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Geographical Variability of Sexual and Age Structure of Populations and the Life Cycle in *Broscus cephalotes* (Coleoptera, Carabidae)

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Abstract—Seasonal dynamics of the activity, life cycle, and sexual and age structure of *Broscus cephalotes* populations were studied in southwestern Moldova (1990) and northwestern Mordovia (1999–2000). In this species, the dynamics of seasonal activity shows two peaks: in early July and mid-August. In Moldova, the abundance peaks are virtually equal, but in Mordovia, the first peak is twice as high as the second. In both regions, larvae and adult beetles overwinter. Overwintered individuals start breeding earlier than those that did not overwinter. However, the largest and the smallest number of egg per single female were equal in hibernated and nonhibernated beetles. Two seasonal reproductive rhythms were observed in *B. cephalotes*. The rhythm characteristic of individuals that hibernate at the larval stage results in a monovoltine life cycle. Another rhythm, observed in individuals that hibernate at the adult stage, results in a semivoltine (two-year) cycle. Thus, *B. cephalotes* possesses a multiple-path life cycle with summer-autumn reproduction, adult beetles being active in different seasons, and larvae, in spring-summer. The geographical variability of the seasonal activity of *B. cephalotes* is compared with that in other closely related species.

During the last ten years, studies of the ecology of ground beetles (Coleoptera, Carabidae) in various natural and climatic zones has usually been accompanied by a discussion of the age and sexual structure of their populations and also of their life cycles. Most frequently, widespread and ecologically plastic polyzonal species, constituting the nucleus of dominants in natural and anthropogenically damaged ecosystems and also in agrocenoses were used as model objects in these studies (Shishova, 1994; Khotuleva, 1997; Matalin, 1997, 1998; Sharova and Denisova, 1997; Filippov, 2000; Budilov, 2002). At the same time, data on stenotopic species, which frequently form a complex of subdominants in separate biotopes or natural zones, are not less interesting.

Broscus cephalotes L. is a species of this kind. This thermophilous and meso-xerophilous species is spread from Central Europe to western Siberia, preferring exposed landscapes with light, occasionally weakly salted soils (Kempf, 1954; Schjøtz-Christensen, 1965; Górny, 1971; Thiele, 1977; Fedorenko, 1988; Lindroth, 1992b; Bulokhova, 1995).

In forests, most frequently in those of flood-land or secondary nature, it is found only occasionally and is not very abundant (Karpińsky and Makólski, 1954; Arnoldi and Matveev, 1973; Feoktistov, 1979). The high abundance of *B. cephalotes* is characteristic of agrocenoses of East Europe. As a rule, it is a member of a group of species dominating on perennial grasses and cereals (Karpova, 1984; Lövei, 1984; Dushenkov and Chernyakhovskaya, 1989), and also on certain row crops (Karpova, 1984). However, monoculture is more favorable for *B. cephalotes* than crop rotation (Lövel, 1984). In addition, its abundance and part in a complex of dominant species in dry lands is much higher than in overflowed lands (Karpova, 1984; Dushenkov and Chernyakhovskaya, 1989, 1990).

According to Larsson's classification (Larsson, 1939), *B. cephalotes* belongs to monovoltine species with autumn reproduction and overwintering larva. All the subsequent authors accepted this point of view (Górny, 1971; Thiele, 1977; Sharova and Dushenkov, 1979), because it well agreed both with experimental data on development of this species (Kempf, 1954) and with dates of records of its larvae in various biocenoses (Górny, 1971; Dushenkov and Chernyakhovskaya, 1989, 1990). However, some authors directly stated that *B. cephalotes* can also overwinter at the adult stage (Larsen, 1936; Budilov, 2002). Moreover, the data of all, without exception, authors concerning the early beginning of activity of adult *B. cephalotes* (in March–May, depending on particular environmental conditions) is an indirect evidence of the occurrence of hibernating adult beetles (Larsson, 1939; Novák, 1964; Mossakowski, 1970; Górny, 1971; Inyaeva, 1983; Lindroth, 1992b; Turin, 2000; Budilov, 2002).

In the present paper, the dynamics of seasonal activity, sexual and age structure of populations and life cycle of *B. cephalotes*, and geographical variability of these characters in the southern and northern parts of the range are discussed (Dushenkov and Chernyakhovskaya, 1989, 1990).

MATERIALS AND METHODS

The study was based on collections made by the first author in southwestern Moldova (May–October 1990, Roshu Vill., flood-land of Prut River, 45°18′N, 28°12′E), and by the second, in northwestern Mordovia (April–October 1999–2000, Elnikovskii district, flood-lands of the Urkat River, 54°44′N, 43°53′E).

