

# Annual reproduction rhythms of ground beetles: a new approach to the old problem

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## Summary

During the consideration of carabids' population dynamics a high variability of their reproductive rhythms has been shown. Species with high and low potential for phenological modifications are distinguished. The phenological polyvariance can be morphological (two types) and dynamical (two types). It is proposed to separate the classification of reproductive cycles from the seasonal dynamics of activity. The possible factors influencing the stability of reproductive rhythms are discussed.

## Historical references

One of the central problems of carabid ecology is the interpretation of their developmental cycles. For this purpose different methods of phenological observations and laboratory studies have been used. Under laboratory conditions the experiments commonly concern a study of different aspects of regulation of reproduction (Thiele 1969; Ferenz 1973; Neudecker & Thiele 1974; Paarmann 1973, 1974, 1977; Hurka 1975; Van Dijk 1977; etc.). The classification of life histories is usually based on the results of pitfall trapping. So, Larsson (1939) using the phenological characteristics distinguished two main reproductive types (*Entwicklungstypen*): spring and autumn ones. Later this classification was corrected many times (Lindroth 1949; Thiele 1977; Paarmann 1979; Sharova & Dushenkov 1979). Thiele (1977) already distinguished seven types of life histories, then Paarmann (1979) added four types peculiar to the tropic and subtropic regions. Simultaneously numerous data about the strong dependence of carabid abundance dynamics on specific

biotopes was accumulated (Lauterbach 1964; Baars 1979; den Boer 1979, 1987; Loreau 1985, 1987; Makarov & Chernjakhovskaja 1989, 1992 etc.). This information has caused doubts about whether the distinguished principal types of development were correct (den Boer 1990).

## Interrelations between catching dynamics and the reproductive rhythms

Following Larsson (1939), researchers have determined the time of reproduction according to the maxima of seasonal activity of carabid beetles. But there is still not any direct proof of this coincidence. Although Wallin (1987) worked out a method of evaluating the demographic structure of carabid populations, this has not been widely used in ecological studies.

Special analyses of demographic patterns in carabid populations were made in our studies to test the correlation between reproductive and locomotory rhythms (Makarov & Chernjakhovskaja 1989, 1992; Chernjakhovskaja & Makarov 1990; Makarov 1990, 1991). The field observations were conducted in Nakhabino suburb (Moscow region) in 1989–1991. In five biotopes (woods: *Tilia-Quercetum*, *Carici-Betuletum*, *Pinetum*, *Piceetum*; agrocenoses: clover field) more than 41 thousand specimens of Carabidae were trapped and analysed.

For the majority of carabid beetles no annually repeated seasonal changes in capture rates were found. This is evidently connected with the plasticity of individual development. In earlier investigations (Thiele 1977; Loreau 1985 and others) species with irregular reproduction rhythms had already been distinguished.

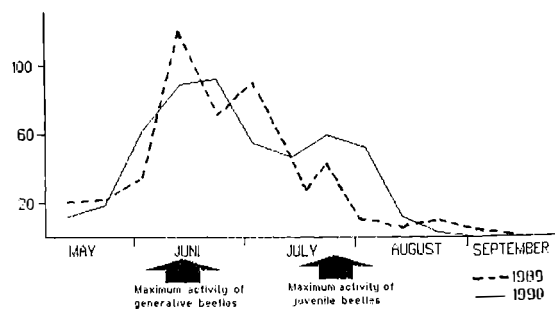


Fig. 1. Seasonal dynamics in catches of *Poecilus cupreus* L. of different age in clover fields (Moscow reg., env. Nakhabino, 1989 & 1990). Ordinates: activity, expressed as numbers of individuals per 10 traps per 10 days.

The rather slight coincidence of locomotory activity in ground beetles (reflected in their capture rates) with their reproduction rhythms is caused, according to our data, by the variation in phenological dates of breeding and development, by the possible existence of two generations in the years with favourable weather conditions and so on.

Based on our material and on the analysis of published data we suggest distinguishing annual (dependent on weather conditions), biotopic and geographical modifications of the reproductive rhythm.

#### Annual differences

In carabid beetles annual changes of reproductive phenology are not rare. For example, in *Loricera pilicornis* (F.), in 1989 (a very warm and wet summer) on the clover field two peaks of larval abundance were recorded (Makarov & Chernjakhovskaja 1990). In the other years this species showed itself as a typical "spring" breeder.

In contrast, another "spring" species also numerous in the same field – *Poecilus cupreus* (L.) – displayed few annual differences in its catch dynamics (Fig. 1).

