

Evolution of biennial life cycles in ground beetles (Coleoptera, Carabidae) of the Western Palaearctic

Andrey V. Matalin

Zoology & Ecology Department, Moscow State Pedagogical University, Kibalchicha str. 6,
build. 5, Moscow 129164, Russia. E-mail: a_matalin@tochka.ru

SUMMARY

Information about the life cycles of 400 Palaearctic carabid species was acquired on the basis of field study and analysis of literature. Five types of biennial development were defined: a biennial life cycle of spring-summer species; a biennial life cycle of summer-autumn species which developed as facultative (only part of the population develops within two years) or obligatory (biennial development occurs in the whole population); biennial life cycle of autumn species which may have appeared in two similar variants – facultative and obligatory. So, biennial life cycles have independently evolved in carabid beetles by at least three means: among spring breeders (type 1, according to Thiele, 1977) with gonad dormancy during hibernation and gonad maturation; males in SD, females after changing SD to LD; among autumn breeders (type 3) without gonad dormancy but with temperature controlled larval dormancy during hibernation; among autumn breeders (type 4) with gonad dormancy during aestivation and gonad maturation after changing LD to SD. The similarity and differences between latitudinal and altitudinal trends in biennial development of Carabidae are discussed. In similar, extreme conditions, the parallel variants of biennial development are observed. However even in favorable environments, some individuals may develop over two years. According to the assimilated data for this study, the proportion of species with biennial life cycles in different habitats within the temperate zone is rather high and biennial development is not unusual.

Keywords: Carabidae, biennial life cycles, Western Palaearctic

INTRODUCTION

The study of life cycles is important in both applied and theoretical biology. Investigations of the features of life cycles under specific conditions allows for detailed study of the structure and dynamics of populations of individual species, as well as of whole communities. Moreover, analysis of the patterns of development along natural gradients makes life cycles an important topic for the discussion of evolution among superspecific taxa (Thiele, 1977; Paarmann, 1979; Sharova, 1981; Hürka, 1986; Makarov, 1989; den Boer & van Dijk, 1996; Matalin, 1998a, 2007; Sota & Ishikawa, 2004).

The problem of the evolution of multi-annual life cycles is one of the most interesting and challenging in modern biology. Among the Coleoptera, multi-annual development patterns are not rare. The longest development, of up to four years, is observed in the larvae of several Lucanidae, Scarabaeidae, Cerambycidae and Elateridae species (Bey-Bienko, 1980; Klausnitzer, 1981). In some Chrysomelidae, especially *Leptinotarsa decemlineata* L., such a phenomenon is known as “super-pause” (Bey-Bienko, 1980; Koval', 2005). In this case, the beetles of a new generation reproduce only two or even three years after pupation. During this period, they remain inert, within their pupation chamber. The development of some arctic Chrysomelidae, such as *Chrysolina subsulcata* Mann., typically lasts for three or four years (Chernov, 1974, 1978), and according to some estimates can extend for up to even five or six years (Khruleva, 1994). An extended developmental period is also known for the lycid, *Pyropterus nigroruber* DeGeer, which has been observed in captivity for five years before pupating (Bourgeois, 1882).

In the Carabidae, however, development does not seem to exceed two years. There is indirect evidence of a possibly triennial development in two species of *Amblystogenium*, which inhabits several sub-antarctic islands (Davies, 1987), *Amara quenseli* (Schönh.) in the Alps (De Zordo, 1979), and some *Carabus* in the barren tundra (Korobeinikov, 1991). Also according to Shelford (1908), the development in some species of Holarctic tiger-beetles lasts for up to three years. But such cases are rather exceptional, because the long development of tiger-beetle larvae is closely related to the features of their life. Stable habitats and food resources are of greater significance to them in comparison with other carabid genera.

Biennial life cycles have traditionally been considered as only occurring among carabid beetles under extreme conditions only, such as high latitudes (Houston, 1981; Refseth, 1980, 1984, 1988; Andersen, 1969; Korobeinikov, 1991; Sharova & Filippov, 2003; Filippov, 2006a-b), high mountains (De Zordo, 1979; Jakuczun, 1979; Brandmayr & Zetto Brandmayr, 1986; Butterfield, 1986, 1996; Chemini & Pizzolotto, 1992; Hemmer & Terlutter, 1991; Schatz, 1994; Sparks et al., 1995; Khobrakova & Sharova, 2005; Sharova & Khobrakova, 2005) and some arid landscapes (Shelford, 1908; Hamilton, 1925).

But how strongly is the biennial life cycle associated with such difficult environments? And how widely is the biennial pattern of development represented amongst the

Carabidae within the temperate belt? Before answering these questions a short review of the evolution of our knowledge concerning the life cycles in Carabidae, including biennial ones, will be provided.

The first classification of the reproductive rhythms of carabid beetles was elaborated in 1939 by Sven Larsson. It was based on a careful analysis of museum collections, primarily representing the Danish fauna. Larsson studied material of more than 270 carabid species caught by pitfall trapping. Using the three parameters of reproduction time, period of imaginal activity and developmental time, he established six groups among the ground beetles: 1) spring reproduction either with high $F+$, 2) moderate $F(+)$ or 3) low autumn activity $F(\div)$, 4) without autumn activity $F\div$, 5) with autumn reproduction H and 6) two-year long development $2F+$.

The proportions of "spring" and "autumn breeders" were about three to one, while biennial development was established for two species only, *Nebria livida* (L.) and *Omophron limbatum* (F.). Larsson correctly observed that the "spring breeders" reproduce during the first half of the vegetation season, hibernating at the stage of an immature imago. In contrast, the "autumn breeders" propagate during the second half of the vegetation season, overwintering as larvae. Paradoxically, he formally grouped the species with a biennial development among "spring breeders", i.e. $2F+$. Such an interpretation could be considered appropriate for *O. limbatum*, but is quite inappropriate for *N. livida*. This has become clear after study of the physiological basis of gonad maturation.

Much study on insect physiology, including that of reproduction, carried out during the latter half of the last century, has greatly extended our knowledge of the life cycles of ground beetles. Thus, the book of Hans-Ulrich Thiele, "Carabid beetles in their environments", which appeared in 1977, recognised six types of annual reproduction rhythms in Carabidae: 1) spring breeders without larval dormancy either with obligatory dormancy in the adult (parapause), mainly governed by photoperiod or 2) facultative dormancy in the adult, governed by photoperiod (photoperiodic quiescence); 3) autumn breeders with larval hibernation, or parapause, either without dormancy in the course of adult development or 4) with adult photoperiodic aestivation or parapause; 5) species with unstable conditions of hibernation and potentially lacking dormancy; or 6) species requiring two years to develop.

Thiele (1977) discussed a two-year long pattern of development using three species as examples. In 1972, van Dijk suggested that during the short period of reproduction observed at high latitudes, *Calathus melanocephalus* (L.) may need two years to mature. In 1973, Luff, based on his own observations and the unpublished data of Houston, demonstrated that the development of *Pterostichus madidus* (F.) in sub-arctic conditions is extended for two years. An experimentally proven two-year long development has only been documented for a single species, *Abax ovalis* Duft. In 1975, Lampe described its life cycle in detail, stating that the females of *A. ovalis* show gonad dormancy during hibernation. Maturation is observed only after the day changes from short to long. Contrastingly, males have no photoperiodic gonad dormancy, their maturation being controlled by temperature fluctuations during hibernation.

In 1979, Wilfried Paarmann established a further five types of annual reproduction rhythms among the Carabidae. Two of these are observed in the North African subtropics, and the other three in the Central African tropics. In addition, Paarmann discussed for the first time the possible pathways of evolution of annual reproduction rhythms under the seasonal climate of the temperate zone. In contrast to Thiele (1977), he distinguished two modifications of biennial development in Carabidae. Paarmann suggested that the biennial development discussed by van Dijk (1972) and Luff (1973) could have evolved from the reproductive cycle of “autumn breeders,” with obligatory larval hibernation but without dormancy during adult development (Type 3, according to Thiele, 1977). On the other hand, he considered that the biennial cycle of *A. ovalis* (Lampe, 1975) might not have originated from the same type of annual cycle, because the control of gonad dormancy and adult maturation is drastically different in this case. Paarmann isolated this life cycle as a separate modification.

In 2004, Teiji Sota and Ryosuke Ishikawa reconstructed the phylogenetic and life-history evolution within the genus *Carabus* (sensu lato) on the basis of molecular data. They suggested that the biennial life cycles in Carabina could have evolved from “spring breeders”. As a direct shift from spring to autumn breeders in warm temperate climates is unlikely, they surmised that larval overwintering might have evolved among spring breeders in cool temperate conditions with a short warm season, resulting in the evolution of species with summer breeding. After that, such species with larval hibernation might have either colonized sub-arctic habitats, where they develop for two years, or re-colonized the warmest habitats, where a reproduction summer aestivation parapause in adult is observed, i.e. this evolved adaptation could confer a fitness advantage under certain climatic conditions.

So, the evolutionary scenario of Sota and Ishikawa (2004) contradicts that proposed by Paarmann (1979). On the other hand, my own observations regarding the time of development of overwintering larvae in several species of ground beetles with spring reproduction rather support Paarmann’s hypothesis.

MATERIALS AND METHODS

During the preparation of the current paper, numerous publications referring to the seasonal dynamics of activity, the demographic structure of populations, gonad maturation and larval development in Palaearctic Carabidae have been critically reviewed (Gilbert, 1956; Briggs, 1965; Inyaeva, 1965; Thiele, 1977; Murdoch, 1967; Vlijm & van Dijk, 1967; Andersen, 1969; Penney, 1969; Krehan, 1970; Kasandrova & Sharova, 1971; Potapova, 1972; van Dijk, 1972, 1979, 1994; Hürka, 1973, 1975; Paarmann, 1974, 1976a-b, 1990, 1994; Bauer, 1974; Ferenz, 1975, 1977; Kúrka, 1975; Lampe, 1975; van Heerdt et al., 1976; Jørum, 1976, 1980, 1985; Jones, 1979; Sharova & Dushenkov, 1979; Houston, 1981; Zetto Brandmayr, 1983; Refseth, 1984, 1988; Sota, 1985, 1986, 1987, 1994, 1996; Loreau, 1985; Butterfield, 1986, 1996; Brandmayr & Zetto Brandmayr, 1986; van Schaick Zillesen et al.,

1986; Nekuliseanu, 1987, 1990, 1994; Nelemans, 1987; Wallin, 1987; Kruchkova & Panov, 1988; Makarov & Chernyakhovskaya, 1989, 1990; Dushenkov & Chernyakhovskaya, 1990; Chernyakhovskaya, 1990; Makarov, 1994; Chemini & Pizzolotto, 1992; Ernsting et al., 1992; Basedow, 1994; Cárdenas, 1994; Schatz, 1994; Cárdenas & Hidalgo, 1995, 1998, 2004; Sharova & Denisova, 1995, 1997; Chaabane et al., 1996; Ortuño & Marcos, 1997; Purvis, 1998; Turin, 2000; Sharova & Filippov, 2003; Turin et al., 2003; Khobrakova & Sharova, 2005; Sharova & Khobrakova, 2005; Filippov, 2006, 2006a). As a result, data on the life cycles of more than 250 carabid species have been obtained.