The material was collected and analyzed by a standard method. Beetles were collected in soil traps, i.e., 0.5-l glass jars with a 72-mm trap orifice diameter, 1/3-filled with a 4% formalin solution (Skuhravý, 1970). In Moldova, beetles were collected on the second over-floodland terrace of the Prut River along the banks of Fundul-Roshu Brook, where 40 traps were exposed during the season; in Moldova, traps were placed in a recently abandoned field (30 traps). In both habitats, *B. cephalotes* was among dominant species. A total of 762 specimens were trapped during the entire period of investigation: 427, 169, and 171 beetles in 1990, 1999, and 2000, respectively.

The sexual and age structure of populations was analyzed according to Wallin (1987), with 5 physiological states distinguished in adult males and females: juvenile, immature, generative of the first year of life, generative of the second year of life, and postgenerative individuals. The number of mature eggs was counted in ovarioles of all the generative females. In plotting graphs illustrating the seasonal activity of separate ages, the resulting curves were calculated only for females. This made it possible to distinguish the reproductive periods more precisely.

The dates when larvae were recorded were taken into account in compiling a scheme of the life cycle. For this purpose, 10 soil samples (0.25 × 0.25 × 0.25 m) were taken once a week, using a standard method (Gilyarov, 1965). A total of 188 larvae were caught, including 23, 60, and 105 larvae of the 1st, 2nd, and 3rd instars, respectively.

In comparing the seasonal dynamics of *B. cephalotes* in different parts of the range, the data from previous publications (Larsson, 1939; Novák, 1964; Mossakowski, 1970; Górny, 1971; Inyaeva, 1983; Lindroth, 1992a; Turin, 2000) were represented as monthly records, which permitted a discussion of its geographical variability.

The material was processed statistically with a STATISTICA software package (version 5.5a). In the text, means ± SD are given.

RESULTS

Seasonal Dynamics of Activity, Sexual and Age Structure of the Population and Life Cycle of B. cephalotes in Southwestern Moldova

In southwestern Moldova, *B. cephalotes* is found in soil traps from late May till early September. Two distinct, virtually equal peaks of abundance are revealed in the seasonal dynamics of its activity (Fig. 1). The first somewhat smaller rise in abundance occurs in late June. More than 85% of this peak is accounted for by the activity of overwintered generative adults breeding in this period. During this peak, the sex ratio is close to one (Fig. 1*a*). The largest number of eggs in repeatedly breeding females (8–10 eggs) was recorded in the last ten-day period of June and first ten-day period of July. The average number of eggs per one female was 3.1 ± 2.1.

In the middle of July, the activity noticeably decreases. During this period of time, generative specimens of the second year of life, which finish their breeding, occur together with juvenile and immature beetles that emerged from overwintered larvae in the population of *B. cephalotes*. From the end of July till the middle of August, the second peak of abundance is observed, which is associated with breeding of young adults. The largest number of mature beetles was recorded in early and mid-August, when their fraction in the population was as high as 80–90%. During this period of time, sex ratio was shifted toward males (Fig. 1*b*). At this same time, the largest number of eggs per single female (10–11) was also recorded, with the average number constituting 3.4 ± 2.0. Thus, both the largest and the average number of eggs were virtually the same in females breeding for the first time and females breeding repeatedly. From the beginning of August, postgenerative individuals appear

