

Typology of Life Cycles of Ground Beetles (Coleoptera, Carabidae) in Western Palaearctic

A. V. Matalin

Moscow State Pedagogical University, Moscow, 129278 Russia

e-mail: a_matalin@tochka.ru

Received April 12, 2006

Abstract—An original classification of the life cycles of ground beetles from Western Palaearctic is proposed. The classification is based on a combination of five criteria: duration, number of generations per season, phenology of reproduction, stability, and repeatability of reproduction. According to the individual lifespan, the cycles are subdivided into annual and biennial ones. The annual life cycles may be uni- and bivoltine, whereas biennial ones are always univoltine. By the time of reproduction, winter-spring, spring, spring-summer, early summer, summer, late summer, summer-autumnal, autumnal, autumn-winter, winter, and aseasional species are distinguished. The biennial and bivoltine cycles may be of both facultative and obligate nature. Species living only one season and having a continuous reproductive period are designated as semelparous, while those breeding during two or more years or having several distinct periods of reproduction in one season, as iteroparous. By now, 30 variants of life cycles in Carabidae from western Palaearctic have been established. Repeated similarly directed modifications of the life cycle may produce essentially different seasonal rhythms in some individuals. In this case, two subpopulation groups usually appear within the population. Under the most unfavorable conditions, these groups become practically isolated and hibernate at different ontogenetic stages. The individual development in each of these groups takes two years with the same seasonal rhythm. Among the types considered, only obligate-bivoltine life cycles are always polyvariant, but annual univoltine and obligate-biennial ones are always univariant. The facultative-bivoltine and biennial life cycles may be realized as uni- and polyvariant ones, depending on the environmental conditions.

DOI: 10.1134/S0013873807080027

In zoology, life cycles are usually considered either as an aspect of morphogenesis (alternation of ontogenetic stages, generations, life forms, etc.), or from the viewpoint of developmental physiology (Beklemishev, 1942; Cole, 1954; Stearns, 1976, 1992; Wilbur, 1980; Roff, 1992; Galaktionov and Dobrovolskii, 1998). Both approaches have been applied to insects (Mazokhin-Porshnyakov, 1954; Danilevskii, 1961, 1972; Hinton, 1963; Danilevskii and Kuznetsova, 1968; Glinyanaya, 1972; Rotenberg, 1977; Loreau and Ebenhöf, 1994; Kundu and Dixon, 1995; Truman and Riddiford, 1999; Sugonyaev, 2001), including ground beetles (Murdoch, 1966; Sharova, 1971, 1981; Thiele, 1977; Paarmann, 1979; Sota, 1987, 1988; Makarov, 1989). Evaluation of the possible variants of the life cycles under specific natural conditions is necessary for understanding the structure and dynamics of populations of individual species and the functioning of the community as a whole. The study of the geographic and biotopic variability of the types of development may be used in bioindication, evaluation of recolonization of the disturbed habitats, or prediction of the

population dynamics of mass species, including those of economic importance. Besides that, comprehensive analysis of the life cycles allows one to reveal the cases of their parallel development and use them as a criterion for discussing the evolution of differently ranked taxa (Brandmayr and Zetto Brandmayr, 1979; Paarmann, 1979; Sharova, 1981; Makarov, 1989; den Boer and van Dijk, 1996; Matalin, 1997a, 1998; Sota and Ishikawa, 2004).

The history of study of the life cycles of ground beetles covers over 150 years. The first data on the biology of some European species were published in the middle of the XIX century—early XX century (Schiødte, 1867; Zang, 1901; Mjöberg, 1906; Schelford, 1908; Burges, 1911). However, a systematic study of the life cycles of Carabidae started only in the 1920s (Claassen, 1919; van Lengerken, 1921; Zikan, 1929; Znoiko, 1929, 1935; Delkeskamp, 1930; Kochetova, 1936; Chaboussou, 1938). The data accumulated by that time were analyzed by S.G. Larsson (1939), who proposed the first classification of the types of development in Carabidae. The factual basis for this

classification was formed by thoroughly processed museum collections, mostly representing the fauna of Denmark. Larsson used three parameters: the period of development, the period of activity of the adults, and duration of the life cycle. As a result, the European ground beetles were subdivided into the forms with spring reproduction and a high (F+), moderate (F(+)), or weak autumnal activity (F(÷)) or without autumnal activity (F(-)), and into the forms with autumnal reproduction (H) and biennial development (2F+). This classification proved to be rather convenient and became broadly accepted in later periods.

The rapid development of insect physiology, including the reproductive aspects, in the 1950–1970s brought significant progress in understanding the life cycles of ground beetles. Having summarized all the available data, H.-U. Thiele (1977) recognized seven types of reproductive rhythms in the ground beetles of the temperate zone: those with reproduction in spring, photoperiodic control of gonad development, and an imaginal parapause (1) or diapause (2); those with reproduction in autumn, a larval parapause, and with (3) or without (4) photoperiodic aestivation in the adults; those with unstable wintering conditions (5); those with biennial development, a larval parapause, and temperature (6) or photoperiodic (7) control of the gonad development. Later, W. Paarmann (1979) described five more variants of reproductive rhythms, of which two were characteristic of the ground beetles living in the subtropical zone of North Africa, and three, of those inhabiting the Central African tropics. In both cases, the principal parameters considered were the temperature control of development of the resting stage, and the photoperiodic control of the gonad development.

Thus, two directions in the study of the life cycles of ground beetles—phenological and physiological—were established by the 1980s. At the same time, it was repeatedly noticed that the diversity of the life cycles of ground beetles, especially considering their geographic and biotopic variability, could not be fitted into the schemes proposed by Larsson and Thiele. Numerous attempts at expanding and modifying these schemes were made (Lindroth, 1945; van Dijk, 1972; Luff, 1973; Paarmann, 1979; Sharova and Dushenkov, 1979; Loreau, 1985; Hůrka, 1986; Drioli, 1987; den Boer and den Boer-Daanje, 1990; den Boer and van Dijk, 1996; Matalin, 1998a, 2005).

A reconsideration of approaches to classification of the life cycles of Carabidae has been largely facilitated

by the research performed in the last three decades. By now, a huge amount of data has been accumulated concerning the phenology, seasonal dynamics of activity, gonad maturation, and preimaginal development of Carabidae (Inyaeva, 1965; Thiele, 1966, 1969, 1971, 1975, 1977; Andersen, 1969; Thiele and Krehan, 1969; Krehan, 1970; Kaufmann, 1971; Paarmann, 1973, 1974, 1976a, 1976b, 1977, 1979, 1990, 1994; Neudecker and Thiele, 1974; Ferenz, 1975, 1977; Kůrka, 1975; Lampe, 1975; Lamprecht and Weber, 1975; Könen, 1978; Jørum, 1980; Zetto Brandmayr, 1983; Sota, 1984, 1985a, 1985b; Brandmayr and Zetto Brandmayr, 1986; Nekuliseanu, 1987, 1990, 1994; Kryuchkova and Panov, 1988; Karpova and Matalin, 1990a; Cárdenas, 1994; Matalin, 1994; Telfer and Butterfield, 2004). In addition, data have been obtained indicating both the high lability of the oviposition time (van Dijk, 1972, 1979a, 1979b, 1983, 1994; Jones, 1979; Basedow, 1994; Makarov, 1994; Sharova and Denisova, 1995, 1996, 1997a, 1997b; Matalin, 2006) and the variability of the time of development of some ontogenetic stages in many species of ground beetles (Manga, 1972; Thiele, 1977; Houston, 1981; Andersen, 1983; Refseth, 1984; Butterfield, 1986, 1996; Sota, 1986; Nelemans, 1987; Makarov and Chernyakhovskaya, 1990; Chaabane et al., 1996; Matalin, 1997b, 1998b). Analysis of the dynamics of the demographic structure of populations of many species (Vlijum and van Dijk, 1967; van Dijk, 1972; van Heerdt et al., 1976; Jørum, 1980; Loreau, 1985; Wallin, 1987; Fadl et al., 1996; Sharova and Denisova, 1996, 1997a, 1997b; Matalin, 1997c, 1998b, 2006; Tselishcheva, 2000; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Khobrakova and Sharova, 2005; Sharova and Khobrakova, 2005; Filippov, 2006a, 2006b), together with the established concepts of the polyvariant nature of development (Makarov and Chernyakhovskaya, 1989; Makarov, 1990, 1994; Matalin, 1998b, 2006; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Filippov, 2006a, 2006b) and its synchronization (Neudecker and Thiele, 1974; Sota, 1985a; van Schaick-Zillesen et al., 1986; Matalin, 1997c, 1998b) have noticeably changed our understanding of the life cycles of Carabidae.

The life cycles of a number of Palaearctic species of ground beetles have been described or redescribed in the last 20 years. A detailed analysis of the geographic and biotopic variability of the demographic structure of populations has been performed for some of these species (Sota, 1985a, 1986, 1994, 1996; Colombini

and Chelazzi, 1992; Shishova, 1994; Sharova and Denisova, 1996, 1997; Matalin, 1997b, 1998b; Khotuleva, 1997; Sharova and Khobrakova, 2005), including the areas lying at the boundaries of their distribution ranges (Houston, 1981; Andersen, 1984; Refseth, 1984; Sota, 1996b; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Filippov, 2006a, 2006b; Matalin, 2006). The data obtained allowed many life cycles to be characterized as polyvariant (Makarov, 1990, 1994; Shishova, 1994; Sharova and Denisova, 1995; 1996, 1997a, 1997b; Khotuleva, 1997; Matalin, 1997a, 1997b, 1998a, 2006; Filippov, 2000; Tselishcheva, 2000; Budilov, 2002; Khobrakova, 2003; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Khobrakova and Sharova, 2005; Sharova and Khobrakova, 2005). However, the “polyvariant nature” of the life cycles was often differently understood and too broadly interpreted in the cited publications. This resulted in inconsistent interpretation of some life cycles, especially the variants with development taking more than one year, and also the cycles with repeated hibernation and subsequent reproduction of the adults.

In view of the above, a necessity arose to organize the presently available data on the demography and biology of individual species and to establish the criteria on which a modern classification of the life cycles of Carabidae of the Western Palaearctic can be developed. Some results of this work have been published earlier (Makarov, 1994; Matalin, 1998a, 2005).

MATERIALS AND METHODS

Methods of Data Collection and Analysis

The study is based on the critical analysis of the vast published data on the seasonal dynamics of activity, the demographic structure of the populations, the life cycles, and the specific features of preimaginal development of the ground beetles in the Palaearctic (see references in the Introduction and table), and also the collections made by the author in 1982–2006 in 15 regions of Russia and the former USSR.

The material was collected using standard methods: soil, light, and window traps, soil sampling, net sweeping, and manual collection (Matalin, 1996). These methods resulted in a huge amount of data reflecting the various aspects of ecology and biology of the most common ground beetle species in the European part of Russia. The adults and larvae were maintained under laboratory conditions, which allowed us to estimate

the occurrence and duration of individual development phases in different seasons.

The sex and age structure of populations was analyzed using the modified method of H. Wallin (1987), distinguishing five reproductive states in the adults of both sexes: teneral, immature, mature of the first and the second year of life, and spent. The dormant periods occurring during a season were described using the terminology proposed by H.J. Müller (1970).

As a result, we have obtained data on the demographic structure of local populations of 365 Palaearctic species of ground beetles, belonging to 70 genera. The complete or partial life cycles of these species have been described in detail. The schemes of the life cycles were built taking into account the periods of occurrence and development of the larvae, either determined by the original field and laboratory studies (Matalin, 1997b, 1997c, 1998b, 2006) or obtained from the publications of other workers (Larsson, 1939; Gilbert, 1956; Andersen, 1969; Kasandrova and Sharova, 1971; Hürka, 1973, 1975; Vasil'eva, 1978; Loreau, 1985; Nelemans, 1987; Arndt, 1989; Budilov, 1990; Dushenkov and Chernyakhovskaya, 1990; Nekuliseanu, 1990, 1994; Chaabane et al., 1996; Turin et al., 2003).

The Main Terms and Concepts

At different times, the life cycle of a ground beetle was interpreted either as a set of ontogenetic features (Thiele, 1977; Paarmann, 1979), or as an aspect of the population dynamics (den Boer, 1979; Sharova and Dushenkov, 1979; den Boer and van Dijk, 1996). In this communication, the following terms will be used to discuss the specific features of life cycles in Carabidae and their classification.

Ontogenesis—development of an individual from a fertilized egg until the moment of its natural death, which may occur either before the reproductive period (interrupted or incomplete ontogenesis) or after it (complete ontogenesis). Thus, we consider ontogenesis as subdivided into two phases: morphogenesis, resulting in the formation of a sexually mature individual, and reproduction, increasing the number of individuals (Rasnitsyn, 1965; Sharova, 1981; Afonin, 2004).

Seasonal (annual) rhythm—change of the active and resting periods of the development stages during the vegetation season (year).

Types of life cycles of Carabidae realized in the Western Palaearctic

Type of life cycle		Species	References
Annual univoltine:			
aseasonal	Y	<i>Aphaenops cerberus</i> Dieck	Deleurance and Deleurance, 1964a, 1964b
winter-spring iteroparous	WVi	[<i>Agonum thoreyi</i> (Dej.)]	Ortuño and Marcos, 1997
spring semelparous	Vs	<i>Stenolophus skrimshiranus</i> Steph.	Larsson, 1939; Matalin, 1996b, 1997a, 1997b; Ortuño and Marcos, 1997
spring iteroparous	Vi	<i>Anisodactylus signatus</i> (Panz.)	Larsson, 1939; Kasandrova and Sharova, 1971; Shilenkov, 1978; Karpova, 1990; Karpova and Matalin, 1990a, 1990b; Fazekas et al., 1997; Matalin, 1994, 1997
spring-summer semelparous	VsS	<i>Tachys micros</i> (F.-W.)	Matalin, 1997a
spring-summer iteroparous	VSi	<i>Poecilus cupreus</i> L.	Larsson, 1939; Lindroth, 1945; Skuhřavý, 1959; Briggs, 1965; Greenslade, 1965; Inyaeva, 1965, 1983; Louda, 1968; Kabacik-Wasylik, 1970; Krehan, 1970; Thiele, 1971, 1977; Vasil'eva, 1978; Karpova, 1990; Nekuliseanu, 1990; Wallin, 1987
early summer semelparous	eSs	<i>Bembidion hyperboraeorum</i> Munst.	Andersen, 1969, 1983
early summer iteroparous	eSi	<i>Carabus creutzeri</i> F.	Brandmayr and Zetto Brandmayr, 1986; Chemini and Pizzolotto, 1992; Turin et al., 2003
summer semelparous	Ss	<i>Bembidion petrosum</i> Gebl.	Andersen, 1969, 1983
summer iteroparous	Si	<i>Carabus schoenherri</i> F.-W.	Tselishcheva, 2000
summer-autumnal semelparous	SAs	<i>Epaphius secalis</i> (Payk.)	Larsson, 1939; Inyaeva, 1983; Wallin, 1987; Refseth, 1988; den Boer and van Dijk, 1996
summer-autumnal iteroparous	SAi	[<i>Harpalus rufipes</i> DeGeer]	Larsson, 1939; Lindroth, 1945; Skuhřavý, 1959; Briggs, 1965; Greenslade, 1965; Inyaeva, 1965, 1983; Louda, 1968; Kabacik-Wasylik, 1970; Vasil'eva, 1978; den Boer, 1979; Jones, 1979; Wallin, 1987; Budilov, 1990; Dushenkov and Chernyakhovskaya, 1990; Karpova, 1990; Karpova and Matalin, 1990b; Matalin, 1994, 1997a, 1997b, 1998a, 1998b, 1998c; den Boer and van Dijk, 1996; Hatvani and Kádár, 2002
autumnal semelparous	As	<i>Nebria brevicolis</i> (F.)	Larsson, 1939; Lindroth, 1945; Gilbert, 1958; Williams, 1959; Greenslade, 1965; Penney, 1969; Murdoch, 1967; Thiele, 1969, 1971, 1977; Manga, 1972; Jørum, 1976; den Boer, 1979; Jones, 1979; Kålås, 1985; Loreau, 1985; Nelemans, 1987; den Boer and van Dijk, 1996; Fadl and Purvis, 1998
autumnal iteroparous	Ai	<i>Calathus granatensis</i> Vuill.	Cárdenas and Bach, 1992; Cárdenas, 1994; Cárdenas et al., 1996
autumn-winter iteroparous	AWi	[<i>Calathus mollis</i> (Marsh.)]	Gilbert, 1956; Zaballos, 1986
winter semelparous	Ws	[<i>Bradycellus harpalinus</i> (Serv.)]	den Boer, 1979; den Boer and van Dijk, 1996
winter iteroparous	Wi	<i>Carabus lusitanicus</i> (F.)	Cárdenas and Hidalgo, 1995
Annual facultative-bivoltine:			
spring-summer semelparous	(VS) ² s	[<i>Loricera pilicornis</i> (F.)]	Larsson, 1939; Loreau, 1985; Dushenkov and Chernyakhovskaya, 1990; Makarov and Chernyakhovskaya, 1990
Annual obligate-bivoltine:			
spring-summer semelparous	VS ² s	[<i>Stenolophus discophorus</i> (F.-W.)]	Matalin, 1996b, 1997a, 1997b