Moreover, my own long-term observations from 1982 to 2007 in 20 regions of the former USSR and Russia have been summarized as well (Karpova & Matalin, 1990; Matalin, 1994, 1997a-c, 1998a-b, 2003, 2006, 2007; Matalin & Budilov, 2003; Matalin & Makarov, 2006; Matalin et al., 2007). This has provided detailed material on the life cycles of an additional 150 species.

For discussion of developmental variations, the criteria annual and biennial development are defined. In the case of annual life cycles, the beetles of a new generation emerge every year. Therefore, the hibernation of parental and daughter generations is observed in the same ontogenetic phase (Figs 2A, 4A). In the case of biennial life cycles, the beetles of the daughter generation appear once in two years. Their first hibernation is observed in a different ontogenetic stage compared to the parental generation (Figs 2B, 4B-C).

RESULTS

At the present time, the following modifications of biennial development are recognised among carabid species in the temperate climates of the Western Palearctic.

The first such species to be considered is *Harpalus affinis* Schrank (Matalin, 1998b). According to Larsson (1939), *H. affinis* is a "spring breeder" with adult hibernation. In the steppe zone, the seasonal dynamics of its activity are characterized by two peaks, one at the end of May to the middle of June, the second in the middle of August to early September (Fig. 1). The first peak represents overwintering beetles. Their reproduction commences in mid-May and ceases towards the beginning of August. The first instar larvae appear 12 days after egg-laying in late spring. Their development averages 14-15 days. At the end of June to early July, the first instar larvae molt to the second instar. The second instar development lasts c. 20 days. On average, the third instar larvae complete their development in 26 days. The first pupae are to be found at the beginning of August. The average duration of pupation is 16 days. So the development of *H. affinis* from adult to adult takes about 90 days. Similar developmental periods are observed in the first instar larvae taken by soil sampling at the end of May (Table 1). From the end of August, mass emergences of beetles of the new generation can be observed. This generation forms the second peak of locomotor activity. Later on, the young adults, as well as some beetles of the parental generation, hibernate. In this case the life cycle of *H. affinis* can be characterized as annual (Fig. 2A).

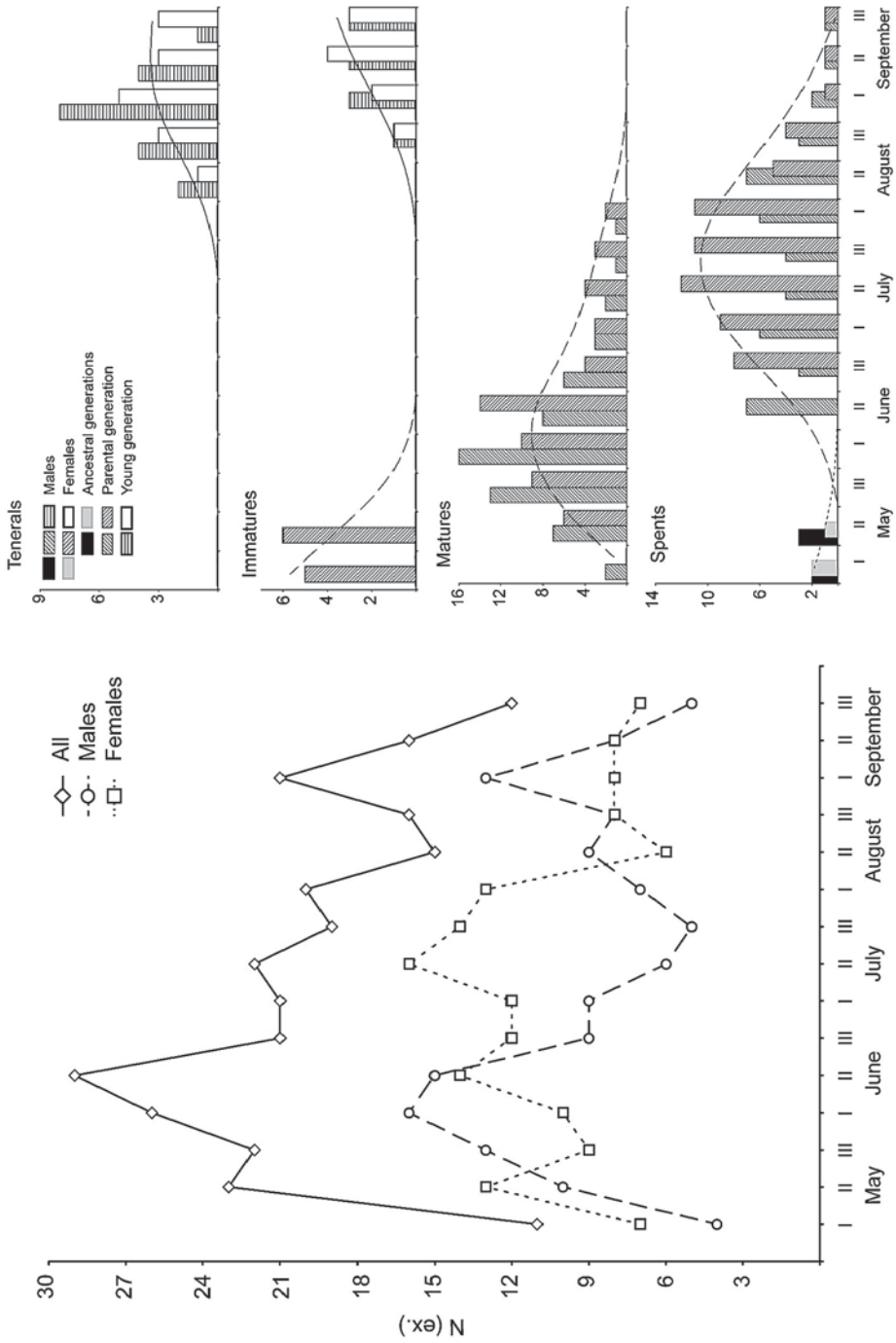


Fig. 1. Seasonal dynamics of activity, and sex and age structure of populations of *Harpalus affinis* in the steppe zone (south-western Moldavia, 1990).

Table 1. Developmental time of pre-imaginal stages of *Harpalus affinis* in south-western Moldavia (data from 1990, semi-natural conditions).

Developmental stages	Non-overwintering		Overwintering	
	Calendar times of development	Average duration of development ± SD	Calendar times of development	Average duration of development ± SD
Eggs	21.V -14.VI	14.5±8.7 (n = 4)		
L ₁	10.VI -27.VI	16.7±6.4 (n = 4)		
L ₂	21.VI -19.VII	21.8±2.4* (n = 7)	12.V -3.VII	49.5±0.5* (n = 2)
L ₃	12.VII -12.VIII	^{NS} 25.5±0.6** (n = 7)	14.V -28.VII 30.VI -2.VIII (after L ₂)	69.2±2.8** ^{NS} 29.5±2.1 (after L ₂) (n = 2)
Pupa	5.VIII -27.VIII	^{NS} 15.3±0.5*** (n = 7)	16.V -27.VIII 28.VII -26.VIII (after L ₂) 20.VII -30.VIII (after L ₃)	102±2.0*** (n = 2) ^{NS} 20.5±6.4 (after L ₂) (n = 2) ^{NS} 28.9±7.5 (after L ₃) (n = 12)

Notes: *, **, *** - significant differences (p<0.05, T-test); NS – not significant differences.

In *H. affinis*, also older instar larvae, as well as pupae, hibernate in addition to mature and immature adults. This is well supported both by personal soil sampling data taken in early May and literature sources (Briggs, 1965; Inyaeva, 1965; Budiolov, 1990; Dushenkov, Chernyakhovskaya, 1990). According to my own observations, the ratio of overwintering pre-imaginal stages of *H. affinis* in the steppe zone is: 1 pupa, 2 second instars larvae, 20 third instars larvae. It is noteworthy that the development of overwintering larvae

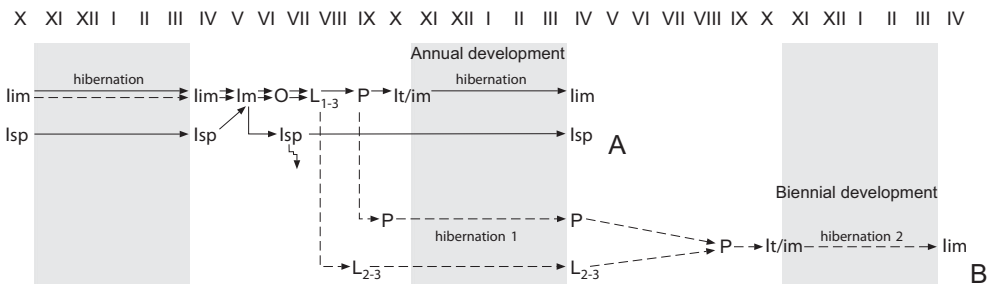


Fig. 2. A scheme of the facultatively biennial life cycle with spring-summer reproduction (an example of *Harpalus affinis*). It/im - teneral; Iim - immature; Im - mature; Isp - spent beetles; O - eggs; L₁₋₃ - larvae of first-third instars, respectively; P - pupae.

and pupae is greatly prolonged. On average, the second instar larvae molt into the third instar 58 days after hibernation. After that, the development of the third instar larvae usually lasts 25 days, and the pupae, 23 days. So the time of appearance of young beetles, starting from the overwintering second instar larvae, averages 106 days. The development of the overwintering third instar larvae takes longer, and they can be encountered in the soil at the beginning of May, but on average, they pupate only in mid to late July, i.e. in 68 days. The emergence of young beetles is observed after another 36 days, in the mid to late August. So the average developmental time from the overwintering third instar larvae until the beetles of the new generation, takes 105 days. The maximum delay in development is observed in the hibernated pupae. In 1991, two pupae were collected on the 16th of May. The beetles (a male and a female) emerged only on the 23rd and 27th of August, that is, after 100 and 104 days, respectively (Table 1).

In spite of the delayed development of the overwintering pre-imaginal stages, the emergence of teneral beetles is observed at the same time as mentioned above, that is, from the end of August to early September. On the other hand, these beetles do not reproduce in the same season. So the total duration of their development period increases to two years (Fig. 2B).