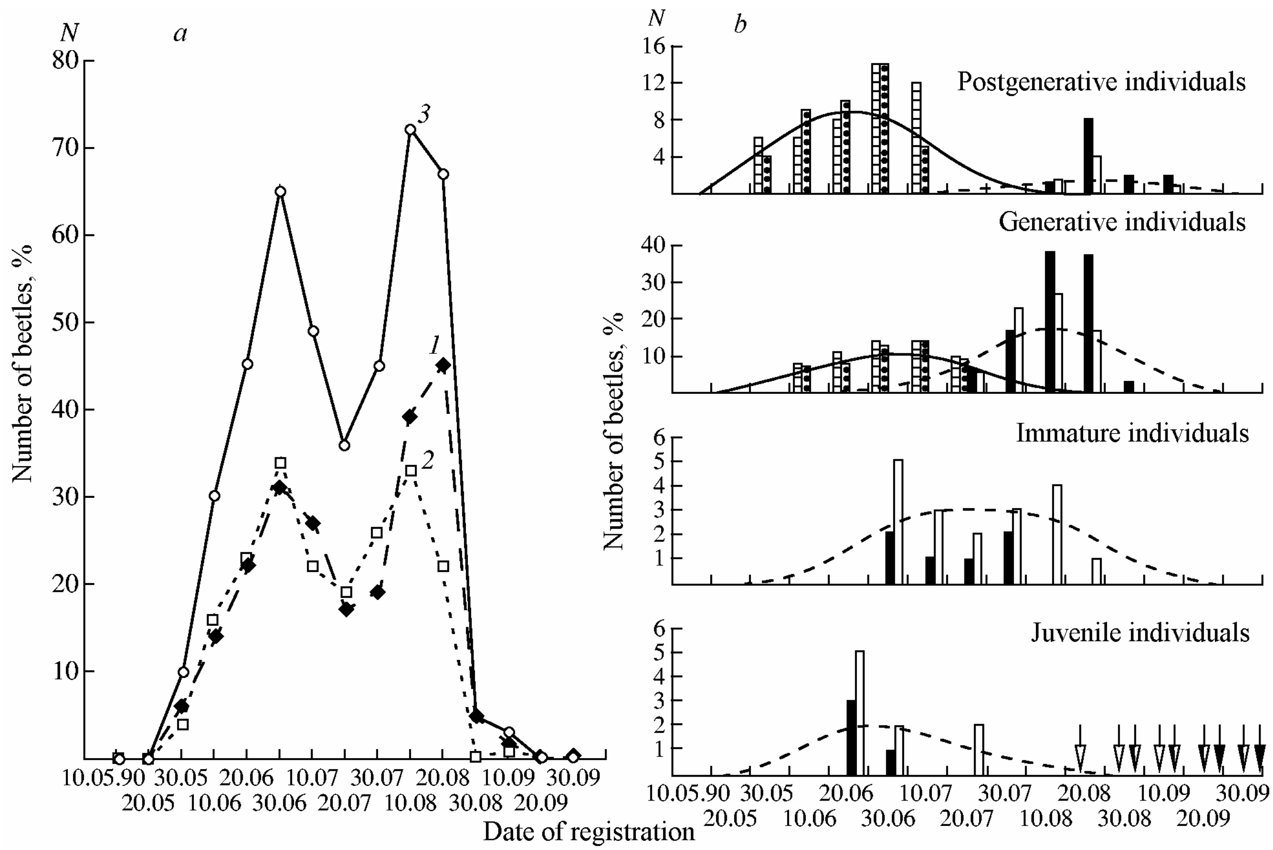

Fig. 1. (*a*) Seasonal dynamics of activity and (*b*) the sexual and age structure of the population of *B. cephalotes* in southwestern Moldova; (a): *1*, males; *2*, females; *3*, total number of specimens; (*b*): columns with horizontal hatching show overwintered males; columns with dotted hatching and continuous lines, overwintered females; white columns and dotted lines, females that did not overwinter; downwards-pointed arrows, larvae beginning wintering process: open, 1st instar larvae; half filled, 2nd instar larvae; filled, 3rd instar larvae.

in the population of *B. cephalotes* again; these specimens are found in the population during the entire period of vegetation. Part of these beetles overwinter and breed in the next season.

Larvae of the 1st instar emerge from mid-August till the beginning of September from eggs laid in June–August; larvae of the 2nd instar are recorded from the end of August till the end of September; and larvae of the 3rd instar, from mid-September till the end of the vegetative period. Further development of larvae of late instars occurs only in the next season, after the winter diapause (Fig. 1*b*).

Thus, two seasonal reproductive rhythms are combined in *B. cephalotes* in southwestern Moldova. One of these is characteristic of specimens wintering at the larval stage. In this case, the developmental cycle from larva to larva is entirely completed during the vegetative period. The second rhythm was found in wintering adults. In this case, the development is longer and lasts for two years. During the first year, it goes rather slowly, because only larvae have time to develop during the vegetative period from eggs laid. Their development finishes after the winter diapause, i.e., during the next season. In such conditions, *B. cephalotes* possesses a multi-path life cycle, because it combines a monovoltine cycle with wintering larvae and a two-year (semivoltine) cycle with wintering postgenerative adults (see Fig. 4).

Seasonal Dynamics of Activity, Age and Sexual Structure of the Population and Life Cycle of B. cephalotes in Northwestern Mordovia

In Mordovia, *B. cephalotes* is active on soil from the beginning of May till the beginning of October. Two peaks of activity also occur in the early–mid-July and early August, with the first peak being twice as high as the second (Figs. 2, 3).

