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Altitudinal Variation of the Life Cycle of *Poecilus fortipes* (Coleoptera, Carabidae) in Eastern Siberia

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Abstract—Altitudinal variation of the demographic structure of populations of *Poecilus fortipes* (Chaud.) was studied in four mountain localities in the south of Eastern Siberia, and the life cycle of the species was reconstructed for each locality. The size of adults of both sexes decreased along the altitudinal gradient: the beetles from the Selenga middle mountains (600–650 m above sea level) were much larger, while those at the upper boundary of the forest-steppe belt in the Eastern Sayan (1500–1700 m asl) were smaller than others. Their linear dimensions decreased more distinctly in the transitional zone between middle and high mountains. The duration of the reproductive period did not depend on the altitude. However, the onset of oviposition shifted along the altitudinal gradient to the beginning of the vegetation season, due to its shortening and a decrease in the sum of effective temperatures. As the altitude increased, the mean number of eggs per female declined significantly from 15.9 ± 6.1 to 8.6 ± 5.8, whereas the maximum number of eggs increased from 26–28 to 40–43. On the contrary, the dates of emergence shifted gradually from the beginning and middle of the vegetation period to its middle and end. Populations from the Selenga middle mountains, the Vitim Plateau, and the lower margin of the forest-steppe belt in the Eastern Sayan mountains were characterized by a relatively low catch index and the absence of rebreeding old individuals, both these features increasing the risk of spontaneous local extinction. The annual life cycle with summer breeding was replaced along the altitudinal gradient with an obligate biennial life cycle with summer and early-summer breeding. This transition was observed as the altitude increased from 600–650 to 900–950 m asl while the sum of effective temperatures dropped below 1400°C, i.e., the value needed for implementation of the annual life cycle.

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In the last 30 years, latitudinal variation of life cycles of Carabidae was described in detail (Paarmann, 1979; Sharova and Dushenkov, 1979; Andersen, 1984; Sharova, 1990; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Matalin, 2006; Filippov, 2006a, 2006b, etc.); variation of the demographic composition of populations of some species along the altitudinal gradient was studied in the mountain systems of Europe (De Zordo, 1979; Brandmayr and Zetto Brandmayr, 1986; Butterfild, 1986, 1996; Refseth, 1988; Sparks et al., 1995), South Siberia (Sharova and Khobrakova, 2005), and Japan (Sota, 1986, 1987, 1996). These studies allowed the researchers to characterize the reproductive strategies of some species in different parts of their ranges (Paarmann, 1976; Thiele, 1977; Jørum, 1980; Refseth, 1980, 1984, 1986; Müller, 1987; Weber and Klener, 1987; Korobeinikov, 1991; Sota, 1996; Matalin, 1997, 1998; Filippov, 2008, etc.) and to summarize the data on the realization of life cycles of ground beetles in the Western Palaearctic (Matalin, 2007, 2012).

This communication is devoted to the altitude-related changes in the sex and age composition of local populations of one of the common Siberian ground beetle species, *Poecilus fortipes* (Chaudoir, 1850), and to the realization of its life cycle. In the South of Siberia and the Russian Far East, this species inhabits steppe, meadow, and forest communities (Shilenkov, 1978; Khobrakova and Sharova, 2004, 2005; Eremeeva and Efimov, 2006; Ivanov and Dudko, 2006; Khobrakova, 2006, 2008; Averinskii et al., 2008; Rogatnykh, 2008; Lyubechanskii, 2009; Moroldoev and Khobrakova, 2010a, 2010b; Bespalov, 2011; Pankratov, 2011) as well as anthropogenically modified landscapes: barren lands (Shilenkov, 1978), fallow lands (Lapshin and Lapshin, 1978), and city dumps (Filip-

Table 1. The climatic conditions of the localities studied

Field station locality	Air temperature, °C				Mean precipitation, mm	Total solar radiation, kcals/cm^2	Sum of effective temperatures, °C	Timing and duration of vegetation season
	mean		absolute					
	January	July	max	min				
Selenga middle mountains (600–650 m above sea level)	–22 ... –27	18–20	40	–53	200–250	106	1800	2.V–26.IX 147 days
Vitim Plateau (900–950 m)	–24 ... –26	16–18	35	–57	300–350	106	1400	12.V–15.IX 126 days
Eastern Sayan, lower forest-steppe belt (1300–1400 m)	–22 ... –24	14–16	31	–55	350–400	110	841	23.V–10.IX 110 days
Eastern Sayan, upper forest-steppe belt (1500–1700 m)	–20 ... –22	12–10	28	–54	400–500	>110	600	30.V–10.IX 100 days

pov and Khobrakova, 2005; Khobrakova and Filippov, 2007). Within most of its distribution range, *P. fortipes* belongs to the dominant ground beetle communities in different variants of forest-steppes. In South Siberia, this beetle can be found in the vast under-mountain depressions, extending into the mountain boreal forest along the south-facing slopes. In the latter case, *P. fortipes* often acts as a superdominant in the peculiar mountain forest-steppes of the Eastern Sayan, the so-called uburs (Garmazhapov and Baskhaeva, 2002; Khobrakova and Sharova, 2004).

MATERIALS AND METHODS

The material was collected by the first author at four seasonal field stations:

(1) The Selenga mid-altitude mountain area, the Kuitunka River valley, forb-grass meadow steppe, 600–650 meters above sea level (m asl), May–September 2007;

(2) The Vitim Plateau, Eravninskaya [=Sosnoozerskaya] depression, the Indola River valley, meadow steppe, 900–950 m asl, May–September 2004;

(3) The Eastern Sayan (the lower forest-steppe belt), the Oka Plateau, the Oka River valley, light forb larch-birch forest, 1300–1400 m asl, June–September 2005;

(4) The Eastern Sayan (the upper forest-steppe belt), Belskie goltzi area, the Ekhe-Kheregte River valley, mountain forb-grass meadow steppe, 1500–1700 m asl, May–September 2001.

The four field stations were considerably different in their temperature regime, precipitation, total solar radiation, and the duration of the vegetation season (Table 1; *Atlas of the Transbaikalia…*, 1967; *Atlas of the Republic of Buryatia*, 2000).

The beetles were collected in soil traps made of 200-ml plastic beakers with the upper diameter 75 mm, filled with 4% formalin solution to 1/2 of their volume. Ten traps were placed in each biotope; the material was removed from them every 10 days. The total body length was measured in all the specimens collected, from the anterior margin of the labrum to the apical margin of the elytra, using an eyepiece micrometer. The sex ratio index (I_s) was calculated by the formula $I_s = (f - m)/(f + m)$, where f is the number of females and m is the number of males (Šustek, 1984). The reproductive state of adult beetles of both sexes was assessed by the method of Wallin (1987). The life cycle was reconstructed based on the seasonal dynamics of activity, timing of reproduction, quantitative parameters of egg production, and the occurrence of larvae, and was classified according to the system by Matalin (2007).

The data were statistically processed using the Statistica 8.0 software. The resulting curves for the diagrams illustrating the seasonal activity dynamics of the tenerale and reproducing females were drawn by the weighted least-squares method. The significance of differences between samples was determined by the Mann–Whitney U-test and the Kruskal–Wallis H-test for independent variables, with a 95% confidence interval (Borovikov, 2001).

RESULTS

In the Selenga mid-altitude mountain area, the population of *P. fortipes* occupying a floodland patch of a forb-grass meadow steppe was found to be relatively sparse: only 209 beetles were captured during the study period. The sex ratio was even ($I_s = 0.005$), whereas the mean size of the males and females was the same: 14.7 ± 0.5 mm.

The period of epigeic activity lasted from the end of May to the beginning of August and was characterized by two waves of the catch index (Fig. 1*a*). The first wave, recorded at the beginning of June, was related to the activity of the immature and teneral beetles that developed from the overwintered larvae. The second wave, composed of two peaks recorded in the first two decades of July and at the beginning of August, was determined by the activity of immature and mature individuals. An abrupt drop in the number of individuals recorded during the third decade of July and the subsequent increase during the first decade of August almost to the mid-July level (Fig. 1*b*) reflect the influence of local weather factors. The reproductive period started in the middle of June and lasted until the beginning of August. Both the maximum absolute number of eggs (28) and the maximum mean number of eggs per female (22.4 ± 5.6) were recorded in the first decade of July (Table 2). The eggs laid during this period developed into wintering larvae. Spent adults were recorded at the end of June and in mid-July; however, since they constituted a very small fraction (less than 2% of the total number) and were completely absent in the samples during the first half of the vegetation season, this population can be regarded as monocyclic. Based on the regular change from teneral adults to immature and then to mature ones, the life cycle of *P. fortipes* in the Selenga mid-altitude mountains can be interpreted as annual with reproduction in summer (Fig. 5*a*).