Thus, in the populations of *H. affinis* in Moldova, two subpopulations with different seasonal rhythms are formed. Due to this, the life cycle of *H. affinis* is characterized as multivariant. In the case of adult hibernation, the development is completed in one year. But in the case of larval and pupal hibernation, the development is increased to two years. Since only a part of the whole population develops during two years, the life cycle of *H. affinis* is realized as facultatively biennial with spring-summer reproduction (Fig. 2). The extended period of reproduction seems to be the cause of *H. affinis* hibernation in the atypical ontogenetic phases. As a result, desynchronization of the life cycle is observed. Yet the completion of the development of both hibernated and non-hibernated larvae at the same time supports its life cycle synchronization. It is noteworthy that these two sub-populations are not isolated from each other. The daughter generation which hibernates in the different ontogenetic stages can develop in either of the two ways described above. Thus, the biological integrity of the species is maintained.

An analysis of the sex and age structures of the population showed that gonad maturation in *H. affinis* males is completed in short-day conditions. On the contrary, the gonad maturation in females is observed only after the daytime changes from short to long (Fig. 1). Hence the above pattern of a biennial life cycle could have evolved in response to the annual reproduction rhythms of "spring breeders" (Type 1, according to Thiele, 1977), with the same mechanism of gonad maturation. A similar life cycle is observed in *Harpalus distinguendus* (Duft.), *Ophonus azureus* (F.), *Chlaenius vestitus* (Payk.), *Omophron limbatum* (F.) and possibly also in *Abax ovalis* Duft.

As a second example, *Pterostichus melanarius* (Ill.), one of the most common and abundant Palaearctic ground beetle species (Matalin, 2006), has been chosen. According to Larsson (1939), *P. melanarius* is an "autumn breeder" with larval hibernation. The overwintering third instars occur in pitfall traps and soil samples at the beginning of the vegetation season. In mixed forests, the duration of larval development after hibernation averages 24

days, and the pupal stage only seven days. As a rule, the beetles of a new generation emerge at the end of June/early July. The reproduction period continues from the end of July until mid-September (Fig. 3). The first instar larvae appear at the beginning of August. The second instar larvae are to be found at the end of August while the third instars are to be seen in the middle of September. The larvae of the older instars hibernate. So, the life cycle of *P. melanarius* in such conditions is annual, because the emergence and reproduction of teneral beetles are observed during the same season and the hibernation of parental and daughter generations take place during the same ontogenetic phase (Fig. 4A).

However some reports (Jørum 1980; Wallin, 1987; Kryuchkova & Panov, 1988; Nekuliseanu, 1990; Sharova & Filippov, 2003) present direct evidence of a possible biennial development of *P. melanarius*. In addition, some indirect data concerning a two-year long development in at least part of *P. melanarius* populations are contained in virtually any publication dealing with the ecology of this species (Lindroth, 1945; Skuhřavý, 1959; Greenslade, 1965; Vasil'eva, 1978; Jones, 1979; Desender et al., 1985; Kålås, 1985; Makarov & Chernyakhovskaya 1989; Sharova & Denisova 1997; Faddl & Purvis, 1998). Both larvae and adults are known to hibernate all over the distribution area of *P. melanarius*. The imagines are represented by mature individuals of the ancestral generations, as well as by non-copulated individuals of the new generation. A delayed maturation of the teneral beetles is due to their late emergence in mid to late August, which implies a less than minimum sum of effective temperatures. According to Krehan (1970), *P. melanarius* females and males attain sexual maturity in more or less three weeks at about 20°C. At lower temperatures, a thermic quiescence occurs.

The overwintered beetles form an early summer peak of locomotor activity. At the same time, specimens of ancestral generations start their reproduction at least ten days earlier than the immature ones (Fig. 3). In mixed forests, oviposition is observed from the end of June to early July. On average, eggs develop for 9.5 days, the first instar larvae for 17.5 days, and the second instars are found in mid to late July. During August, some of them molt into the third instar, whereupon the older instar larvae hibernate. In this case, emergence and reproduction of teneral beetles are observed over a year. Besides this, they pass the first hibernation as adults while the parental generation hibernates as larvae. Thus, the overwintering immature specimens of *P. melanarius* need two years to develop (Fig. 4B).

As with *H. affinis*, the populations of *P. melanarius* show two temporally, partly overlapping, sub-populations with different seasonal rhythms. Larval hibernation ensures an annual development, though the hibernation of immature adults maintains a two-year long development. Thus, over most of the area of natural habitats, ranging from the steppe to the middle taiga (= boreal forest) zones, the life cycle of *P. melanarius* is multivariant and could be defined as facultatively biennial with summer-autumn reproduction. The prolonged period of emergence of the new generation together with the heterogeneous maturation of the beetles, is the cause of desynchronisation of *P. melanarius*' life cycle, though here the larval hibernation maintains its overall synchronisation.

In adverse conditions, however, such as those observed near the northern range limits of *P. melanarius*, the life cycle is sharply different. In the northern taiga zone, its reproduction

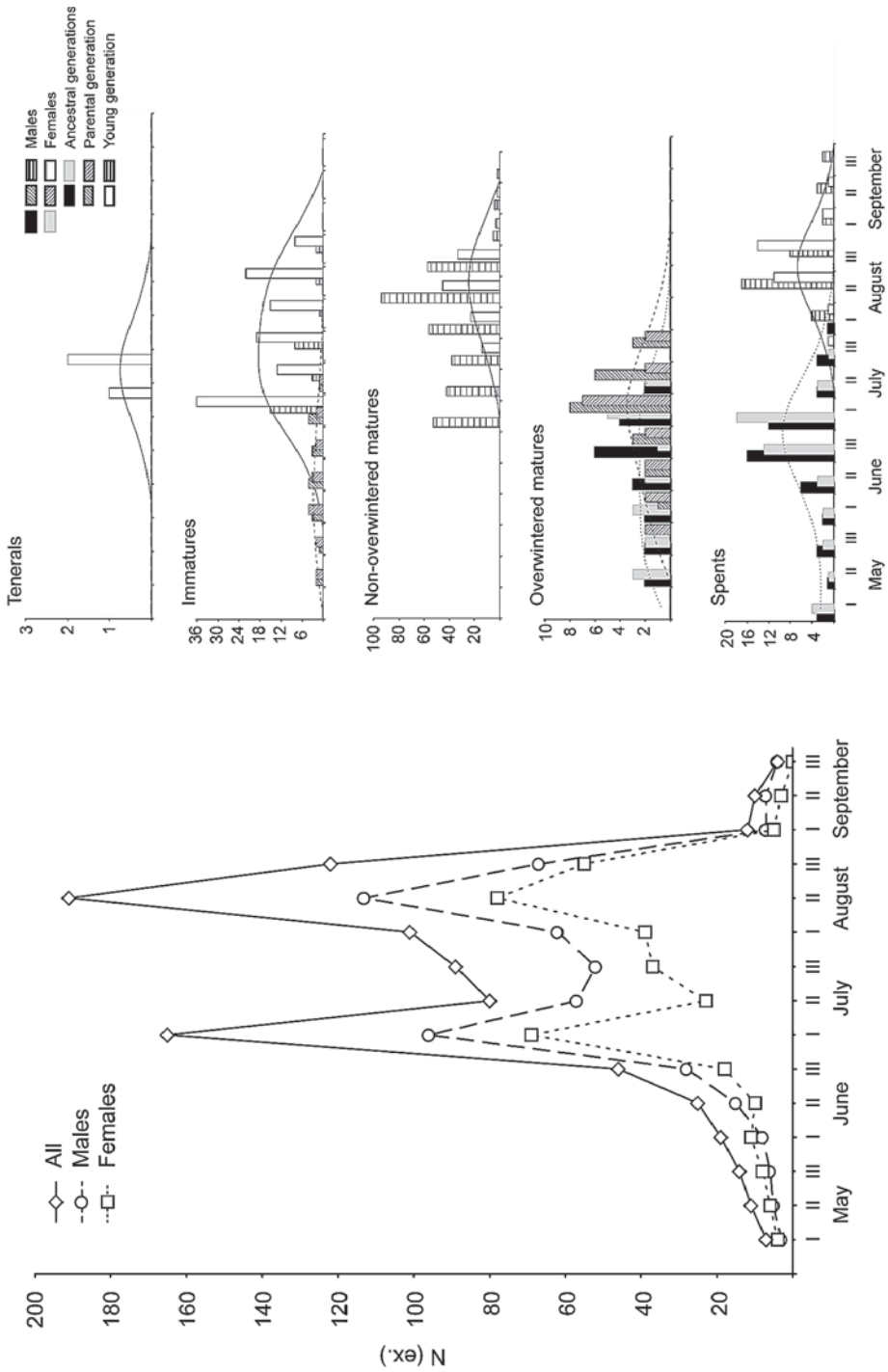


Fig. 3. Seasonal dynamics of activity, and sex and age structure of populations of *Pterostichus melanarius* in the steppe zone (south-western Moldavia, 1990).