From the middle of May till the middle of June, the population of *B. cephalotes* is represented only by overwintered immature individuals. The first generative beetles appear in the second and third ten-day period of June. About 50–70% of the activity peak

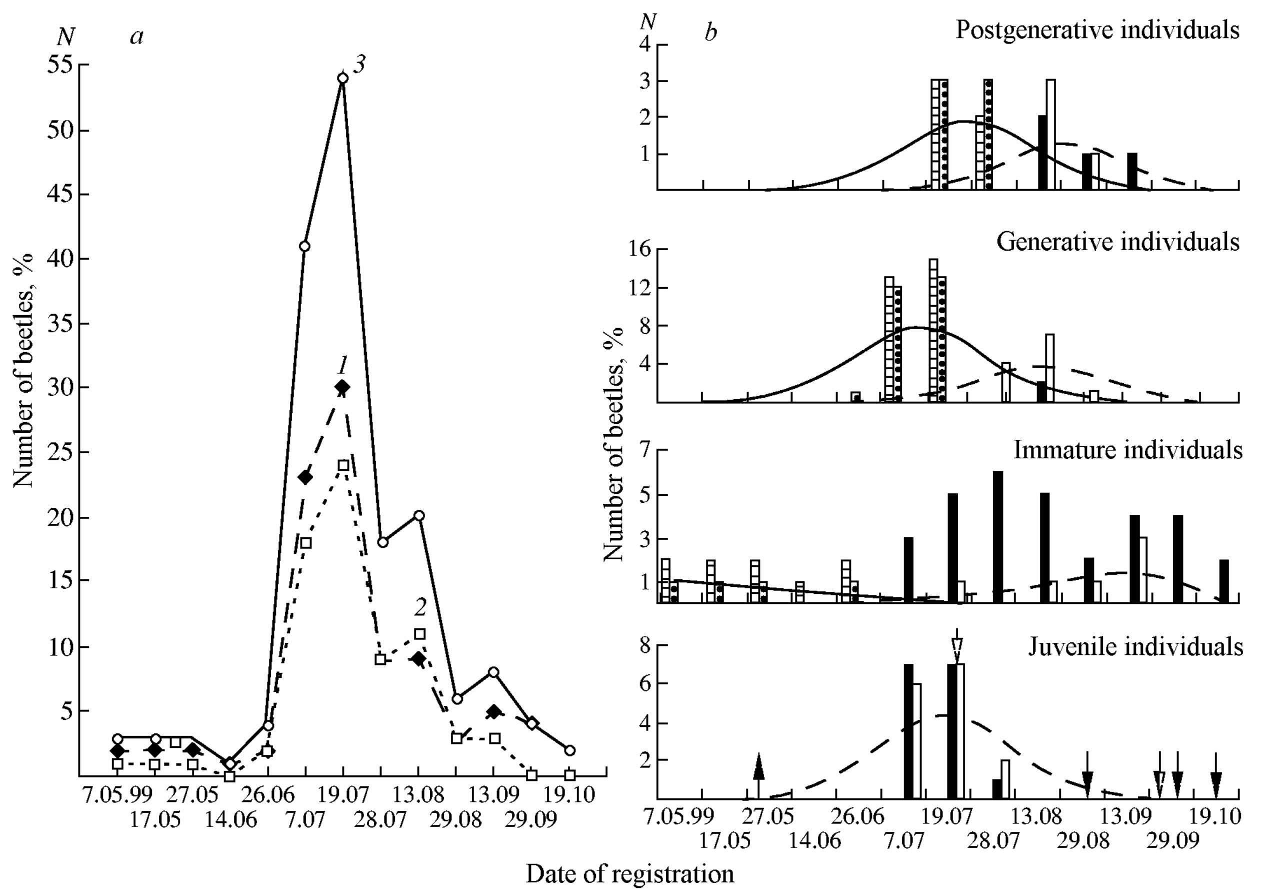

Fig. 2. (*a*) Seasonal dynamics of activity and (*b*) the sexual and age structure of the population of *B. cephalotes* in Mordovia (upwards-pointed arrows indicate 3rd instar larva finishing wintering process. Other designations, as in Fig. 1).

observed in early and mid-July is accounted for just these beetles (Figs. 2*b*, 3*b*). During this period of time, males are trapped twice more frequently than females (Fig. 3*a*). The largest number of eggs in females breeding in this period is 8–10, and their average number 5.0 ± 2.6. In mid-July, the abundance of immature females strongly decreases, and at the end of July, the same occurs with generative females (Figs. 2*b*, 3*b*), which indicates that the reproductive period of overwintered beetles is over.