The population of *P. fortipes* studied on the Vitim Plateau was also characterized by low abundance: the total capture for the season barely exceeded 300 ind., with a slight prevalence of males ($I_s = -0.1$). The mean size of the females was 14.2 ± 0.8 mm, that of males, 14.0 ± 0.7 mm.

Epigeic activity was recorded from the third decade of May to the third decade of August. The seasonal dynamics of abundance revealed a distinct wave limited by three decades, with a peak at the end of June (Fig. 2*a*), when the population mostly consisted of overwintered mature adults. The period of oviposition lasted from the beginning of June to the end of July (Fig. 2*b*). Both the maximum absolute number of eggs (33) and the greatest mean number of eggs per female (15.1 ± 7.7) were recorded in the second decade of June (Table 2). A minor wave of abundance recorded in late July–early August was related to the activity of spent individuals that had finished reproduction, and of immature ones that had developed from the overwintered larvae. The appearance of the latter cohort corresponded to the presence of teneral adults in the samples of the first decade of July. It should be noted that these adults hibernated without reproducing in the same season. The spent adults occurred in samples from the second decade of June to the third decade of August, reaching the maximum abundance in the third decade of July. However, since they were not recorded at the beginning of the active period, their repeated breeding was hardly possible. Based on the data obtained, the life cycle of *P. fortipes* under the Vitim Plateau conditions can be characterized as obligate biennial with reproduction in early summer (Fig. 5*b*).

The material collected in the lower forest-steppe belt of the Eastern Sayan included 335 individuals, with an almost 1.5-fold prevalence of males ($I_s = -0.16$). The mean size of females was 14.1 ± 1.1 mm, that of males, 13.8 ± 0.9 mm.

The beetles were active from the second decade of June to the third decade of August (Fig. 3*a*). According to the decade survey data, their abundance remained almost at the same level from the end of June to the beginning of August, with small fluctuations. In our opinion, this fact can be explained by convergence and partial overlap of the periods of activity of individuals which overwintered at different phases of development. Between the third decade of June and the third decade of July, the population was mostly represented by overwintered immature and mature beetles. The period of oviposition lasted for 6 decades, from the end of June to the middle of August (Fig. 3*b*). The maximum number of eggs in one female (43) was recorded in the second decade of July, the mean number being 22.4 ± 9.7 (Table 2). Spent individuals were recorded only in the third decade of July and the second decade of August; their fraction was very small (barely exceeding 5%), so that the population studied can be regarded as monocyclic. Teneral and immature individuals which developed from overwintered larvae were recorded in the population from mid-July to mid-August. The peak of their abundance was

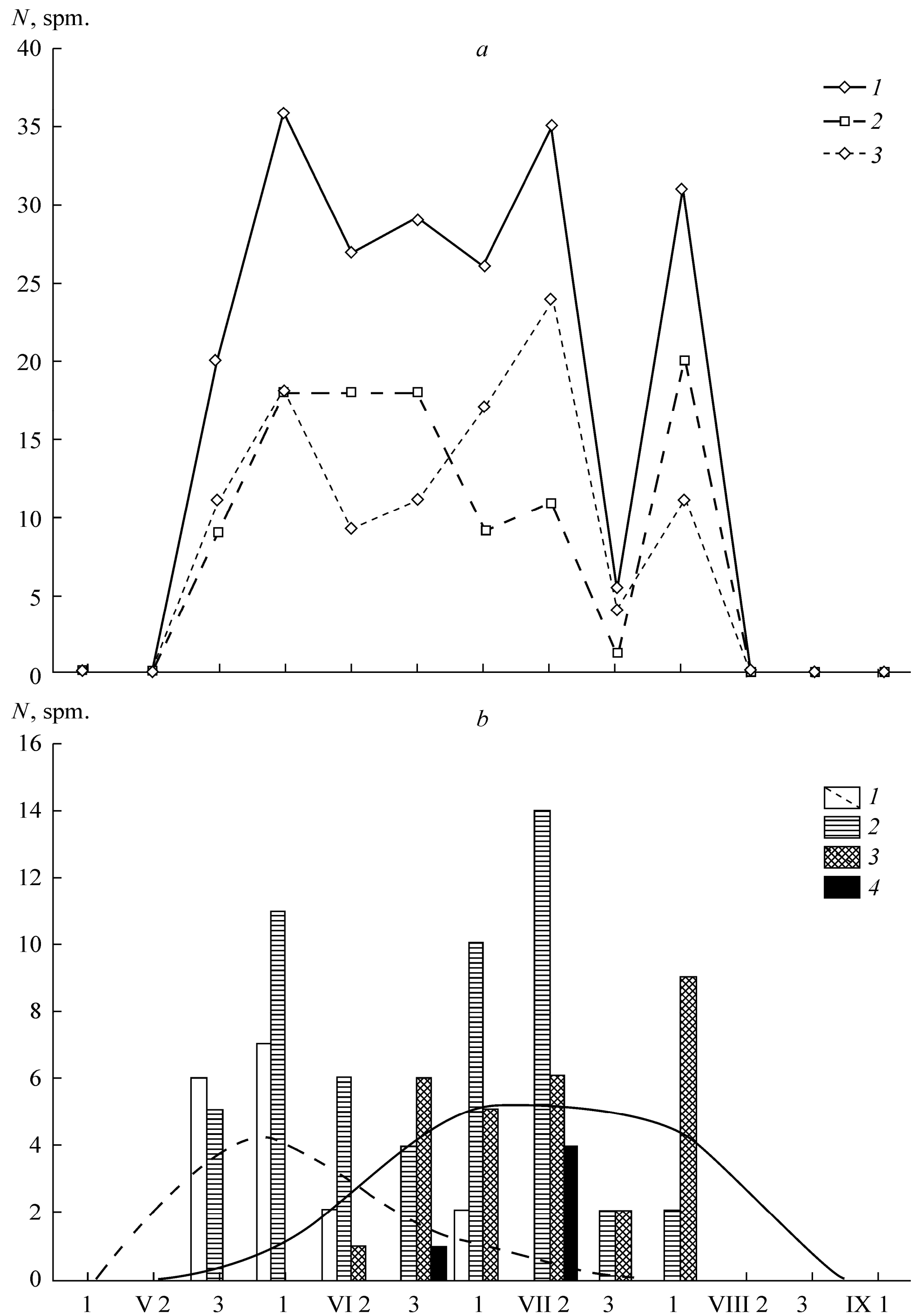

Fig. 1. Seasonal dynamics of activity (*a*) and the demographic spectrum of the population of *Poecilus fortipes* (females only) (*b*) in the Selenga mid-altitude mountain area; *a*: *1*, all individuals; *2*, males; *3*, females; *b*: *1*, teneral; *2*, immature; *3*, mature; *4*, spent; the resulting curves are shown only for the teneral and mature individuals.

observed in the first decade of August against the background of declining reproductive activity of the overwintered beetles. Thus, in the lower forest-steppe belt of the Eastern Sayan, *P. fortipes* has an obligate biennial life cycle with reproduction in summer (Fig. 5*c*).

