt. subaeneus* Chaudoir 1850, and *Pt. turanensis* Jedlicka 1959. These species reproduce in spring, winter as imago, and their populations develop synchronously by a single pattern. The monovariant life cycle features a spring peak of imago activity and a spring peak of egg production. It can be described by the phenological sequence of ontogenetic stages during a season (from wintering to wintering) shown in Figs. 1 and 2.

(2) ISuP, one-year summer polyvariant development was observed in *Poecilus fortipes* Chaudoir 1850, *Pterostichus dilutipes* (Motschulsky 1844), and *Bembidion infuscatum* Dejean 1831. These species reproduce in summer and, partially, early autumn; the imago activity and egg production peak in mid-summer; imago and larvae winter, intrapopulation groups develop by two patterns as described in Figs. 3 and 4.

The abundance of the first population variant is higher than the second one, which suggests that summer reproduction with the wintering of imagoes only is the primary variant. Monovariant development is a consequence of species adaptation to mountain conditions.

II. Two-year life cycles of species development from eggs to reproduction feature polyvariant development and the presence of two intrapopulation groups with asynchronous development and alternating reproduction once in two years. This provides for annual reproduction of the species. We observed two-year development in the genus *Carabus: C. spasskianus* Fischer–Waldheim 1822, *C. henningi* Fischer–Waldheim 1817, *C. odoratus melleus* Lapouge 1909, *C. canaliculatus* Adams 1812, and *C. loschnikovi* Fischer–Waldheim 1823 as well as in the genus *Curtonotus: Curt. fodinae* (Mannerheim 1825) and *Curt. tumidus* (A. Morawitz 1862). All these species demonstrated multiseasonal reproduction and differed only by the timing of seasonal activity and egg production.

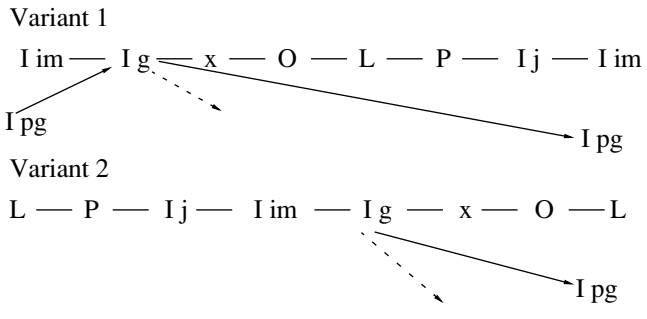

Fig. 3. ISuP, one-year summer polyvariant development.

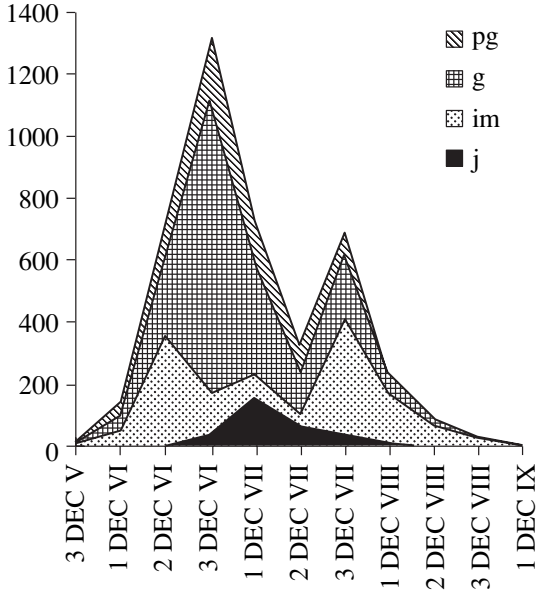

Fig. 4. *P. fortipes* seasonal activity in mountain steppe of the Okinskoe Plateau.