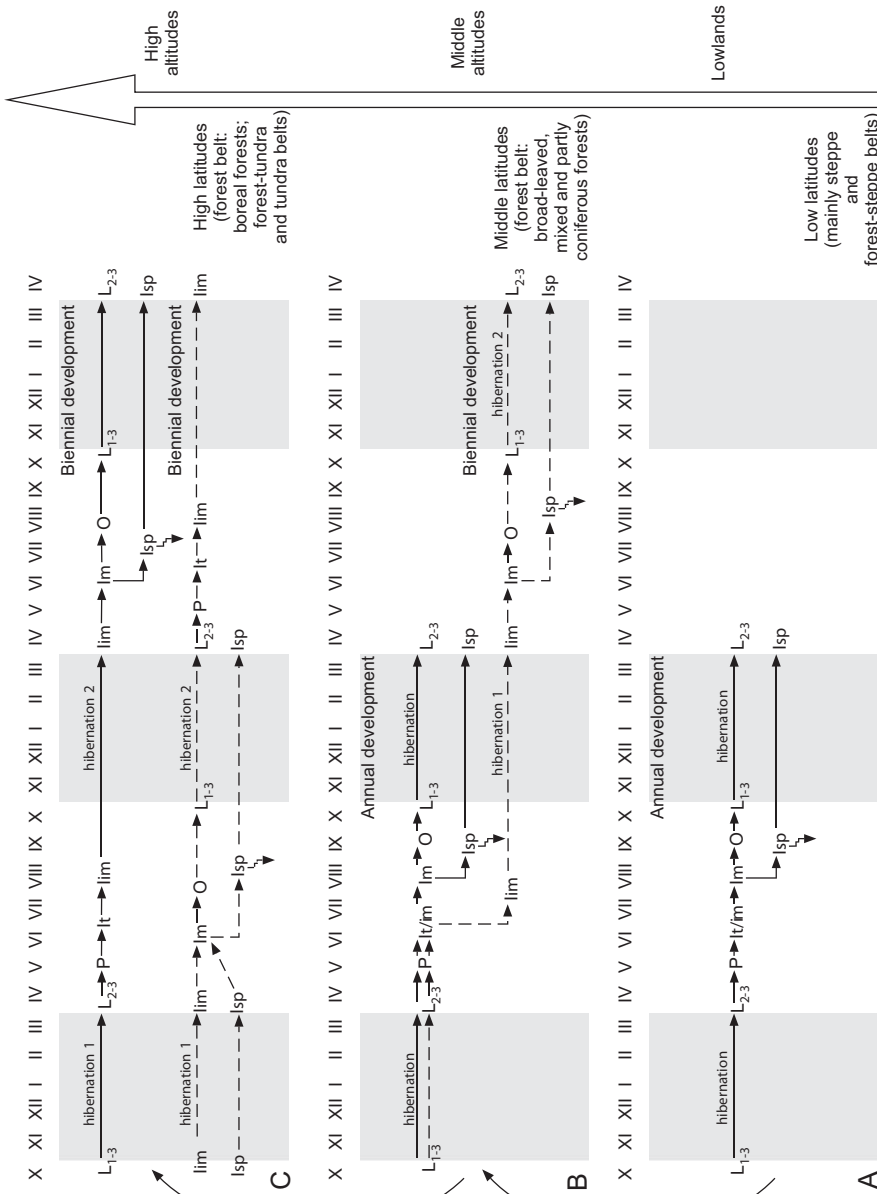


Fig. 4. A scheme of modifications of the *Pterostichus melanarius* life cycle across a climatic gradients. A - annual life cycle with summer-autumn reproduction; B - facultatively biennial life cycle with summer-autumn reproduction; C - obligate biennial life cycle early summer reproduction; other explanations as in Fig. 2.

lasts from mid-June until early August. Then only the overwintered beetles, both mature and immature, breed. The new generation cohort that emerges from the overwintering larvae during the current season remain sexually immature until the following year (Sharova & Filippov, 2003: fig. 3B). In this case, both adult and larval hibernation is the cause of a two-year long development. As a result, an almost complete separation of the sub-populations overwintering in different ontogenetic phases is observed. However, individuals from the ancestral generations represent a connecting link between the sub-populations, thus maintaining the biological integrity of the species. In such conditions, the life cycle of *P. melanarius* is altered from facultatively biennial with summer-autumn reproduction to obligate biennial with early-summer reproduction. A new generation in either sub-population appears only once in two years. But thanks to the emergence alternately every second year of teneral beetles in each subpopulation, a new generation in the population as a whole is produced every year. The development of beetles in each subpopulation is realized on the basis of the same seasonal rhythms shifted by a year (Fig. 4C). Earlier, such populations were termed as by-side (Matalin, 2006). In this way, in the northern taiga the multivariant pattern of the *P. melanarius* life cycle is replaced by a monovariant one.

Gonad maturation of both males and females of *P. melanarius* is well known to be independent from photoperiod (Krehan, 1970; Thiele, 1977). However, normal completion of metamorphosis is observed only in overwintering larvae (Hürka, 1975; Thiele, 1977). Then the described biennial life cycle could have evolved on the basis of annual reproduction rhythms of "autumn breeders" (Type 3, according to Thiele, 1977), with a similar mechanism of gonad maturation.

The life cycle of *P. madidus* is just as in *P. melanarius*. According to Luff (1973), in the south of Northumberland (UK), the life cycle of this species is facultatively biennial, because some immature specimens hibernate and are then to be found in May. Still, according to unpublished data of Houston (quoted by Luff, 1973), in the Moor House National Reserve (UK), all populations of *P. madidus* develop in two years. In this case, its life cycle is obligate biennial. Similar results have been obtained by Butterfield (1996) after a study of the *P. madidus* life cycle across an altitudinal gradient in Great Dun Fell (UK). In addition, similar life cycles are observed in numerous carabid beetles, such as *Carabus glabratus* Payk., *C. violaceus* L., *C. aurolimbatus* Dej., *Broscus cephalotes* L., *Pterostichus niger* (Shall.), *Harpalus rufipes* Degeer and so on.

As an example of the third type of biennial development among carabid beetles, *Carabus problematicus* Herbst has been selected. Larsson (1939) and later Lindroth (1945), considered *C. problematicus* to be a "spring breeder." However this is not entirely true. In fact this species is an "autumn breeder" with larval hibernation. The dynamics of its locomotor activity are characterized by two peaks. The first is observed in late spring to early summer, while the second is in late summer to mid-autumn (van der Drift, 1951, 1958; Greenslade, 1965; Thielle, 1977; Houston, 1981; Jørum, 1985; Loreau, 1985; Butterfield, 1986, 1996; Sparks et al., 1995). In the temperate zone, the first peak is due to the activity of both the overwintering parental generation and the freshly emerged teneral beetles. The subsequent activity decline is related to a short aestivation period,

only then followed by reproduction. The larvae appearing during the autumn hibernate. In this case, the life cycle of *C. problematicus* is annual.

But in sub-arctic conditions, its life cycle is sharply altered. According to Houston (1981: fig. 3), in the Moor House National Reserve (UK), the first activity peak in the population of *C. problematicus* is observed in June. At this time, the overwintering beetles both from the parental and daughter generations are active. However, there is no reproduction until the end of July. As a result, the life cycle of *C. problematicus* is strongly synchronized, with oviposition observed during the same period. The peak of reproduction activity is restricted to the middle to the end of August and this coincides with the emergence of the new generation. The locomotor activity finishes at the end of September, whereafter the larvae, some of the adults of the parental generation as well as all beetles of the new generation hibernate. The development of the overwintering larvae and adults lasts two years. In these conditions the life cycle of *C. problematicus* is obligate biennial with late summer reproduction.

Presumably there must be a gradual transition between these extremely different life cycle patterns. Under certain conditions, cohorts of both the annual and biennial development cycles can coexist in the same population. In this case, the life cycle is facultatively biennial with autumn reproduction. This is well-supported by studies on the *C. problematicus* population structure across an altitudinal gradient in northern England (Butterfield, 1986, 1996) and northern Wales (Sparks et al., 1995). In the lowlands, the life cycle of *C. problematicus* is either annual or a small proportion of specimens develops over two years. At intermediate altitudes (100–300 m), the proportion of individuals with biennial development is greater. At high altitudes (500–850 m), the life cycle is purely biennial. It is noteworthy that, as in *H. affinis* and *P. melanarius*, the facultative biennial life cycle of *C. problematicus* is multivariant, because both subpopulations show different seasonal rhythms.

According to the dominant opinion, *C. problematicus* exhibits a larval hibernation parapause, as well as an adult photoperiodic aestivation parapause (van der Drift, 1951, 1958; Thielle, 1977; Houston, 1981; Jørum, 1985; Loreau, 1985; Butterfield, 1986). Gonad maturation in this species is observed only after the transition from long-day to short-day conditions. Thus, this kind of biennial development could have evolved on the basis of annual reproduction rhythms of “autumn breeders” (Type 4, according to Thiele, 1977). The same type of life cycle is found in *Carabus hortensis* L., *C. exaratus* Quens., *Calathus erratus* (Sahlb.), *C. fuscipes* (Goeze), *Curtonotus alpinus* (Payk) etc.

DISCUSSION

An analysis of the geographic variability of the sex and age population structures in Carabidae shows that a development over two years is quite often observed among species with phenologies differing in various natural zones, ranging from the tundra to the steppe (Jørum, 1980, 1985; Houston, 1981; Butterfield, 1986, 1996; Sharova & Denisova, 1997; Matalin, 1997c, 1998b, 2006; Matalin & Budilov, 2003; Sharova & Filippov, 2003; Filippov, 2006a–b). Numerous carabid species have quite broad distributions. So they

have to cope with a great variation in weather and climatic conditions, as well as with different landscape-habitat and vegetation patterns. As a result, across such considerable gradients, regular changes can be observed in the duration of locomotor activity, breeding time and development of pre-imaginal stages, as well as adult maturation.

With increasing latitude or altitude, the reproduction period in “spring breeders” is not only shortened but also shifts to a later time. Spring reproduction is replaced by a spring-summer or early-summer one. Amongst “autumn breeders,” the period of reproduction is shifted to an earlier date, being observed in late, mid or even early summer (Briggs, 1965; Jørum, 1980, 1985; Sota, 1985, 1994, 1996; Butterfield, 1986, 1996; Refseth, 1988; Sparks et al., 1995; Matalin, 1997c, 1998b, 2006; Sharova & Filippov, 2003; Khobrakova & Sharova, 2005; Filippov, 2006a-b). Because of the shorter vegetation season, the oviposition time is greatly reduced, while the duration of larval development and adult maturation is increased. For the reasons given above, hibernation may be observed in atypical ontogenetic phases, such as larva and pupa for “spring breeders” and as immature beetles for “autumn breeders”. Therefore, in numerous carabid beetle species some individuals of the population develop in two years.

In southern regions or over the plains, most individuals show annual life cycles and the proportion of beetles with a biennial development is small. When moving to higher altitudes or latitudes, the proportion of species with biennial development increases. At the northern range peripheries, and at high altitudes, entire populations demonstrate biennial life cycles. So not only facultatively biennial life cycles might have evolved across gradients of climate conditions, but also their gradual transformations into obligate biennial ones (Fig. 4).

At the same time, in various habitats of the same climatic zone, even with relatively favourable conditions, different types of biennial life cycle can be realized. According to Sharova and Denisova (1997), hibernated specimens of *P. melanarius*, both mature and immature, reproduce in oak woods of the Tambov area of Russia at the end of spring to early summer. On the other hand, from mid-summer until early autumn, the teneral beetles of the new generation breed as well (Sharova & Denisova, 1997: fig 4b). In this case, the life cycle is facultatively biennial and multivariant. In contrast, only hibernated beetles reproduced in pine forests. Specimens of the new generation, which emerged from the overwintering larvae, hibernated as immature adults (Sharova & Denisova, 1997: fig 4a). Thus, the life cycle in this case is obligate biennial and monovariant. Besides this, a facultatively biennial life cycle adapting to an obligate biennial one has been observed under anomalous weather conditions. Thus, according to Jørum (1980), in Denmark in years with a long and cold winter, and a short and cool summer, the life cycles of *P. melanarius* and *P. niger* are solely obligate biennial.

