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On Life History Tactics in Carabid Beetles: are there only Spring and Autumn Breeders?

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Abstract

Since the classical paper of Larsson (1939) carabid species have been divided into spring and autumn breeders. However, if we rank the 68 most common carabid species of Drenthe (The Netherlands) according to the period of reproduction (data from at least 10 years of pitfall sampling in more than 80 sites) we find a continuous sequence from early spring to late autumn, including seven species that mainly reproduce in winter, some species that show two reproduction periods in the same year, and species that uninterruptedly reproduce during the greater part of the year. The adults of most species hibernate after reproduction and again participate in reproduction in following years, so that also a division in adult and larval hibernators is inadequate. Comparison with data from other carabidologists (Lindroth, Schjøtz-Christensen, Thiele, Paarmann, etc.) show that these features are not restricted to Drenthe, but are common to Western Europe.

To discriminate between two groups of West European carabid species with fundamentally different life history tactics one may distinguish species with summer larvae from species with winter larvae.

The Role of Ground Beetles in Ecological and Environmental Studies

Introduction

In 1939 Larsson published his classical paper 'Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden', in which he tried to bring each of the Danish, and more generally Scandinavian, Carabidae species to one of two groups: *spring breeders* or *autumn breeders*. Although he only used the distribution of numbers of specimens collected by hand in the different months of the year, his division was generally accepted. Even Carl Lindroth (1945) for Scandinavia conformed to Larsson's scheme. He noted, however, that some species seem to show an unstable reproduction period, so that in 1949 he suggested to discriminate between 'adult hibernators' and 'larval hibernators'.

From about 1953 onwards the use of pitfall traps for studying the distribution and life history of carabid beetles gave detailed information about activity and resting periods, by which it became clear that many hand catches concerned inactive beetles. For instance, the high numbers of *Nebria brevicollis* usually collected in summer (Larsson 1939: 316) concerned aestivating specimens (e.g. Gilbert 1958). Gradually, more and more deviations from Larsson's scheme were discovered. In his excellent book *Carabid Beetles in their Evironments* Thiele (1977, Ch. 6B) gives a survey of these findings. For the temperate zones he came to the following types of annual rhythms in carabids (see also Paarmann 1979):

1. Spring breeders with summer larvae and adult hibernation;
2. Species with winter larvae and reproduction in summer and/or autumn, but without adult dormancy;
3. Species with winter larvae and young adults in spring which undergo aestivation prior to reproduction;
4. Species with a flexible reproduction period, in which both spring and autumn breeding may occur, and in which larvae seem to develop equally well in summer as in winter;
5. Carabid beetles that require more than one year to develop.

Schjøtz-Christensen (1965) was probably the first to dissect sufficient females to discriminate between reproductive and other locomotory activities. He discovered (1965, 1966) that in Denmark in some *Harpalus* species old beetles reproduce again in following years, and callow beetles can be caught in periods that do not match a single, fixed reproductive period (type 4 of Thiele).

Reproduction and Age Composition

During 30 years of pitfall sampling in the surroundings of Wijster we found that in nearly all carabid species studied more closely many beetles reproduce during two or three succeeding years (e.g. den Boer 1979; Table 1; van Dijk 1982); until the present only *Nebria brevicollis* appeared to be virtually semelparous (Nelemans 1987). This means that discriminating between 'adult hibernators' and 'larval hibernators' is not very useful: in nearly all species at least part of the old beetles hibernate. The reproduction of old and young beetles may show rather complicated patterns in time, which may differ again between years and/or between sites (van Dijk 1972, 1973), without leading to an unstable reproductive cycle. As old beetles usually reproduce earlier than young ones, often reproduction extends over a longer period, sometimes suggesting more than one period. These shifts in time of reproduction and in age composition could mainly result from spatial and/or temporal differences in dominant physical factors, such as temperature. So far, only the reproductive cycle of *Abax parallelepipedus* (= *A. ater*) actually seems to be unstable (Löser 1972).

Also, the occurrence of callow individuals outside the normal periods need not point to an unstable cycle. For example, the presence of a few callow beetles in autumn does not mean that the autumn breeder *Nebria brevicollis* would show two hatching peaks, as is suggested by Muggleton (1969). Neither does the often occurring spring catch of a single, or a few, callow beetle(s) of *Pterostichus oblongopunctatus*, *P. versicolor*, or *Agonum assimile* mean that the cycles of these evident spring breeders would be unstable. Depending on the amount of food and temperature young beetles of these and other species may stay callow or lightly coloured for up to ten weeks (e.g. Nelemans *et al.* 1989), and in winter possibly even longer.