In spring, from the end of April till the beginning of June, larvae of the 3rd instar are recorded in the population of *B. cephalotes*. The emergence of young adults begins in the mid and late June. After that, in the end of July–beginning of August, the second rise in the abundance of immature beetles is observed, and in the beginning and end of August, also in that of generative ones. This peak was the most pronounced in 2000 (Fig. 3). The largest number of eggs in females breeding in this period (7–11) is observed in the second ten-day period of August. The average number of eggs per female constitutes 5.0 ± 2.6. Thus, the largest and the average amounts of eggs in overwintered immature females, which breed earlier, and in females that emerged from overwintered larvae are equal. Postgenerative individuals are recorded till early–mid-September, but, in contrast to beetles from southern regions, do not survive wintering. At the same time, a part of beetles of the new generation that had no time to breed in the current season, go to wintering

Beginning from late July–early August, larvae of the 1st instar appear in the Mordovian population of *B. cephalotes*. Larvae of the 2nd instar are recorded from the end of August–beginning of September, and larvae of the 3rd instar, from the beginning or middle of September till the end of the vegetative period. Larvae of two last instars go to wintering (Figs. 2*b*, 3*b*).

Thus, a combination of two seasonal reproductive rhythms is also observed in northwestern Mordovia. As in Moldova, *B. cephalotes* possesses a multi-path life cycle that combines a monovoltine development with wintering larvae of late instar, and a two-year-long (semivoltine) cycle with wintering immature adults (Fig. 4).

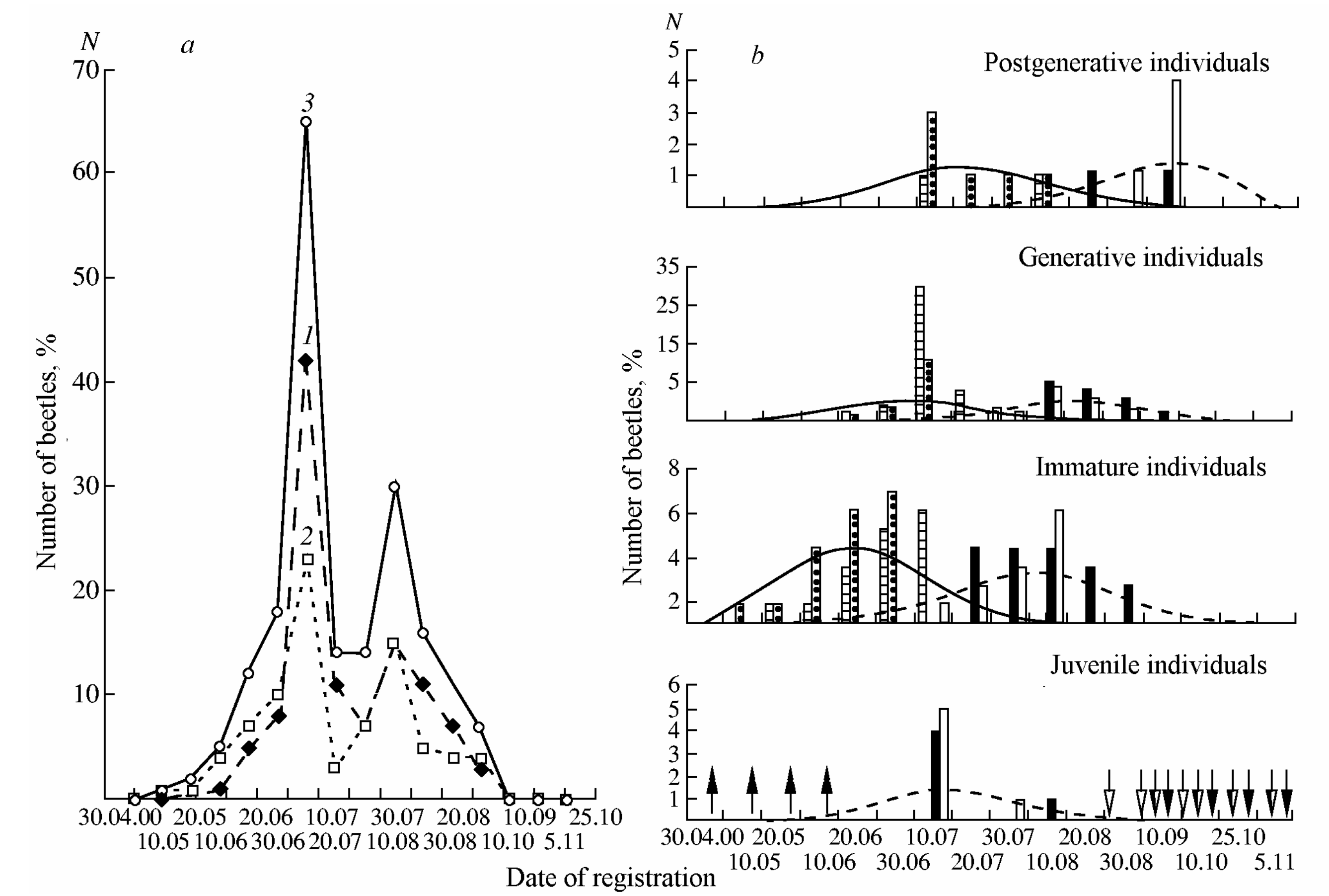

Fig. 3. (*a*) Seasonal dynamics of activity and (*b*) the sexual and age structure of the population of *B. cephalotes* in Mordovia. Designations as in Fig. 1.