According to this evidence, one can derive a very important conclusion. In the temperate zone of the Western Palaearctic, biennial life cycles among carabid beetles have evolved independently at least three times (Fig. 5). Under these conditions, the following versions of biennial development may have developed:

- Facultatively biennial with spring-summer reproduction (on the basis of the annual rhythm of “spring-breeders” – Type 1, according to Thiele, 1977);

- Facultatively biennial with summer-autumn reproduction and then
- Obligate biennial with early summer reproduction (on the basis of the annual rhythm of “autumn breeders” – Type 3, according to Thiele, 1977);
- Facultatively biennial with autumn reproduction and then
- Obligate biennial with late summer reproduction (on the basis of the annual rhythm of “autumn breeders” – Type 4, according to Thiele, 1977).

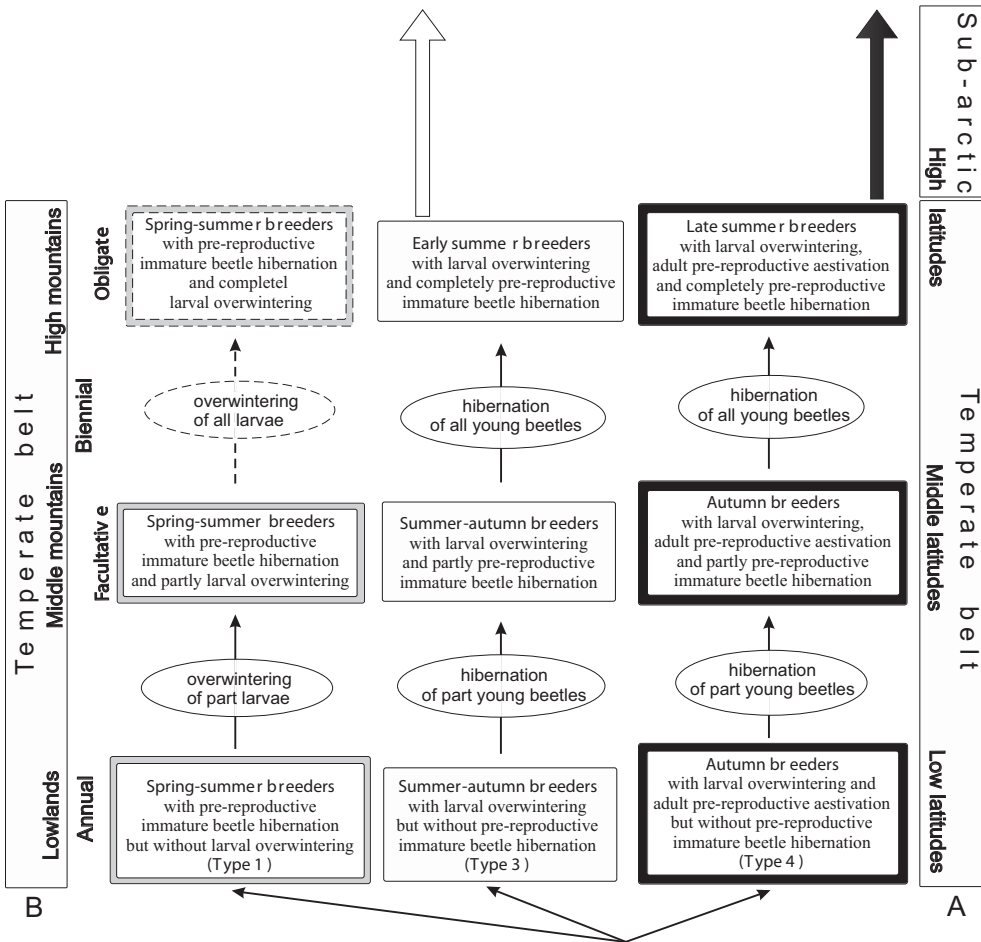


Fig. 5. A scheme of possible evolution of biennial life cycles among Carabid beetles of Western Palearctic. A - latitudinal trend; B - altitudinal trend; large arrows indicate immigration of “autumn breeders,” with different biennial life cycles in sub-arctic regions; dotted lines indicate a possible pathway of biennial life cycle among “spring breeders.”

The existence of an obligate biennial life cycle among “spring breeders” remains open to question. At present there is no firmly established evidence that would support such a type of biennial development. Colonization of northern habitats by numerous carabid species with spring or spring-summer reproduction e.g. all *Harpalus*, most *Amara* and *Pterostichus* spp. is limited first of all by the lack of suitable habitats, coupled with both poor food resources and the developmental features of overwintering larval stages. Unlike species with autumn reproduction and hibernating larvae, “spring breeders” have no pre-adaptations for larval overwintering. The hibernation of pre-imaginal stages amongst “spring breeders” can only be successful in relatively mild conditions, such as those observed in the southern regions, partly also in the middle part of the temperate zone, as well as in regions with a mild coastal climate.

The development of overwintering pre-imaginal stages amongst “spring breeders” seems to be controlled by photoperiod. Indeed, successful completion of metamorphosis in this case is only observed under daylight changing from long to short, or even under short-day conditions alone. This is suggested by the development of overwintering *H. affinis* larvae and pupae in the steppe zone as described above (Table 1). Apparently, under constant illumination conditions at high latitudes, the development of overwintering larvae and pupae of “spring breeders” is suppressed.

In any case, in the northern taiga, sub-arctic and barren tundra, all carabid beetles with initial spring reproduction fully complete their annual development even during the short vegetation season (Andersen, 1969, 1984; Butterfield, 1996; Sharova & Filippov, 2003; Filippov, 2006a, 2007). So, at high latitudes, among ground beetles with biennial development, only “autumn breeders” are found (Lindroth, 1945; Refseth, 1988; Butterfield, 1996; Filippov, 2007).

However, by considering the characteristic sex and age structure of a population, I am able to postulate a mechanism by means of which a certain type of biennial life cycle might have evolved. A study by Houston (1981) is a good example of this. He studied the phenology and life cycles of *C. glabratus* and *C. problematicus* under sub-arctic conditions.

Reproduction in hibernated specimens of *C. glabratus* has been observed in June to July, while the emergence of teneral beetles - in August to September (Houston, 1981: fig. 2). Under sub-arctic conditions, its life cycle is obligate biennial with early-summer reproduction. In southern and central Europe, this species shows a summer-autumn reproduction pattern without gonad dormancy (Stiprais, 1970; Hürka, 1973; Grüm, 1975; Feoktistov & Dushenkov, 1982; Dülge, 1994; Günther & Assmann, 2000; Turin et al., 2003). Thus, the biennial life cycle in *C. glabratus* could have evolved on the basis of the annual, Type 3 reproduction rhythm of Thiele, (1977). Similar patterns are observed in *Carabus violaceus* (Refseth, 1984), *C. aurolimbatus* (Sharova & Filippov, 2003), *Pterostichus melanarius* and *P. niger* (Jørum, 1980; Sharova & Filippov, 2003), as well as in *P. madidus* (Luff, 1973; Butterfield, 1996).

Contrastingly, in *Carabus problematicus* the reproduction of overwintering beetles and the emergence of a new generation are observed concurrently, from late July until

mid-September (Houston, 1981: fig. 3). Thus, in the sub-arctic, the life cycle of *C. problematicus* is obligate biennial with late summer reproduction. However, in middle Europe this species is characterized by autumn reproduction with gonad dormancy during aestivation and by gonad maturation after daylength changing from long to short (van der Drift, 1951, 1958; Thiele, 1977; Jørum, 1985; Loreau, 1985; Turin et al., 2003). The biennial life cycle of *C. problematicus* could have evolved on the basis of the Type 4 annual reproduction rhythm, as described by Thiele (1977). At high latitudes, the life cycles of *Carabus hortensis* (Refseth, 1988), *Calathus erratus* (Kålås, 1985; Refseth, 1988) and *C. fuscipes* (Kålås, 1985; Butterfield, 1996) are similar.

Because the vegetation season at high latitudes and altitudes is short, whilst the reproduction time in all carabid species is markedly shortened, reproductive monotony and a restricted spectrum of life cycles in different habitats is observed. As a result, the contradiction arises that phenologically, the species are biennials with “early-summer” or “late-summer” reproduction, whereas their life cycles could have evolved starting from either of the two annual autumn breeder rhythms. Perhaps this paradox led to the mistake in Sota and Ishikawa’s (2004) hypothesis.

My studies allow me to conclude that biennial life cycles among “spring breeders” (Type 1, according to Thiele, 1977) and “autumn breeders” (Type 4, according to Thiele, 1977), could have originated independently from one another (Fig. 5). The most important feature in both cases is the hibernation of some individuals in atypical ontogenetic stages. The developmental time of such individuals is then increased to two years and the life cycle is thus transformed from annual to facultatively biennial. As one can easily see, the reproduction time both in spring and autumn breeders remains unchanged. Under cooler environmental conditions, further transformations of a biennial life cycle in autumn breeders can be observed. This results from the replacement of a facultative biennial development with an obligate biennial one. In this case, the period of reproduction is shifted from autumn to late summer. A similar transformation is observed in a different group of “autumn breeders” (Type 3 of Thiele, 1977).

In theory, an obligate biennial life cycle among “spring breeders” is possible in mountains, because the photoperiodic conditions there do not change so sharply. Here lies the principal difference between two general trends in biennial development in carabid beetles: latitudinal and altitudinal.

At high latitudes, obligate biennial life cycles seem to have evolved on the basis of annual reproduction rhythms of “autumn breeders,” Types 3 and 4 only (Fig. 5A). In contrast, at high altitudes, in addition to the types mentioned above, an obligate biennial life cycle in “spring breeders,” Type 1, is theoretically possible (Fig. 5B). However, as is the case with high latitudes, no reliable data exist for mountains which would support obligate biennial carabids with a spring or spring-summer reproduction pattern (De Zordo, 1979; Jakuczun, 1979; Sota, 1985, 1994, 1996; Brandmayr & Zetto Brandmayr, 1986; Butterfield, 1986, 1996; Chemini & Pizzolotto, 1992; Hemmer & Terlutter, 1991; Schatz, 1994; Sparks et al., 1995; Khobrakova & Sharova, 2005; Sharova & Khobrakova, 2005).

At present, we have sufficient knowledge concerning both gonad maturation and the exogeneous regulation of annual reproduction rhythms in carabid beetles. However, there is an obvious knowledge gap regarding the study of the main features of larval development regulation. Further collection of such data would expand our understanding biennial life cycles. The biennial development patterns as observed in some individuals in the populations of numerous carabids in different habitats within the temperate zone are clearly of adaptive importance. The long reproduction period and asynchronous appearance of the subsequent generations causes age heterogeneity. These factors stabilize the population structure and decrease the risk of extinction of local populations (Weber & Klenner, 1987; Matalin, 1998b) and it is probably not coincidental that the majority of brood-watching Pterostichines, many of which inhabit mountainous habitats, have a biennial life cycle (Brandmayr, 1977). Individuals with a prolonged development form a strategic reserve in the whole population in force-majeure situations. Maybe thanks to such features as their life cycles, these species show vast distributions and occur in high numbers, not only in natural but also in man-made habitats, including agrocoenoses. According to my estimates, the proportions of such species in different communities within the temperate zone is very high, well over one-third of the fauna of dominants. So a biennial development in Carabidae is rather the rule than the exception.

