

Life Cycles of Carabids of the Genus *Stenolophus* (Coleoptera, Carabidae) in the Steppe Zone of Europe

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Abstract—Peculiarities of life cycles in *Stenolophus* species are discussed based on field experiments performed in SW Moldova. Two life cycle patterns are observed in the European steppes. *S. skrimshiranus* has a monovoltine one-year life cycle with hibernating imago. *S. discophorus*, *S. mixtus*, and *S. persicus* are characterized by a polyvariant bivoltine one-year life cycle; the hibernating stages are imago, older larval instars, and pupa. Preimaginal stages complete development by the beginning of the following vegetation season, without prolongation and subsequent synchronization. This life cycle pattern shows high flexibility with regard to environmental factors. In unfavorable seasons, the development and activity periods of certain stages may be strongly shortened; however, this does not affect the life cycle pattern in general.

During the recent decade, the carabid life cycles have been in the focus of attention of researchers (Neculiseanu, 1990, 1994; Chernyakhovskaya, 1990; Cardenas, 1994; Kegel, 1994; Makarov, 1994; Neculiseanu, 1994). New experimental data (Brandmayer and Goruppi, 1985; Pearson and Knisley, 1985; Butterfield, 1986; Makarov and Chernyakhovskaya, 1990; Matalin, 1993; Luff, 1994; Makarov, 1994; Paarmann, 1994; Schatz, 1994; Matalin, 1996a; Sharova and Denisova, 1996, 1996a) suggest that the previously established views on carabid life cycles in the moderate zone (Larsson, 1939; Briggs, 1965; Van Dijk, 1972; Luff, 1973; Paarmann, 1979) need to be reconsidered. This was largely facilitated by the studies of sex and age structure of carabid populations (Wallin, 1987) and by the concept of the polyvariant nature of life cycles in Carabidae (Makarov, 1990, 1991, 1994).

In the present communication, peculiarities of the life cycles in species belonging to the genus *Stenolophus* Steph. in European steppes are discussed. Species of this genus are characterized by a mixed feeding type and are most abundant in various intrazonal biotopes (Petrusenko and Petrusenko, 1968, 1973; Thiele, 1977; Vasil'eva, 1984; Hieke and Wrase, 1988; Karpova and Matalin, 1991). However, no data on their life cycles have been so far presented in the available literature; only the periods of seasonal or diurnal activity have been reported for some species (Larsson, 1939; Chernyshev, 1961; Belousov, 1986; Karpova and Matalin, 1990; Matalin, 1990, 1994, 1996; Lindroth, 1992).

Our data on the preimaginal development and phenology allowed the life cycles of the species studied to be described in detail for the first time. Some aspects of this work were previously considered by the author (Matalin, 1996a).

MATERIALS AND METHODS

The investigation was performed during the entire vegetation seasons of 1990–1991 in SW Moldova

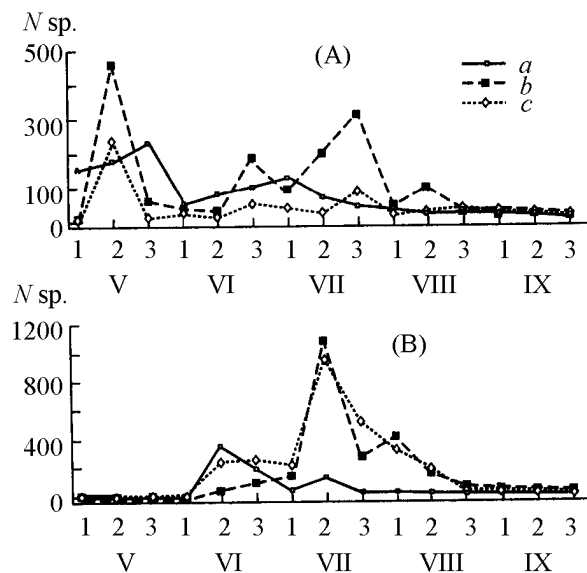


Fig. 1. Seasonal activity dynamics in *Stenolophus* species with spring and spring-summer types of reproduction (combined data for all traps). a—*S. skrimshiranus*; b—*S. discophorus*; c—*S. mixtus*. (A) Data of 1990; (B) data of 1991; 1–3—10-day intervals of a month; V–IX—months.