Table (Contd.). Types of life cycles of Carabidae realized in the Western Palaearctic

Type of life cycle		Species	References
spring-summer iteroparous	VS ² i	[<i>Notiophilus biguttatus</i> F.]	Sharova and Filippov, 2003
Facultative-biennial:			
spring-summer semelparous	(2VS)s	[<i>Asaphidion pallipes</i> Duft]	Andersen, 1969
spring-summer iteroparous	(2VS)i	[<i>Harpalus affinis</i> Schrank]	Inyaeva, 1965; Budilov, 1990; Matalin, 1998a, 1998b
summer iteroparous	(2S)i	[<i>Nebria rufescens</i> (Ström)]	Lindroth, 1945; Forsskåhl, 1972; Refseth, 1988
summer-autumnal iteroparous	(2SA)i	[<i>Pterostichus melanarius</i> (Ill.)]	Larsson, 1939; Lindroth, 1945; Skuhrový, 1959; Green-slade, 1965; Vasil'eva, 1978; Wallin, 1987; Kryuchkova and Panov, 1988; Makarov and Chernyakhovskaya, 1989; Fadl et al., 1996; Sharova and Denisova, 1997a, 1997b; Fadl and Purvis, 1998; Matalin, 2006
autumnal iteroparous	(2A)i	[<i>Carabus hortensis</i> L.]	Refseth, 1988
Obligate-biennial:			
early summer iteroparous	2eSi	<i>Carabus aurolimbatus</i> Dej.	Sharova and Filippov, 2003; Turin et al., 2003
summer iteroparous	2Si	<i>Carabus loschnikovi</i> F.-W.	Khobrakova, 2003; Khobrakova and Sharova, 2005; Sharova and Khobrakova, 2005
late summer iteroparous	2lSi	[<i>Carabus problematicus</i> Herbst]	Houston, 1981; Butterfield, 1986, 1996
summer-autumnal semelparous	2SAs	<i>Bembidion hasti</i> Sahlb.	Andersen, 1969, 1983
summer-autumnal iteroparous	2SAi	[<i>Carabus coriaceus</i> (L.)]	Larsson, 1939; Lindroth, 1945; Hürka, 1973; Kålås, 1985; Refseth, 1988; Arndt, 1989; Turin et al., 2003

Note: Data on all the 365 species analyzed cannot be presented here due to the limited volume of the publication, therefore only one example is given for each type of the life cycle. The species shown in square brackets may have more than one variant of the life cycle. For designation of the life cycle abbreviation see Fig. 8.

Diapause (in the broad sense)—a phase of the seasonal rhythm including an obligatory (parapause) or facultative (diapause proper) dormant period at one or several development stages.

Reproductive rhythm (gonad cycle)—periodic changes in the rate of the gonad development in response to the key environmental factors, ensuring reproduction.

In view of the above, the life cycle is regarded as a regular combination of the seasonal and reproductive rhythms, reproduced consistently under specific biotopic and seasonal (climatic) conditions.

RESULTS

Typology of the Life Cycles of Ground Beetles in the Western Palaearctic

The typology of the life cycles of ground beetles proposed in this paper is based on the combination of five criteria: duration of the life cycle, in years; the number of generations per season, or voltinism; phe-

nology of reproduction, or seasonality; stability or consistency; and repeatability of reproduction.

With respect to duration, the life cycles of Carabidae can be subdivided into annual and biennial. Their principal difference consists in the periodicity of appearance of the young generation. In particular, in the annual life cycles the beetles of the new generation appear every year, because the overwintered individuals reproduce in the same season; the parental and filial generations enter diapause at the same stage of development (Figs. 1, 2, 3a, 5a, 6, 7). In the case of a biennial life cycle, the young generation is produced only once in two years; individuals of the new generation reproduce not in the current but in the subsequent season, and hibernate at a stage different from that of the parental generation (Figs. 3 b, 4, 5b).

With respect to the number of generations, the annual life cycles may be univoltine, if only one generation develops during a season (Figs. 1, 6, 7), or bivoltine, when two generations are produced in one

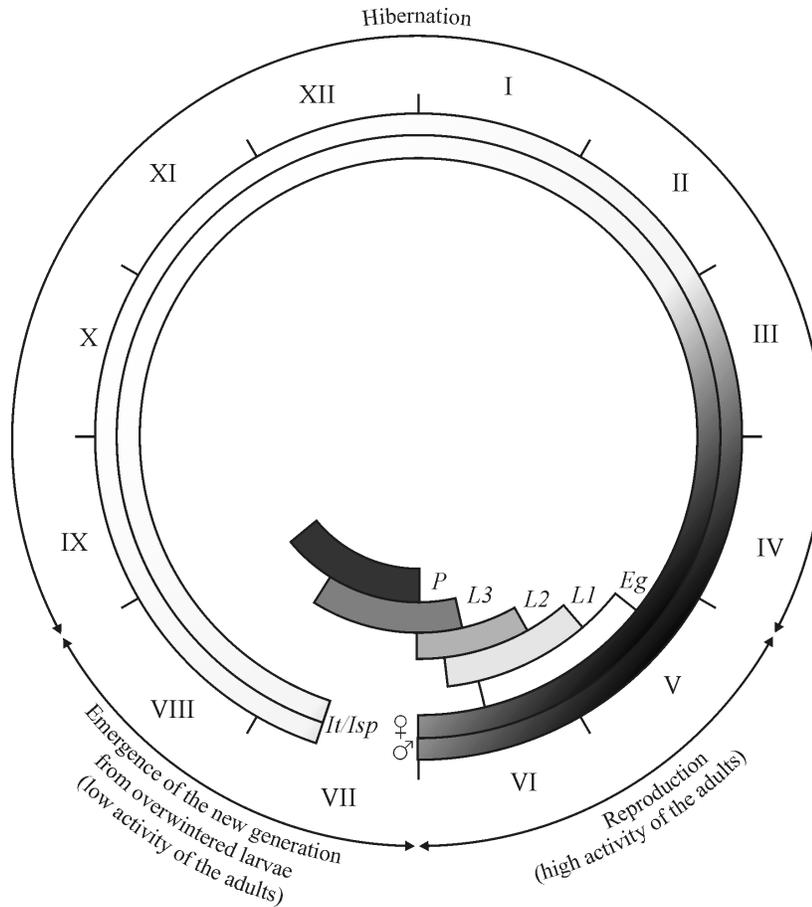


Fig. 1. An annual spring iteroparous life cycle by the example of *Anisodactylus signatus* Panz. (after Karpova and Matalin, 1990): oviposition (*Eg*), larvae of the first (*L1*), second (*L2*), and third (*L3*) instars, pupae (*P*), teneral adults (*It*), and spent adults of the parental generation (*Isp*). The intensity of shading corresponds to the degree of gonad maturation.

season (Fig. 2). In the latter case, reproduction of the filial generation often coincides with repeated reproduction of the parental generation. The biennial life cycles are always univoltine (Figs. 3–5).

The seasonality of the life cycle is determined by the period of reproduction and, consequently, by the hibernating stage. Following the established tradition (Larsson, 1939; Lindroth, 1945; Thiele, 1977; Paarman, 1979; Sharova and Dushenkov, 1979; Loreau, 1985; Drioli, 1987; den Boer and den Boer-Daanje, 1990; den Boer and van Dijk, 1996) and taking into account the original data (Matalin, 1997a, 1998, 2005), we distinguish the following categories of carabid species: winter-spring, spring, spring-summer, early summer, summer, late summer, summer-autumnal, autumnal, autumn-winter, winter, and aseasonal (aperiodic).

The spring species reproduce at the very beginning of the vegetation period and always hibernate as adults

(Fig. 1). Under favorable conditions, oviposition in some of them starts already in late winter, and reproduction ends completely by mid-spring. Such forms are placed in the group of winter-spring species.

The spring-summer species reproduce from the middle or end of spring to the second half of summer. The annual and bivoltine species hibernate only as adults, the first generation in the bivoltine species developing without a diapause, and the second one, with a diapause (Fig. 2). The biennial spring-summer species can hibernate both as adults (Fig. 3a) and as larvae (Fig. 3b).

Reproduction of the summer species is observed from mid-June to the middle or end of August. The immature adults of the new generation usually hibernate. However, in high latitudes and alpine areas the reproduction period of both spring and autumnal species shifts to summer, owing to the general reduction of the vegetation season from which the spring and

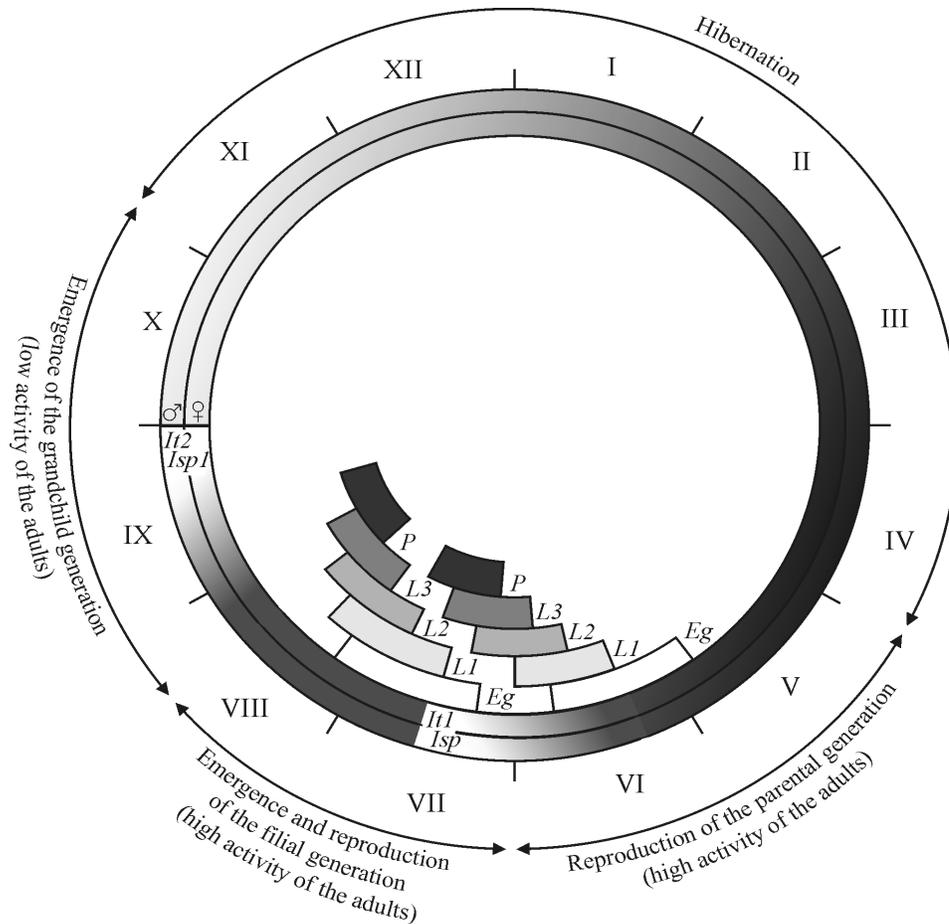


Fig. 2. Bivoltine spring-summer iteroparous life cycle by the example of *Loricera pilicornis* (F.) (after Makarov and Chernyakhovskaya, 1990): teneral adults of the first (*It1*) and second (*It2*) generations, and spent adults of the first generation (*Isp1*). For other designations, see Fig. 1.

autumn months are excluded. It should be noted that under these conditions, the originally spring species can complete their development and preserve the annual life cycle. Contrariwise, in the originally summer-autumnal and autumnal species, the adults of the new generation, having developed from the overwintered larvae, start to reproduce only in the subsequent year, and their life cycle therefore becomes biennial (Figs. 4, 5b). Some of these species (the early summer ones) reproduce in the first half of summer, and others (the late summer ones), in the second half of summer. This difference reflects their physiological specificity, primarily the nature of the adult diapause and gonad maturation.

The summer-autumnal species (often referred to as “multi-seasonal”) reproduce from the end of summer to mid-autumn and hibernate as old-instar larvae (Fig. 5a). In some species, however, part of the adults

may also hibernate; this fraction includes both the individuals from the parental generation, which have already reproduced in the current season, and still immature ones from the filial generation. In the latter case, the duration of the life cycle increases to two years (Fig. 5b).

The autumnal species reveal a stable and obligatory larval parapse that has formed because of the long and cold winter typical of the greatest part of the region in question. Reproduction in this case is observed from late summer to the middle or end of autumn, and the new generation appears in the middle or end of spring (Fig. 6). It should be noted that in the species with biennial development the immature beetles of the new generation hibernate together with the larvae.