The highest abundance of *P. fortipes* was observed in the upper forest-steppe belt (the uburs) of the Eastern Sayan where 1960 individuals were captured. The catch index of the species was 6–9 times as great as in the other model populations, with a more than 1.5-fold prevalence of females ($I_s = 0.25$). The mean size

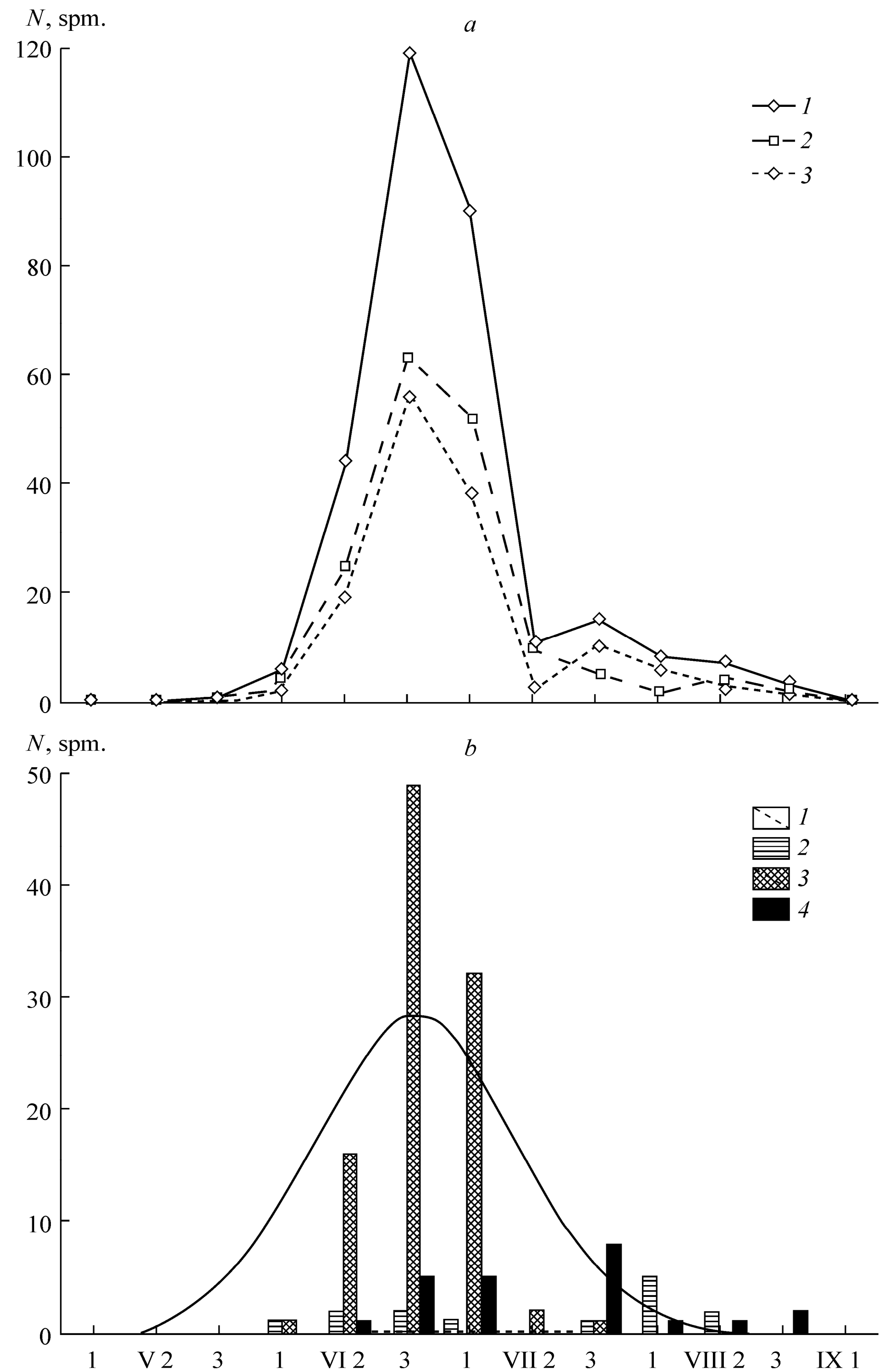

Fig. 2. Seasonal dynamics of activity (*a*) and the demographic spectrum of the population of *Poecilus fortipes* (females only) (*b*) on the Vitim Plateau. For designations, see Fig. 1.

of females was 13.0 ± 0.3 mm, that of males, 11.9 ± 0.5 mm.

The period of epigeic activity lasted from the third decade of May to the first decade of September. Two waves of the catch index were recorded during the season (Fig. 4*a*). The first, more pronounced wave was observed in late June–early July and was determined by the activity of overwintered immature and spent individuals which started laying eggs simultaneously at the beginning of June. The maximum abundance of mature individuals was recorded in the third decade of June; the reproductive period ended late in July

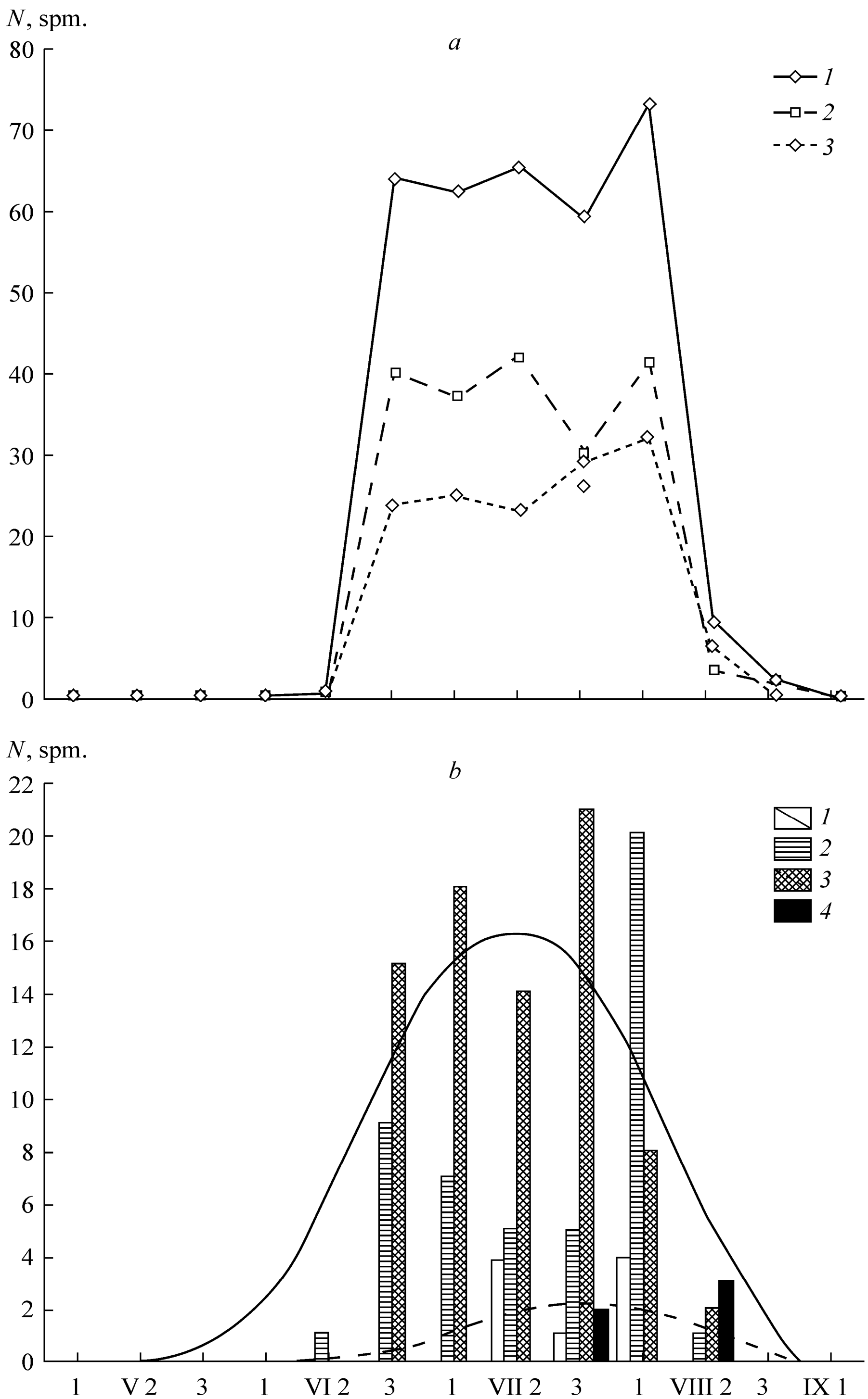

Fig. 3. Seasonal dynamics of activity (*a*) and the demographic spectrum of the population of *Poecilus fortipes* (females only) (*b*) in the lower forest-steppe belt of the Eastern Sayan. For designations, see Fig. 1.

(Fig. 4*b*). The greatest mean number of eggs per female was observed in the second and third decades of June (9.8 ± 5.1 and 9.8 ± 6.5, respectively), whereas the maximum number of eggs in one female (40) was also recorded in the third decade of June (Table 2). Larvae of the II instar were recorded from the third decade of July to the third decade of August, and those of the III instar, from the first decade of August to the first decade of September. Teneral beetles, whose appearance marked the end of development of the overwintered larvae, were captured from the third decade of June to the third decade of July.