ACKNOWLEDGEMENTS

I would like to thank all of my carabidologist colleagues who have helped with this study and who have contributed material for analysis and discussion. In particular, I would like to express my gratitude to my teacher, Professor Inessa Khristianovna Sharova, as well as to my colleague and friend, Professor Kirill Vladimirovich Makarov (both from the Moscow State Pedagogical University, Russia), for the important critiques and fruitful discussions of the presented contribution. I would also like to address special thanks to Professor Sergei Il'ich Golovach (Institute of Problems of Ecology and Evolution, Moscow, Russia) and Dr. Stephen Venn (University of Helsinki, Finland) for a critical review of the text.

This study was financially supported by the Russian Foundation for Basic Research (projects No. 06-04-49456, 07-04-08381) as well as the Presidential Support Program for Leading Academic Schools (project No. HIII-2154.2003.4).

REFERENCES

- Andersen, J.M. (1969). Habitat choice and life history of *Bembidiini* (Col., Carabidae) on river banks in central and northern Norway. – *Norsk ent. Tidsskr.* 17: 17-65.
- Andersen, J.M. (1984). A re-analysis of the relationships between life cycle patterns and the geographical distribution of Fennoscandian carabid beetles. – *J. Biogeography*. 11: 479-489.
- Basedov, Th. (1994). Phenology and egg production in *Agonum dorsale* and *Pterostichus melanarius* (Col., Carabidae) in winter wheat fields of different growing intensity in

- Northern Germany. – In: Carabid beetles: ecology and evolution (Desender, K., Dufrêne, M., Loreau, M., Luff, M.L. & Maelfait, J-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 101-108.
- Bauer, T. (1974). Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae). – Oecologia. 14: 139-196.
- Bey-Bienko, G.Ya. (1980). General entomology (3-d edition). – High School Press, Moscow, 416 pp. [in Russian].
- Brandmayr, P. (1977). Ricerche etologiche e morfofunzionali sulle cure parentali in Carabidi Pterostichini (Coleoptera, Carabidae:Pterostichini). – Redia, 60:275-316.
- Brandmayr, P. & Zetto Brandmayr, T. (1986). Phenology of ground beetles and its ecological significance in some of the main habitat types of Southern Europe. – In: Carabids beetles: their adaptations and dynamics (den Boer, P.J., Mossakowski, D., Luff, M.L. & Weber, F., eds). Gustav Fisher Verlag, Stuttgart-New York, p. 195-220.
- Briggs, J.B. (1965). Biology of some ground beetles (Col. Carabidae) injurious to strawberries. – Bull. Entomol. Res. 56: 79-93.
- Budilov, V.V. (1990). Autumnal distribution of ground beetles in agrocenosis of Mordovian ASSR. – In: Structure and dynamics of populations of edaphic and herpetobiotic invertebrates (Sharova, I.Kh., ed). Moscow State Pedagogical Institute Press, Moscow, 1: 51-57 [in Russian].
- Bourgeois, J. (1882). Monographie des Lycides de l'Ancirnt-Monde. – L'Abeille. 20: 1-120.
- Butterfield, J. (1986). Changes in life-cycle strategies of *Carabus problematicus* over a range of altitudes in Northern England. – Ecol. Entomol. 11: 17-26.
- Butterfield, J. (1996). Carabid life cycle strategies and climate change: a study on an altitudinal transect. – Ecol. Entomol. 21: 9-16.
- Cárdenas, A.M. (1994). On the life history of *Calathus granatensis* (Coleoptera, Carabidae) in southwest Iberian Peninsula. – In: Carabid beetles: ecology and evolution (Desender, K., Dufrêne, M., Loreau, M., Luff, M.L. & Maelfait, J-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 109-116.
- Cárdenas, A.M. & Hidalgo, J.M. (1995). Datos sobre la biología de reproducción desarrollo larvario de *Carabus (Hadrocarabus) lusitanicus* (Fabricius, 1801) (Coleoptera: Carabidae). – Elytron. 9: 139-145.
- Cárdenas, A.M. & Hidalgo, J.M. (1998). Data on the biological cycle of *Steropus globosus* (Coleoptera Carabidae) in the south west of Iberian Peninsula. – Vie Milieu. 48: 35-39.
- Cárdenas, A.M. & Hidalgo, J.M. (2004). Life cycles of riparian ground beetles (Coleoptera, Carabidae): strategies for reproduction in the bank of a temporary stream in the southern Iberian peninsula. – Vie Milieu. 54: 47-56.
- Chaabane, K., Loreau, M. & Josens, G. (1996). Individual and population energy budgets of *Abax ater* (Coleoptera, Carabidae). – Ann. Zool. Fenn. 33: 97-108.
- Chemini, C. & Pizzolotto, R. (1992). Comunità di carabidi in siti forestali dei Monti Lessini (Trentino) (Coleoptera: Carabidae). – Studi Trentini Sci. Nat. Acta Biol. 67: 197-227.
- Chernov, Yu.I. (1974). Some regularities of the adaptation of terrestrial animals to landscape-zonal conditions. – Zh. Obshch. Biol. 35: 846-857 [in Russian].
- Chernov, Yu.I. (1978). Adaptive features of the life cycles of the tundra zone insects. – Zh. Obshch. Biol. 39: 394-402 [in Russian].
- Chernyakhovskaya, T.A. (1990). Seasonal dynamics of activity and structure of populations of carabid species *Pterostichus niger* Schaller in different biotopes. – In: Structure and

- dynamics of populations of edaphic and herpetobiotic invertebrates (Sharova, I.Kh., ed). Moscow State Pedagogical Institute Press, Moscow, 1: 44-49 [in Russian].
- Davies, L. (1987). Long adult life, low reproduction and competition in two sub-Antarctic carabid beetles. – *Ecol. Entomol.* 12: 149-162.
- den Boer, P.J. & van Dijk, Th.S. (1996). Life history patterns among carabid species. – *Tijdschr. Ent.* 139: 1-16.
- Desender, K., van den Broeck, D. & Maelfait, J.-P. (1985). Population biology and reproduction in *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) from a heavily grazed pasture ecosystem. – *Med. Fac. Landbouww. Rijksuniv.* 50: 567-575.
- De Zordo, I. (1979). Phänologie von Carabiden im Hochgebirge Tirols (Obergurgl, Österreich) (Insecta: Coleoptera). – *Ber. Nat. -med. Ver. Innsbruck.* 66: 73-83.
- Dülge, R. (1994). Seasonal activity of carabid beetles in wooded habitats in northwest Germany (Coleoptera, Carabidae). – In: *Carabid beetles: ecology and evolution* (Desender, K., Dufrêne, M., Loreau, M., Luff, M.L. & Maelfait, J.-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 125-131.
- Dushenkov, V.M. & Chernyakhovskaya, T.A. (1990). Carabid larvae in agricultural areas of the Moscow region. – In: *Structure and dynamics of populations of edaphic and herpetobiotic invertebrates* (Sharova, I.Kh., ed). Moscow State Pedagogical Institute Press, Moscow, 1: 84-99 [in Russian].
- Ernsting, G., Isaaks, J.A. & Berg, M.P. (1992). Life cycle and food availability indices in *Notiophilus biguttatus* (Coleoptera, Carabidae). – *Ecol. Entomol.* 17: 33-42.
- Fadl, A. & Purvis, G. (1998). Field observations on the lifecycles and seasonal activity patterns of temperate carabid beetles (Coleoptera: Carabidae) inhabiting arable land. – *Pedobiologia.* 42: 171-183.
- Feoktistov, V.F. & Dushenkov, V.M. (1982). Seasonal dynamics of activity of the ground beetles (Coleoptera, Carabidae) in forests of different types at the southern taiga boundary. – *Zool. Zh.* 61: 227-232 [in Russian].
- Ferenz, H.-J. (1975). Photoperiodic and hormone control of reproduction in male beetles, *Pterostichus nigrita*. – *J. Insect Physiol.* 21: 331-341.
- Ferenz, H.-J. (1977). Two-step photoperiodic and hormonal control of reproduction in the female beetle *Pterostichus nigrita*. – *J. Insect Physiol.* 23: 671-676.
- Filippov, B.Yu. (2006a). Seasonal aspects of life cycles in the ground beetles *Carabus granulatus* and *C. glabratus* (Coleoptera, Carabidae) in the northern taiga. – *Zool. Zh.* 85: 1076-1084 [in Russian].
- Filippov, B.Yu. (2006b). Seasonal aspects of life cycles in the ground beetles *Calathus melanocephalus* and *C. micropterus* (Coleoptera, Carabidae) in the northern taiga. – *Zool. Zh.* 85: 1196-1204 [in Russian].
- Filippov, B.Yu. (2007). Seasonal life cycles in some species of ground beetles in southern tundra. – *Russ. Entomol. J.* 16: [in press].
- Gilbert, O. (1956). The natural histories of four species of *Calathus* (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. – *Oikos.* 7: 22-47.
- Greenslade, P.J.M. (1965). On the ecology of some British carabid beetles with special reference to life histories. – *Trans. Soc. Brit. Ent.* 16: 149-179.
- Grüm, L. (1975). Growth rate of the *Carabus* L. larvae (Col. Carabidae). – *Ekol. Polska, Ser. A.* 23: 667-671.