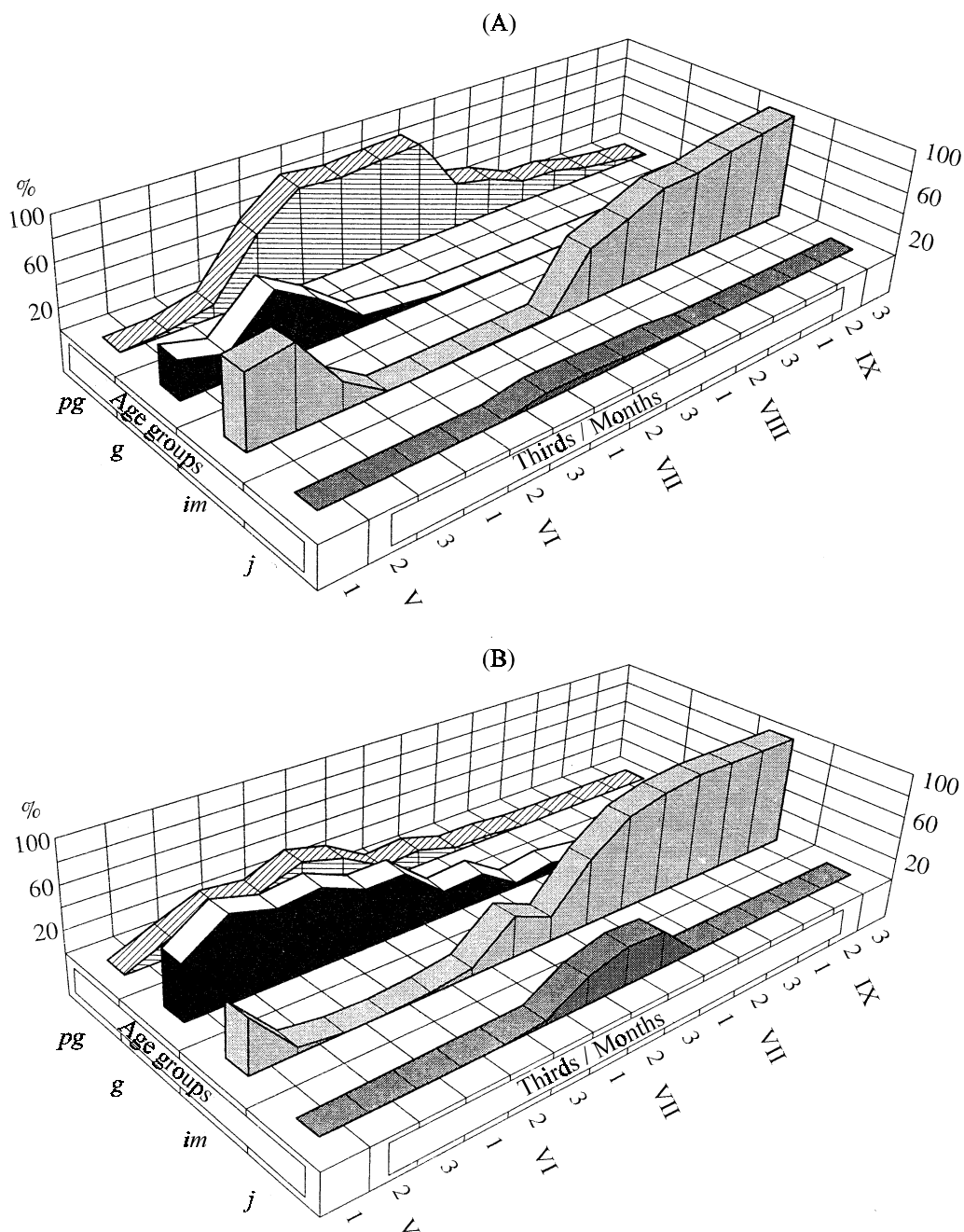


Fig. 2. Age spectrum of populations, % (average for 1990–1991, combined data for all traps). (A) *S. skrimshiranus*; (B) *Anisodactylus signatus*; j—juveniles; im—immatures; g—generatives; pg—postgeneratives; 1–3, 10-day intervals of a month; V–IX, months.

(Prut River floodlands, 2 km N of Kakhul; 45°18' N, 28°12' E). Of the 7 *Stenolophus* species found in the region (Karpova and Matalin, 1993), 4 most abundant species were selected as models: *S. discophorus* F. = W., *S. mixtus* (Herbst), *S. persicus* Mnnh., and *S. skrimshiranus* Steph.