In short, without a more careful, experimental, check of the findings of Schjøtz-Christensen we consider type (4) of Thiele as mainly resulting from environmental heterogeneity, which in cold-blooded animals may easily lead to appreciable local differences in time of development. We expect that the deviating features, which gave rise to the conception of type (4) of annual rhythms (Thiele 1977), may occur in all species, without necessarily signifying more than individual variability. Type (5) of Thiele will generally be restricted to the Northern parts of Europe (see also van Dijk 1972). Summarizing, about ten years ago we concluded that the first three types of annual rhythms of Thiele, one kind of spring breeders and two kinds of autumn breeders, would cover the reproductive cycles of the majority of the carabid species of Drenthe.

Testing Larsson's Scheme

To test further Larsson's scheme the second author studied the continuous pitfall catches of the 68 species most abundantly caught in the surroundings of Wijster for about 10 years or longer. Females belonging to 34 species, caught throughout the year, were dissected to discover which locomotory activities are directly connected with reproduction. For the other species the main reproduction period(s) were derived from indirect information, such as the time of the year with most pronounced locomotory activities (when males show a protruding penis), or when tenerals or larvae were present. To define the reproduction period(s), as a common characteristic for about 10 or more years, we fixed the weeks in which nearly exclusively reproducing beetles (females with ripening eggs) were caught, or during which 90–95% of the higher week-catches of reproducing beetles were obtained, covering at least 100 individuals. In most species after a few 'introductory' individuals, which are ignored, reproduction starts quite suddenly, and after some months with high week-catches of reproducing beetles more and more individuals become 'spent', so that during a number of weeks the catches gradually diminish and hardly contain reproducing beetles any longer. This 'tail' of lower catches of mainly 'spent' individuals is disregarded.

Next, the reproductive periods thus defined were ranked according to the starting week, beginning with early March. It then appeared that these 68 periods are uninterruptedly spread over the whole year (see den Boer 1985, Fig. 5), so that spring and autumn breeders could not be separated (see Fig. 1)

If we take into account additional information, in particular on the period of larval development and that of hatching of young adults, both from our own data and from literature, the first 25 species, which mainly reproduce in April-June, can still be considered spring breeders (Fig. 1). Among the next 17 species, most of which reproduce between May and August, eight species with winter larvae (*) are about evenly spread, whereas the other nine species (x) are dubious spring breeders, either because our data contradict those of Lindroth (1945), or because the majority of the tenerals become active in the wrong period of the year (Fig. 1). The following 19 species, the reproduction periods of which are uniformly spread over the second half of the year, can be called autumn breeders (*). Finally, the remaining seven species mainly reproduce in winter. In these species, reproduction starts in October and continues, depending on winter conditions, until either February/March, or until April/May. In Scandinavia, where winters will often start too early for these species and also are severe, probably they are rightly considered early spring breeders (x) (Lindroth 1945).

In typical spring breeders, the 25 first species of Fig. 1, the larvae develop in late spring and summer and both young and old adults hibernate. The just hatched adults, usually together with part of the old ones, often show some locomotory activities in autumn, most probably to add to the fat reserves before overwintering (Mols 1988). These autumn activities are remarkably variable between years as well as between species (see den Boer 1979: 9)

Fig. 2 shows a number of apparently deviating activity cycles. *Calathus erratus* and *C. melanocephalus* are autumn breeders without dormancy of young adults: type (2) of Thiele (1977). The larvae develop in winter and early spring, young beetles hatch in July and start reproduction soon thereafter. The overwintered old beetles sometimes show some non-