In the areas with mild frost-free winter where the air temperature does not drop below +5°C, some representatives of Carabidae reveal winter activity. Repro-

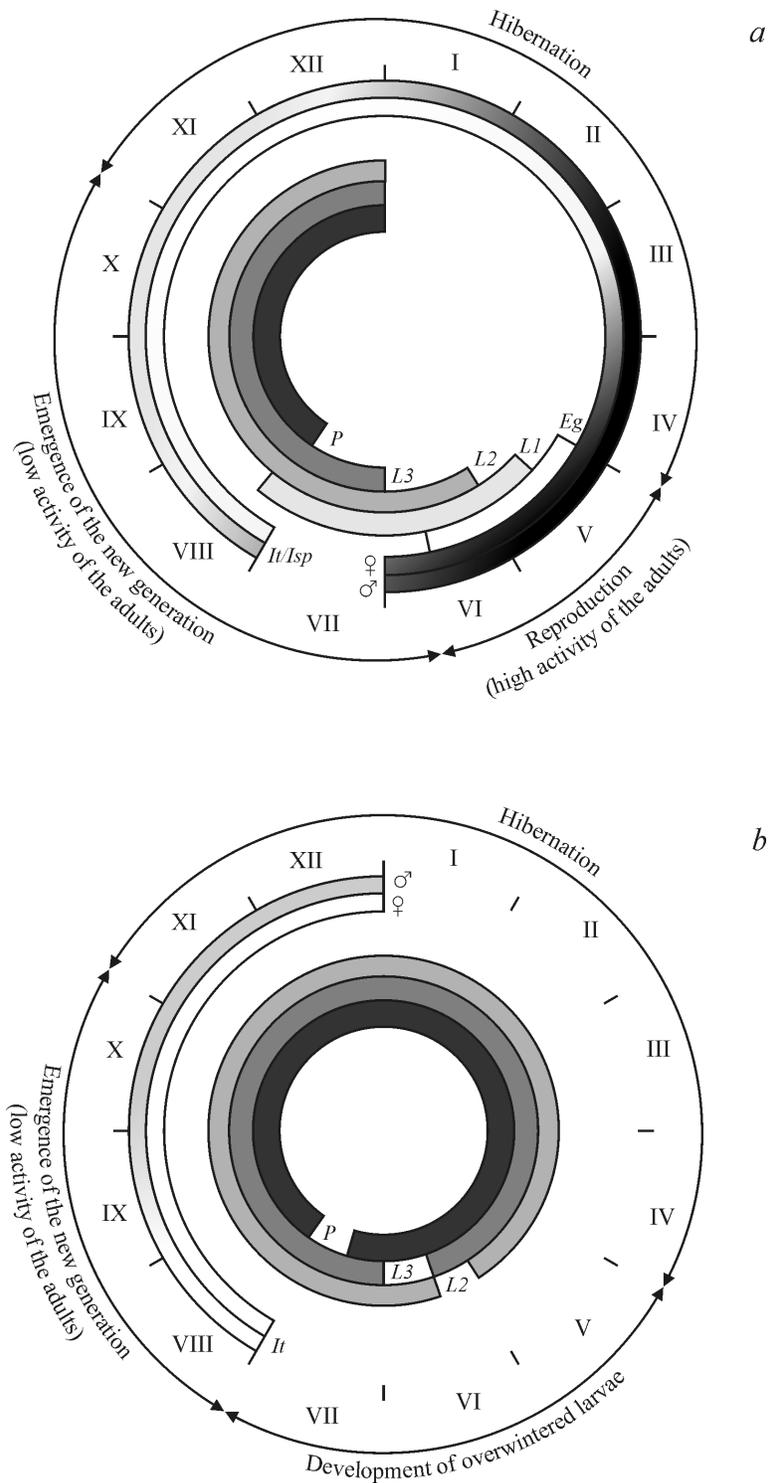


Fig. 3. Facultative-biennial spring-summer iteroparous life cycle by the example of *Harpalus affinis* Schrank (after Matalin, 1998b): the annual variant with hibernating adults (a) and the biennial variant with hibernating old-instar larvae and pupae (b). For other designations, see Fig. 1.

duction in this case takes place from late autumn to early spring; larval development is completed during the period of low positive temperatures and often in-

cludes no diapause. The adults of the new generation, emerging in the middle or end of spring, have a summer dormant period, or an aestivation parapause

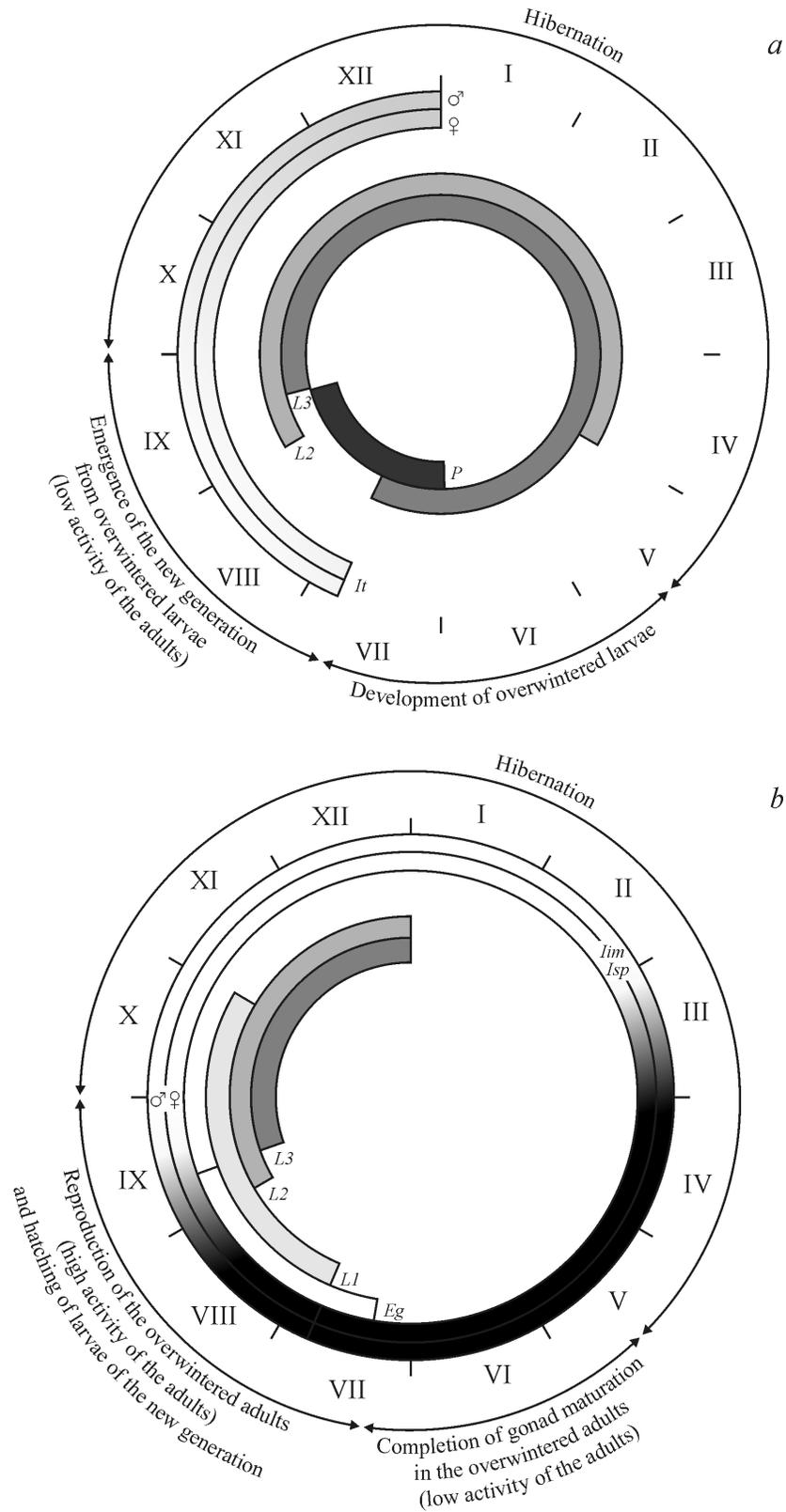


Fig. 4. Obligate-biennial late spring iteroparous life cycle by the example of *Carabus problematicus* Herbst (after Houston, 1981): the variants with hibernating old-instar larvae (a) and teneral adults (b). Immature adults are designated as *Im*. For other designations, see Fig. 1.

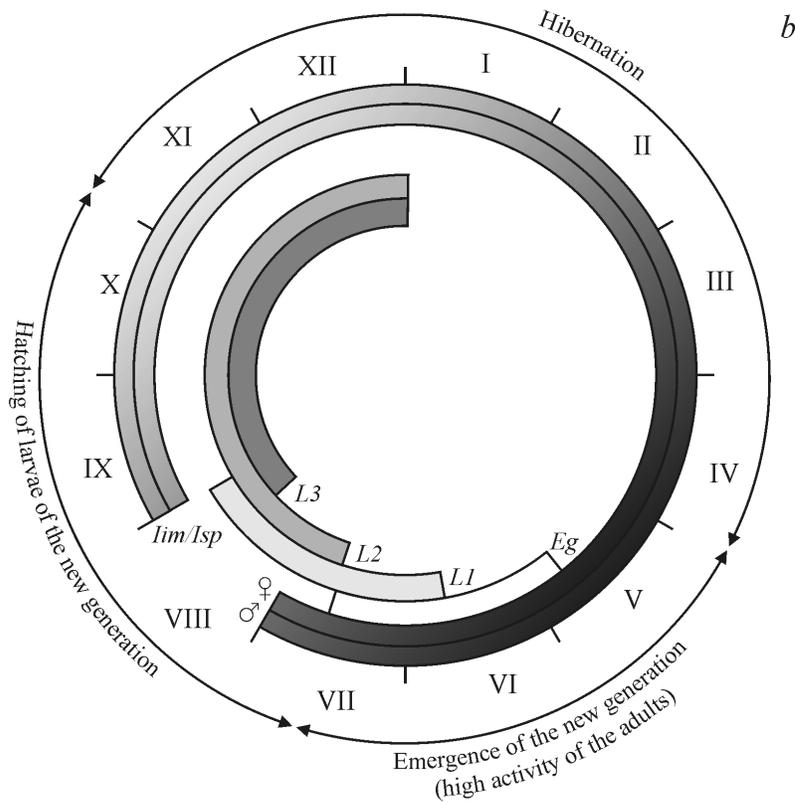
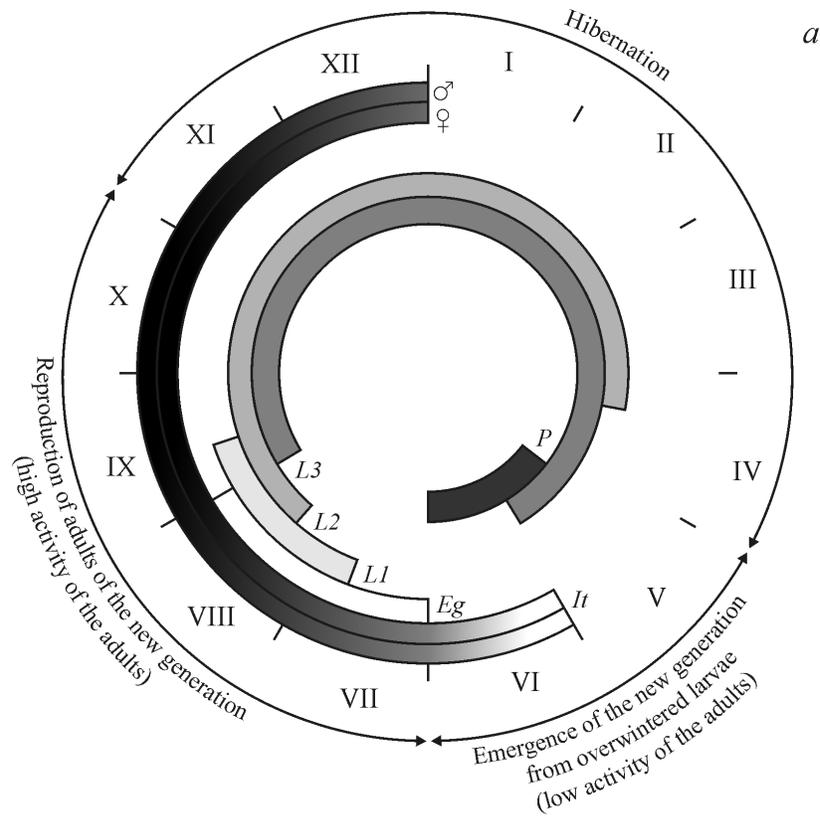


Fig. 5. Facultative-biennial summer-autumnal iteroparous life cycle by the example of *Pterostichus melanarius* (III.) (after Matalin, 2006): the annual variant with hibernating old-instar larvae (a) and the biennial variant with hibernating teneral adults (b). For designations, see Fig. 4.

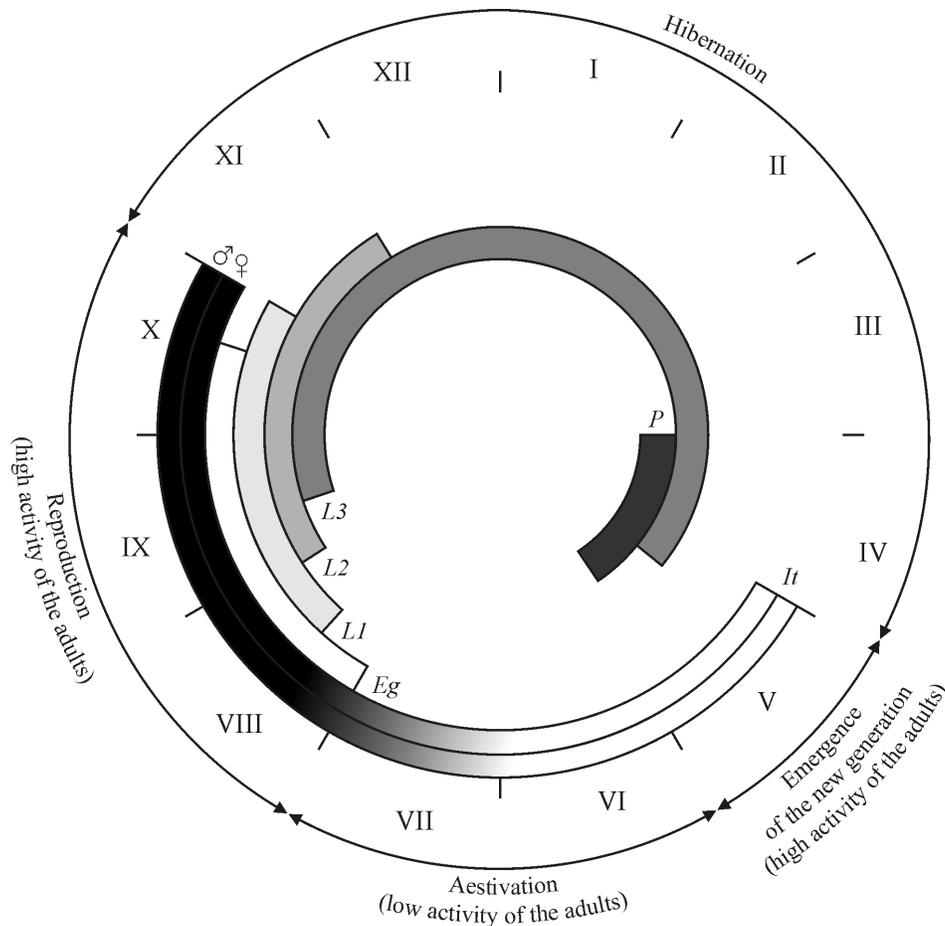


Fig. 6. Annual autumnal semelparous life cycle by the example of *Nebria brevicolis* (F.) (after Nelemans, 1987). For designations, see Fig. 1.

(Fig. 7). In case of brief cold spells in late autumn and early winter, the larvae of these species may enter a short facultative diapause. Such species belong to the autumn-winter group.

Reproduction of the aseasonal species occurs not in any specific period but all the year round; correspondingly, such species have no diapausing stage.

The constancy of the life cycle, previously referred to as determinacy (Matalin, 2005), is understood as the influence of specific biotopic conditions, and also the weather and climatic conditions of individual seasons within one or several natural zones, on the parameters of the life cycle. For example, the biennial life cycles can be obligatory, when development of all individuals in the population takes more than one year under any conditions, or facultative, when, depending on the conditions, only part of individuals follow the biennial development pattern. The bivoltine cycles can also be obligatory or facultative. In the former case, two generations develop in the population regardless of the

conditions, and in the latter case, the second generation appears only in the most favorable seasons or only in part of the distribution area. Although similar variants of such life cycles are sometimes difficult to distinguish, their consistency is insured by the discrete nature of the hibernating stages and the synchronized development of both larvae and adults.