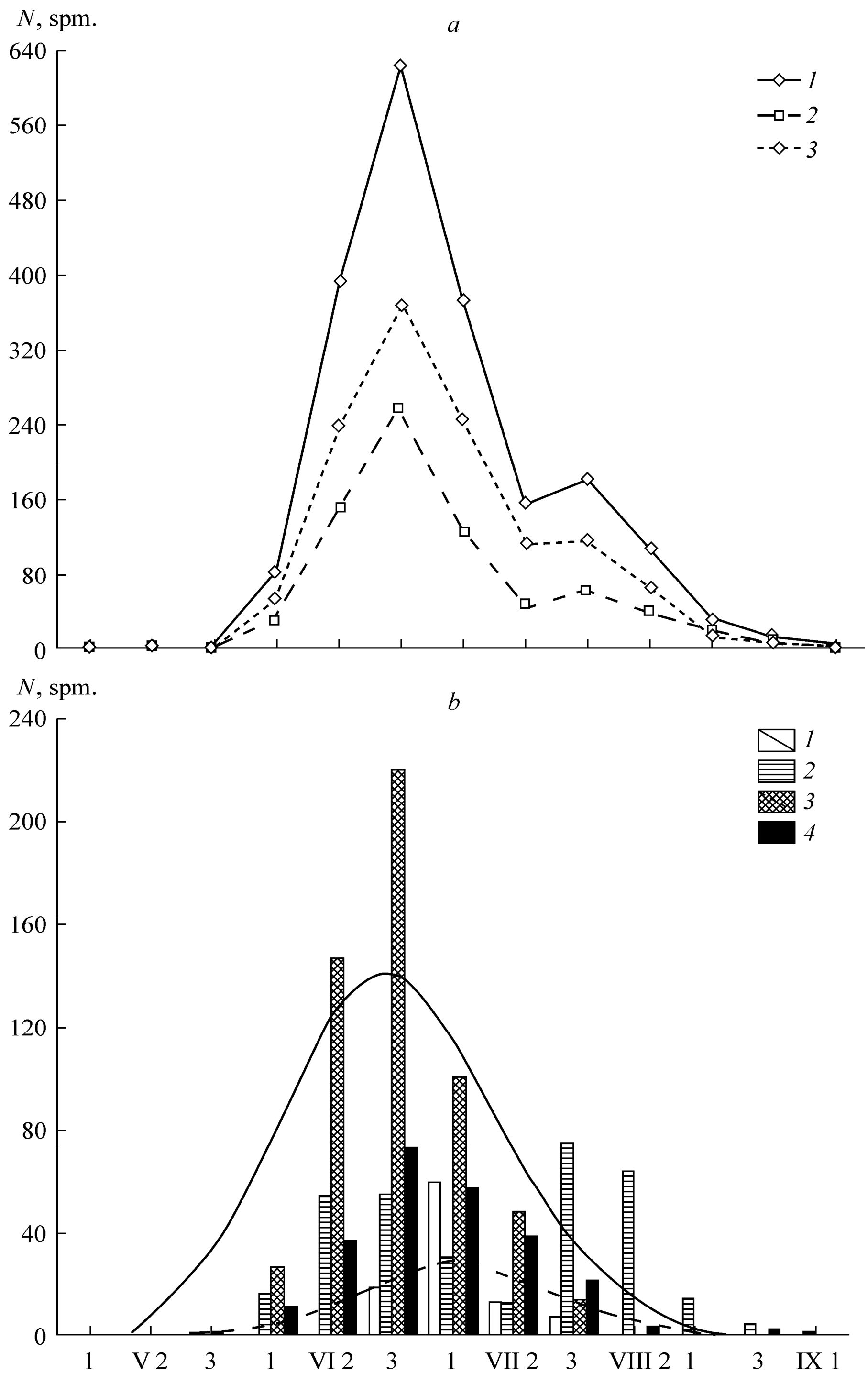

Fig. 4. Seasonal dynamics of activity (*a*) and the demographic spectrum of the population of *Poecilus fortipes* (females only) (*b*) in the upper forest-steppe belt of the Eastern Sayan. For designations, see Fig. 1.

High epigeic activity of the corresponding immature cohort was observed in late July–early August, after which only immature and spent individuals were recorded in the population until the very end of the active period. Thus, the life cycle of *P. fortipes* in the upper forest-steppe belt of the Eastern Sayan is realized as an obligate biennial one with reproduction in early summer (Fig. 5*d*).

DISCUSSION

Despite the fact that beetles were studied in different years and during only one season at each field

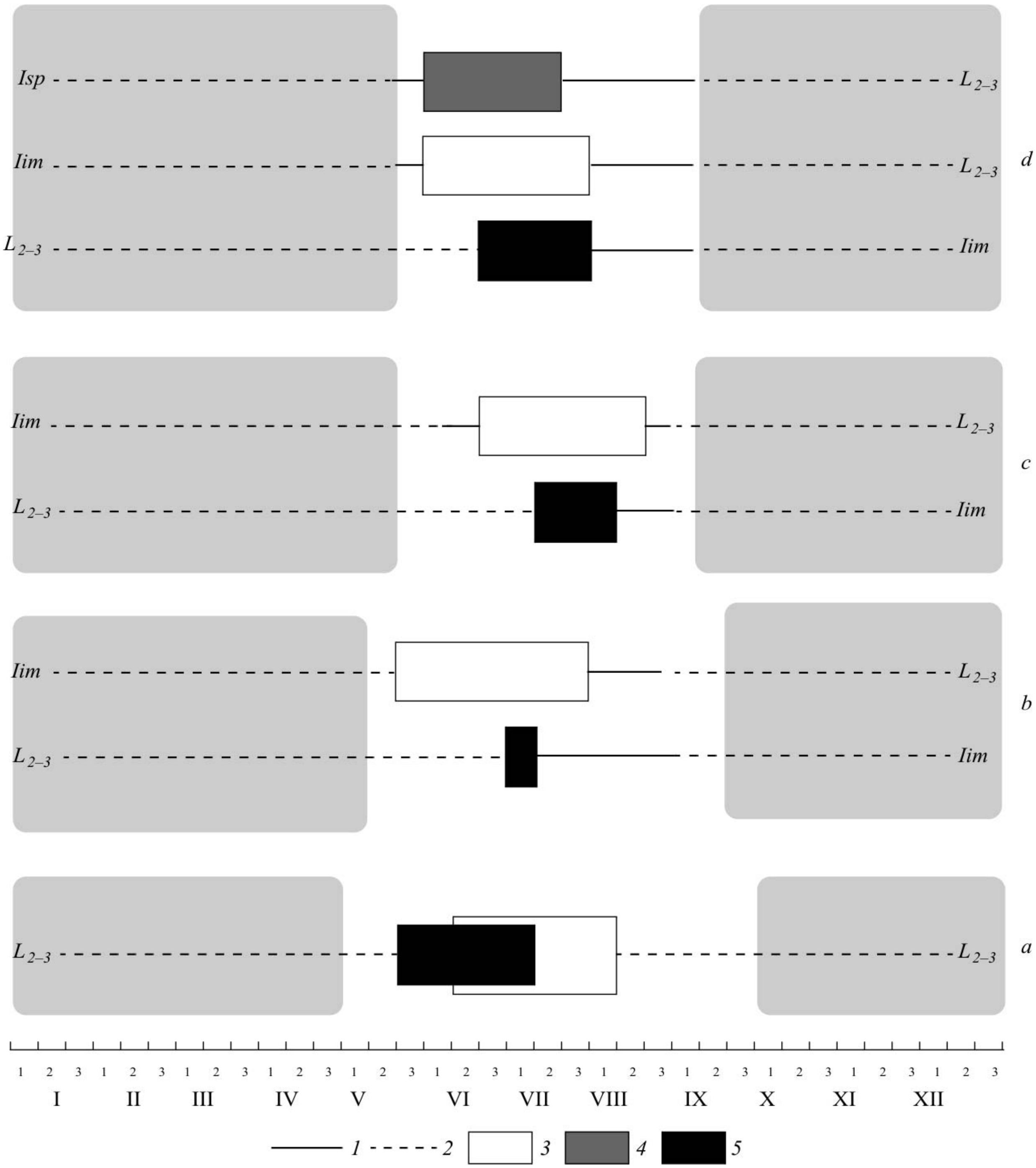

Fig. 5. Diagrammatic representations of the life cycle of *Poecilus fortipes* along the altitude gradient; (*a*) Selenga mid-altitude mountains (600–650 m asl); (*b*) Vitim Plateau (900–950 m asl); (*c*) lower forest-steppe belt of the Eastern Sayan (1300–1400 m asl); (*d*) upper forest-steppe belt of the Eastern Sayan (1500–1700 m asl); *Iim*, immature adults; *Isp*, spent adults (remaining from the generations of the previous seasons); L_{2-3}, larvae of the II and III instars; *1*, soil trap survey data; *2*, inferred periods of activity; *3*, reproductive period of adults breeding for the first time; *4*, reproductive period of adults remaining from the previous generations; *5*, period of emergence of adults developing from the overwintered larvae.

station, the research carried out in different altitudinal belts allowed us to reveal certain trends both in the morphological characters and in the population parameters of the species in question.