The material was collected using ground and light traps in 3 natural and 2 agricultural biotopes. Ten

ground traps consisting of glass jars with a volume of 0.5 l and an opening diameter of 72 mm (Barber, 1931) were set in each biotope. The light trap consisted of a "Pennsylvania" light source (Frost, 1957) with an original collecting device designed by the author (Matalin, 1992); light traps were set at permanent sites during the entire investigation period. The sex and age spectra of populations were analyzed us-

ing the method proposed by Wallin (1987), allowing one to distinguish 4 imaginal age states for both sexes, judging from the degree of the gonad development: juvenile, immature, generative, and postgenerative. A total of 3187 specimens of *S. discophorus*, 3610 of *S. mixtus*, 220 of *S. persicus*, and 856 of *S. skrimshiranus* were collected and dissected during the investigation.

To monitor the larvae, 10 soil samples (0.25 × 0.25 × 0.25 m) were taken once a week using the standard technique (Gilyarov, 1975). The collected larvae were kept in field cages, allowing the individual development time to be determined. The state of the larvae was checked daily. In addition to larvae, beetles of different species were kept in separate cages, which also allowed one to determine the imaginal and larval development time. In all, observations were made of the development of 4 *S. discophorus* larvae, 14 *S. mixtus* larvae, and 10 *S. persicus* larvae.

The statistical data processing was performed using an IBM PC AT computer.

RESULTS AND DISCUSSION

On the basis of phenological data, the studied species are divided into 2 groups, with spring and spring-summer reproduction. The "spring" species are characterized by high activity in May–June and also in August, whereas the "spring-summer" species are active during the entire vegetation period. The pattern of their seasonal dynamics is characterized by considerable changes of the abundance (Fig. 1).

S. skrimshiranus belongs to the first group. The spring peak of its activity is formed by overwintered immatures whose abundance reaches a maximum by mid-May and decreases afterwards. The oviposition occurs since the beginning of May till the end of June. The maximal abundance of generatives is observed in the end of May–beginning of June; no generatives are found in *S. skrimshiranus* populations since mid-July. Postgeneratives start to appear in the end of May, with the maximal abundance in mid-June–mid-July.

The increased activity in mid-summer–early autumn is associated with emerging beetles of the young generation. First juveniles are found in *S. skrimshiranus* populations since the last third of June. Correspondingly, the abundance of immatures gradually increases starting from mid-July until the end of the vegetation period. The age spectrum of populations prior to hi-

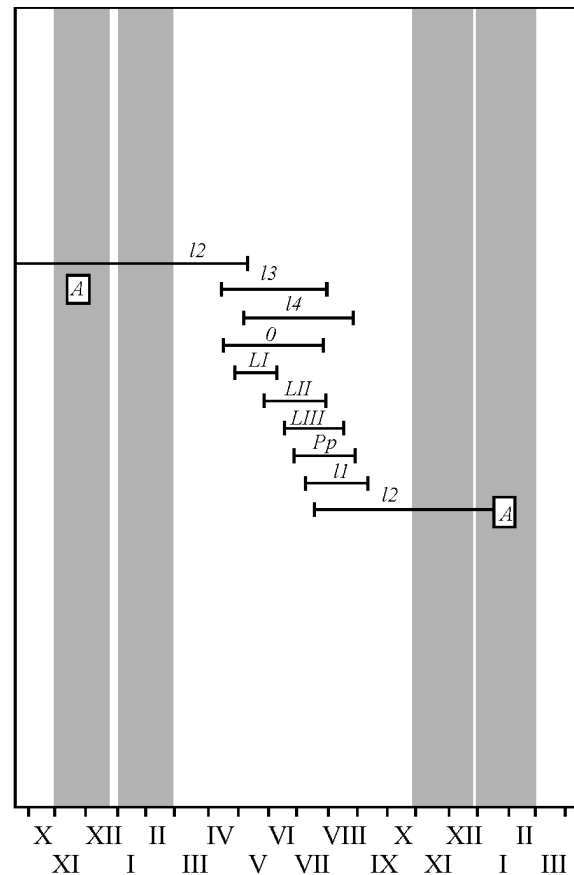


Fig. 3. Diagram of *S. skrimshiranus* life cycle. O—Oviposition period; LI–LIII—larvae of 1st, 2nd, and 3rd instars, respectively; Pp—pupae; I1–I4—juvenile, immature, generative, and postgenerative imagoes, respectively; A—hibernation at the stage of immature imago; shaded area—period of winter temperatures; X–III—months.

bernation includes only immatures of the new generation (Fig. 2A).