The repeatability of reproduction, which was quite inadequately referred to as polycyclic in an earlier publication (Matalin, 2005), reflects the ability of individuals to reproduce more than once during either one or several seasons. Based on this criterion, the species that live during only one season and have a continuous period of reproduction are termed semelparous, while those capable of reproduction during two or more years or having several distinct periods of reproduction during one season are referred to as iteroparous.

The combinatorial analysis of the above parameters produces a considerable number of theoretically pos-

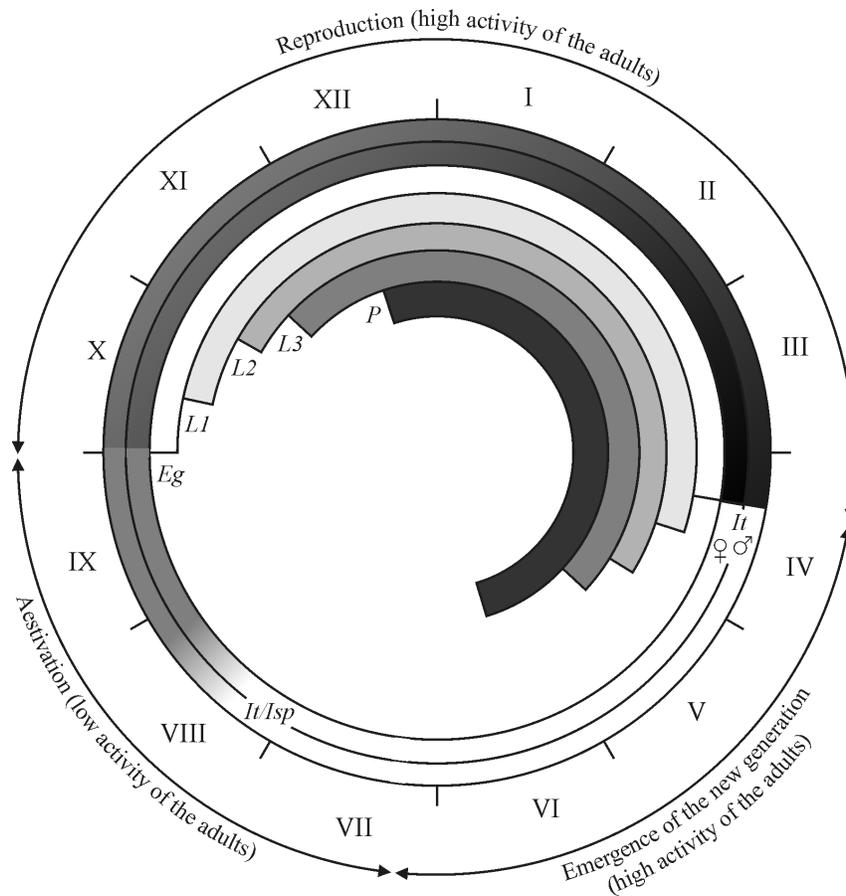


Fig. 7. Annual winter iteroparous life cycle by the example of *Carabus lusitanicus* (F.) (after Cárdenas and Hidalgo, 1995). For designations, see Fig. 1.

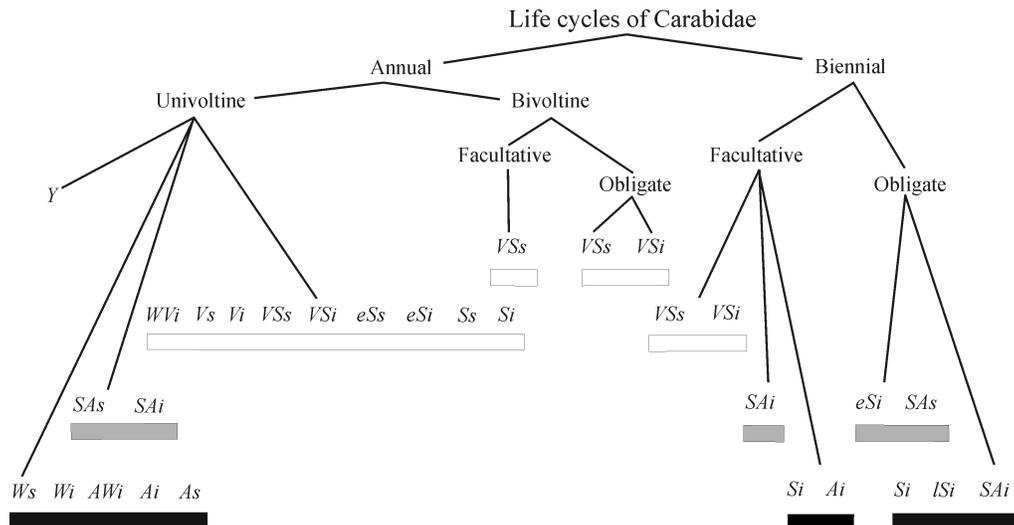


Fig. 8. Typology of the life cycles of Carabidae in the Western Palearctic: aseasonal (Y), winter-spring iteroparous (WVi), spring semelparous (Vs), spring iteroparous (Vi), spring-summer semelparous (VSs), spring-summer iteroparous (VSi), early summer semelparous (eSs), early summer iteroparous (eSi), summer semelparous (Ss), summer iteroparous (Si), late summer iteroparous (lSi), summer-autumnal semelparous (SAs), summer-autumnal iteroparous (SAi), autumnal semelparous (As), autumnal iteroparous (Ai), autumn-winter iteroparous (AWi), winter semelparous (Ws), and winter iteroparous (Wi). The cycles with obligatory hibernation of the adults are shown as white rectangles, the cycles with obligatory hibernation of the larvae but no aestivation of the adults, as gray rectangles, and those with obligatory hibernation of the larvae and aestivation of the adults, as black rectangles.

sible combinations: $2 \times 2 \times 11 \times 2 \times 2 = 176$. However, most of these variants cannot be realized due to obvious restrictions. It is known that the duration of development of each ontogenetic stage in Carabidae is affected by many factors: the temperature regime of the soil and the near-ground air layer, humidity, day length, the quantity and quality of food, its availability, etc. The eggs, first-instar larvae, and pupae usually develop most rapidly, whereas the development of old-instar larvae takes much more time (Kasandrova and Sharova, 1971; Hürka, 1975; Nekuliseanu, 1987; Matalin, 1998b). Even under the most favorable conditions there exists a minimum time of development, comprising from 1 to 1.5 months in the ground beetles of the temperate belt. It should also be taken into account that the gonad development in many species is controlled by the photoperiod and has strict temporal limitations. Thus, the “forbidden” combinations are the bivoltine spring, summer-autumnal, autumnal, autumn-winter, winter, and winter-spring cycles. In addition, bivoltine development cannot be combined with a biennial or perennial life cycle for obvious reasons.

By now, 30 variants of the life cycles of Carabidae realized in the Western Palaearctic have been described and analyzed (Fig. 8; table). The following notation is proposed: the period of reproduction is designated by capital letters, and the periodicity, in lowercase letters: Vs or SAi; the duration of the cycle is designated by the preceding coefficient: As or 2SAi, while the number of generation is shown in superscript: VS² (omitted for annual and univoltine cycles); the parentheses indicate the facultative nature of the cycle: (2VS)i, as compared to the obligatory one: 2SAs.

The Polyvariant Nature of the Life Cycle and Variability of the Seasonal Rhythm

The quantitative parameters of the life cycles are often changed under the influence of environmental factors. Many representatives of Carabidae are characterized by high variability of the duration of the reproduction period (van Dijk, 1972, 1983; Jones, 1979; Basedow, 1994; Matalin and Budilov, 2003; Sharova and Filippov, 2003), the number of eggs laid (Grüm, 1975; Desender et al., 1985; Aukema, 1987; Matalin, 2006), and the development time and survival rates of specific ontogenetic stages (Andersen, 1983; Butterfield, 1986; Sota, 1986; Nelemans, 1987; Chaabane et al., 1996). However, all these fluctuations can be

partly compensated for by the synchronized development of the larval or adult phase, because of which the demographic structure of populations of most species displays more or less regular dynamics.

The synchronized development of preimaginal phases was described earlier by the example of *Harpalus affinis* (Matalin, 1998b). In general, the sex and age structure of populations of this species corresponds to the spring-summer type with hibernating adults. The overwintered beetles reproduce in May–June, and preimaginal development is completed during summer, each ontogenetic stage taking on the average from 15 to 20 days. As a result, individuals of the new generation appear in August–September and hibernate (Fig. 3a). However, not only adults of *H. affinis* but also old instar larvae and pupae can hibernate. Their development after hibernation is strongly extended and may take 2–3 months in the larvae and 3.5–4 months in the pupae. The teneral adults, as in the preceding case, emerge in August–September (Fig. 3b). Thus, prolonged development of the overwintered larvae and pupae insures synchronization of the life cycle as a whole.

Synchronized development of the adults was described in *Carabus problematicus* (Houston, 1981; Jørum, 1985; Loreau, 1985). This species is characterized by autumnal reproduction, a larval parapause and, according to most researchers, also an aestivation parapause at the adult stage (van der Drift, 1951, 1958; Thiele, 1977; Jørum, 1985; Butterfield, 1986). The seasonal dynamics of *C. problematicus* displays two peaks of surface activity, one of which, depending on the conditions, is observed in late spring—mid-summer, and the other, in late summer—early autumn (van der Drift, 1951, 1958; Greenslade, 1965; Rijnsdorp, 1980; Houston, 1981; Jørum, 1985; Loreau, 1985). Individuals of the new generation emerge during the first peak, which is followed by a short period of summer dormancy (aestivation). It is only after this period that the beetles start to reproduce, and the hatched larvae hibernate. At the same time, some of the spent individuals of *C. problematicus* can hibernate for the second time, their fraction being much greater in high latitudes (Houston, 1981) and alpine areas (Butterfield, 1986; Sparks et al., 1995). However, the overwintered individuals do not reproduce till the end of summer (Houston, 1981: Fig. 3; Jørum, 1985: Fig. 1; Loreau, 1985: Figs. 8–9). This is related to the fact that reactivation of their gonads (as well as gonad maturation in the immature adults) takes

place only when the day length decreases (Thiele, 1977). In this case, synchronization of the life cycle is facilitated by a delay in gonad reactivation in the spent adults after their second hibernation (Fig. 4). It is interesting that besides the physiological limitations, the trophic ones also play a significant role. In particular, if the overwintered spent adults started reproducing immediately in late spring–early summer, larvae hatched by mid-summer could face a shortage of food. Such data were obtained in the studies of larval feeding and development in some North American (Lenski, 1982, 1984) and Japanese (Sota, 1985b) *Carabus* species with similar life cycles.

The variability of the life cycles may result in facultative bivoltinism (Bauer, 1974; Paarmann, 1976a; Loreau, 1985; Sota, 1988; Adis et al., 1998; Makarov and Chernyakhovskaya, 1990; Sharova and Filippov, 2003), with hibernation at different ontogenetic stages. For example, the larval development in the species with spring and spring-summer reproduction is completed within the vegetation season, and the immature beetles of the new generation hibernate. However, many species have strongly prolonged periods of reproduction and emergence of larvae. In some cases, part of the larvae have to hibernate without pupation, which, as mentioned above, results in strongly prolonged development (see also Matalin, 1998b). On the contrary, in the summer–autumnal and autumnal species with a larval parapause, the hibernation of immature adults increases the time of individual development to two years (Jørum, 1980; Houston, 1981; Butterfield, 1986; Matalin and Budilov, 2003; Sharova and Filippov, 2003; Matalin, 2006). Because of the repeated similarly directed modifications of the life cycle, the population may simultaneously include individuals with essentially different seasonal rhythms (Chaabane et al., 1996; Sharova and Denisova, 1997a; Matalin, 1998b, 2006; Matalin and Budilov, 2003). This phenomenon was referred to earlier as phenological polyvariance (Makarov, 1990, 1991, 1994).

It should be borne in mind that phenological polyvariance may be differently manifested in different populations even within the same natural and climatic zone. Under certain conditions, the population may be represented by two fractions, whose individuals reproduce synchronously (Fig. 3) or asynchronously (Fig. 5) during a season (Makarov and Chernyakhovskaya, 1990; Sharova and Denisova, 1996, 1997a, 1997b; Matalin, 1997c, 1998b; Matalin and Budilov, 2003; Sharova and Denisova, 1995). It often happens, how-

ever, that the population is represented by only one of these fractions (Makarov and Chernyakhovskaya, 1989; Chernyakhovskaya, 1990; Khotuleva, 1997). Under the least favorable conditions, for example, at the periphery of the distribution range or in the years with anomalous weather conditions, the population can be subdivided into two almost completely separated groups (Fig. 4), one of which hibernates as adults, and the other as larvae (Houston, 1981; Refseth, 1984; Sota, 1985a; Butterfield, 1986; Sharova and Filippov, 2003; Khobrakova and Sharova, 2005; Sharova and Khobrakova, 2005; Matalin, 2006). Even though individual development in each fraction takes two years, it follows the same pattern, i.e., it is based on the same seasonal rhythm with a one-year lag. The phenological polyvariance in this case is replaced by univariance. This type of the life cycle was previously referred to as “compensatory monovariant,” and the populations in which it is observed, as “byside populations” (from the expression “side by side”) (Matalin, 2006). It should be noted that the spent individuals hibernating for the second time provide a link between the two subpopulation groups, maintaining the biological integrity of the species (Matalin, 1997c, 1998b; Sharova and Khobrakova, 2005). Thus, the presence of subpopulation groups does not necessarily indicate the polyvariant nature of the life cycle, as was erroneously assumed by some researchers (Sharova and Filippov, 2003; Khobrakova and Sharova, 2005; Sharova and Khobrakova, 2005).

The phenological polyvariance of the life cycle means that the same population includes individuals with different seasonal rhythms, resulting from diapausing in an atypical phenophase or from development of several generations during a season. Repeated reproduction during several seasons (iteroparity) cannot be considered as a manifestation of phenological polyvariance (Sharova and Denisova, 1995, 1996, 1997a, 1997b; Filippov, 2000; Khobrakova, 2003; Sharova and Filippov, 2003; Khobrakova and Sharova, 2005), because the individuals show the same seasonal rhythm in the case of the first or repeated reproduction, hibernation takes place at the same ontogenetic stage, and development of the filial generation proceeds in the same way.

Among the life cycles considered above (table), only the obligate-bivoltine ones are always polyvariant, because one of their generations develops with a diapause, and the other without a diapause. On the contrary, the annual univoltine and obligate-biennial

life cycles are always univariant. The facultative bivoltine and biennial life cycles may be realized both as univariant (univoltine, and also annual or biennial) and polyvariant ones (bivoltine or combining annual and biennial individual development), depending on the seasonal, biotopic, and climatic conditions.

At the same time, the influence of environmental factors may also result in qualitative changes in the life cycles, such as reduction of certain development stages or appearance of additional dormant phases owing to morphological and functional differentiation of the larvae (Makarov, 1994; Kirk, 1974). Such cases are referred to as morphological polyvariance (Makarov, 1991). Unfortunately, a detailed analysis of this phenomenon is presently impossible due to the insufficient experimental data. When such data become available in the future, they will certainly expand the proposed classification of the life cycles in Carabidae.