The length of individuals of both sexes decreased regularly in the altitudinal gradient. Beetles from the Selenga mid-altitude mountains (600–650 m asl) were significantly larger, and those from the upper

Table 2. Parameters of egg production in the model populations of *Poecilus fortipes*

Months and decades of surveys		Selenga mid-altitude mountains			Vitim Plateau			Eastern Sayan					
								lower forest-steppe belt			upper forest-steppe belt		
		number of females with eggs	number of eggs		number of females with eggs	number of eggs		number of females with eggs	number of eggs		number of females with eggs	number of eggs	
			min–max	mean ± *SD*		min–max	mean ± *SD*		min–max	mean ± *SD*		min–max	mean ± *SD*
V	1												
	2												
	3										1	4	
VI	1				1	12					26	2–20	9.8 ± 5.1
	2	1	12		16	9–33	15.1 ± 7.7				147	1–40	9.8 ± 6.5
	3	6	10–26	15.8 ± 5.6	49	1–28	13.0 ± 6.5	15	2–22	13.5 ± 5.9	220	1–31	9.4 ± 6.0
VII	1	5	13–28	22.4 ± 5.6	32	2–27	10.1 ± 6.5	18	7–34	18.2 ± 7.8	100	1–15	5.3 ± 3.2
	2	6	4–15	8.3 ± 4.3	2	12	12.0 ± 0	14	12–43	22.4 ± 9.7	48	3–26	8.9 ± 5.3
	3	2	15–18	16.5 ± 2.1	1	7		21	1–24	9.4 ± 7.8	13	1–9	4.1 ± 27
VIII	1	9	14–23	17.6 ± 2.8				8	6–21	11.3 ± 5.0			
	2							2	1	1.0 ± 0			
	3												
Season	29	4–28	15.9 ± 6.1^{AD}	101	1–33	12.3 ± 6.7^{Bd}	78	1–43	14.5 ± 9.0^{C}	555	1-40	8.6 ± 5.8^{abc}	

Notes: *SD* is standard deviation. Comparison of the median values marked with different letters (U-test, $p < 0.05$) yielded the following results: ^{Aa} U = 2960.0 ($z = 5.74$, $p = 0.0$); ^{Bb} U = 17717.5 ($z = 5.88$, $p = 0.0$); ^{Cc} U = 12476.0 ($z = 6.06$, $p = 0.0$); ^{Dd} U = 942.0 ($z = 2.92$, $p = 0.003$).

Table 3. Significance of differences in the body length of *Poecilus fortipes* from the model populations (based on the Kruskal–Wallis *H*-test: $\chi^2 = 988.86$, df = 7, $p = 0.0$)

			Selenga middle mountains		Vitim Plateau		Eastern Sayan, forest-steppe			
							lower belt		upper belt	
			males	females	males	females	males	females	males	females
Selenga middle mountains		males	*2409.6*							
		females	0.05 / 1.0	*2404.2*						
Vitim Plateau		males	**4.34** / 0.0	**4.29** / 0.001	*1970.1*					
		females	3.13 / 0.05	3.08 / 0.06	1.17 / 1.0	*2079.8*				
Eastern Sayan, forest-steppe	lower belt	males	**3.74** / 0.01	**3.69** / 0.01	0.51 / 1.0	0.64 / 1.0	*2017.6*			
		females	**5.39** / 0.0	**5.35** / 0.0	1.07 / 1.0	2.22 / 0.74	1.54 / 1.0	*1879.0*		
	upper belt	males	**13.48** / 0.0	**13.48** / 0.0	**10.12** / 0.0	**10.77** / 0.0	**10.02** / 0.0	**9.37** / 0.0	*1293.0*	
		females	**18.82** / 0.0	**18.84** / 0.0	**16.68** / 0.0	**16.82** / 0.0	**16.14** / 0.0	**16.36** / 0.0	**12.74** / 0.0	*811.56*

Notes: Numerators: standardized *z* values; denominators: confidence intervals (*p*); the mean ranks are shown in italics; the values significant at $p < 0.05$ are shown in bold.

forest-steppe belt of the Eastern Sayan (1500–1700 m asl) were significantly smaller than all the others. Females were larger than males in all the localities except the Selenga mid-altitude mountains, but the difference was statistically significant only in the population from the upper forest-steppe belt of the Eastern Sayan (Table 3, Fig. 6). It should be noted that the body length of females changed more smoothly along the altitudinal gradient than that of males. The most abrupt decrease in the body length was observed in transition from the middle mountains to the lower margin of the high mountain belt. In particular, as the altitude changed from 600–650 to 1300–1500 m asl, the body length of females and males of *P. fortipes* decreased on average by 0.6 and 0.9 mm, whereas with transition from 1300–1400 to 1500–1700 m asl it decreased by 1.1 and 1.9 mm, respectively. Similar changes in the body length were observed in *Carabus problematicus* Herbst, 1786 in North Wales, along the altitudinal gradient from 660 to 1055 m asl (Sparks et al., 1995), and in *Carabus kumagaii* Kimura et Komiya, 1974, whose populations were studied in the Honshu Island at altitudes of 20, 60, and 1100 m asl (Sota, 1987). As in our case, females were larger than males, whereas the differences in the body length of individuals from the plain and mountain populations were statistically significant (Sota, 1987). Similar trends in the body size of Carabidae were observed along the latitudinal gradient. For example, according to the data of Filippov (2008), the body size of males and females of 12 out of 15 ground beetle species was smaller in the northern parts of their ranges than in the central and southern ones.

Changes in the sex ratio index I_s along the altitudinal gradient were not so clear. Under the conditions of the Selenga mid-altitude mountains (600–650 m asl), the sex ratio in the model population of *P. fortipes* was 1 : 1 ($I_s = 0.005$). As the altitude increased, the fraction of males also gradually increased to the populations, resulting in a 1.2-fold prevalence of males ($I_s = -0.1$) on the Vitim Plateau (900–950 m asl) and in an almost 1.5-fold prevalence of males ($I_s = -0.16$) in the lower forest-steppe belt of the Eastern Sayan (1300–1400 m asl). However, in the upper forest-steppe belt of the Eastern Sayan (1500–1700 m asl) the sex ratio in the model population of *P. fortipes* was shifted towards a 1.5-fold prevalence of females ($I_s = 0.25$). The different catch indices of individuals of different sexes, affecting the I_s values, seem to reflect the specific conditions of epigeic activ-