Unfortunately, no larvae of *S. skrimshiranus* were collected or reared during the investigation; the trapping data were, therefore, not confirmed by the timing of development of preimaginal stages. However, the seasonal activity dynamics and the sex and age spectrum of *S. skrimshiranus* populations, when compared to the data for other "spring" species (Kasandrova and Sharova, 1971; Karpova and Matalin, 1990a) suggested a similar pattern of their life cycles. In particular, in the steppe zone, similar data were obtained for *Anisodactylus signatus* Panz. (Karpova and Matalin, 1990a) (Fig. 2B).

I instar larvae are found in populations since the beginning of May till mid-June; their molt into II instar is observed since the beginning of June till end of July,

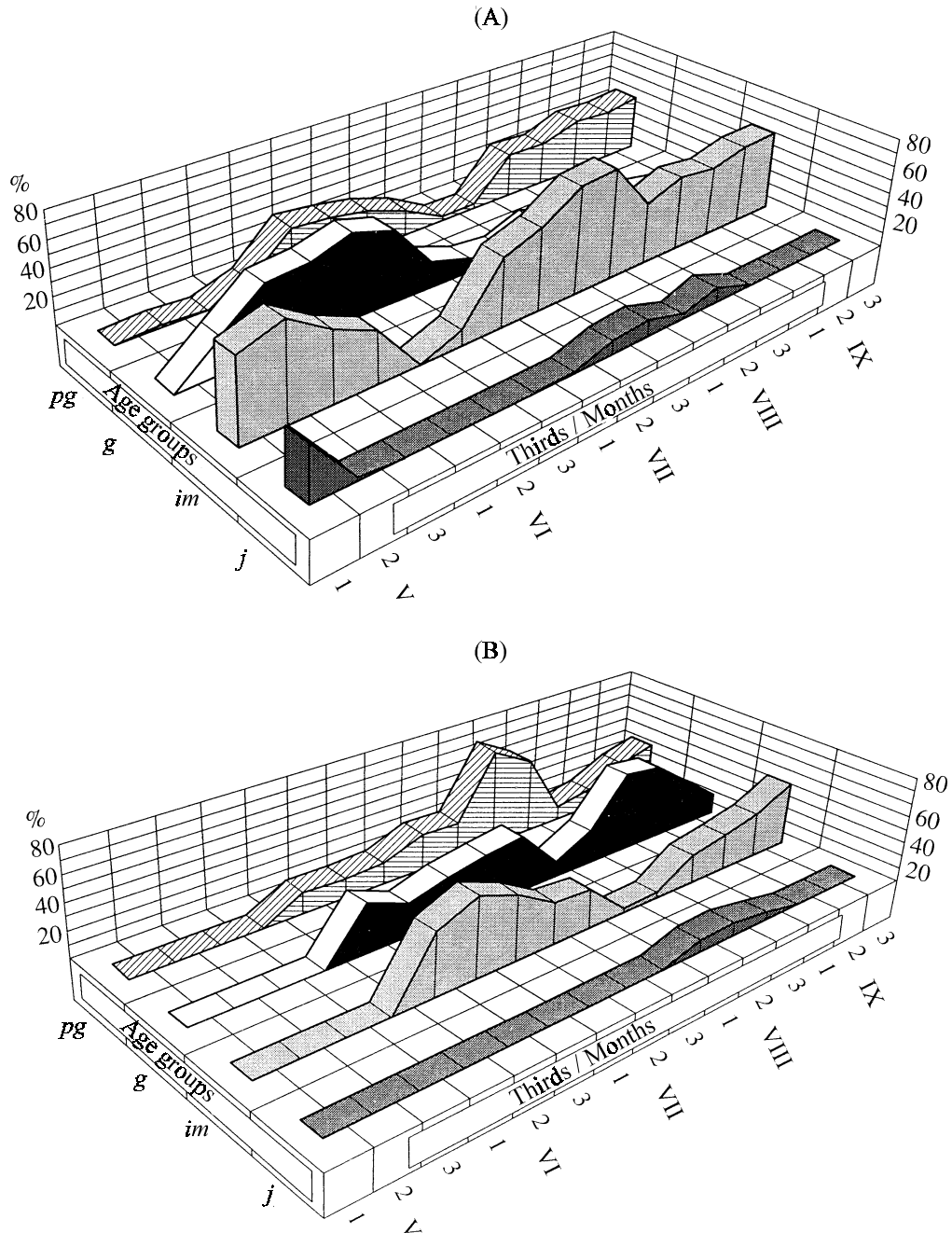


Fig. 4. Age spectrum of *S. discophorus* populations, % (combined data for all traps). *j*—Juveniles; *im*—immatures; *g*—generatives; *pg*—postgeneratives. (A) Data of 1990; (B) data of 1991; 1–3—10-day intervals of a month; V–IX—months.

and into III instar, since the end of June till end of August. Pupation occurs since the beginning of July till beginning of September. Since mid-September, no preimaginal stages are found in populations of these species, which indicates that their development is completed. The only hibernating stage is immature imagoes of the young generation.