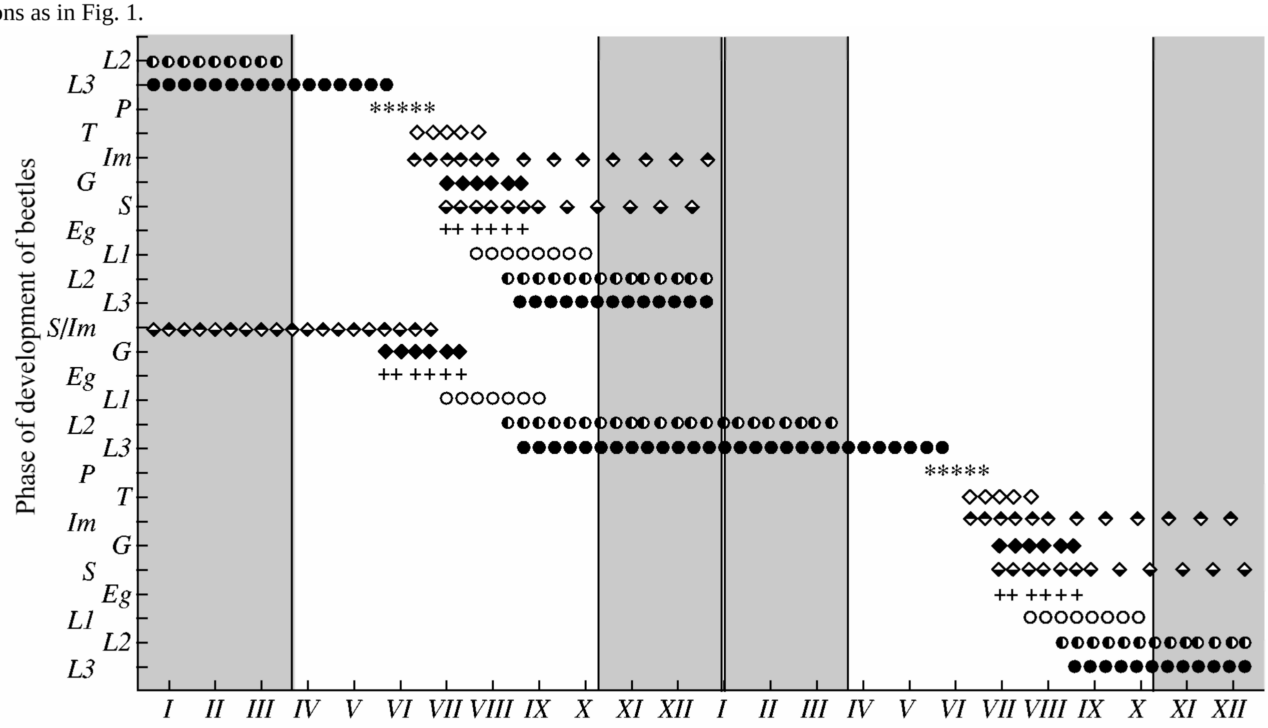

Fig. 4. Scheme of the life cycle of *B. cephalotes*. [*T*, juvenile; *Im*, immature; *G*, generative; *S*, postgenerative adult beetles; *Eg*, egg-laying; *L1*, 1st instar larvae; *L2*, 2nd instar larvae; *L3*, 3rd instar larvae; *P*, pupae; hatched area, period of winter diapause; double vertical line, border between seasons.

Geographical Variability of Seasonal Activity Dynamics, Sexual and Age Structure, and Life Cycle of B. cephalotes

The study revealed some similarities and differences in the seasonal activity and the sexual and age structure of populations of *B. cephalotes* from southern and northern parts of the range. Its life cycle was also described in detail.