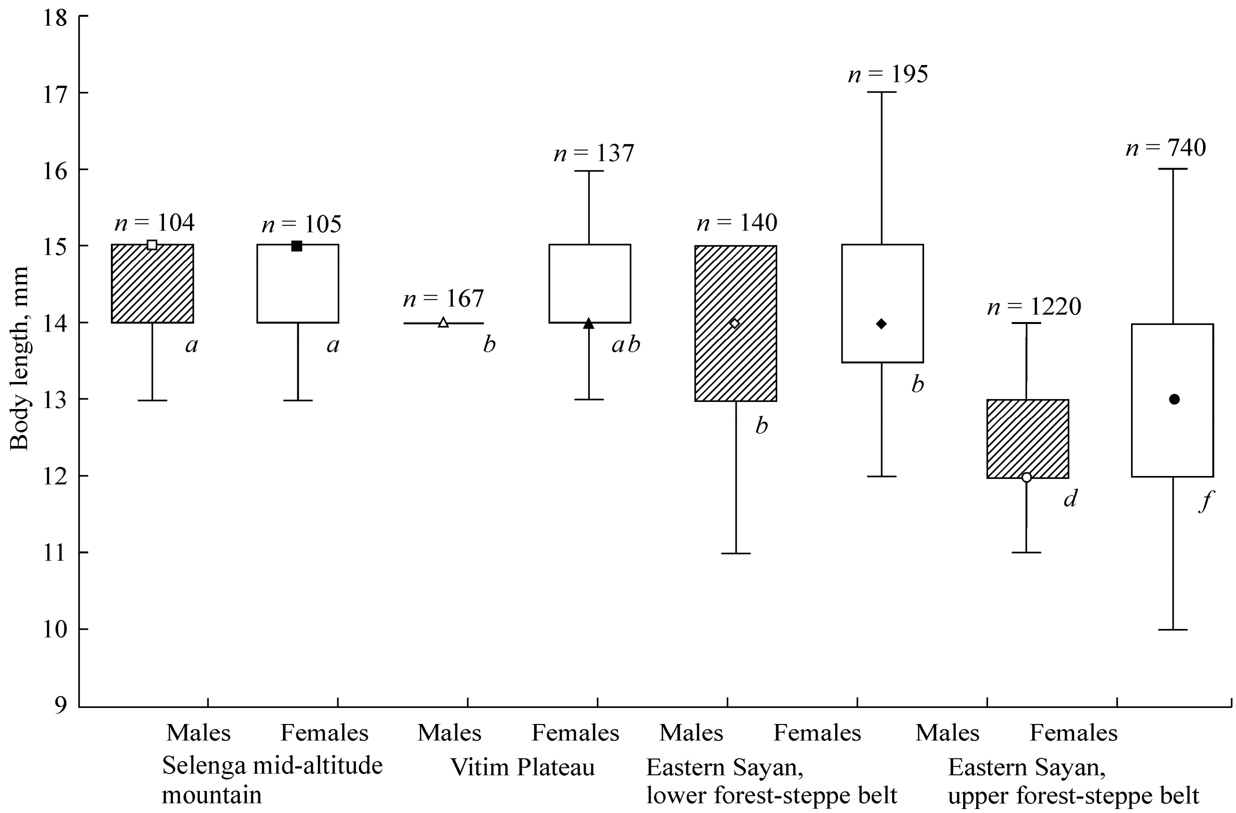

Fig. 6. Changes in the mean body length (determined by the median values) of *Poecilus fortipes* along the altitudinal gradient. Rectangles mark the second and third quartiles; vertical bars mark the ranges with the outlier values neglected; *n* is the number of observations. Different letters mark statistically significant differences; identical letters, statistically non-significant differences (Kruskal–Wallis *H*-test with a 95% confidence interval).

ity in each particular case. At the same time, the observed fluctuations of I_s generally stayed within the limits of the biological norm. Similar trends were observed for *Pterostichus tomensis* (Gebler, 1847) in Rudny Altai, where the sex ratio varied from 0.84 to 1.33 within the mountain boreal forests (at altitudes from 1200 to 1800 m asl), which is the optimum zone for the species (Matalin, 1990).

The duration of the reproductive period of *P. fortipes* was 6–7 decades and almost did not depend on the altitude, but the time of the onset of oviposition changed regularly along the altitudinal gradient. In particular, under the conditions of the Selenga middle mountains, oviposition started two decades after the onset of epigeic activity; the delay was only one decade on the Vitim Plateau and in the lower forest-steppe belt of the Eastern Sayan, whereas in the upper forest-steppe belt oviposition started simultaneously with epigeic activity of the species (Fig. 5). This trend was obviously determined by the shortening of the vegetation season and the decrease in the sum of effective temperatures (Table 1). The same picture was observed in the populations of *Patrobus atrorufus* (Ström, 1768) in central Norway: the reproductive period lasted from July to August at altitudes below 120 m asl, and from June to July at an altitude of 830 m asl (Refseth, 1980). Similar changes in the terms of reproduction can be determined by the shortening of the frost-free season along the latitudinal gradient (Filippov, 2008). For example, *Calathus melanocephalus* (L., 1758), broadly distributed in Europe, reproduces from August to mid-November in Denmark, from July to August in Moscow Province, and from June to August in Arkhangelsk Province (Filippov, 2006b). The populations of *P. fortipes* from the Selenga mid-altitude mountains, the Vitim Plateau, and the lower forest-steppe belt of the Eastern Sayan were characterized not only by relatively low catch indices but also by the absence of rebreeding individuals of the preceding generations. These features may lead to strong fluctuations of abundance from season to season, and also increase the risk of spontaneous extinction of local populations; such phenomena were observed in *Carabus auronitens* F., 1792 (Weber and Klenner, 1987) and *Carabus bessarabicus concretus* F.-W., 1823 (Matalin and Makarov, 2008).

The reproductive potential of populations also changed regularly along the altitudinal gradient. The mean number of eggs per female decreased from 15.9 ± 6.1 to 8.6 ± 5.8 as the altitude increased from 600–650 to 1500–1700 m asl. The population from the upper forest-steppe belt of the Eastern Sayan was significantly different from others in this parameter. The maximum number of eggs, on the contrary, increased from 26–28 in the population from the Selenga mid-altitude mountains to 40–43 in those from the Eastern Sayan forest-steppe (Table 2). A similar decrease in the mean number of eggs was observed in populations of *C. problematicus* in northern England. In particular, the mean number of eggs per female was 6.31 ± 0.59 at 102 m asl and 2.7 ± 0.28 at 800–850 m asl (in these two cases, the data are expressed as the mean ± standard error) (Butterfield, 1986).

Changes in the dates of emergence of adults developing from the overwintered larvae were no less significant. In the Selenga mid-altitude mountains, emergence of tenerals started simultaneously with the onset of epigeic activity and lasted until the first decade of July. On the Vitim Plateau and the lower forest-steppe belt of the Eastern Sayan emergence started in the first decade of July and ended in the first decade of August. The period of activity of teneral beetles was the longest in the upper forest-steppe belt of the Eastern Sayan, where it started at the end of June and continued until the beginning of September (Fig. 5). The same trend was observed in populations of *Carabus caelatus schreiberi* Kraatz, 1887 from the mountain forests growing in a karst landscape in the environs of Trieste (Italy). Emergence of adults that developed from overwintered larvae was observed from May to July at altitudes ranging from 120 to 420 m asl, whereas at 950 m asl it was shifted to August (Brandmayr and Zetto Brandmayr, 1986).

Despite the fact that *P. fortipes* is one of the most common ground beetle species in South Siberia, data on its seasonal activity and life cycle are still incomplete. In the south of West Siberia, the period of its epigeic activity lasts from the beginning of July to the beginning of August. Reproduction is observed during this entire period, while the teneral beetles recorded in late July and early August hibernate for the winter (Bespalov, 2011). In the South Cisbaikalia, the species is active from mid-May to mid-August; oviposition takes place in June–July, and tenerals appear from the end of July to mid-August (Shilenkov, 1978). In these two cases, the demographic spectrum is almost identical to that observed in the lower forest-steppe belt of the Eastern Sayan (Fig. 3), which allows one to assume that the life cycle must be realized in a similar way. In the upper reaches of the Lena River, *P. fortipes* was active from June to mid-August (Averenskii et al., 2008). In the overgrown fallow lands in the South Primorskii Territory the species was dominant from mid-July to the beginning of September, with the peak of abundance in the first decade of August (Lapshin and Lapshin, 1978).

Based on the presence of teneral beetles at the end of the period of epigeic activity, when reproduction is declining, the life cycle of *P. fortipes* was earlier interpreted as annual with "spring" reproduction (Shilenkov, 1978; Khobrakova and Sharova, 2005). However, the data of laboratory rearing of the species contradicted this assumption. First, preimaginal development of the species was found to be the most successful under the conditions of the changing temperature regime (+24°C → +5°C → +24°C). Second, development of no less than 20% of III instar larvae was considerably prolonged, both at constant and changing photoperiods (Makarov, 1994; Matalin and Makarov, 2011). These facts suggest that wintering at the larval stage is a common phenomenon for *P. fortipes*. Some larvae completed development under the laboratory conditions without a temperature-induced diapause, regardless of the photoperiodic regime (Berlov, 1989; Matalin and Makarov, 2011). However, preimaginal development took more than 4 months in the latter case, which means that under the natural conditions it would be inevitably interrupted by diapause. Thus, the reproductive rhythm of *P. fortipes* does not depend on the photoperiod and is characterized by a facultative temperature-induced diapause (Matalin and Makarov, 2011). Similar data were obtained for two closely related species: the European *P. lepidus* (Leske, 1785) (Paarmann, 1990; Budilov, 2002) and the Far Eastern *P. samurai* (Lutshnik, 1916) (Matalin and Makarov, 2011).