In our opinion, *S. skrimshiranus*, like *A. signatus*, has a monovariant monovoltine one-year life cycle, with reproduction in spring and hibernation at the stage of immature imago (Fig. 3).

The group with spring-summer reproduction includes *S. discophorus*, *S. mixtus*, and *S. persicus* (Figs. 4–6).

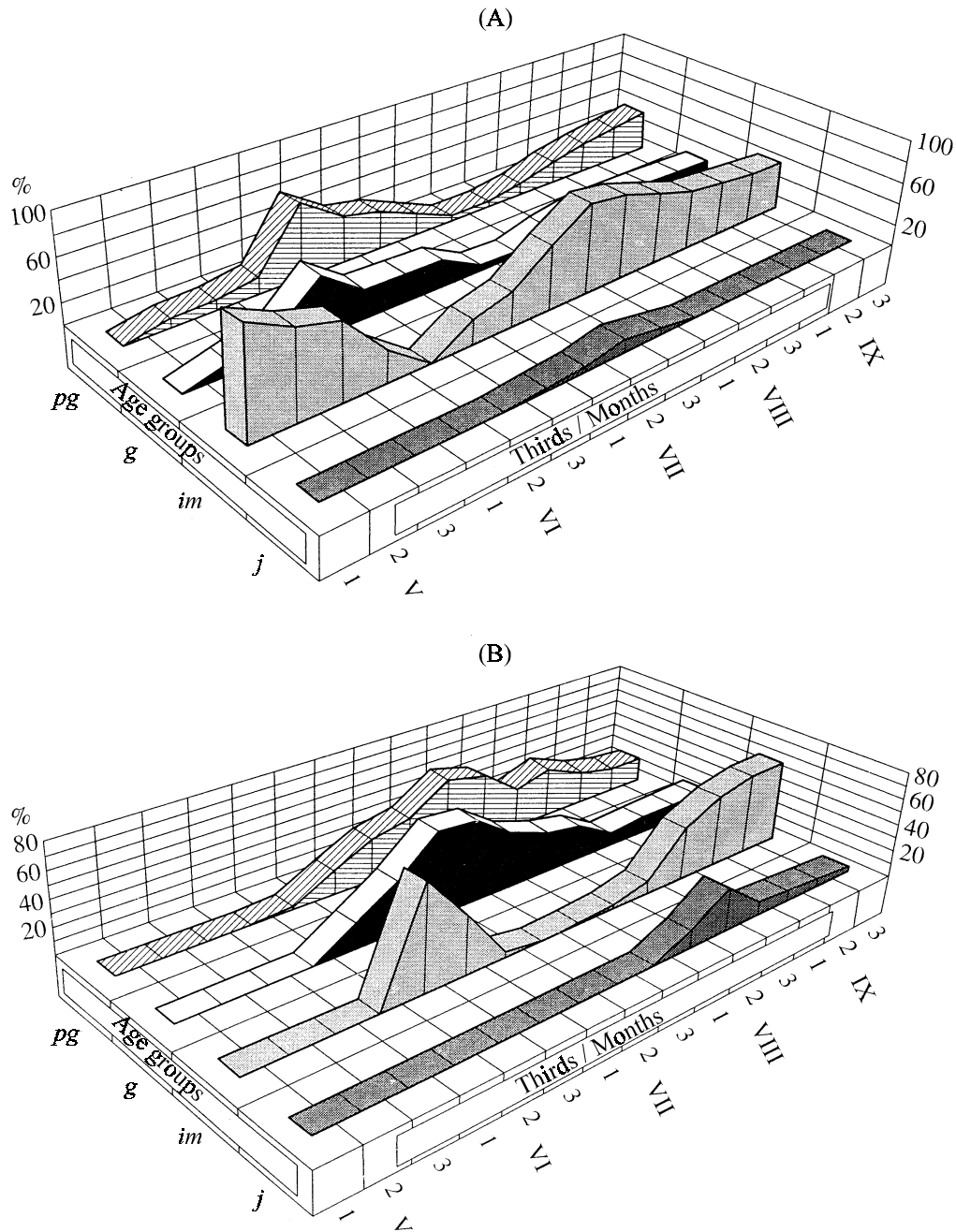


Fig. 5. Age spectrum of *S. mixtus* populations, % (combined data for all traps). Designations as in Fig. 4.