Over the entire range, *B. cephalotes* overwinters both at larval and at adult stages. Postgenerative beetles overwinter in southern regions, and immature beetles, in the north. In both cases, overwintered individuals begin breeding earlier than beetles of the new generation. The largest and the average amounts of eggs per female are virtually the same in overwintered specimens and in those that did not hibernate. Overwintered individuals of *B. cephalotes* finish breeding somewhat earlier, by mid-July in southwestern Moldova (Fig. 1*b*) and continue breeding till the end of July in northwestern Mordovia (Fig. 3*b*). The emergence of young adults from overwintered larvae begins in mid-June in southern regions (Fig. 1*b*), and only in early July in northern regions (Figs. 2*b*, 3*b*). In spite of this circumstance, the largest number of generative individuals corresponding to these juvenile adults was observed in early August in both cases. However, the fraction of mature beetles remains very low in the Mordovian population (Figs. 2*b*, 3*b*), being very high in the Moldavian population (Fig. 1*b*).

This phenomenon accounts for the differences in the dynamics of seasonal activity of *B. cephalotes* in southern and northern parts of the range. In both cases, it shows two peaks, one in the end of June–beginning of July and the other in the beginning of August. The first peak of activity is only slightly lower than the second in the south (Fig. 1*a*), being twice as high in the north (Figs. 2*a*, 3*a*). The favorable climatic conditions in the southern regions provide opportunity not only for breeding of all the individuals of the new generation, but also for a repeated reproduction of a significant part of postgenerative beetles after the overwintering. In these conditions, the high abundance of both repeatedly breeding generative beetles and young imagoes breeding for the first time provides their equal participation in breeding and leads to two equal peaks of activity (Fig. 1*a*). In northern regions, by contrast, a significant part of immature individuals of the new generation, which have not enough time for breeding, overwinter, and breed only in the next summer. Just this phenomenon is responsible for the low level of the August peak of activity and high level of the July peak (Figs. 2*a*, 3*a*).

Over the entire range, the life cycle of *B. cephalotes* combines two variants of development: one-year- and two-year-long, thus demonstrating a multi-path development. Wintering larvae of late instars, which have enough time to finish development during the vegetative season, provide the monovoltine variant of the life cycle. Wintering at the stage of imago always results in a semivoltine (two-year-long) life cycle, because a larva can finish its development successfully only after the winter diapause (Fig. 4). The shares of the two described variants of the life cycle vary between different parts of the range. In the south, wintering occurs to the same extent at the larval and adult stages, which points to equilibrium between mono- and semivoltine types of development of *B. cephalotes* in these conditions. The virtually equal abundances of beetles at two peaks of activity, in June and August, confirms this conclusion. (Fig. 1*a*). In northern parts of the range, wintering at the stage of imago and semivoltine (two-year-long) life cycle prevail. This indicated by the fact that the peak of activity in July is twice as high as that in August (Figs. 2*a*, 3*a*).

DISCUSSION

A comparison of the results of preceding studies with the data obtained by the authors revealed main trends in the geographical variability of the seasonal dynamics of activity and the life cycle of *B. cephalotes*.

According to the data of monthly records, only a single peak occurs in the seasonal dynamics of activity of *B. cephalotes* over most part of its range. This peak can be observed in different dates from June to August, depending on a region, season, and biotope. For example, the peak of abundance was recorded in July in the Netherlands (Turin, 2000), Germany (Mossakowski, 1970), Moscow Province (Inyaeva, 1983), and Mordovia (Budilov, 2002), and even in June in Poland (Górny, 1971) and southern Sweden (Lindroth, 1992a) (this, however, can reflect peculiarities of particular seasons). In the north, in Denmark (Larsson, 1939), *B. cephalotes* is the most active in August. By contrast, two peaks of activity (in June and August) are observed in southern regions, such as Czechia (Novák, 1964) and southwestern Moldova (Fig. 5).