DISCUSSION

After the publication of Larsson (1939), subdivision of the ground beetles into the “spring” and “autumnal” species was firmly established in the literature. However, in the course of subsequent work it became evident that each of these types of development could be realized on the basis of two different reproductive rhythms (Thiele, 1977; Paarmann, 1979). It was also found out that in the absence of below-zero temperatures, some “autumnal” species could develop during the winter months (Paarmann, 1970; van Dijk, 1972; den Boer, 1977; den Boer and den Boer-Daanje, 1990; Cárdenas, 1994; Cárdenas and Hidalgo, 1995, 1998; den Boer and van Dijk, 1996). Finally, many species of ground beetles were observed to hibernate both as larvae and as adults and to have a prolonged reproductive period, extending from late spring—early summer to late summer—early autumn. The forms showing the former trait were referred to as “species with unstable wintering conditions” (Lindroth, 1945; Thiele, 1977; Paarmann, 1979; Drioli, 1987; Loreau, 1985), and the species revealing the latter trait were termed “multi-seasonal” ones (Sharova and Dushenkov, 1979).

The type of reproduction was used as the main criterion for the development of all classifications of the life cycles of Carabidae following that of Larsson (1939). However, approaches to this task varied. For example, Thiele (1977), Paarmann (1979), and Drioli (1987) considered each type of reproduction to correspond strictly to a specific reproductive rhythm.

P.J. den Boer and co-authors (den Boer and den Boer-Daanje, 1990; den Boer and van Dijk, 1996) subdivided the species not only by the period of reproduction but also by their migration capacities and preferred habitats. Sharova and Dushenkov (1979) considered not only the type of reproduction but also the pattern of seasonal activity of the adults and larvae. Finally, Hürka (1973, 1986) tried to find the relation between the type of development and the taxonomic position of ground beetle species. The common drawback of all these classifications was lack of any options, each species being characterized by one and only one type of the life cycle. Even though the selected parameters or even the entire life cycle was quite often observed to vary between different biotopes or climatic zones (Lindroth, 1945; Paarmann, 1979; Jørum, 1980; Houston, 1981; Loreau, 1985; Sota, 1985a, 1986; Refseth, 1988), it was not reflected in any of the previous schemes.

The classification of life cycles of Carabidae proposed in this communication essentially differs from the preceding ones in that it provides for the possible alternatives. Since each of the parameters considered above varies to some extent depending on the zonal, climatic, or biotopic conditions, many species of ground beetles can be characterized by a certain set of life cycles, rather than by a single type. This approach allows one not only to characterize their biotopic and geographical variability, but also to estimate their polyvariance.

Most ground beetles of the temperate belt are characterized by annual development (Larsson, 1939; Lindroth, 1945; Thiele, 1977; Paarmann, 1979; Andersen, 1984). Until recently, it was believed that the biennial life cycles were realized only under the most extreme conditions, for example in high latitudes (Kaufmann, 1971; Paarmann, 1979; Houston, 1981; Andersen, 1983; Korobeinikov, 1984, 1988; Refseth, 1984; Sharova and Filippov, 2003), alpine areas (Butterfield, 1986, 1996; Schatz, 1994; Sparks et al., 1995; Khorakova and Sharova, 2005; Sharova and Khorakova, 2005), and arid landscapes (Shelford, 1908; Hamilton, 1925). However, the data obtained by a number of researchers indicate that biennial development is often observed in phenologically different species in various natural zones: from the middle taiga to the steppes (Luff, 1966, 1973; Jørum, 1980; Kryuchkova and Panov, 1988; Chaabane et al., 1996; Sharova and Denisova, 1997b; Matalin, 1998b, 2006; Matalin and Budilov, 2003). The fraction of individuals with an-

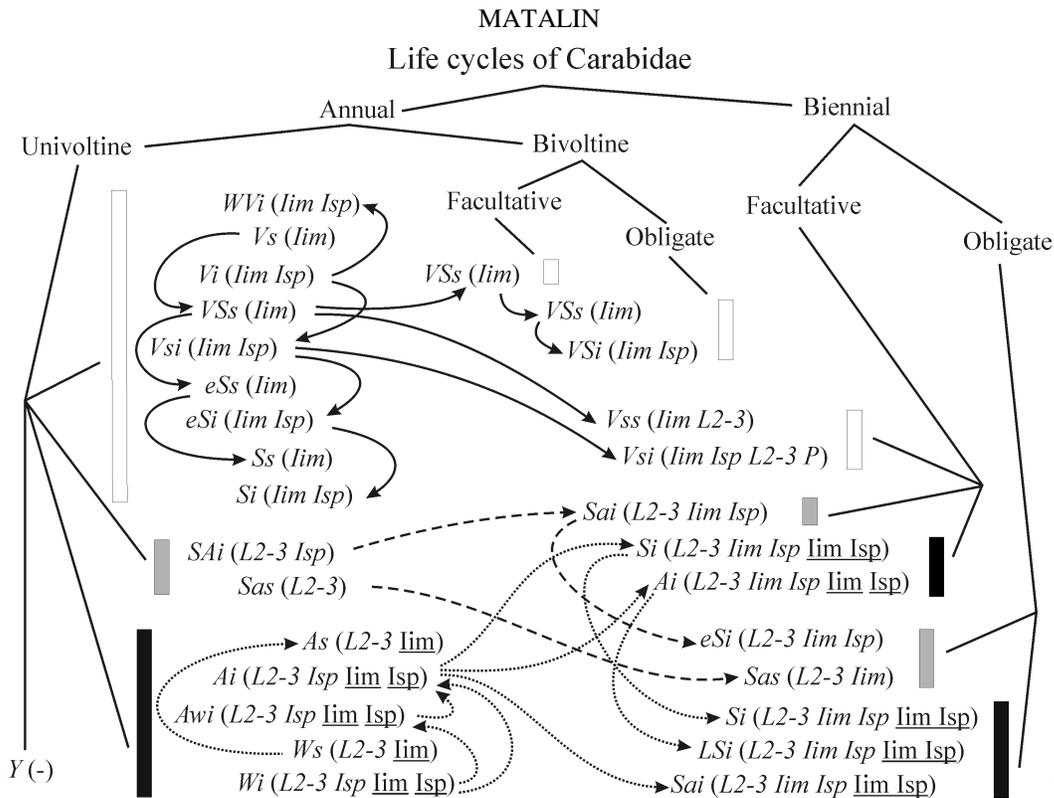


Fig. 9. Possible directions of transformation of the life cycles of Carabidae in the Western Palearctic. Designations: immature adults (*Im*), spent adults (*Isp*), old-instar larvae (*L2-3*), and pupae (*P*). The hibernating phases are shown in italics, and the aestivating phases are underlined. The cycles with obligatory hibernation of the adults are shown as white rectangles and solid arrows, the cycles with obligatory hibernation of the larvae but no aestivation of the adults, as gray rectangles and dashed arrows, and those with obligatory hibernation of the larvae and aestivation of the adults, as black rectangles and dotted arrows. The arrows show the direction and sequence of cycle transformations. For other designations, see Fig. 8.

annual or biennial type of development changes regularly with latitude (Matalin, 1998b, 2006; Matalin and Budilov, 2003). At the same time, the ratio of fractions with annual and biennial development may vary considerably between different biotopes even within the same natural zone (Makarov and Chernyakhovskaya, 1989; Chernyakhovskaya, 1990; Sharova and Denisova, 1997b). It is interesting to note that biennial development in Carabidae has appeared on the basis of at least three different reproductive rhythms (Fig. 9).

The triennial life cycles can be considered only as a theoretical possibility. Such a scenario could be realized if a new generation appeared once in three years. This could be possible if the first hibernation occurred at the immature adult stage, the second one, at the young-instar larval stage, and the third one, at the third-instar larval and/or pupal stage. This variant of life cycle is possible only under strictly limited environmental conditions, for example in the Subarctic. It is known at least in several Arctic leaf beetles, whose development may take from three to four years (Chernov, 1974, 1978), and, according to some data, even four to five and possibly six years (Khruleva, 1994).

However, no reliable reports of this phenomenon have been published for Carabidae. There is only indirect evidence on the possibly triennial development of two *Amblystogenium* species from some subantarctic islands of the Indian Ocean (Davies, 1987). The phenomenon of “superpause,” when the adult remains inactive in the pupal chamber for two or three years and only then starts reproducing, is known for some coleopterans, in particular leaf beetles (Koval, 2005), but not for ground beetles.

Most of Carabidae are iteroparous, i.e., they can reproduce during two or more years or several times per season. This may be explained by the fact that many species of ground beetles can hibernate as adults and are therefore pre-adapted to repeated reproduction. The resulting age heterogeneity of the population increases its stability, preventing abrupt changes in the abundance and reducing the risk of elimination (Matalin, 1997c, 1998b; Weber and Klenner, 1987). Some representatives of Carabidae are, however, obligatorily semelparous. This is typical of some spring species (for example, *Pterostichus strenuus*, *Stenolophus skrimshiranus*) with a considerable gap between the

two periods of reproduction. A similar situation is observed in the species with a long aestivation diapause in the adult phase (*Nebria brevicollis*, *Amara bifrons*, *Leistus rufomarginatus*, etc.), when the emergence of young beetles and their reproduction are separated by no less than 2–3 months. In this case, individuals of the parental generation cannot survive the long dormant period, therefore, the small number of old overwintered individuals present in the population in spring die out before the beginning of the reproductive period in late summer—early autumn. Such species were even specially referred to as “virtually semelparous” (den Boer, 1979; Nelemans, 1987). In both cases, the death of old adults appears to be determined by the specificity of their water-salt metabolism and deficiency of water in the organism that develops during the long dormant period coinciding with the warmest months in the season.

It is well known that multivoltine species, especially obligate-multivoltine ones, are rare among ground beetles. Such species produce no more than two generations per season even under the most favorable conditions. The main reason for this is the specific physiology of both adults and larvae. The species with obligatory hibernation of the larva (all summer-autumnal, autumnal, and winter ones), and those in which the gonad maturation is strictly determined by changes in the day length (some spring, spring-summer, autumnal, and winter ones) cannot produce more than one generation per season under any circumstances. An important condition for the development of the second generation is the availability of trophic resources and the relative stability of the habitat. This is why the bivoltine life cycles are most often observed in the populations of small specialized predators, such as *Loricera* (Makarov and Chernyakhovskaya, 1989) or *Notiophilus* (Loreau, 1985; Ernsting et al., 1992; Sharova and Filippov, 2003), consuming various springtails. The high abundance of their prey insures survival of the second generation in these species not only in the southern parts of their distribution ranges, but also in the northern areas (Sharova and Filippov, 2003). The bivoltine cycles often occur in the populations of small non-specialized predators of the genera *Elaphrus* (Bauer, 1974) and *Pogonus* (Paarmann, 1976a) and some mixophagous forms, such as *Stenolophus* (Matalin, 1997b). Two generations usually develop in the southern parts of their ranges, and only one generation, in the northern parts (Paarmann, 1976a; Matalin, 1997b). Accord-

ing to the theoretical estimations (Sota, 1988), the bivoltine life cycle can be stable only if the fraction of the filial generation among the overwintered individuals exceeds that of the parental generation; otherwise, the bivoltine pattern is changed back to the univoltine one. This accounts for the phenomenon of the facultative-bivoltine life cycles, observed in some basically univoltine ground beetles in the temperate belt: a second generation can develop in some parts of the distribution range or only in the most favorable years.

The most variable parameter of the life cycle is the seasonality, i.e., the position of the reproductive period. Many species of ground beetles have vast distribution ranges and occur within considerable gradients of weather and climatic conditions, overlapping with the mosaic pattern of landscapes and biotopes. The total duration of the active period, the time of reproduction, preimaginal development, and maturation of the adults change regularly along these gradients. In particular, as the latitude increases, reproduction of many spring species not only shortens but also shifts onto a later period: spring-summer and even summer (Fig. 9). For example, *Pterostichus oblongopunctatus*, broadly distributed in Europe, reproduces from early April to late July in the forest-steppe (Sharova and Denisova, 1997b), from late April to the middle or end of July in the broad-leaved forests (van Heerd et al., 1976), from early May to mid-July in the southern taiga (Vasil'eva, 1978), and from early June to early July in the northern taiga (Sharova and Filippov, 2003). The reproductive period in the summer-autumnal and some autumnal species, on the contrary, shifts onto earlier dates. For example, *Carabus glabratus* reproduces from July to September in southern and middle Europe (Larsson, 1939; Lindroth, 1945; Hürka, 1973; Kozyrev, 1989; Turin, 2000) and from June to July in the northern Europe (Lindroth, 1945; Houston, 1981; Refseth, 1988; Luff, 1998; Filippov, 2006a). However, the reproductive period of some autumnal species may expand considerably under favorable climatic conditions. For example, *Leistus rufomarginatus*, *Amara infima*, *Bradycellus harpalinus*, *Trichocellus placidus*, and *T. cognatus* reproduce during the autumn months in most parts of Europe (Larsson, 1939; Lindroth, 1945; Loreau, 1985), whereas in the mild coastal climate of Belgium and the Netherlands their reproduction occurs not only in autumn but also in winter (den Boer, 1977; den Boer and van Dijk, 1996; Turin, 2000).

Changes in the climatic and biotopic conditions often affect the constancy of the life cycle. For example, the main variant of development of the widespread Palaearctic species *Pterostichus melanarius* is the annual univoltine summer-autumnal semelparous cycle with obligatory hibernation (parapause) of the old-instar larvae (Larsson, 1939; Hürka, 1975; Thiele, 1977; Matalin, 2006). However, under unfavorable conditions, part of the beetles of the new generation that develops from the overwintered larvae hibernate without reproducing (Jørum, 1980; Matalin, 2006). Development of these individuals takes two years, so that the originally annual semelparous life cycle becomes the facultative-biennial iteroparous one (Fig. 5). Under the most pessimal conditions, for example, near the northern border of the range, all adults of the new generation hibernate without reproducing (Sharova and Filippov, 2003; Matalin, 2006). The facultative-biennial life cycle is thus transformed into the obligate-biennial one.

It should be noted that not only the type of the life cycle, but also its variability is changed in the above case. The original annual summer-autumnal life cycle is univariant because all individuals have the same seasonal rhythm with the hibernating larva (Fig. 5a). Hibernation of the immature adults increases their development to two years, resulting in the facultative-biennial variant (Fig. 5b); the life cycle then becomes polyvariant. As a result, two subpopulation groups, partly overlapping in time, are formed within the same population. If these groups become completely isolated and the obligate-biennial life cycle is established, the population reverts to the uniform seasonal rhythm, which is, however, shifted by one year between the two groups. As a result, the polyvariant development is again replaced by the univariant one.

The different variants of the life cycle may be often realized in different biotopes within the same natural and climatic zone and in the same season. For example, in the grassless birch forests and grass oak groves of Tambov Province, the overwintered immature and spent individuals of *P. melanarius* reproduce from late spring to early summer, while the adults of the new generation, having developed from the overwintered larvae, reproduce from mid-summer to early autumn (Sharova and Denisova, 1997b: Figs. 4b, 4c). The life cycle is polyvariant in both cases and is realized as the facultative-biennial summer-autumnal iteroparous variant. On the contrary, in the forb-meadow pine forests only the overwintered adults start

to reproduce, whereas the beetles of the new generation hibernate without reproduction (Sharova and Denisova, 1997b: Fig. 4a). In this case, we observe the univariant obligate-biennial early summer iteroparous life cycle.

The proposed typology of the life cycles of Carabidae reflects two most important characteristics of a species: its discreteness and integrity. In many cases, examination of individual populations allows us to reveal only some variants of the life cycle or its local (zone or landscape) specificity. Although these data are important for various ecological studies, the exact type of life cycle for the species as a whole can be determined only by studying the variety of its realizations.