#### Biotopic peculiarities

As examples of the significant biotopic modification of reproductive phenology two carabid beetles of the genus *Pterostichus* could be men-

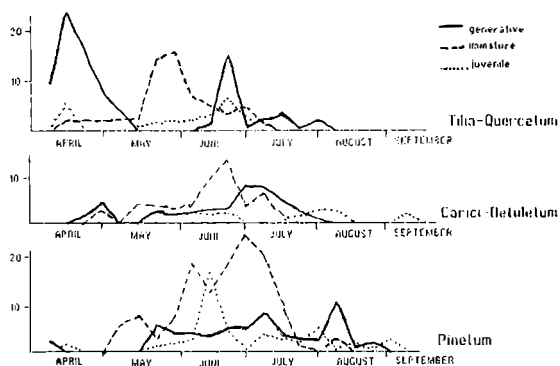


Fig. 2. Changes in the age spectrum of *Pterostichus melanarius* Ill. in different forest types (Moscow reg., env. Nakhabino, 1989). Ordinates: activity, expressed as numbers of individuals per 10 traps per 10 days.

tioned: *P. niger* Schall. (Chernjakhovskaja 1990b) and *P. melanarius* Ill. (Fig. 2). It is important that, in different habitats, not only the catch dynamics of separate age-groups, but also the periods of mass oviposition varied.

A similar situation (but only for activity dynamics) was observed by Lauterbach (1964) in *Abax ater* Villers: in rather open habitats this species had a two-peaked curve of activity with maxima in June and September, and in the strongly shaded woods a unimodal curve. Loreau (1985) demonstrated with his data the large variability of seasonal rhythms, including the time of egg laying, in carabid beetles inhabiting different forest types.

At the same time, opposite examples are also known. Thus, during our studies the demographic parameters dynamics of *P. oblongopunctatus* (F.) were uniform within habitat types.

#### Zonal differences

Geographical variation in phenology is well demonstrated by *Pseudoophonus rufipes* De Geer. This widespread species is often numerous in agrocenoses and has distinct phenological peculiarities in different natural zones (Kasandrova 1970; Dushenkov 1984; Popova 1984; Karpova 1986; Chernjakhovskaja 1990a). In the steppe and forest-steppe zones this species has two pronounced peaks of activity occurring in May and August–

September. It is important that the individuals of spring and autumn peaks differ in morphology (Matalin, pers. comm.). To the north (for example in Moscow region) these peaks are less pronounced, and in the taiga zone the curve of activity has only one maximum in July (Dushenkov, pers. comm.).

### Subdivision of the cases of phenological variation

We consider it necessary to distinguish within carabid beetles two groups of species according to the restriction of their reproductive period to a particular season of the year and to the longevity of this breeding activity: the species with variable and stable life cycles.

For the description of species with a stable type of development the use of traditional terms (Larsson 1939; Thiele 1977 etc.) is quite possible.

In the species with variable breeding phenology the adaptive changes of reproductive cycle could be the result both of direct environmental influence (delay in development at low temperatures) and of changes in their type of development (wintering larvae or wintering imago, development with two or three larval stages etc.). As a definition for all such phenomena we suggest using the term *polyvariance*, adopted from botanical studies (Zhukova & Komarov 1990).

Two aspects of such polyvariance can be separated for carabid beetles: the morphological and dynamical ones.

Dynamical polyvariance can be expressed in terms of speed and rhythms of development.

In the first case (including many "spring" breeders) pronounced acceleration of separate stages is possible. As a result the development can be completed as quickly as possible, i.e., normally, by the middle of summer. In favorable conditions these species can optionally be polyvoltine (Gilbert 1956; Paarmann 1966, 1976; Krehan 1970; Bauer 1979; Loreau 1985; Makarov & Chernjakhvskaya 1990). Evidently, obligatory univoltinism is rarely found in ground beetles, occurring mainly in species with ephemeral type of activity and rather short life longevity.

In the second case (typical example – *Pseudophonus*), more or less separated generations are distinguished within one population and winter

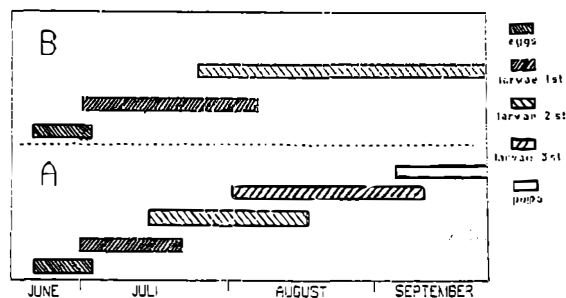


Fig. 3. Pre-imaginal development of the *Poecilus fortipes* (Gebli.) in different conditions (see text).

diapause is usually the differentiating factor: some individuals spend winter in the larval stage, others as adults. Similar results are known for *Harpalus* Latr. (Schjøtz-Christensen 1965, 1966) and *A. ater* (Löser 1970). Usually, when the vegetation growth period is rather long, these generations are well separated in time and can differ even in morphology. In the conditions close to extreme, the only breeding type in the whole population of this species is usually established. It is clear that well developed phenological polyvariance can form part of a biennial life cycle (Larsson 1939; Sharova & Dushenkov 1979) that is not always proved during the following researches.