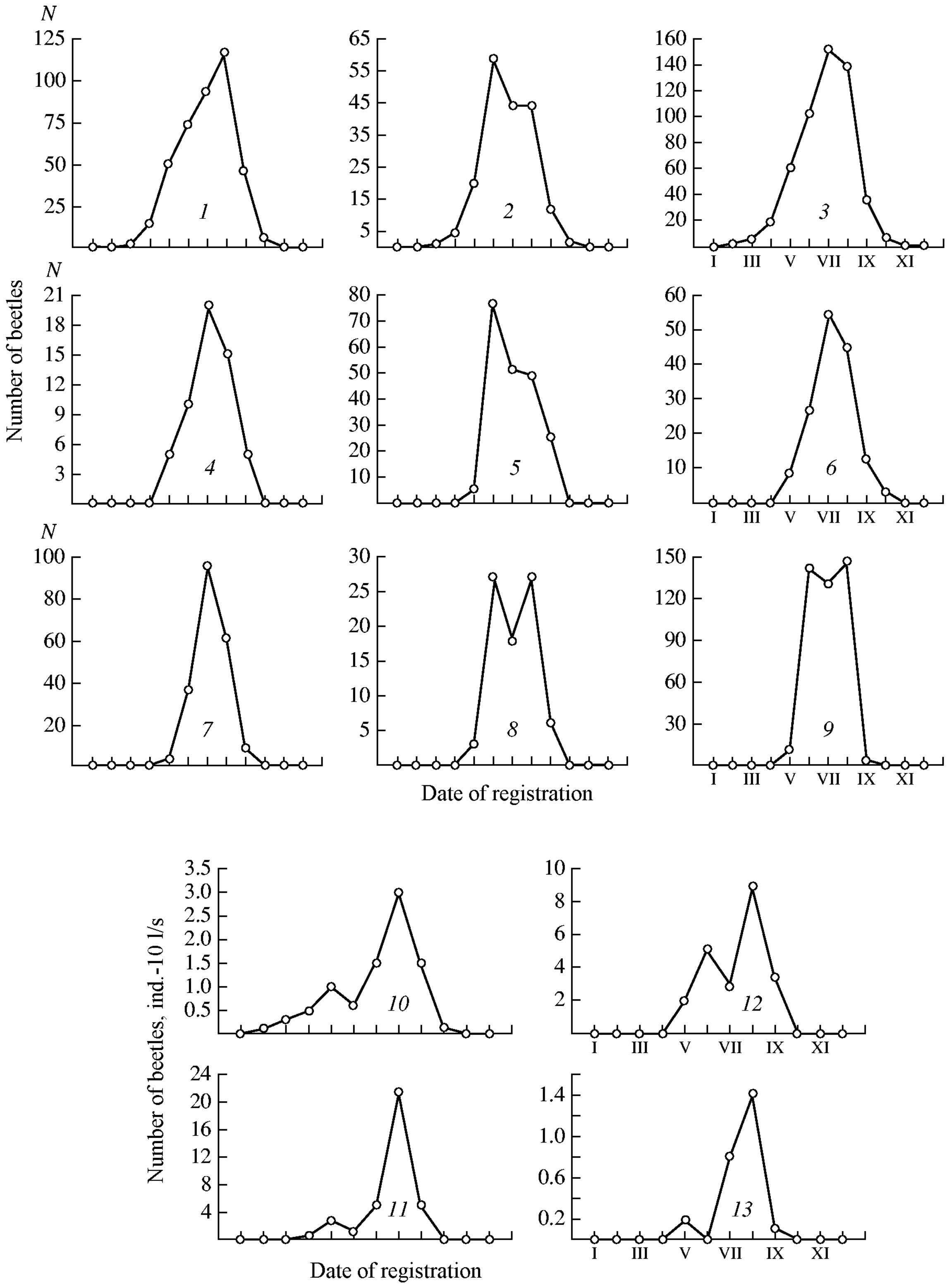

Fig. 5. Seasonal dynamics of activity of *B. cephalotes* (*1–9*) and *B. semistriatus* (*10–13*) in different parts of the range: (*1*) Denmark (Larsson, 1939); (*2*) southern Sweden (Lindroth, 1992a); (*3*) Netherlands (Turin, 2000); (*4*) Germany (Mossakowski, 1970); (*5*) Poland (Górny, 1971); (*6*) Moscow Province (Inyaeva, 1983); (*7*) northwestern Mordovia (1999); (*8*) Czechia (Novák, 1964); (*9*) southwestern Moldova (1990); (*10*) Crimea (Eidelberg, 1989); (*11*) Daghestan (Saipulaeva, 1990); (*12*) Volgograd Province (Karpova, 2001); (*13*) northwestern Kazakhstan (Potapova, 1972).

It is interesting that, according to the data of monthly recordings, the dynamics of activity of a closely related species, *B. semistriatus* Dej., is also characterized by two peaks. For example, they occur in May and August in the Crimea (Eidelberg, 1981), Daghestan (Saipulaeva, 1990), and northwestern Kazakhstan (Potapova, 1972), and in June and August in Volgograd Province (Karpova, 2001). According to Potapova (1972) and Eidelberg (1989), *B. semistriatus* overwinters mainly as larvae. This is also indicated by the August peak of abundance, which is significantly higher than those in May or June (Fig. 5). It is noteworthy that *B. cephalotes* and *B. semistriatus* were long treated as subspecies (Kryzhanovskij, 1983; Sharova and Makarov, 1984), and their species status was reestablished rather recently (Kryzhanovskij *et al.*, 1995) In the north African *B. laevigatus* (Dej.), the reproductive period of young beetles that had emerged from diapausing larvae shifts to even later dates and is observed from November till March. In this species, the diapause is characteristic of exclusively late instar larvae (Paarmann, 1973).

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