ACKNOWLEDGMENTS

The author expresses his sincere gratitude to Prof. I.Kh. Sharova and Prof. K.V. Makarov (Moscow State Pedagogical University) for valuable advice and discussion of this work and for the overall help and support.

This work was financially supported by the Russian Foundation for Basic Research (grants no. 03-04-49251, 06-04-49456) and the Presidential Support Program for Leading Academic Schools (grant no. 2154.2003.4).

REFERENCES

1. Adis, J., Paarmann, W., Amorin, M.A., Arndt, E., and Fonseca, C.R.V., "On Occurrence, Habitat Specificity and Natural History of Adult Tiger Beetles (Coleoptera: Carabidae: Cicindelinae) near Manaus, Central Amazonia, and Key to the Larvae of Tiger Beetle Genera," *Acta Amazonica* **28** (3), 247–272 (1998).
2. Afonin, A.A., "Periodization of Ontogenesis in RS-Strategists," in *Prof. V.V. Stanchinskii Memorial Lectures, Issue 4* (Gos. Ped. Univ., Smolensk, 2004), pp. 322–326 [in Russian].
3. Andersen, J.M., "Habitat Choice and Life History of *Bembidiini* (Col., Carabidae) on River Banks in Central and Northern Norway," *Norsk Entomol. Tidsskr.* **17**, 17–65 (1969).
4. Andersen, J.M., "The Life Cycle of the Riparian Species of *Bembidion* (Coleoptera, Carabidae) in Northern Norway," *Notul. Entomol.* **63** (4), 195–202 (1983).
5. Andersen, J.M., "A Re-Analysis of the Relationships between Life Cycle Patterns and the Geographical Distribution of Fennoscandian Carabid Beetles," *J. Biogeography* **11** (6), 479–489 (1984).
6. Arndt, E., "Beiträge zur Insektenfauna der DDR: Gattung *Carabus* Linné (Coleoptera: Carabidae)," *Beitr.*

- Entomol. **39** (1), 63–103 (1989).
7. Aukema, B., "Differences in Egg Production and Egg Laying Period between Long- and Short-Winged *Calathus erythroderus* (Coleoptera, Carabidae) in Relation," Acta Phytopath. Entom. Hung. **22** (1–4), 45–56 (1987).
 8. Basedow, Th., "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. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 101–108.
 9. Bauer, T., "Ethologische, autökologische und ökophysiologische Untersuchungen an *Elaphrus cupreus* Dft. und *Elaphrus riparius* L. (Coleoptera, Carabidae)," Oecologia **14**, 139–196 (1974).
 10. Beklemishev, V.N., "Comparative Study of the Life Cycles of Bloodsucking Arthropods," Med. Parazitol. **11** (3), 39–44 (1942).
 11. Brandmayr, P. and Zetto Brandmayr, T., "The Evolution of Parental Care Phenomena in Pterostichine Ground Beetles with Special Reference to the Genera *Abax* and *Molops* (Col. Carabidae)," in *On the Evolution of Behavior in Carabid Beetles. Miscellaneous Papers of Agricultural University Wageningen* (H. Veeningen & Zonen B.V. Publ., Wageningen, 1979), pp. 35–49.
 12. 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.
 13. Briggs, J.B., "Biology of Some Ground Beetles (Col. Carabidae) Injurious to Strawberries," Bull. Entomol. Res. **56**, 79–93 (1965).
 14. Budilov, V.V., "Autumnal Distribution of Ground Beetles in Agrocenoses of Mordvinian ASSR," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990), Vol. 1, pp. 51–57 [in Russian].
 15. Budilov, P.V., *Candidate's Dissertation in Biology* (Moscow, 2002).
 16. Burges, A.F., "*Calosoma sycophanta*: Its Life History, Behavior and Successful Colonization in New England," U.S. Dep. Agric. Entomol., No. 101, 1–94 (1911).
 17. Butterfield, J., "Changes in Life-Cycle Strategies of *Carabus problematicus* over a Range of Altitudes in Northern England," Ecol. Entomol. **11** (1), 17–26 (1986).
 18. Butterfield, J., "Carabid Life Cycle Strategies and Climate Change: a Study on an Altitudinal Transect," Ecol. Entomol. **21** (1), 9–16 (1996).
 19. Cárdenas, A.M., "On the Life History of *Calathus granatensis* (Coleoptera, Carabidae) in Southwest Iberian Peninsula," in *Carabid Beetles: Ecology and Evolution. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 109–116.
 20. Cárdenas, A.M. and Bach, C., "The Effects of Photoperiod and Temperature Cycle on the Larval Development of *Calathus granatensis* Vuill. (Col. Carabidae)," in *Actas do I Congresso ibérico de Entomologia* (1992), Vol. 1, pp. 453–464.
 21. Cárdenas, A.M. and Hidalgo, J.M., "Datos sobre labiología de reproducción desarrollo larvario de *Carabus (Hadrocarabus) lusitanicus* (Fabricius, 1801) (Coleoptera: Carabidae)," Elytron **9**, 139–145 (1995).
 22. Cárdenas, A.M. and Hidalgo, J.M., "Data on the Biological Cycle of *Steropus globosus* (Coleoptera Carabidae) in the Southwest of Iberian Peninsula," Vie Milieu **48**, 35–39 (1998).
 23. Cárdenas, A.M. and Hidalgo, J.M., "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** (1), 47–56 (2004).
 24. Cárdenas, A.M. Heras, A.M. de la, and Molina, M.D., "The Influence of Some Abiotic Factors on the Developmental Type of *Calathus granatensis* Vuillefroy, 1866 (Coleoptera Carabidae)," Bol. Mus. Reg. Sci. Nat. Torino **14** (2), 379–387 (1996).
 25. Chaabane, K., Loreau, M., and Josens, G., "Individual and Population Energy Budgets of *Abax ater* (Coleoptera, Carabidae)," Ann. Zool. Fenn. **33** (1), 97–108 (1996).
 26. Chaboussou, F., "Remarques sur *Lebia grandis* Hentz," Rev. Zool. Agric. **37**, 165–171 (1938).
 27. Chemini, C. and Pizzolotto, R., "Comunita di carabidi in siti forestali dei Monti Lessini (Trentino) (Coleoptera: Carabidae)," Studi Trentini Sci. Nat. Acta Biol. **67** (1990), 197–227 (1992).
 28. Chernov, Yu.I., "Some General Aspects of Adaptation of Terrestrial Animals to Landscape and Zonal Conditions," Zh. Obshch. Biol. **35** (6), 846–857 (1974).
 29. Chernov, Yu.I., "Adaptive Features of the Life Cycles of Insects in the Tundra Zone," Zh. Obshch. Biol. **39** (3), 394–402 (1978).
 30. Chernyakhovskaya, T.A., "Seasonal Activity Dynamics and Population Structure of the Ground Beetle *Pterostichus niger* Schaller in Different Biotopes," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990), Vol. 2, pp. 44–49 [in Russian].
 31. Claassen, P., "Life History and Biological Notes on the *Chlaenius impunctifrons* Say," Ann. Entomol. Soc. Amer. **12**, 95–100 (1919).
 32. Cole, L.C., "The Population Consequences of Life History Phenomena," Quart. Rev. Biol. **29**, 103–137 (1954).
 33. Colombini, I. and Chelazzi, L., "A Comparison between the Life Cycles of Different Populations of *Eurynebria complanata* (Linnaeus, 1767) (Coleoptera: Carabidae)," Elytron **5**, 5–14 (1992).

34. Danilevskii, A.S., *Photoperiodism and Seasonal Development of Insects* (Len. Gos. Univ., Leningrad, 1961) [in Russian].
35. Danilevskii, A.S., "The System of Ecological Adaptations of Insects to Seasonal Zonality," in *Problems of Photoperiodism and Diapause in Insects* (Len. Gos. Univ., Leningrad, 1972), pp. 15–25 [in Russian].
36. Danilevskii, A.S. and Kuznetsova, I.A., "Intraspecific Adaptations of Insects to Climatic Zonality," in *Photoperiodic Adaptations in Insects and Acarines* (Len. Gos. Univ., Leningrad, 1968), pp. 5–51 [in Russian].
37. Davies, L., "Long Adult Life, Low Reproduction and Competition in Two Sub-Antarctic Carabid Beetles," *Ecol. Entomol.* **12** (2), 149–162 (1987).
38. Deleurance, S. and Deleurance, E.P., "Reproduction et cycle évolutif larvaire des *Aphaenops* (*A. cerberus* Dieck, *A. crypticola* Lindner), insectes Coléoptères cavernicoles," *C. R. Acad. Sci. Paris* **258**, 4369–4370 (1964a).
39. Deleurance, S. and Deleurance, E.P., "L'absence de cycle saisonnier de reproduction chez les insectes Coléoptères troglobies (Bathysciines et Tréchinés)," *C. R. Acad. Sci. Paris* **258**, 5995–5997 (1964b).
40. Delkeskamp, K., "Biologische Studien über *Carabus nemoralis* Müll.," *Zeitschr. Morph. Ökol. Tiere* **19**, 1–57 (1930).
41. den Boer, P.J., "Dispersal Power and Survival. Carabids in a Cultivated Countryside (with a Mathematical Appendix by J. Reddingius)," in *Misc. Papers Landbouwhogeschool Wageningen* (1977), No. 14, pp. 1–190.
42. den Boer, P.J., "Some Remarks in Retrospect. On the Evolution of Behavior in Carabid Beetles," in *Misc. Papers Agricultural Univ. Wageningen* (1979), pp. 213–222.
43. den Boer, P.J. and den Boer-Daanje, W., "On Life History Tactics in Carabid Beetles: Are There Only Spring and Autumn Breeders?," in *The Role of Ground Beetles in Ecological and Environmental Studies* (Intercept Publ., Andover-Hampshire, 1990), pp. 247–258.
44. den Boer, P.J. and van Dijk, Th.S., "Life History Patterns among Carabid Species," *Tijdschr. Entomol.* **139** (1), 1–6 (1996).
45. Drioli, G., *Tipi e tempi di sviluppo dei Coleoptteri Geoadefagi presenti sul basso Carso triestino* (Trieste, 1987).
46. Dushenkov, V.M. and Chernyakhovskaya, T.A., "Carabid Larvae in Agricultural Areas of Moscow Region," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990), Vol. 1, pp. 84–99 [in Russian].
47. Ernsting, G., Isaaks, J.A., and Berg, M.P., "Life Cycle and Food Availability Indices in *Notiophilus biguttatus* (Coleoptera, Carabidae)," *Ecol. Entomol.* **17** (1), 33–42 (1992).
48. Fadl, A. and Purvis, G., "Field Observations on the Lifecycles and Seasonal Activity Patterns of Temperate Carabid Beetles (Coleoptera: Carabidae) Inhabiting Arable Land," *Pedobiologia* **42** (2), 171–183 (1998).
49. Fadl, A., Purvis, G., and Towey, K., "The Effect of Time of Soil Cultivation on the Incidence of *Pterostichus melanarius* (Illig.) (Coleoptera: Carabidae) in Arable Land in Ireland," *Ann. Zool. Fenn.* **33** (1), 207–214 (1996).
50. Fazekas, J., Kádár, F., Sárospataki, M., and Lövei, G., "Seasonal Activity, Age Structure and Egg Production of the Ground Beetle *Anisodactylus signatus* (Coleoptera: Carabidae) in Hungary," *Eur. J. Entomol.* **94** (4), 473–484 (1997).
51. Ferenz, H.-J., "Photoperiodic and Hormonal Control of Reproduction in Male Beetles, *Pterostichus nigrita*," *J. Insect Physiol.* **21**, 331–341 (1975).
52. Ferenz, H.-J., "Two-Step Photoperiodic and Hormonal Control of Reproduction in the Female Beetle *Pterostichus nigrita*," *J. Insect Physiol.* **23** (6), 671–676 (1977).
53. Filippov, B.Yu., *Candidate's Dissertation in Biology* (Moscow, 2000).
54. 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)].
55. 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)].
56. Forsskåhl, B., "The Invertebrate Fauna of the Kilpisjaervi Area, Finnish Lapland 9. Carabidae. With Special Notes on Ecology and Breeding Biology," *Acta Soc. Faun. Flora Fenn.* **80**, 99–119 (1972).
57. Galaktionov, K.V. and Dobrovolskii, A.A., *Origin and Evolution of Life Cycles of Trematoda* (Nauka, St. Petersburg, 1998) [in Russian].
58. Gilbert, O., "The Natural Histories of Four Species of *Calathus* (Coleoptera, Carabidae) Living on Sand Dunes in Anglesey, North Wales," *Oikos* **7** (1), 22–47 (1956).
59. Gilbert, O., "The Life History Patterns of *Nebria degenerata* Schaufuss and *N. brevicollis* Fabricius (Coleoptera, Carabidae)," *J. Soc. Brit. Entomol.* **6**, 11–14 (1958).
60. Glinyanaya, E.I., "The Role of Photoperiodic Conditions in Reactivation after Winter and Summer Diapause," in *Problems of Photoperiodism and Diapause in Insects* (Len. Gos. Univ., Leningrad, 1972), pp. 88–102 [in Russian].
61. Greenslade, P.J.M., "On the Ecology of Some British Carabid Beetles with Special Reference to Life Histories," *Trans. Soc. Brit. Entomol.* **16**, 149–179 (1965).
62. Grüm, L., "An Attempt to Estimate Production of a Few *Carabus* L. Species (Col. Carabidae)," *Ekol. Polska* **23** (4), 673–680 (1975).
63. Hamilton, C.C., "Studies on the Morphology, Taxon-