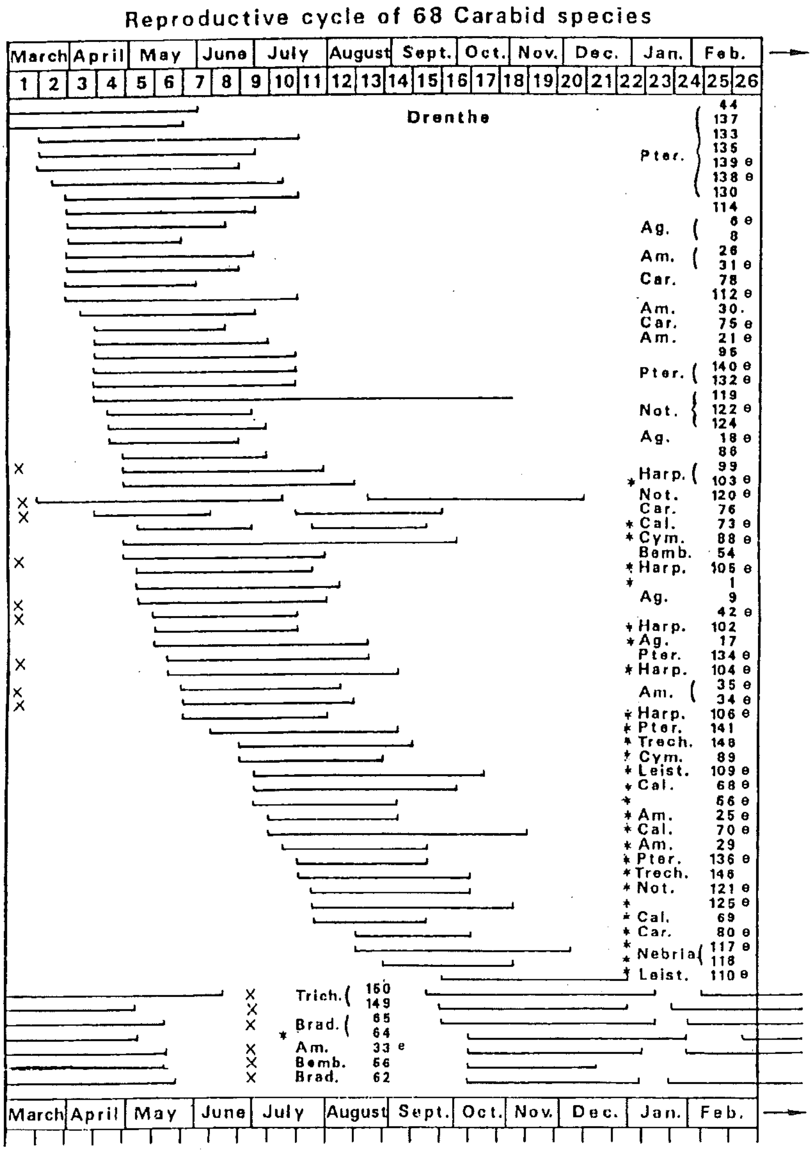

Figure 1. Reproduction periods of the 68 most abundant carabid species of Drenthe (The Netherlands) averaged per species over all sites and over more than 10 years. The procedure for delimiting these periods is described in the text. The numbers and abbreviations at right, which refer to the species, are explained in Table 1. Females of species indicated with 'e' at right were dissected to directly determine the period(s) of reproduction. Species with '*' are considered autumn breeders, species with 'x' are dubious spring breeders. All other species (without '*' or 'x' are considered evident spring breeders.