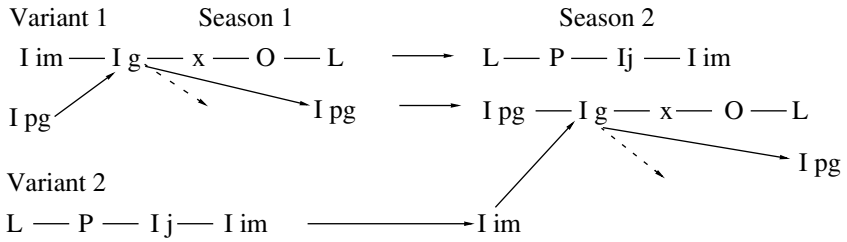

Fig. 5. IIMsP, two-year multiseasonal polyvariant development.

A set of parameters is indicative of two-year development: (1) wintering of imago and larvae, (2) single reproduction peak of a population fraction that wintered as imagoes, (3) wintered larvae develop into immature imagoes and winter once more, (4) reproducing beetles of one group occur together with larvae, pupae, and juvenile imagoes of another group.

The phenological sequence of ontogenetic stages for two-year multiseasonal polyvariant development is shown in Figs. 5 and 6.

The only difference between studied species with two-year life cycles was different timing of egg production: spring–early summer in *C. odoratus melleus* Lapouge 1909; early summer in *C. spasskianus* Fischer–Waldheim 1822 and *C. henningi* Fischer–Waldheim 1817; mid-summer in *C. canaliculatus* Adams 1812 and *Curt. fodinae* (Mannerheim 1825); and mid-summer–late-summer in *C. loschnikovi* Fischer–Waldheim 1823 and *Curt. tumidus* (A. Morawitz 1862).

I/II. One/two-year life cycles have the most complex polyvariant development: a population fraction develops from egg to reproduction in one year; another fraction, in two years. Individuals of both one- and two-year life cycles participate in reproduction.

Multiseasonal activity of imagoes is typical for such species. Among the studied species with one/two-year development, *Harpalus major* Motschulsky 1850 and *H. aequicollis* Motschulsky 1844 demonstrated a mid-summer maximum of imago activity. The one-year fraction of the population, wintering as immature or even generative imago, reproduces in the first half of the season, while the two-year fraction largely reproduces in the second half. The mid-summer peak of beetle activity is due to simultaneous reproduction of beetles with one- and two-year development.

Reproduction of two intrapopulation groups is indicated by two ways of juvenile imago appearance: in the first half of the season (for IIMsP) and at the end of the season (for ISpM). Only two out of three groups reproduce. The formula of the one/two-year life cycle is as follows I/IIMsP = ISpSuM + IIMsP (Figs. 7, 8).

DISCUSSION

Analysis of the demographic structure of ground beetles allowed us to compile the system of life cycles for 15 dominant species in the mountain taiga and mountain forest–steppe belts in the Okinskoe Plateau of the Eastern Sayan. The ontogenetic timing allows the recognition of one-year, two-year, and one/two-year cycles. According to the seasonal activity and reproduction period, all these carabid life cycles can be divided into spring and multiseasonal ones. Multiseasonal cycles can be further divided according to the peak reproduction activity into spring–early summer, mid-summer, and late-summer. The seasonal dynamics of certain species varies by the total duration and reproduction timing with altitude and slopes in the mountain taiga belt. Life cycles of ground beetles in the studied region are realized as monovariant and polyvariant, while autumn and bivoltine life cycles, typical for European carabid species, are missing.