According to our data, the annual life cycle with reproduction in summer, characteristic of the population of *P. fortipes* from the Selenga mid-altitude mountains, is regularly replaced along the altitudinal gradient by the obligate biennial life cycle with reproduction in summer or early summer, which was observed in the lower and upper forest-steppe belts of the Eastern Sayan. Transition from annual to obligate biennial development takes place as the altitude increases from 600–650 to 900–950 m asl (Fig. 5), which corresponds to the sum of effective temperatures dropping to 1400°C. The latter value appears to be insufficient for implementation of the annual variant of the life cycle (Table 1). Similar transformations of the life cycles are known for many ground beetle species occupying different habitats along altitudinal gradients (Refseth, 1980; Butterfield, 1986, 1996; Sota, 1986; Sparks et al., 1995; Brandmayr and Zetto Brandmayr, 1996, etc.).

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REFERENCES

1. Andersen, J.M., "A Re-analysis of the Relationships between Life Cycle Patterns and the Geographical Distribution of Fennoscandian Carabid Beetles," J. Biogeogr. **11** (6), 479–489 (1984).
2. *Atlas of the Republic of Buryatia* (Moscow, 2000) [in Russian].
3. *Atlas of the Transbaikalia (Buryat ASSR and Chita Province)* (Irkutsk, 1967) [in Russian].
4. Averenskii, A.I., Nogovitsyna, S.N., and Stepanov, A.D., *Insects of Yakutia. Coleoptera* (Bichik, Yakutsk, 2008) [in Russian].
5. Berlov, O.E., "Rearing of Ground Beetles (Coleoptera, Carabidae) from the Cisbaikalia," in *Insects and Arachnids of Siberia* (Irkutsk State Univ., Irkutsk, 1989), pp. 71–76 [in Russian].
6. Bespalov, A.N., Candidate's Dissertation in Biology (Novosibirsk, 2011).
7. Borovikov, V., *STATISTICA: Computer-Assisted Data Analysis for Professionals* (Piter, St. Petersburg, 2001) [in Russian].
8. Brandmayr, P. and Zetto Brandmayr, T., "Phenology of Ground Beetles and Its Ecological Significance in Some of the Main Habitat Types of Southern Europe," in *Carabid Beetles: Their Adaptations and Dynamics* (Gustav Fisher Verlag, Stuttgart, 1986), pp. 195–220.
9. Budilov, P.V., Candidate's Dissertation in Biology (Moscow, 2002).
10. Butterfield, J.E.L., "Changes in Life-Cycle Strategies of *Carabus problematicus* over a Range of Altitudes in Northern England," Ecol. Entomol. **11**, 17–26 (1986).
11. Butterfield, J.E.L., "Carabid Life Cycle Strategies and Climate Change: a Study on an Altitudinal Transect," Ecol. Entomol. **21** (1), 9–16 (1996).
12. De Zordo, I., "Phänologie von Carabiden im Hochgebirge Tirols (Obergurgl, Österreich) (Insecta: Coleoptera)," Ber. Naturwiss.-Medizin. Vereins Innsbruck **66**, 73–83 (1979).
13. Eremeeva, N.I. and Efimov, D.A., *Ground Beetles (Coleoptera, Carabidae) of Natural and Urbanized Territories of the Kuznetsk Depression* (Nauka, Novosibirsk, 2006) [in Russian].
14. Filippov, B.Yu., "Seasonal Aspects of the Life Cycles of *Carabus granulatus* L. and *C. glabratus* Payk. (Coleoptera, Carabidae) in the Northern Taiga," Zool. Zh. **85** (9), 1076–1084 (2006a) [Entomol. Rev. **86** (7), 751–759 (2006)].
15. Filippov, B.Yu., "Seasonal Aspects of the Life Cycles of *Calathus melanocephalus* and *C. micropterus* (Coleoptera, Carabidae) in the Northern Taiga," Zool. Zh. **85** (10), 1196–1204 (2006b) [Entomol. Rev. **86** (8), 901–909 (2006)].
16. Filippov, B.Yu., Doctoral Dissertation in Biology (Moscow, 2008).
17. Filippov, E.V. and Khobrakova, L.Ts., "Seasonal Dynamics of Activity of Ground Beetles under the Natural and Anthropogenic Conditions of a Siberian City," in *Ecology of South Siberia and Adjacent Territories. Issue 9, Vol. 1* (Khakass State Univ., Abakan, 2005), p. 99 [in Russian].
18. Garmazhapov, Z.N. and Baskhaeva, T.G., "On Some Characteristic Phytocenoses of the Okinskoe Plateau Mountain Forest-Steppe (by the Example of Kheregte Hollow)," in *The Future of Buryatia as Viewed by the Young* (Buryat State Univ., Ulan-Ude, 2002), pp. 77–79 [in Russian].
19. Ivanov, S.B. and Dudko, R.Yu., "Spatio-Temporal Organization of the Ground Beetle (Coleoptera, Carabidae) Population of the Middle- and High-Mountain Parts of Northeast Altai," Sibir. Ekol. Zh. **4**, 457–467 (2006).
20. Jørum, P., "Life Cycles and Annual Activity Patterns of *Pterostichus melanarius* (Illig.) and *P. niger* (Schall.) (Coleoptera: Carabidae) in a Danish Beech Wood," Entomol. Medd. **48** (1), 19–25 (1980).
21. Khobrakova, L.Ts., "Ordination of the Ground Beetle Population (Coleoptera, Carabidae) in the Mountain

Forest-Steppe of the East Sayan," in *Biodiversity of Ecosystems of Inner Asia* (Russian Acad. Sci., Ulan-Ude, 2006), pp. 189–191 [in Russian].