- Günther, J.M. & Assmann, Th. (2000). Competition in the woodland? Phenology, body mass and body length of coexisting *Carabus* species – preliminary results (Coleoptera, Carabidae). – In: Natural history and applied ecology of Carabid beetles (Brandmayr, P., Lövei, G.L., Zetto-Brandmayr, T., Casale, A. & Vigna Taglianti, A, eds). Pensoft, Sofia-Moscow, p. 185-195.
- Hamilton, C.C. (1925). Studies on the morphology, taxonomy and ecology of the larvae of Holarctic tiger beetles (family Cicindelidae). – Proc. U.S. Nat. Mus. 65: 1-87.
- Hemmer, J & Terlutter, H. (1991). Untersuchungen zur Höhenverbreitung von Carabiden am Alpen-Nordrand (Coleoptera, Carabidae). – NachrBl. Bayer. Ent. 40: 72-79.
- Houston, W.W.K. (1981). The life cycles and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst. (Col.: Carabidae) on moorland in northern England. – Ecol. Entomol. 6: 263-271.
- Hürka, K. (1973). Fortpflanzung und Entwicklung der mitteleuropäischen *Carabus* und *Procerus*-Arten. – Studie ESAV. 9: 1-78.
- Hürka, K. (1975). Laboratory studies on the life cycle of *Pterostichus melanarius* (Ill.) (Coleoptera, Carabidae). – Věst. Čs. Společ. Zool. 39: 265-274.
- Hürka, K. (1986). The developmental type of Carabidae in the temperate zones as a taxonomic character. – In: Carabids beetles: their adaptations and dynamics (den Boer, P.J., Mossakowski, D., Luff, M.L. & Weber, F., eds). Gustav Fisher Verlag, Stuttgart-New York, p. 187-193.
- Inyaeva, Z.I. (1965). Ground beetles on the field crops. – Thesis of diss. PhD. Moscow State University Press, Moscow, p. 1-20 [in Russian].
- Jakuczun, L. (1978). Fenologia rozrodu czterech wysokogórskich gatunków chrząszczy biegaczowatych (Coleoptera, Carabidae) w Tatrach. – Polskie pismo Entomol. 48: 573-581.
- Jones, M.G. (1979). The abundance and reproductive activity of common carabidae in a winter wheat crop. – Ecol. Entomol. 4: 31-43.
- Jørum, P. (1976). Life cycle and population density of *Nebria brevicollis* F. (Coleoptera: Carabidae) in a Danish beech forest. – Vidensk. Medd. Dansk. nat. Foren. 139: 245-261.
- Jørum, P. (1980). Life cycles and annual activity patterns of *Pterostichus melanarius* (Illig.) and *P. niger* (Schall.) (Coleoptera: Carabidae) in a Danish beech wood. – Ent. Medd. 48: 19-25.
- Jørum, P. (1985). Life cycle and phenology of *Carabus problematicus* Herbst, 1786 in Denmark (Coleoptera: Carabidae). – Ent. Medd. 53: 27-30.
- Kålås, J.A. (1985). Species composition and seasonal activity patterns of Carabidae (Col.) in a small deciduous forest in western Norway. – Fauna Norvegica. Ser. B. 32: 28-32.
- Karpova, V.E. & Matalin, A.V. (1990). Functional age structure of *Anisodactylus signatus* Panz. populations (Coleoptera, Carabidae) in the steppe zone. – In: Advances of entomology in USSR: Coleoptera (Medvedev, G.S. & Korotyayev, B.A., eds). Zoological Institute of USSR Acad. Sci. Press, Leningrad, p. 62-63 [in Russian].
- Kasandrova, V.I. & Sharova, I.Kh. (1971). Development of *Amara ingenua*, *Anisodactylus signatus* and *Harpalus distinguendus* (Coleoptera, Carabidae). – Zool. Zh. 50: 215-220 [in Russian].
- Khobrakova, L.Ts. & Sharova, I.Kh. (2005). Life cycles of ground beetles (Coleoptera, Carabidae) from the mountain taiga and mountain forest-steppe in the Eastern Sayan. – Izv. Ross. Acad. Nauk, Ser. Biol. 6: 688-693 [in Russian].

- Khruleva, O.A. (1994). Life cycle of the leaf beetle *Chrysolina subsulcata* (Coleoptera, Chrysomelidae) on Wrangel Island. – Zool. Zh. 73: 29-38 [in Russian].
- Klausnitzer, B. (1991). Wunderwelt der Käfer. – Edition Leipzig, 212 ss.
- Koval', A.G. (2005) Ground beetles (Coleoptera, Carabidae) of fields of vegetable nightshade (species composition, ecology, biology, entomophages of Colorado beetle). – Thesis of diss. Ph.D. All-Russian Institute of Plant Protection Press, St.-Petersburg, p. 1-22 [in Russian].
- Korobeinikov, Yu.I. (1991). About some features of seasonal dynamics activity and reproduction of ground beetles in sub-Arctic conditions. – In: The problems of soil zoology (Mordkovich, V.G., Stebaeva, S.K. & Grishina, L.G., eds). Eastern-Siberian Forest Factory Press, Novosibirsk, p. 127-128 [in Russian].
- Krehan, I. (1970). Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imago-überwintern der Gattung *Pterostichus* (Col., Carab.). – Oecologia. 6: 58-105.
- Kürka, A. (1975). The life cycle of *Bembidion tibiale* (Coleoptera, Carabidae). – Acta Entomol. Bohemoslov. 72: 374-382.
- Kryutchkova, E.E. & Panov, A.A. (1988). Activity alterations in cerebral neurosecretory cells in three species of ground-beetles (Coleoptera, Carabidae) related to the annual reproduction cycle. – Zool. Zh. 67: 1661-1669 [in Russian].
- Lampe, K.H. (1975). Die Fortpflanzungsbiologie und Ökologie des Carabiden *Abax ovalis* Dft. und der Einfluss der Umweltfaktoren Bodentemperatur, Bodenfeuchtigkeit und Photoperiode auf die Entwicklung in Anpassung an die Jahreszeit. – Zool. Jb. Syst. 102: 128-170.
- Larsson, S.G. (1939). Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Kommission Hos P. Haase & Søns Forlag, København. – Entomologiske Meddelelser. 20: 277-562.
- Lindroth, C.H. (1945). Die fennoskandischen Carabidae, Eine tiergeographische Studie. I. Spezieller Teil. – Bröderna Lager-ström Boktryckare, Göteborgs, 709 p.
- Loreau, M. (1985). Annual activity and life cycles of carabid beetles in two forest communities. – Holarctic Ecology. 8: 228-235.
- Luff, M.L. (1973). The annual activity pattern and life cycle of *Pterostichus madidus* F. (Col. Carabidae). – Ent. Scand. 4: 259-273.
- Makarov, K.V. (1989). Morpho-ecological characteristics of life cycles in the ground beetles of genus *Carabus* (L.) Thoms. – In: Life forms and strategy of organisms and their use for bioindication of environment conditions (Bogach, Ya.Ya., ed). Institute of Landscape Ecology of Acad. Sci. of Czech. SSR, České Budějovice, p. 22-23 [in Russian].
- Makarov, K.V. (1994). Annual reproduction rhythm of ground beetles: a new approach to the old problem. – In: Carabid beetles: ecology and evolution (Desender, K., Dufrêne, M., Loreau, M., Luff, M.L. & Maelfait, J-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 177-182.
- Makarov, K.V. & Chernyakhovskaya, T.A. (1989). Variability of the seasonal dynamics activity of the ground beetle *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in different types of forest. – In: Ecological aspects of adequate nature management (Tyuryapin, I, Ventin'sh, Ya., Il'in, V., Tarvid, I., Utrans, A. & Sheshukova, T., eds). Institute of Biology of Acad. Sci. of Lithuanian SSR Press, Riga, p. 55-56 [in Russian].
- Makarov, K.V. & Chernyakhovskaya, T.A. (1990). Phenology of development and population structure of *Loricera pilicornis* (F.) (Coleoptera, Carabidae) in an agrocenosis. – In: Structure

- and dynamics of populations of edaphic and herpetobiotic invertebrates (Sharova, I.Kh., ed). Moscow State Pedagogical Institute Press, Moscow, 1: 21-32 [in Russian].
- Matalin, A.V. (1994). The strategy of dispersal behaviour in some Carabidae species of southeastern Europe. – In: Carabid beetles: ecology and evolution (Desender, K., Dufrière, M., Loreau, M., Luff, M.L. & Maelfait, J-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 183-188.
- Matalin, A.V. (1997a). Peculiarities of spatial and temporal differentiation of carabids (Coleoptera, Carabidae) in the steppe zone. – Entomol. Rev. 77: 1155-1166.
- Matalin, A.V. (1997b). Life cycles of carabids of the genus *Stenolophus* (Coleoptera, Carabidae) in the steppe zone of Europe. – Entomol. Rev. 77: 1181-1190.
- Matalin, A.V. (1997c). Specific features of life cycle of *Pseudoophonus* (s. str.) *rufipes* Deg. (Coleoptera, Carabidae) in southwestern Moldova. – Biol. Bull. 24: 371-381.
- Matalin, A.V. (1998a). Life cycles of ground beetles of the tribe Harpalini (Coleoptera, Carabidae) on the European subcontinent: the possible ways of their origin and transformation. – In: The problems of entomology in Russia (Medvedev, G.S., ed). Zoological Institute of Russ. Acad. Sci. Press, St.-Petersburg, 2: 25-26 [in Russian].
- Matalin, A.V. (1998b). Polyvariance of *Harpalus affinis* Schrank (Coleoptera, Carabidae) and its adaptive significance. – Biol. Bull. 25: 402-410.
- Matalin A.V., 2003. Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. – Pedobiologia. 47: 311-319.
- Matalin, A.V. (2006). Geographic variability of the life cycle in *Pterostichus melanarius* (Coleoptera, Carabidae). – Entomol. Rev. 86: 409-422.
- Matalin, A.V. (2007). Typology of life cycles of ground beetles (Coleoptera, Carabidae) from Western Palaearctic. – Zool. Zh. 86: 1196-1220 [in Russian].
- Matalin, A.V. & Budilov, P.V. (2003). Geographical variability of sexual and age structure of populations and the life cycle in *Brosicus cephalotes* (Coleoptera, Carabidae). – Entomol. Rev. 83: 1037-1045.
- Matalin, A.V. & Makarov, K.V. (2006). Life cycle of the halophilic carabid beetle *Pogonus* (s. str.) *transfuga* Chaudoir, 1871 (Coleoptera: Carabidae) in the Elton region. – In: Biodiversity and problems of nature management in Elton region (Kursakova, N.A., Nekrutkina, Yu.A., Sokhina, E.N. & Chernobai, V.F. eds). PrinTerra, Volgograd, p. 40-46.
- Matalin, A.V., Makarov, K.V. & Bokhovko, E.E. (2007). Estimation of abundance and spatial distribution of the ground beetles (Coleoptera, Carabidae) in natural and anthropogenic conditions. – In: Problems and perspectives of general entomology (Zamotailov, A.S. ed). KubGAU Press, Krasnodar, p. 224-225 [in Russian].
- Murdoch, W.W. (1967). Life history patterns of some British Carabidae (Coleoptera) and their ecological significance. – Oikos. 19: 25-32.
- Nekuliseanu, Z.Z. (1987). Biology of *Pogonus litoralis* Duft. (Coleoptera, Carabidae). – In: The problems of soil zoology (Kurashvili, B.E., ed). Metscniereba, Tbilisi, p. 199 [in Russian].
- Nekuliseanu, Z.Z. (1990). Specific biological features of some ground beetles of genus *Pterostichus* Bon. (Coleoptera, Carabidae) in Moldova. – In: Advances of entomology in USSR: Coleoptera (Medvedev, G.S. & Korotyayev, B.A., eds). Zoological Institute of USSR Acad. Sci. Press, Leningrad, p. 96-98 [in Russian].
- Nekuliseanu, Z.Z. (1994). Biologia unor Carabidae ale genului *Amara* Bon. (Coleoptera, Carabidae) din Moldova. – Bul. Acad. Ştiin. Rep. Moldova. Ştiin. boil. chim. 1: 37-41 [in Moldavian].