Bi- and multiannual cycles are usually formed as a response to very hard environmental conditions – for example, in Subarctic (Kaufmann 1971; Korobeinikov 1991), highlands (Weidemann 1971; Hurka 1973), or extremely dry landscapes (Hamilton 1925). Among these species the forms with variable type of development usually prevail.

Morphological polyvariance is expressed as morphological differences between individuals within one stage of development. The dissimilarity of larvae of *Poecilus fortipes* (Gebli.), developing in different circumstances, can serve as a good example of such polyvariance (Fig. 3).

A pair of adult beetles of this species was brought from the Far East in June 1990; 54 eggs were obtained, and were separated into two series. The first one (group A) developed in normal conditions (LD 16/8, optimal humidity), the second one (group B) under short days (LD 8/16) and with periodical desiccations. By the end of

the first week of developments L1 of group B were significantly larger due to their fat body growth and almost stopped feeding. In this state they existed from 2 to 3 weeks when 60% of the larvae moulted into L2. These larvae fed actively during 7–10 days, then entered an inactive state and remained without changes until winter. The larvae of group A by this time had already pupated. Formation of the delayed larval forms was accompanied also by the modifications in their chaetae. Significant prolongation of the reproductive cycles was observed also by Paarmann (1990) in the related species *P. lepidus* Leske.

Morphological polyvariance has been recorded in carabid beetles rather rarely (mostly in xerophilic forms) and needs special studies.

### Factors influencing the dynamics of development

In native coenoses, reproductive cycles are reflected in the seasonal dynamics of the abundance/activity indirectly. Summarizing the results of our observations and data from earlier publications (Thiele 1977; Paarmann 1979; Van Schaick-Zillesen *et al.* 1986 and others) it seems to be possible that some factors determine the coincidence of these processes.

Among the factors that stabilize reproductive cycles and, therefore, the seasonal activity of ground beetles we consider:

1. synchronized development of separate stages, connected with trigger characters for physiological processes;
2. high abilities of migration, which support the possibility of sexes meeting and promote the selection of surrounding conditions by moving from one microsite to another;
3. interspecific relations of closely related and coexisting sympatric species;
4. ecological specialization;
5. short lifespan and obligatory univoltinism;
6. development of different forms of parental care.

As destabilizing factors we treat:

1. unsynchronized development, connected with individual differences in growth and maturation rates;
2. low migration abilities, complicating search for

a sex partner and limiting the choice of optimal locations inside the biotope;

3. ecological flexibility and no absence of species-competitors;
4. long individual life and multivoltinism.

Interactions of these and other factors make it sometimes impossible properly to interpret capture dynamics as a result of reproductive rhythms. For example, "multiseasonal" type of activity can be a consequence of prolongation of the reproductive period or/and obligatory multivoltinism or/and considerably overlapped periods of activity in separate generations.

### Criteria for classification of reproductive rhythms and capture dynamics

We suggest distinguishing between the classifications of reproductive cycles (reflecting biological peculiarities of species) and those of seasonal dynamics of activity/abundance (reflecting mostly the habitat). This will help to avoid many discrepancies in interpreting experimental data and improve knowledge about the functioning of carabid populations.

In order to distinguish abundance dynamic types, the following features must be taken into account (in decreasing order of significance):

1. breeding season;
2. wintering stages (mainly preimaginal);
3. occurrence and type of parapause (according to Müller 1970);
4. duration of individual life;
5. time of maximal locomotory activity.

The earlier suggested classification of "types of development" (Larsson 1939; Thiele 1977 etc.) is based mainly on phenological data.

For systematization of reproductive cycles we consider the following criteria:

1. cycle stability;
2. type of polyvariance (morphological: optional, obligatory; dynamical: in rhythms, in rates);
3. mechanism of exogenous regulation (temperature, photoperiod, humidity etc.);
4. uni- and multivoltinism.

This approach can be useful in connection with the problem of the evolution of carabid reproductive cycles (Paarmann 1979).

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