The initial spring activity of these species is due to overwintered immatures, whose abundance reaches the maximum in the beginning and middle of May. It is interesting that in *S. discophorus* populations, juveniles are also observed during this period (Fig. 4A). One may conclude that the hibernating stage in this case can be either the pupa or the older larval instars, because juvenile imagoes are quite vulnerable and hibernation at this stage is almost impossible (Müller,

1985). Therefore, in the beginning of the spring activity (probably as early as April), the preimaginal stages complete development very quickly (Fig. 7A). This is an important feature, because this pattern is exactly opposite to that shown by some *Harpalus* Latr. and *Pseudoophonus* Motch. (Matalin, 1993), characterized by a considerable prolongation and subsequent synchronization of development of overwintered larvae. As a result, development of III instar larvae and

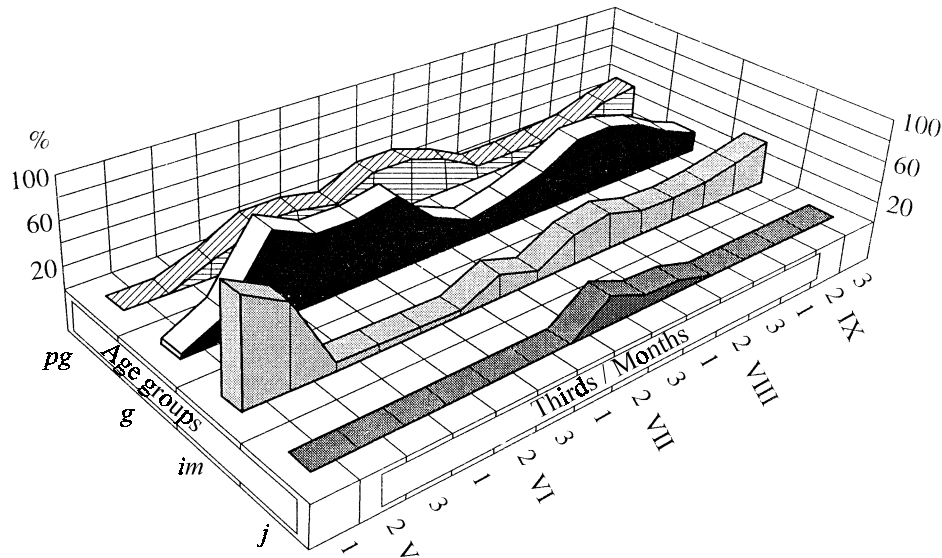


Fig. 6. Age spectrum of *S. persicus* populations, % (combined data for all traps). Designations as in Fig. 2.

pupae may take more than 2.5–3.0 months (Figs. 7B, 7C). Judging from the specific age spectra of the populations (Figs. 5, 6), the preimaginal development in *S. mixtus* and *S. persicus* follows the same pattern as in *S. discophorus*: generatives are found since mid-May with the maximum by mid-June; postgeneratives are observed since the end of May–beginning of June with the maximum in mid-July.

The mass emergence of juveniles of the young generation occurs since mid-July till mid-August, causing the beginning of the autumn rise in abundance. The corresponding peaks of immatures, generatives, and postgeneratives occur in mid-July, mid-August, and the beginning of September, respectively. By the end of the active period, both immatures and generative and postgenerative individuals are represented in populations of these species. However, only immature beetles emerge after hibernation in the following season, whereas generatives and postgeneratives are eliminated during the winter diapause.

The presence of 2 distinct abundance waves for all the 4 age groups of imagoes (Figs. 4–6) makes it possible to conclude that 2 generations appear during a vegetation season; this is also confirmed by the data on larval development. The first wave of larvae is observed since May till July. I instar larvae hatch throughout June; their molt into II instar is observed since the middle third of June till the first third of July, and into III instar, since the last third of June till the

middle third of July. Pupation occurs in July, and emergence of young imagoes is observed since mid-July till mid-August (table, A).