22. Khobrakova, L.Ts., "Ground-Beetle (Coleoptera, Carabidae) Assemblages in the Forest-Steppe of the Southern Vitim Plateau," Entomol. Obozr. **87** (2), 313–324 (2008) [Entomol. Rev. **88** (4), 396–405 (2008)].
23. Khobrakova, L.Ts. and Filippov, E.V., "Ground Beetles in the Ulan-Ude City Dump," in *Synanthropization of Plants and Animals* (Irkutsk, 2007), pp. 208–210 [in Russian].
24. Khobrakova, L.Ts. and Sharova, I.Kh., *Ecology of Ground Beetles in the East Sayan* (Ulan-Ude, 2004) [in Russian].
25. Khobrakova, L.Ts. and Sharova, I.Kh., "Life Cycles of Ground Beetles (Coleoptera, Carabidae) in the Mountain Taiga and Forest-Steppe of the East Sayan," Izv. Akad. Nauk, Ser. Biol., No. 6, 688–693 (2005).
26. Korobeinikov, Yu.I., "On Some Traits in the Seasonal Dynamics of Activity and Reproduction of Ground Beetles in the Subarctic," in *Problems of Soil Zoology* (Novosibirsk, 1991), pp. 127–128 [in Russian].
27. Lapshin, L.V. and Lapshin, A.V., "The Ground Beetle Complexes of Fallow Lands in the Southern Primorskii Territory," in *Problems of Soil Zoology* (Nauka i Tekhnika, Minsk, 1978), pp. 138–139 [in Russian].
28. Lyubechanskii, I.I., "The Ground Beetle Population (Coleoptera, Carabidae) of Typical Biotopes of the West Siberian Southern Forest-Steppe," Evraziat. Entomol. Zh. **8** (3), 315–318 (2009).
29. Makarov, K.V., "Annual Reproduction Rhythm of Ground Beetles: a New Approach to the Old Problem," in *Carabid Beetles: Ecology and Evolution. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 177–182.
30. Matalin, A.V., "The Use of the Sex Ratio in Determining the Biotopic Preferenda (by the Example of *Pterostichus tomensis* Gebl.)," in *Population Structure and Dynamics in Edaphic and Epigeic Invertebrates. Vol. 2* (Moscow, 1990), pp. 16–21 [in Russian].
31. Matalin, A.V., "Life Cycles of Carabids of the Genus *Stenolophus* (Coleoptera, Carabidae) in the Steppe Zone of Europe," Zool. Zh. **76** (10), 1141–1149 (1997) [Entomol. Rev. **77** (9), 1181–1190 (1997)].
32. Matalin, A.V., "The Polyvariant Nature of the Life Cycle of *Harpalus* (s. str.) *affinis* Schrank and Its Adaptive Significance," Izv. Ross. Akad. Nauk, Ser. Biol., No. 4, 496–505 (1998).
33. Matalin, A.V., "Geographic Variability of the Life Cycle in *Pterostichus melanarius* (Coleoptera, Carabidae)," Zool. Zh. **85** (5), 573–585 (2006) [Entomol. Rev. **86** (4), 409–422 (2006)].
34. Matalin, A.V., "Typology of Life Cycles of Ground Beetles (Coleoptera, Carabidae) in Western Palaearctic," Zool. Zh. **86** (10), 1196–1220 (2007) [Entomol. Rev. **87** (8), 947–972 (2007)].
35. Matalin, A.V., Doctoral Dissertation in Biology (Moscow, 2012).
36. Matalin, A.V. and Budilov, P.V., "Geographical Variability of Sexual and Age Structure of Populations and the Life Cycle in *Broscus cephalotes* (Coleoptera, Carabidae)," Zool. Zh. **82** (12), 1445–1453 (2003) [Entomol. Rev. **83** (8), 1037–1045 (2003)].
37. Matalin, A.V. and Makarov, K.V., "Seasonal Dynamics and the State of Local Populations of *Carabus bessarabicus concretus* F.-W. under the Conditions of the Elton Nature Park," in *Biodiversity and Biological Resources of the Urals and Adjacent Territories: Proceedings of the Institute of Biological Resources and Applied Ecology, Issue 7* (Orenburg State Ped. Univ., Orenburg, 2008), pp. 200–201 [in Russian].
38. Matalin, A.V. and Makarov, K.V., "The Effects of Temperature and Photoperiod on Preimaginal Development of *Poecilus fortipes* Chaud. and *P. samurai* (Lutsh.) (Coleoptera: Carabidae)," in *Fundamental Problems of Entomology* (St. Petersburg State Univ., St. Petersburg, 2011), p. 103 [in Russian].
39. Moroldoev, I.V. and Khobrakova, L.Ts., "Seasonal Dynamics of the Age Structure of Mass Ground Beetle Species (Coleoptera, Carabidae) in the Vitim Plateau Forest-Steppe," Vestnik Tomsk. Gos. Ped. Univ. **3** (93), 27–31 (2010a).
40. Moroldoev, I.V. and Khobrakova, L.Ts., "A Review of the Ground Beetle Communities (Coleoptera, Carabidae) in the South of Vitim Plateau," Vestnik Altai. Gos. Agric. Univ., Issue 4, 45–50 (2010b).
41. Müller, J.K., "Period of Adult Emergence in Carabid Beetles: an Adaptation for Reducing Competition?" Acta Phythopathol. Entomol. Hung. **22** (1–4), 409–415 (1987).
42. Paarmann, W., "The Annual Periodicity of the Polyvoltine Ground-Beetle *Pogonus chalceus* Marsh. (Col. Carabidae) and Its Control by Environmental Factors," Zool. Anz. **196**, 150–160 (1976).
43. Paarmann, W., "Ideas about the Evolution of the Various Annual Reproduction Rhythms in Carabid Beetles of the Different Climatic Zones," Misc. Papers L. H. Wageningen **18**, 119–132 (1979).
44. Paarmann, W., "*Poecilus lepidus* Leske (Carabidae, Coleoptera), a Species with the Ability to be a Spring and Autumn Breeder," in *The Role of Ground Beetles in Ecological and Environmental Studies* (Intercept Publ., Andover-Hampshire, 1990), pp. 259–267.
45. Pankratov, A.A., Candidate's Dissertation in Biology (Irkutsk, 2011).
46. Refseth, D., "Differences in Seasonal Activity Pattern and Breeding Time of *Patrobus atrorufus* (Carabidae) in Central Norway," Holarctic Ecol. **3**, 87–90 (1980).
47. Refseth, D., "The Life Cycle and Growth of *Carabus glabratus* and *C. violaceus* in Budalen, Central

Norway," Ecol. Entomol. Oxford **9** (4), 449–455 (1984).
48. Refseth, D., "Phenological Adaptation in *Patrobus assimilis* and *P. atrorufus* (Col., Carabidae)," Fauna Norvegica, Ser. B **33**, 57–63 (1986).
49. Refseth, D., "Annual Patterns of Activity, Reproduction and Development in Some Norwegian Carabidae (Col.)," Fauna Norvegica **35** (1), 21–30 (1988).
50. Rogatnykh, D.Yu., Candidate's Dissertation in Biology (Vladivostok, 2008).
51. Sharova, I.Kh., "Factors Determining the Seasonal Dynamics of Activity of Ground Beetles (Coleoptera, Carabidae) in Agrocenoses," in *Population Structure and Dynamics in Edaphic and Epigeic Invertebrates. Vol. 1* (Moscow, 1990), pp. 1–12 [in Russian].
52. Sharova, I.Kh. and Dushenkov, V.M., "Types of Development and Types of Seasonal Activity in Ground Beetles (Coleoptera, Carabidae)," in *Fauna and Ecology of Invertebrates* (Moscow, 1979), pp. 15–25 [in Russian].
53. Sharova, I.Kh. and Filippov, B.Yu., "Specific Features of the Life Cycles of Ground Beetles (Coleoptera, Carabidae) in Northern Taiga," Zool. Zh. **82** (2), 229–238 (2003) [Entomol. Rev. **83** (8), 982–992 (2003)].
54. Sharova, I.Kh. and Khobrakova, L.Ts., "Specific Features of the Life Cycles of *Pterostichus montanus* (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) (Coleoptera, Carabidae) in the Mountain Taiga Belt of the Eastern Sayan," Izv. Ross. Akad. Nauk, Ser. Biol., No. 1, 36–46 (2005).
55. Shilenkov, V.T., "Biological Characteristics of Abundant Species of Carabidae (Coleoptera) in Southern Cisbaikalia," Entomol. Obozr. **57** (2), 290–301 (1978) [Entomol. Rev. **57** (2), 202–209 (1978)].
56. Sota, T., "Carabid Populations along an Altitudinal Gradient: Life History Variation of *Leptocarabus kumagaii* (Coleoptera; Carabidae)," in *Carabid Beetles: Their Adaptations and Dynamics* (Gustav Fisher Verlag, Stuttgart, 1986), pp. 429–437.
57. Sota, T., "Effects of Temperature and Photoperiod on the Larval Hibernation and Adult Aestivation of *Leptocarabus kumagaii* (Coleoptera: Carabidae)," Appl. Entomol. Zool. **22** (4), 617–623 (1987).
58. Sota, T., "Altitudinal Variation in Life Cycles of Carabid Beetles: Life-Cycle Strategy and Colonization in Alpine Zones," Arctic Alpine Res. **28** (4), 441–447 (1996).
59. Sparks, T.H., Buse, A., and Gadsden, R.J., "Life Strategy of *Carabus problematicus* (Coleoptera, Carabidae) at Different Altitudes on Snowdon, North Wales," J. Zool. Lond. **236** (1), 1–10 (1995).
60. Šustek, Z., "The Indicative and Prognostic Significance of Sex Ratio in Carabidae," Ecology (ČSSR), No. 3, 3–22 (1984).
61. Thiele, H.-U., *Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behavior* (Springer-Verlag, Berlin, 1977).
62. Wallin, H., "Distribution, Movements and Reproduction of Carabid Beetles (Coleoptera, Carabidae) Inhabiting Cereal Fields," in *Plant Protection Reports and Dissertations of the Swedish Univ. for Agric. Sci., No. 15* (SLU/Repro, Uppsala, 1987), pp. 1–109.
63. Weber, F. and Klenner, M., "Life History Phenomena and Risk of Extinction in a Subpopulation of *Carabus auronitens*," Acta Phytopathol. Entomol. Hung. **22** (1–4), 321–328 (1987).