- Nelemans, M.N.E. (1987). On the life history of the carabid beetle *Nebria brevicollis* (F.). Egg production and larval growth under experimental conditions. – Neth. J. Zool. 37: 26-42.
- Ortuño, V.M. & Marcos, J.M. (1997). Carabidofauna (Insecta, Coleoptera) del área natural de Salburua (Vitoria, Álava). – Ecologia. 11 457-482.
- Paarmann, W. (1974). Der Einfluss von Temperatur und Lichtwechsel auf die Gonadenreifung des Laufkäfers *Brosicus laevigatus* Dej. (Coleoptera, Carabidae) aus Nordafrika. – Oecologia. 15: 87-92.
- Paarmann, W. (1976a). The annual periodicity of the polyvoltine ground-beetle *Pogonus chalcus* Marsh. (Col. Carabidae) and its control by environmental factors. – Zool. Anz. 196: 150-160.
- Paarmann, W. (1976b). Die Bedeutung exogener Faktoren für die Gonadenreifung von *Orthomus barbarus atlanticus* (Coleoptera, Carabidae) aus Nordafrika. – Ent. Exp. et Appl. 19: 23-26.
- Paarmann, W. (1979). Ideas about the evolution of the various annual reproduction rhythms in carabid beetles of the different climatic zones. – In: On the evolution of behaviour in Carabid beetles (den Boer, P.J., Thiele, H.U. & Weber, F., eds). H. Veeneman & Zonen B.V. Publ., Wageningen. 18: 119-132.
- Paarmann, W. (1990). *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 (Stork, N.E., ed). Intercept Publishers, Andover-Hampshire, p. 259-267.
- Paarmann, W. (1994). Temperature and photoperiodic influence on development stages and adults of the subarctic carabid beetles *Pterostichus adstrictus* (Coleoptera). – In: Carabid beetles: ecology and evolution (Desender, K., Dufrière, M., Loreau, M., Luff, M.L. & Maelfait, J.-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 201-205.
- Penney, M.M. (1969). Diapause and reproduction in *Nebria brevicollis* (F.) (Coleoptera, Carabidae). – J. Anim. Ecol. 38: 219-233.
- Potapova, N.A. (1972). Seasonal dynamics of activity of Carabidae (Coleoptera) in semidesert of the north-west Kazakhstan. – Zool. Zh. 60: 1651-1658 [in Russian].
- Refseth, D. (1980). Differences in seasonal activity pattern and breeding time of *Patrobus atrorufus* (Carabiade) in central Norway. – Holarctic Ecology. 3: 87-90.
- Refseth, D. (1984). The life cycle and growth of *Carabus glabratus* and *C. violaceus* in Budalen, central Norway. – Ecol. Entomol. 9: 449-455.
- Refseth, D. (1988). Annual patterns of activity, reproduction and development in some Norwegian Carabidae (Col.). – Fauna Norvegica. 35: 21-30.
- Schatz, I. (1994). Life strategy of an alpine Carabid: *Pterostichus jurinei* (coleoptera, Carabidae). – In: Carabid beetles: ecology and evolution (Desender, K., Dufrière, M., Loreau, M., Luff, M.L. & Maelfait, J.-P., eds). Kluwer Acad. Publ., Dordrecht-Boston-London, p. 213-217.
- Sharova, I.Kh. (1981). Morpho-ecological typification of life cycles of ground beetles (Coleoptera, Carabidae). – Proc. All-Union Entomol. Soc. 63: 59-61 [in Russian].
- Sharova, I. Kh. & Denisova, M.I. (1995). Life cycles and reproduction rhythms of *Calathus erratus* C.R. Sahlberg and *C. micropterus* Duftschmidt (Coleoptera, Carabidae) in the forest of Russian forest-steppe zone. – Russ. Ent. J. 4: 159-165.
- Sharova, I.Kh. & Denisova, M.I. (1997). Seasonal dynamics of carabid populations from the genus *Pterostichus* (Coleoptera, Carabidae). – Zool. Zh. 76: 418-427 [in Russian].

- Sharova, I.Kh. & Dushenkov, V.M. (1979). Types of development and types of seasonal activity in ground beetles. – In: Fauna and ecology of invertebrate animals (Chernova, N.M., ed), Moscow State Pedagogical Institute Press, Moscow, p. 5-25 [in Russian].
- Sharova, I.Kh. & Filippov, B.Yu. (2003). Peculiarities of ground beetles (Coleoptera, Carabidae) life cycles in northern taiga. – Zool. Zh. 82: 229-238 [in Russian].
- Sharova, I.Kh. & Khobrakova, L.Ts. (2005). Features of the life cycles of *Pterostichus montanus* (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) in conditions of the mountain taiga zone in the Eastern Sayan. – Izv. Ross. Acad. Nauk, Ser. Biol. 1: 36-46 [in Russian].
- Shelford, V.E. (1908). Life-histories and larval habits of the tiger beetles (Cicindelidae). – J. Linn. Soc. London. 30: 157-184.
- Skuhřavý, V. (1959). Příspěvek k bionomii polních střelíkovitých (Col. Carabidae). – Rozpr. Českosl. Akad. Věd. Řada matemat. a přírodn. věd. 69: 3-64.
- Sota, T. (1985). Life history patterns of carabid beetles belonging to the subtribe Carabina (Coleoptera, Carabidae) in the Kinki district, W. Japan. – Kontyū. 53: 370-378.
- Sota, T. (1986). Effects of temperature and photoperiod on the larval development and gonad maturation of a carabid beetle, *Carabus yaconinus* (Coleoptera: Carabidae). – Appl. Ent. Zool. 21:89-94.
- Sota, T. (1987). Effects of temperature and photoperiod on the larval hibernation and adult aestivation of *Leptocarabus kumagaii* (Coleoptera: Carabidae). – Appl. Ent. Zool. 22: 617-623.
- Sota, T. (1994). Variation of carabid life cycles along climatic gradients: an adaptive perspective for life-history evolution under adverse conditions. – Series Entomologica. 52: 91-112.
- Sota, T. (1996). Altitudinal variation in life cycles of carabid beetles: life-cycle strategy and colonization in Alpine zones. – Arctic Alpine Res. 28: 441-447.
- Sota, T. & Ishikawa, R. (2004). Phylogeny and life-history evolution in *Carabus* (subtribe Carabina: Coleoptera, Carabidae) based on sequences of two nuclear genes. – Biol. J. Linn. Soc. 81: 135-149.
- Sparks, T.H., Buse, A. & Gadsden, R.J. (1995). Life strategy of *Carabus problematicus* (Coleoptera, Carabidae) at different altitudes on Snowdon, north Wales. – J. Zool. 236: 1-10.
- Stiprais, M.A. (1970). Growing of *Carabus glabratus* Payk. – LVU Zool. Muz. Raksiti. 4: 103-106 [in Russian].
- Thiele, H.-U. (1977). Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour. Springer-Verlag, Berlin-Heidelberg-New York, XVII+369 p.
- Turin, H. (2000). De Nederlandse loopkevers: verspreiding en oecologie (Coleoptera: Carabidae). – Nat. Natuurhistorisch Mus. Natur., Tekeningen, 666 p.
- Turin, H., Penev, L. & Casale A. (Eds) (2003). The genus *Carabus* in Europe. A synthesis. – Pensoft, Sofia-Moscow, 511 p.
- van der Drift, J. (1951). Analysis of the animal community in a beech forest floor. – Tijdschr. Ent. 94: 1-168.
- van der Drift, J. (1958). Life cycle and phenology of *Carabus problematicus* Herbst. – In: Proceeding of X International Congress of Entomology. 2: 661.
- van Dijk, Th.S. (1972). The significance of the diversity in age composition of *Calathus melanocephalus* L. (Coleoptera, Carabidae) in space and time at Schiermonnikoog. – Oecologia. 10: 111-136.

- van Dijk, Th.S. (1979). Reproduction of young and old females in two carabid beetles and the relationship between the number of eggs in the ovaries and number of eggs laid. – In: On the evolution of behaviour in Carabid beetles (den Boer, P.J., Thiele, H.U. & Weber, F., eds). H. Veeneman & Zonen B.V. Publ., Wageningen. 18: 167-183.
- van Dijk, Th.S. (1994). On the relationship between food, reproduction and survival of two carabid beetles: *Calathus melanocephalus* and *Pterostichus versicolor*. – Ecol. Entomol. 19: 263-270.
- van Heerdt, P.F., Blokhuis, P. & van Haaften, C. (1976). The reproductive cycle and age composition of a population of *Pterostichus oblongopunctatus* F. in the Netherlands (Coleoptera: Carabidae). – Tijdschr. Ent. 119: 1-13.
- van Schaick-Zillesen, P.G., Brunsting, A.M.H. & Siepel, H. (1986). The role of larvae in the synchronization of the life cycle of *Pterostichus oblongopunctatus*. – In: Carabids beetles: their adaptations and dynamics (den Boer, P.J., Mossakowski, D., Luff, M.L. & Weber, F., eds). Gustav Fisher Verlag, Stuttgart-New York, p. 181-185.
- Vasil'eva, R.M. (1978). Specific features of development of some species of ground beetles in the Bryansk province. – In: Fauna and ecology of invertebrates (Naumov, S.P., ed), Moscow State Pedagogical Institute Press, Moscow, p. 40-52 [in Russian].
- Vlijm, L. & van Dijk, Th.S. (1967). Ecological studies on carabid beetles II. General pattern of population structure in *Calathus melanocephalus* L. at Sciermonnikoog. – Zeitschr. Morph. Ökol. Tiere 58: 396-404.
- Wallin, H. (1987). Distribution, movements and reproduction of Carabid beetles (Coleoptera, Carabidae) inhabiting cereal fields. Plant Protection Reports and Dissertations of the Swedish Univ. for Agric. Sci., Uppsala, 25 + 109 p.
- Weber, F. & Klenner, M. (1987). Life history phenomena and risk of extinction in a subpopulation of *Carabus auronitens*. – Acta Phytopath. Entom. Hung. 22: 321-328.
- Zetto Brandmayr, T. (1983). Life cycle, control of propagation rhythm and fecundity of *Ophonus rotundicollis* Fairm. et. Lab. (Coleoptera, Carabidae, Harpalini) as an adaption to the main feeding plant *Daucus carota* L. (Umbelliferae). – In: The synthesis of field studies and laboratory experiment (Brandmayr, P., den Boer, P.J. & Weber, F., eds). Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, p. 93-103.