The second wave of larvae is observed in the second half of summer, since July till September. I instar larvae hatch since the last third of July till the middle third of August; the molt into II instar occurs in August, and into III instar, since the last third of August till the first third of September. Pupation takes place in September, and young imagoes emerge since mid-September till the end of the vegetation period (table, B). It should be noted that part of II and III instar larvae and pupae have not enough time to complete development and overwinter; their development is resumed only in April–May of the following season.

It is important to note that the life cycles of the species in question have highly flexible periods of activity, depending on environmental factors. In particular, in 1991, because of continuous rains in May–June, the spring activity period was 1.5 months longer than usual. As a result, the autumn peak was shifted by 10–20 days and considerably shortened. In spite of this, the general patterns of seasonal activity and life cycles of species remained almost unchanged (Figs. 4A; 5A). This fact represents an essential difference between species with spring and spring-summer types of reproduction, since life cycles of “spring” species are more constant.

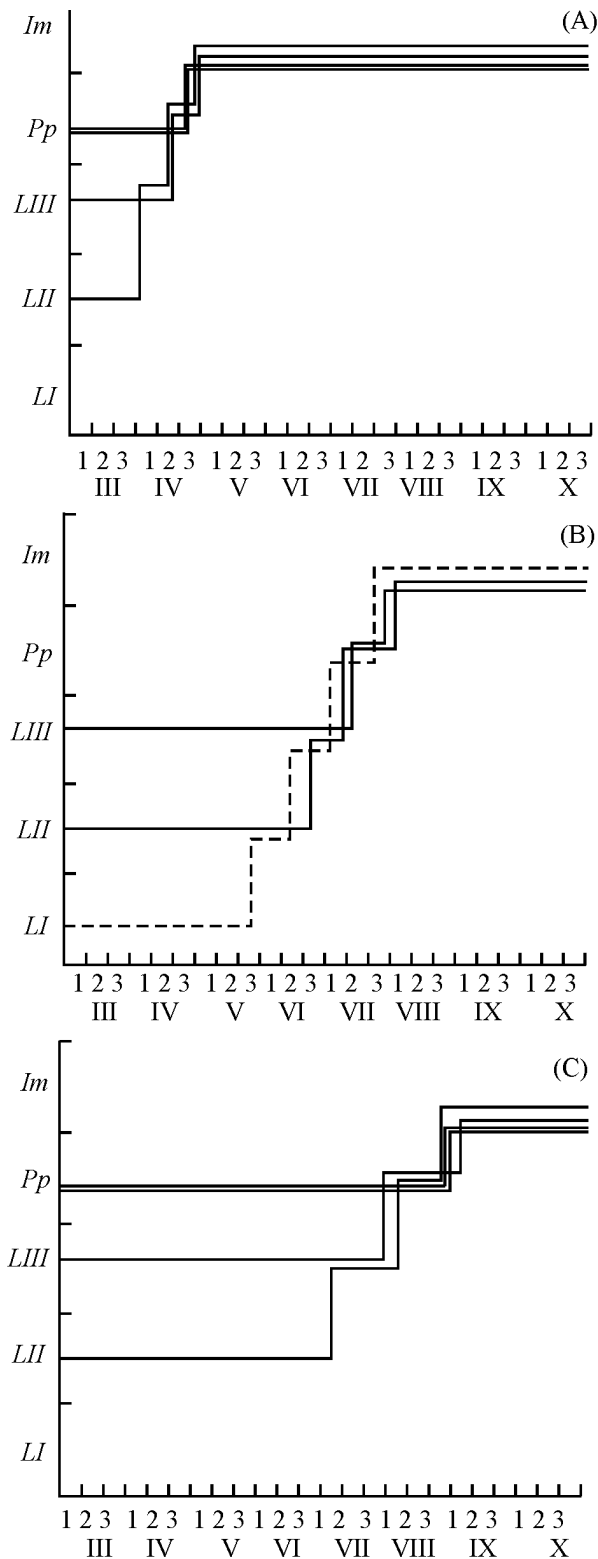


Fig. 7. Development of hibernated larvae. (A) *Stenolophus discophorus*; (B) *Harpalus (Pseudoophonus) rufipes*; (C) *Harpalus (s. str.) affinis*. LI-LIII—Larvae of 1st, 2nd, and 3rd instars, respectively; Pp—pupae; Im—imagoes; 1-3, 10-day intervals of a month; III-IX, months.