- omy and Ecology of the Larvae of Holarctic Tiger Beetles (Family Cicindelidae)," Proc. U. S. Nat. Mus. **65** (17), 1–87 (1925).
64. Hatvani, A. and Kádár, F., "A *Harpalus rufipes* szezonális aktivitása, korszerkezeti és szaporodási jellemzői (Coleoptera: Carabidae)," Növényvédelem **38** (4), 163–168 (2002).
65. Hinton, H.E., "The Origin and Function of the Pupal Stage," Proc. R. Entomol. Soc. Lond. **38** (4–6), 77–85 (1963).
66. Houston, W.W.K., "The Life Cycles and Age of *Carabus glabratus* Paykull and *C. problematicus* Herbst. (Col.: Carabidae) on Moorland in Northern England," Ecol. Entomol. **6** (3), 263–271 (1981).
67. Hůrka, K., "Fortpflanzung und Entwicklung der mitteleuropäischen *Carabus* und *Procerus*-Arten," Studie ÈSAV **9**, 1–78 (1973).
68. Hůrka, K., "Laboratory Studies on the Life Cycle of *Pterostichus melanarius* (Ill.) (Coleoptera, Carabidae)," Věst. Čs. Společ. Zool. **39** (4), 265–274 (1975).
69. Hůrka, K., "The Developmental Type of Carabidae in the Temperate Zones as a Taxonomic Character," in *Carabid Beetles: Their Adaptations and Dynamics* (Gustav Fisher Verlag, Stuttgart, 1986), pp. 187–193.
70. Inyaeva, Z.I., *Candidate's Dissertation in Biology* (Moscow, 1965).
71. Inyaeva, Z.I., "Species Composition and Distribution of Ground Beetles (Coleoptera, Carabidae) in Fields," in *Fauna and Ecology of Invertebrates in Moscow Province* (Nauka, Moscow, 1983), pp. 98–107 [in Russian].
72. Jones, M.G., "The Abundance and Reproductive Activity of Common Carabidae in a Winter Wheat Crop," Ecol. Entomol. **4** (1), 31–43 (1979).
73. Jørum, P., "Life Cycle and Population Density of *Nebria brevicollis* F. (Coleoptera: Carabidae) in a Danish Beech Forest," Vidensk. Meddr. Dansk Naturh. Foren. **139**, 245–261 (1976).
74. 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).
75. Jørum, P., "Life Cycle and Phenology of *Carabus problematicus* Herbst, 1786 in Denmark (Coleoptera: Carabidae)," Entomol. Medd. **53** (1), 27–30 (1985).
76. Kabacik-Wasylik, D., "Ökologische Analyse der Laufkäfer (Carabidae) einiger Agrarkulturen," Ekol. Polska Ser. a **18** (7), 137–209 (1970).
77. Kålås, J.A., "Species Composition and Seasonal Activity Patterns of Carabidae (Col.) in a Small Deciduous Forest in Western Norway," Fauna Norvegica Ser. B. **32** (1), 28–32 (1985).
78. Karpova, V.E., "Seasonal Dynamics of Activity and Behavioral Strategy of Dominant Ground Beetle Species in the Agrocenoses of Different Cultivars," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990), Vol. 1, pp. 32–43 [in Russian].
79. Karpova, V.E. and Matalin, A.V., "Functional Age Structure of *Anisodactylus signatus* Panz. Populations in the Steppe Zone (Coleoptera, Carabidae)," in *Advances in Entomology in the USSR: Coleoptera. Proc. X Congr. of the All-Union Entomological Society* (ZIN, Leningrad, 1990a), pp. 62–63 [in Russian].
80. Karpova, V.E. and Matalin, A.V., "Dynamics of the Flight Activity of Carabids (Coleoptera, Carabidae) in Southern Moldova," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990b), Vol. 1, pp. 43–51 [in Russian].
81. Kasandrova, L.I. and Sharova, I.Kh., "Development of the Field Ground Beetles *Amara ingenua*, *Anisodactylus signatus*, and *Harpalus distinguendus* (Coleoptera, Carabidae)," Zool. Zh. **50** (2), 215–220 (1971).
82. Kaufmann, T., "Hibernation in the Arctic Beetle, *Pterostichus brevicornis*, in Alaska," J. Kansas Entomol. Soc. **44** (1), 81–92 (1971).
83. Khabrakova, L.Ts., *Candidate's Dissertation in Biology* (Moscow, 2003).
84. Khabrakova, L.Ts. and Sharova, I.Kh., "Life Cycles of Ground Beetles (Coleoptera, Carabidae) in the Mountain Taiga and Mountain Forest-Steppe of the Eastern Sayan," Izvestiya Ross. Akad. Nauk Ser. Biol., No. 6, 688–693 (2005).
85. Khotuleva, O.V., *Candidate's Dissertation in Biology* (Moscow, 1997).
86. Khruleva, O.A., "Life Cycle of the Leaf Beetle *Chrysolina subsulcata* (Coleoptera, Chrysomelidae) on Wrangel Island," Zool. Zh. **73** (3), 29–38 (1994).
87. Kirk, V.M., "Biology of a Ground Beetle, *Harpalus erraticus*," Ann. Entomol. Soc. Amer. **67**, 24–28 (1974).
88. Kochetova, A.N., "The Ground Beetle *Amara similata* Gyll. as Pest Damaging the Pericarps of Crucifers and Methods of Its Control," Trudy Timiryazevskoi Sel'skokhoz. Akad. **1** (3), 41–56 (1936).
89. Könen, J., *Physiologisch-Ökologische Untersuchungen zur Steuerung der Gonadenreifung und Fortpflanzungsperiodik von Pterostichus oblongopunctatus* F. (Coleoptera, Carabidae) in Abhängigkeit von Temperate, Fotoperiode und Juvenilhormon, Inaug.-Dissert., 1978.
90. Korobeinikov, Yu.I., "On the Reproductive Behavior of Ground Beetles in the Subarctic," in *Species and Its Productivity within the Distribution Area* (1984), Vol. 3, pp. 66–67 [in Russian].
91. Korobeinikov, Yu.I., "On the Fauna of Ground Beetles (Coleoptera, Carabidae) of Alpine Areas of the Southern Urals," Entomol. Obozr. **67** (4), 738–740 (1988).
92. Koval, A.G., *Candidate's Dissertation in Biology* (St. Petersburg, 2005).
93. Kozyrev, A.V., "Reproduction and Seasonal Activity of Ground Beetles (Coleoptera, Carabidae) in the Middle Urals," in *Insects in the Biogeocenoses of the Urals* (Sverdlovsk, 1989), pp. 27–28 [in Russian].

94. Krehan, I., "Die Steuerung von Jahresrhythmik und Diapause bei Larval- und Imago-überwintern der Gattung *Pterostichus* (Col., Carab.)," *Oecologia* **6** (1), 58–105 (1970).
95. Kryuchkova, E.E. and Panov, A.A., "Changes in the Activity of Cerebral Neurosecretory Cells in Three Species of Ground Beetles (Coleoptera, Carabidae) Related to the Annual Reproduction Cycle," *Zool. Zh.* **67** (11), 1661–1669 (1988).
96. Kundu, R. and Dixon, A.F.G., "Evolution of Complex Life Cycles in Aphids," *J. Animal Ecol.* **64**, 245–255 (1995).
97. Kůrka, A., "The Life Cycle of *Bembidion tibiale* (Coleoptera, Carabidae)," *Acta Entomol. Bohemoslov.* **72**, 374–382 (1975).
98. Lampe, K.H., "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** (1), 128–170 (1975).
99. Lamprecht, G. and Weber, F., "Die Circadian-Rhythmik von drei unterschiedlich weit an ein Leben unter Höhlenbedingungen adaptierten *Laemostenus*-Arten (Coleoptera, Carabidae)," *Anns. Speleol.* **30**, 471–482 (1975).
100. Larsson, S.G., "Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden," in *Entomologische Meddelelser. Bd. 20* (Kommission Hos P. Haase & Sønns Forlag, København, 1939), pp. 277–562.
101. Lenski, R.E., "Effects of Forest Cutting on Two *Carabus* Species: Evidence for Competition for Food," *Ecology* **63** (5), 1211–1217 (1982).
102. Lenski, R.E., "Food Limitation and Competition: a Field Experiment with Two *Carabus* Species," *J. Anim. Ecol.* **53** (1), 203–216 (1984).
103. Lindroth, C.H., "Die fennoskandischen Carabidae, Eine tiergeographische Studie. I. Spezieller Teil," *Göteborgs K. Vet. Vitt. Samh. Handl.: Broderna Lagerstrom Boktryckare Ser. B* **4** (1), 1–709 (1945).
104. Loreau, M., "Annual Activity and Life Cycles of Carabid Beetles in Two Forest Communities," *Holarctic Ecology* **8** (3), 228–235 (1985).
105. Loreau, M. and Ebenhöf, W., "Competitive Exclusion and Coexistence of Species with Complex Life Cycles," *Theor. Pop. Biol.* **46** (1), 58–77 (1994).
106. Louda, J., "Über den Einfluss vom Bebauen und von der chemischen Zusammenetzung des Bodens auf das Erscheinen von Carabidae," *Sborník Pedagogické Fakulty v Hradci Králové* **5**, 219–236 (1968).
107. Luff, M.L., "The Abundance and Diversity of the Beetle Fauna of Grass Tussocks," *J. Anim. Ecol. Oxford* **35**, 189–208 (1966).
108. Luff, M.L., "The Annual Activity Pattern and Life Cycle of *Pterostichus madidus* F. (Col. Carabidae)," *Entomol. Scand.* **4**, 259–273 (1973).
109. Luff, M.L., *Provisional Atlas of the Ground Beetles (Coleoptera, Carabidae) of Britain* (Biological Records Centre, Huntingdon, 1998).
110. Makarov, K.V., "Morpho-Ecological Characteristics of Life Cycles in the Ground Beetles of the Genus *Carabus* (L.)," in *Life Forms and Strategies of Organisms and Their Use for Bioindication of the Environment Conditions* (České Budějovice, 1989), pp. 22–23. [in Russian].
111. Makarov, K.V., "Seasonal Dynamics of Activity and the Reproductive Cycles of Ground Beetles (Coleoptera, Carabidae)," in *Proc. of the All-Union Methodological Workshop of High School Zoology Teachers* (Gos-agroprom DASSR, Makhachkala, 1990), Vol. 1, pp. 181–183 [in Russian].
112. Makarov, K.V., "Polyvariant Nature of the Life Cycle of Ground Beetles (Coleoptera, Carabidae)," in *Problems of Soil Zoology* (Novosibirsk, 1991), p. 132 [in Russian].
113. 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.
114. Makarov, K.V. and Chernyakhovskaya, T.A., "Variability of the Seasonal Activity Dynamics of the Ground Beetle *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Different Types of Forest," in *Ecological Aspects of Adequate Nature Management* (Inst. Biol. Akad. Nauk Latv. SSR, Riga, 1989), pp. 55–56 [in Russian].
115. Makarov, K.V. and Chernyakhovskaya, T.A., "Development Phenology and Population Structure of *Loricera pilicornis* (F.) (Coleoptera, Carabidae) in an Agrocenosis," in *Structure and Dynamics of Populations of Edaphic and Herpetobiotic Invertebrates* (Mos. Ped. Univ., Moscow, 1990), Vol. 1, pp. 21–32 [in Russian].
116. Manga, N., "Population Metabolism of *Nebria brevicollis* (F.) (Coleoptera, Carabidae)," *Oecologia* **10**, 223–242 (1972).
117. Matalin, A.V., "The Strategy of Dispersal Behavior in Some Carabidae Species of Southeastern Europe," in *Carabid Beetles: Ecology and Evolution. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 183–188.
118. Matalin, A.V., "Use of Light Traps in Ecological Studies of Ground Beetles (Coleoptera, Carabidae)," *Zool. Zh.* **75** (5), 744–756 (1996).
119. Matalin, A.V., "Peculiarities of Spatial and Temporal Differentiation of Carabids (Coleoptera, Carabidae) in the Steppe Zone," *Zool. Zh.* **76** (9), 1035–1045 (1997a) [*Entomol. Rev.* **77** (9), 1155–1166 (1997)].
120. 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

- (1997b) [Entomol. Rev. **77** (9), 1181–1190 (1997)].
121. Matalin, A.V., "Specific Features of the Life Cycle of *Pseudoophonus* (s. str.) *rufipes* Deg. (Coleoptera, Carabidae) in Southwestern Moldova," *Izv. Ross. Akad. Nauk. Ser. Biol.*, No. 4, 455–466 (1997c).
 122. Matalin, A.V., "Life Cycles of Ground Beetles of the Tribe Harpalini (Coleoptera, Carabidae) on the European Subcontinent: The Possible Ways of Their Origin and Transformation," in *Problems of Entomology in Russia. Proc. XI Congr. of Russian Entomol. Society (ZIN, St. Petersburg, 1998a)*, Vol. 2, pp. 25–26 [in Russian].
 123. Matalin, A.V., "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 (1998b).
 124. Matalin, A.V., "Typology of Reproductive Rhythms and Their Realization in the Life Cycles of Ground Beetles (Coleoptera, Carabidae) in the Temperate Zone of Western Palaearctic," in *Ecological Diversity of the Soil Biota and Soil Productivity. Proc. IV (XIV) All-Russia Workshop of Soil Zoology (Tsessiya, Tyumen, 2005)*, pp. 154–156 [in Russian].
 125. 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)].
 126. Matalin, A.V. and Budilov, P.V., "Geographical Variability of Sexual and Age Structure of Populations and the Life Cycle in *Brosicus cephalotes* (Coleoptera, Carabidae)," *Zool. Zh.* **82** (12), 1445–1453 (2003) [Entomol. Rev. **83** (8), 1037–1045 (2003)].
 127. Mazokhin-Porshnyakov, G.A., "The Main Adaptive Types of Lepidoptera," *Zool. Zh.* **33** (4), 822–841 (1954).
 128. Mjöberg, E., "Om några svenska insekters biologi och unrväckling," *Ark. Zool.* **3**, 1–22 (1906).
 129. Müller, H.J., "Formen der Dormanz bei Insecten," *Nova Acta Leopoldina* **35**, 7–25 (1970).
 130. Murdoch, W.W., "Population Stability and Life History Phenomena," *Amer. Nat.* **100** (910), 5–11 (1966).
 131. Murdoch, W.W., "Life History Patterns of Some British Carabidae (Coleoptera) and Their Ecological Significance," *Oikos* **19** (1), 25–32 (1967).
 132. Nekuliseanu, Z.Z., "Biology of *Pogonus litoralis* Duft. (Coleoptera, Carabidae)," in *Problems of Soil Zoology: Proc. IX All-Union Workshop (Metsniereba, Tbilisi, 1987)*, p. 199 [in Russian].
 133. Nekuliseanu, Z.Z., "Specific Biological Features of Some Ground Beetles of the Genus *Pterostichus* Bon. (Coleoptera, Carabidae) in Moldova," in *Advances in Entomology in the USSR: Coleoptera. Proc. X Congr. All-Union Entomol. Soc. (ZIN, Leningrad, 1990)*, pp. 96–98 [in Russian].
 134. Nekuliseanu, Z.Z., "Biologia unor Carabidae ale genului *Amara* Bon. (Coleoptera, Carabidae) din Moldova," *Bull. Acad. Ştiin. Rep. Moldova Ştiin. Biol. Chim.*, No. 1, 37–41 (1994).
 135. Nelemans, M.N.E., "On the Life History of the Carabid Beetle *Nebria brevicollis* (F.). Egg Production and Larval Growth under Experimental Conditions," *Neth. J. Zool.* **37** (1), 26–42 (1987).
 136. Neudecker, Ch. and Thiele, H.U., "Die jahreszeitliche Synchronisation der Gonadenreife bei *Agonum assimile* Payk. (Coleopt., Carab.) durch Temperatur und Photoperiode," *Oecologia* **17** (2), 141–157 (1974).
 137. Ortuño, V.M. and Marcos, J.M., "Carabidofauna (Insecta, Coleoptera) del área natural de Salburua (Vitoria, Alava)," *Ecologia*, No. 11, 457–482 (1997).
 138. Paarmann, W., "Untersuchungen über die Jahresrhythmik von Laufkäfern (Coleoptera, Carabidae) in der Cyrenaika (Libyen, Nordafrika)," *Oecologia* **5**, 325–333 (1970).
 139. Paarmann, W., "Bedeutung der Larvenstadien für die Fortpflanzungsrhythmik der Laufkäfer *Brosicus laevigatus* Dej. und *Orthomus atlanticus* Fairm. (Coleoptera, Carabidae) aus Nordafrika," *Oecologia* **13**, 81–92 (1973).
 140. Paarmann, W., "Der Einfluss von Temperatur und Lichtwechsel auf die Gonadenreife des Laufkäfers *Brosicus laevigatus* Dej. (Coleoptera, Carabidae) aus Nordafrika," *Oecologia* **15** (1), 87–92 (1974).
 141. Paarmann, W., "The Annual Periodicity of the Polyvoltine Ground-Beetle *Pogonus chalconus* Marsh. (Col. Carabidae) and Its Control by Environmental Factors," *Zool. Anz.* **196**, 150–160 (1976a).
 142. Paarmann, W., "Die Bedeutung exogener Faktoren für die Gonadenreife von *Orthomus barbarus atlanticus* (Coleoptera, Carabidae) aus Nordafrika," *Entomol. Exp. Appl.* **19** (1), 23–26 (1976b).
 143. Paarmann, W., "Propagation Rhythm of Subtropical and Tropical Carabidae (Coleoptera) and Its Control by Exogenous Factors," *Adv. Invert. Reprod.* **1**, 49–60 (1977).
 144. Paarmann, W., "Ideas about the Evolution of the Various Annual Reproduction Rhythms in Carabid Beetles of the Different Climatic Zones," *Misc. Pap. L. H. Wageningen* **18**, 119–132 (1979).
 145. 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.
 146. Paarmann, W., "Temperature and Photoperiodic Influence on Development Stages and Adults of the Subarctic Carabid Beetles *Pterostichus adstrictus* (Coleoptera)," in *Carabid Beetles: Ecology and Evolution. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 201–205.
 147. Penney, M.M., "Diapause and Reproduction in *Nebria brevicollis* (F.) (Coleoptera, Carabidae)," *J. Anim. Ecol.* **38**, 219–233 (1969).