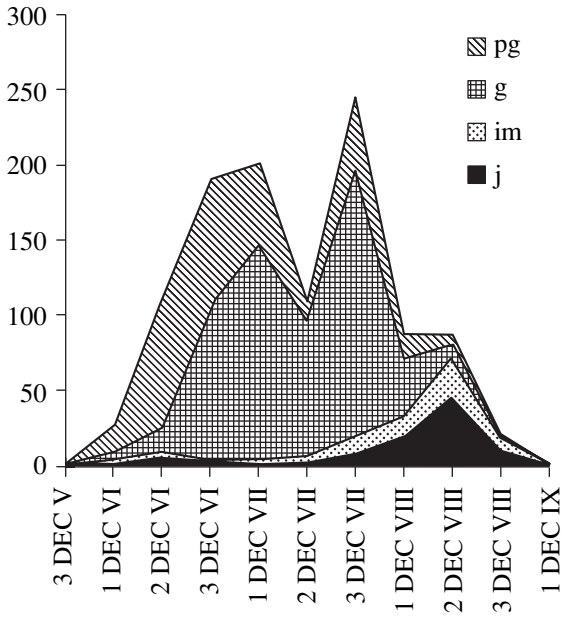

Fig. 6. *C. loschnikovi* seasonal activity in larch forest of the Okinskoe Plateau.

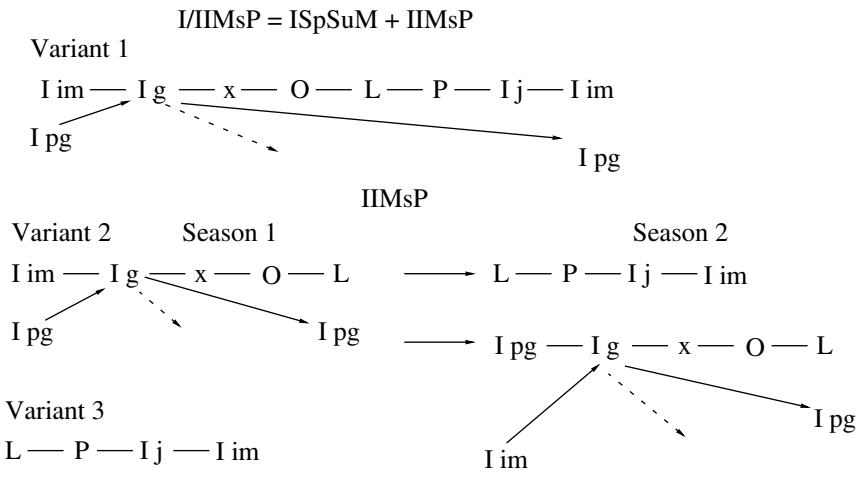

Fig. 7. I/IIMsP, one/two-year multiseasonal polyvariant development including ISpSuM (one-year spring–summer monovariant development) and IIMsP (two-year multiseasonal polyvariant development).

Adaptations of dominant ground beetle species to mountain conditions are manifested as two strategies: accelerated population development in the one-year species and the extension of development to two years in large species of the genus *Carabus*. Polyvariant life cycles provide for multiseasonal reproduction in most species, which increases their fecundity and decreases the risk of offspring death.

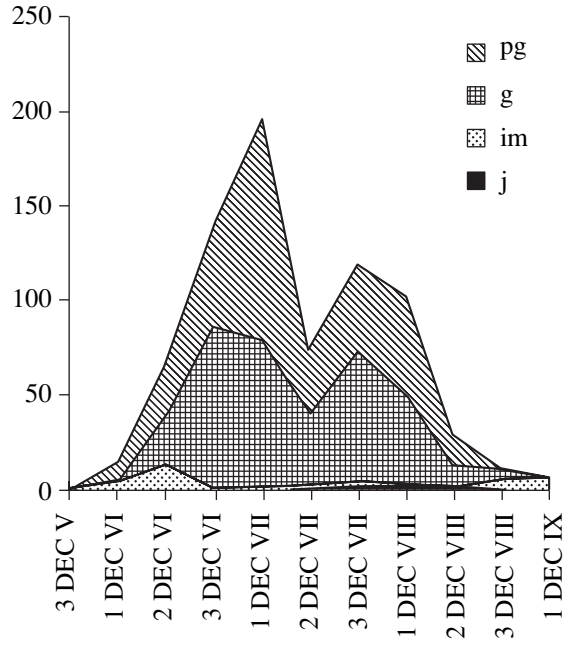

Fig. 8. *H. aequicollis* seasonal activity in mountain forest–steppe of the Okinskoe Plateau.

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