In general, *S. discophorus*, *S. mixtus*, and *S. persicus* in the steppe zone of Europe are characterized by polyvariant bivoltine one-year life cycles, with spring-summer reproduction and hibernation at the stages of immature imagoes and older larval instars, and without synchronization of development of the latter (Fig. 8).

However, occurrence of 2 generations during one season is possible only under favorable conditions, e.g., at a long vegetation period. Under less favorable conditions of Middle and N Europe, the life cycles of these species follow the monovoltine variant. This is true, in particular, for *S. mixtus* in Ryazan and Moscow Provinces (author's unpublished data). In this case, the life cycle is facultatively bivoltine, which is a not unusual phenomenon in carabids (Paarmann, 1976; Krechan, 1970; Bauer, 1974; Makarov and Chernyakhovskaya, 1990).

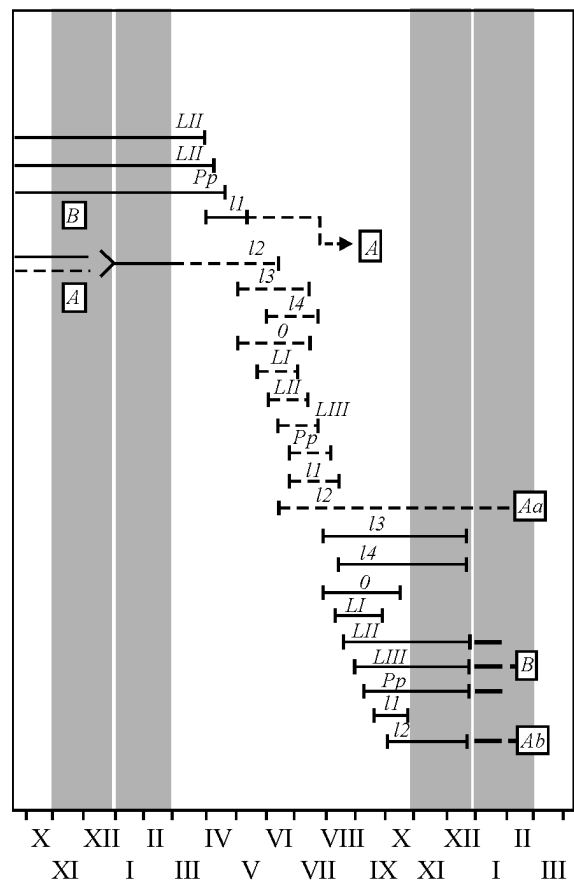


Fig. 8. Diagram of *S. discophorus*, *S. mixtus*, and *S. persicus* life cycles. O—Oviposition period; LI-LIII—larvae of 1st, 2nd, and 3rd instars, respectively; Pp—pupae; II-I4—juvenile, immature, generative, and postgenerative imagoes, respectively; A—hibernation at the stage of immature imago; Aa—first generation; Ab—second generation; B—hibernation at the stage of older larval instars; shaded area—period of winter diapause; X-III—months.

Average larval development time (days) of *Stenolophus* species with a spring-summer type of reproduction

Species	Larval instars			Pupae
	I	II	III	
A. First generation				
<i>S. discophorus</i>	6.0 ± 1.4*	—**	—	—
<i>S. mixtus</i>	7.0 ± 1.5	10.0 ± 1.6	12.4 ± 1.1	10.8 ± 1.3
<i>S. persicus</i>	5.0 ± 2.8	9.8 ± 0.8	12.1 ± 1.9	11.6 ± 1.9
B. Second generation				
<i>S. discophorus</i>	10.0 ± 1.4	—	—	—
<i>S. mixtus</i>	7.5 ± 4.9	11.0 ± 1.4	18.0 ± 0.3	12.0 ± 0.5
<i>S. persicus</i>	10.5 ± 2.1	12.0 ± 1.4	15.5 ± 0.7	9.5 ± 0.7

* Standard deviation.

** No data.

Thus, species of the genus *Stenolophus* in European steppes typically possess 2 patterns of life cycles: a monovoltine, one-year cycle of “spring” species with hibernating imago, and a polyvariant, bivoltine, one-year cycle of “spring-summer” species. The latter is characterized by hibernation at such stages as imago and also older larval instars and pupa. The preimaginal stages complete development in the beginning of the following vegetation season, without prolongation and subsequent synchronization. In addition, this cycle is highly flexible with regard to environmental factors. In unfavorable seasons, the activity periods of certain developmental stages may be strongly shortened; however, this does not affect the life cycle pattern in general.

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