148. Rasnitsyn, A.P., "Some Aspects of the Interactions between Morphogenesis and Growth in the Evolution of Insect Ontogenesis," *Entomol. Obozr.* **44** (3), 548–553 (1965).
149. 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).
150. Refseth, D., "Annual Patterns of Activity, Reproduction and Development in Some Norwegian Carabidae (Col.)," *Fauna Norvegica* **35** (1), 21–30 (1988).
151. Rijnsdorp, A.D., "Pattern of Movement in and Dispersal from a Dutch Forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae)," *Oecologia* **45** (2), 274–281 (1980).
152. Roff, D.A., *The Evolution of Life Histories: Theory and Analysis* (Chapman and Hall, N.Y., 1992).
153. Rotenberg, M., "Mathematical Description of Holometabolous Life Cycles," *J. Theor. Biol.* **64**, 333–353 (1977).
154. Schatz, I., "Life Strategy of an Alpine Carabid: *Pterostichus jurinei* (Coleoptera, Carabidae)," in *Carabid Beetles: Ecology and Evolution. Ser. Entomologica. Vol. 51* (Kluwer Acad. Publ., Dordrecht, 1994), pp. 213–217.
155. Schjødt, J.C., "De metamorphosi Eleuterorum observationes. Bidrag til Insecternes Udviklingshistorie," *Naturhist. Tidsskr.* **3** (4), 415–552 (1867).
156. Sharova, I.Kh., "Change of the Life Forms in the Ontogenesis of Ground Beetles," in *Proc. XIII Int. Entomol. Congr., Moscow, 1968* (1971), Vol. 1, pp. 558–559 [in Russian].
157. Sharova, I.Kh., "Morpho-Ecological Typification of the Life Cycles of Ground Beetles (Coleoptera, Carabidae)," *Vopr. Obshch. Entomol. Trudy VEO* **63**, 59–61 (1981).
158. Sharova, I.Kh. and Denisova, M.I., "Life Cycles and Reproduction Rhythms of *Calathus eratus* C.R. Sahlberg and *C. micropterus* Duftschmidt (Coleoptera, Carabidae) in the Forest of Russian Forest-Steppe Zone," *Russ. Entomol. J.* **4** (1–4), 159–165 (1995).
159. Sharova, I.Kh. and Denisova, M.I., "The Polyvariant Nature of Seasonal Development in Two Species of the Genus *Calathus* Bonelli (Coleoptera, Carabidae) in the Forest-Steppe of Central Russia," *Doklady Akad. Nauk* **348** (1), 140–142 (1996).
160. Sharova, I.Kh. and Denisova, M.I., "Seasonal Dynamics of Forest Populations of the Genus *Pterostichus* (Coleoptera, Carabidae)," *Zool. Zh.* **76** (4), 418–427 (1997a) [*Entomol. Rev.* **77** (8), 1026–1036 (1997)].
161. Sharova, I.Kh. and Denisova, M.I., "Ecological Differentiation of Some Forest Ground Beetles of the Genus *Pterostichus* Bonelli (Coleoptera, Carabidae) in the Forest-Steppe of Central Russia," *Doklady Akad. Nauk* **356** (4), 572–574 (1997b).
162. Sharova, I.Kh. and Dushenkov, V.M., "Types of Development and Types of Seasonal Activity in Ground Beetles," in *Fauna and Ecology of Invertebrates* (MGPI, Moscow, 1979), pp. 5–25 [in Russian].
163. 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)].
164. Sharova, I.Kh. and Khobrakova, L.Ts., "Specific Features of the Life Cycles of *Pterostichus montanus* (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) in the Mountain Taiga Belt of the Eastern Sayan," *Izv. Ross. Akad. Nauk Ser. Biol., No. 1*, 36–46 (2005).
165. Shelford, V.E., "Life-Histories and Larval Habits of the Tiger Beetles (Cicindelidae)," *J. Linn. Soc. London* **30**, 157–184 (1908).
166. Shilenkov, V.T., "Specific Biological Features of the Common Ground Beetle Species (Coleoptera, Carabidae) in the Fauna of the Southern Baikal Area," *Entomol. Obozr.* **57** (2), 290–301 (1978).
167. Shishova, M.I., *Candidate's Dissertation in Biology* (Moscow, 1994).
168. Skuhřavý, V., "Příspevek k bionomii polních střelkovitých (Col. Carabidae)," *Rozpr. Českosl. Akad. Věd. Rada Matemat. Přírodn. Ved. Roč.* **69** (2), 3–64 (1959).
169. Sota, T., "Long Adult Life Span and Polyphagy of a Carabid Beetle, *Leptocarabus kumagaii* in Relation to Reproduction and Survival," *Res. Popul. Ecol.* **26** (2), 389–400 (1984).
170. Sota, T., "Life History Patterns of Carabid Beetles Belonging to the Subtribe Carabina (Coleoptera, Carabidae) in the Kinki District, W. Japan," *Kontyû* **53** (2), 370–378 (1985a).
171. Sota, T., "Activity Patterns, Diets and Interspecific Interactions of Coexisting Spring and Autumn Breeding Carabids, *Carabus yaconinus* and *Leptocarabus kumagaii* (Coleoptera, Carabidae)," *Ecol. Entomol.* **10** (3), 315–324 (1985b).
172. Sota, T., "Effects of Temperature and Photoperiod on the Larval Development and Gonad Maturation of a Carabid Beetle, *Carabus yaconinus* (Coleoptera: Carabidae)," *Appl. Entomol. Zool.* **21** (1), 89–94 (1986).
173. 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).
174. Sota, T., "Univoltine and Bivoltine Life Cycles in Insects: a Model with Density Dependent Selection," *Res. Popul. Ecol.* **30** (1), 135–144 (1988).
175. Sota, T., "Variation of Carabid Life Cycles along Climatic Gradients: an Adaptive Perspective for Life-History Evolution under Adverse Conditions," *Series Entomologica* **52**, 91–112 (1994).

176. Sota, T., "Life-Cycle and Body Size Variation in the Japanese *Leptocarabus* Ground Beetles," *Nature & Insects* **31** (405), 24–30 (1996a).
177. 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 (1996b).
178. Sota, T. and Ishikawa, R., "Phylogeny and Life-History Evolution in *Carabus* (subtribe Carabina: Coleoptera, Carabidae) Based on Sequences of Two Nuclear Genes," *Biol. J. Linn. Soc.* **81** (1), 135–149 (2004).
179. 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).
180. Stearns, S.C., "Life-History Tactics: a Review of the Ideas," *Quart. Review Biol.* **51**, 3–47 (1976).
181. Stearns, S.C., *The Evolution of Life Histories* (Oxford Univ. Press, N.Y., 1992).
182. Sugonyaev, E.S., "Systems of the Chalcid Wasp (Hymenoptera, Chalcidoidea) Adaptations to Parasitizing Soft Scale Insects (Homoptera, Coccidae) in Principal Climatic Zones of the Northern Hemisphere," *Entomol. Obozr.* **80** (1), 8–39 (2001) [*Entomol. Rev.* **81** (3), 253–275 (2003)].
183. Telfer, G. and Butterfield, J.E.L., "The Control of Reproductive Diapause in *Nebria salina* (Coleoptera: Carabidae)," *Ecol. Entomol.* **29** (4), 482–487 (2004).
184. Thiele, H.-U., "Einflüsse der Photoperiode auf die Diapause von Carabiden," *Zeitschr. Angew. Zool.* **58**, 143–149 (1966).
185. Thiele, H.-U., "The Control of Larval Hibernation and Adult Aestivation in the Carabid Beetles *Nebria brevicollis* F. and *Patrobus atrorufus* Stroem," *Oecologia* **2** (2), 347–361 (1969).
186. Thiele, H.-U., "Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren," *Zool. Jb. Syst.* **98** (3), 341–371 (1971).
187. Thiele, H.-U., "Interaction between Photoperiodism and Temperature with Respect to the Control of Dormancy in the Adult Stage of *Pterostichus oblongopunctatus* F. (Coleoptera, Carabidae). I. Experiments on Gonad Maturation under Different Climatic Conditions in the Laboratory," *Oecologia* **19** (1), 39–47 (1975).
188. Thiele, H.-U., *Carabid Beetles in Their Environments. a Study on Habitat Selection by Adaptations in Physiology and Behavior* (Springer-Verlag, Berlin, 1977).
189. Thiele, H.-U. and Krehan, I., "Experimentelle Untersuchungen zur Larvaldiapause des Carabiden *Pterostichus vulgaris*," *Entomol. Exp. Appl.* **12**, 67–73 (1969).
190. Truman, J.W. and Riddiford, L.M., "The Origins of Insect Metamorphosis," *Nature* **401**, 447–452 (1999).
191. Tselishcheva, L.G., "Development Phenology and Population Structure of *Carabus schoenherri* F.-W. (Coleoptera, Carabidae) in the Forests of the Southern Taiga Subzone of the Volga–Vyatka Region," *Vestnik Vyatskogo Gos. Univ.*, No. 2/99, 27–30 (2000).
192. Turin, H., "De Nederlandse loopkevers: verspreiding en oecologie (Coleoptera: Carabidae)," in *Nederlandse fauna. V. 3* (Nat. Natuurhistorisch Mus. Natur., KNNV, Uitgeverij, 2000).
193. Turin, H., Penev, L., Casale, A., et al., "Special Part. Chapter 5. Species Accounts," in *The Genus Carabus in Europe. A Synthesis. Fauna europeae evertebrata № 2* (Pensoft, Sofia, 2003), pp. 151–284.
194. van der Drift, J., "Analysis of the Animal Community in a Beech Forest Floor," *Tijdschr. Entomol.* **94**, 1–168 (1951).
195. van der Drift, J., "Life Cycle and Phenology of *Carabus problematicus* Herbst," *Proc. X Int. Congr. Entomol.* (1958), vol. 2, p. 661.
196. van Dijk, Th.S., "The Significance of the Diversity in Age Composition of *Calathus melanocephalus* L. (Coleoptera, Carabidae) in Space and Time at Schiermonnikoog," *Oecologia* **10**, 111–136 (1972).
197. van Dijk, Th.S., "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 Behavior in Carabid Beetles. Miscellaneous Papers of Agricultural University Wageningen* (H. Veeneman & Zonen B.V. Publ., Wageningen, 1979a), pp. 167–183.
198. van Dijk, Th.S., "On the Relationship between Egg Production, Age and Survival in Two Carabid Beetles: *Calathus melanocephalus* L. and *Pterostichus coeruleus* L. (Coleoptera, Carabidae)," *Oecologia* **40** (1), 63–80 (1979b).
199. van Dijk, Th.S., "The Influence of Food and Temperature on the Amount of Reproduction in Carabid Beetles," in *The Synthesis of Field Studies and Laboratory Experiment. Rep. IV Meeting Europ. Carabidol.* (Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, 1983), pp. 105–123.
200. van Dijk, Th.S., "On the Relationship between Food, Reproduction and Survival of Two Carabid Beetles: *Calathus melanocephalus* and *Pterostichus versicolor*," *Ecol. Entomol.* **19** (3), 263–270 (1994).
201. van Heerdt, P.F., Blokhuis, P., and van Haften, C., "The Reproductive Cycle and Age Composition of a Population of *Pterostichus oblongopunctatus* F. in the Netherlands (Coleoptera: Carabidae)," *Tijdschr. Entomol.* **119** (1), 1–13 (1976).
202. van Lengerken, H., "*Carabus auratus* und seine Larve," *Arch. Natur.* **87**, 31–113 (1921).
203. van Schaick-Zillesen, P.G., Brunsting, A.M.H., and Siepel, H., "The Role of Larvae in the Synchronization of the Life Cycle of *Pterostichus oblongopunctatus*," in *Carabid Beetles: Their Adaptations and Dynamics* (Gustav Fisher Verlag, Stuttgart, 1986), pp. 181–185.

204. Vasil'eva, P.M., "Specific Features of Development of Some Species of Ground Beetles in Bryansk Province," in *Fauna and Ecology of Invertebrates* (Mos. Gos. Ped. Inst., Moscow, 1978), pp. 40–52 [in Russian].
205. Vlijum, L. and van Dijk, Th.S., "Ecological Studies on Carabid Beetles II. General Pattern of Population Structure in *Calathus melanocephalus* L. at Sciermonnikoog," *Zeitschr. Morph. Ökol. Tiere* **58**, 396–404 (1967).
206. 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.* (Uppsala, 1987), No. 15, pp. 1–109.
207. Weber, F. and Klenner, M., "Life History Phenomena and Risk of Extinction in a Subpopulation of *Carabus auronitens*," *Acta Phytopath. Entom. Hung.* **22** (1–4), 321–328 (1987).
208. Wilbur, H.M., "Complex Life Cycles," *Ann. Rev. Ecol. Syst.* **15**, 393–425 (1980).
209. Williams, G., "Seasonal and Diurnal Activity of Carabidae, with Particular Reference to *Nebria*, *Notiophilus* and *Feronia*," *J. Anim. Ecol.* **28**, 309–330 (1959).
210. Zaballos, J.P., "Notas fenológicas sobre los Carábidos de la Península Ibérica (Col., Carabidae)," *Anal. de Biol. (Biol. Anim. 2)* **7**, 11–15 (1986).
211. Zang, R., "Beiträge zur Biologie von *Carabus nemoralis* Müll.," *Allg. Z. Entomol.* **6**, 273–276 (1901).
212. Zetto Brandmayr, T., "Life Cycle, Control of Propagation Rhythm and Fecundity of *Ophonus rotundicollis* Fairm. et Lab. (Coleoptera, Carabidae, Harparini) as an Adaptation to the Main Feeding Plant *Daucus carota* L. (Umbelliferae)," in *The Synthesis of Field Studies and Laboratory Experiment. Rep. IV Meeting Europ. Carabidol.* (Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, 1983), pp. 93–103.
213. Zikan, I.I., "Zur Biologie der Cicindeliden Brasiliens," *Zool. Anz.* **82**, 269–414 (1929).
214. Znoiko, D.V., "A Brief Key to the Larvae of Carabid Genera Present in the USSR and Descriptions of the Larvae of *Zabrus tenebrioides* Gz. and *Harpalus pubescens* Müll.," *Zashchita Rastenii* **6** (3/4), 335–360 (1929).
215. Znoiko, D.V., "Larvae of the Ground Beetles *Zabrus blapoides* Creutz. and *Harpalus calceatus* Duft. (Coleoptera, Carabidae)," *Entomol. Obozr.* **25** (3–4), 232–238 (1935).