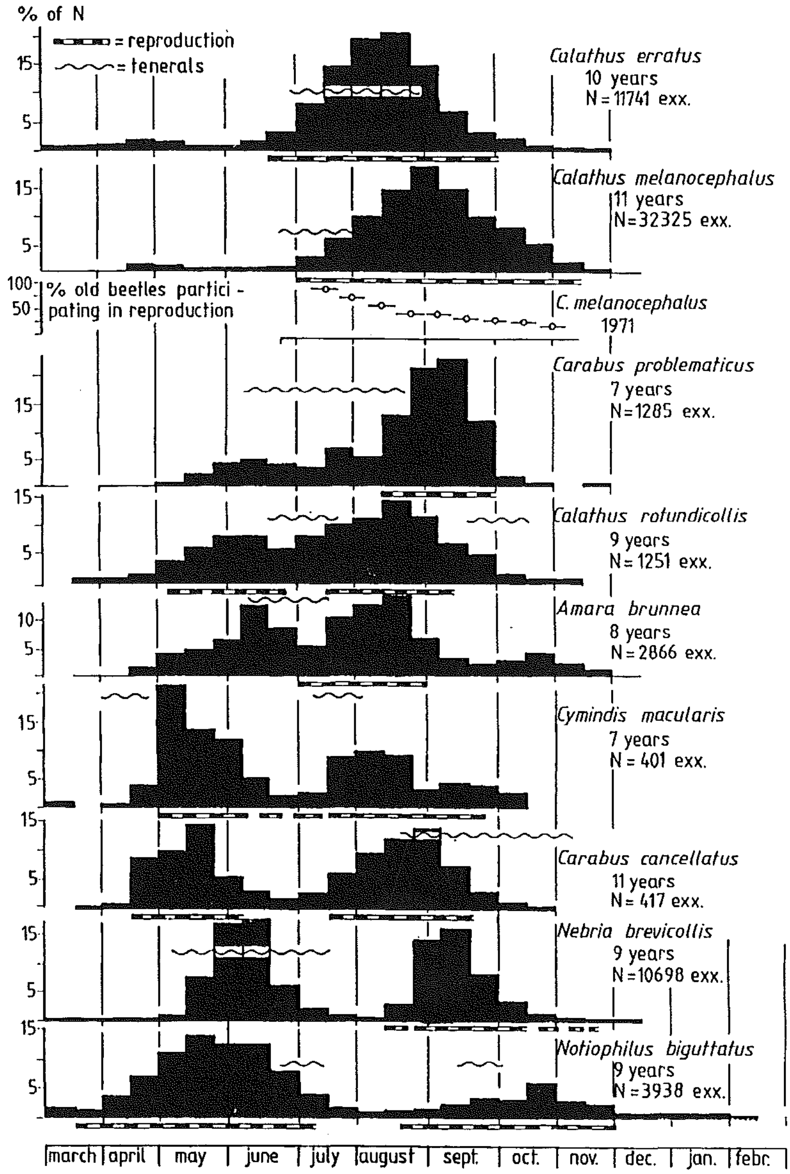

Figure 2. Activity periods of some carabid species of Drenthe (The Netherlands), derived from weekly pitfall-catches in many sampling sites during a number of years (at right). Further explanations in the text.

reproductive, most probably feeding, activities in spring, which vary highly between years, and after a short resting period start reproduction in July before young beetles. Therefore, the participation of old beetles in reproduction decreases in time in favour of the young ones (van Dijk 1973); this pattern is shown in Fig. 2 for *C. melanocephalus*. Sometimes the reproduction of old and young beetles is more separated in time (van Dijk 1972). The reproductive cycle of *Carabus problematicus* in fact is similar, with the locomotory activities of overwintered beetles gradually changing into reproduction. *Calathus rotundicollis* (=*piceus*) shows two reproductive periods, old beetles reproducing in spring and young beetles in summer. The majority of the young beetles hatch in July (den Boer 1979: 7), but a few are caught in autumn. In *Amara brunnea* the overwintered beetles are quite active May–June, but do not start reproduction earlier than July just before the young beetles. It is an autumn breeder with winter larvae (type 2 of Thiele). The reproductive cycles of *Cymindis macularis* and *Carabus cancellatus* have to be studied more closely. There are indications, but nothing more, for two reproduction periods. *Nebria brevicollis* is a late autumn breeder with winter larvae and aestivation of young adults, which hatch May–June and are remarkably active (see Nelemans 1987; Nelemans *et al.* 1989). Old adults do only exceptionally survive winter (den Boer 1979, Table 1). *Notiophilus biguttatus*, which is considered a spring breeder by both Larsson (1939) and Lindroth (1945), shows a second, much smaller reproduction period in autumn, in which both young and old beetles participate.

Possibly, *Notiophilus aquaticus* (Fig. 3) resembles *N. biguttatus*, but without any separation between spring and autumn activities. Because tenerals can be caught throughout the entire period, for the moment, with Lindroth (1945), we consider it to show an unstable cycle. The two *Leistus*-species are extremely late autumn breeders with winter larvae, and aestivation of young adults (type 3 of Thiele 1977). In the surroundings of Wijster the last six species of Fig. 3 reproduce in winter and early spring They are considered spring breeders by Lindroth (1945), and in most cases also by Larsson (1939). We agree with Lindroth (1945) that *Bradycellus harpalinus* will be an autumn breeder, because in July and August very high numbers of tenerals are flying around and caught in window traps (see den Boer 1977, Table 3), and will reproduce October–December, and possibly later. Most probably this does not apply to the other five species. For instance, high numbers of tenerals of *Bradycellus ruficollis* (=*similis*) are caught November–December, which indicates spring breeding. The seven winter breeders of Drenthe deserve extra attention in other parts of Europe.

Summer and Winter Larvae

Fig. 1 showed that a division of the carabid species of Drenthe into spring and autumn breeders would leave about a third of the species unclassified:

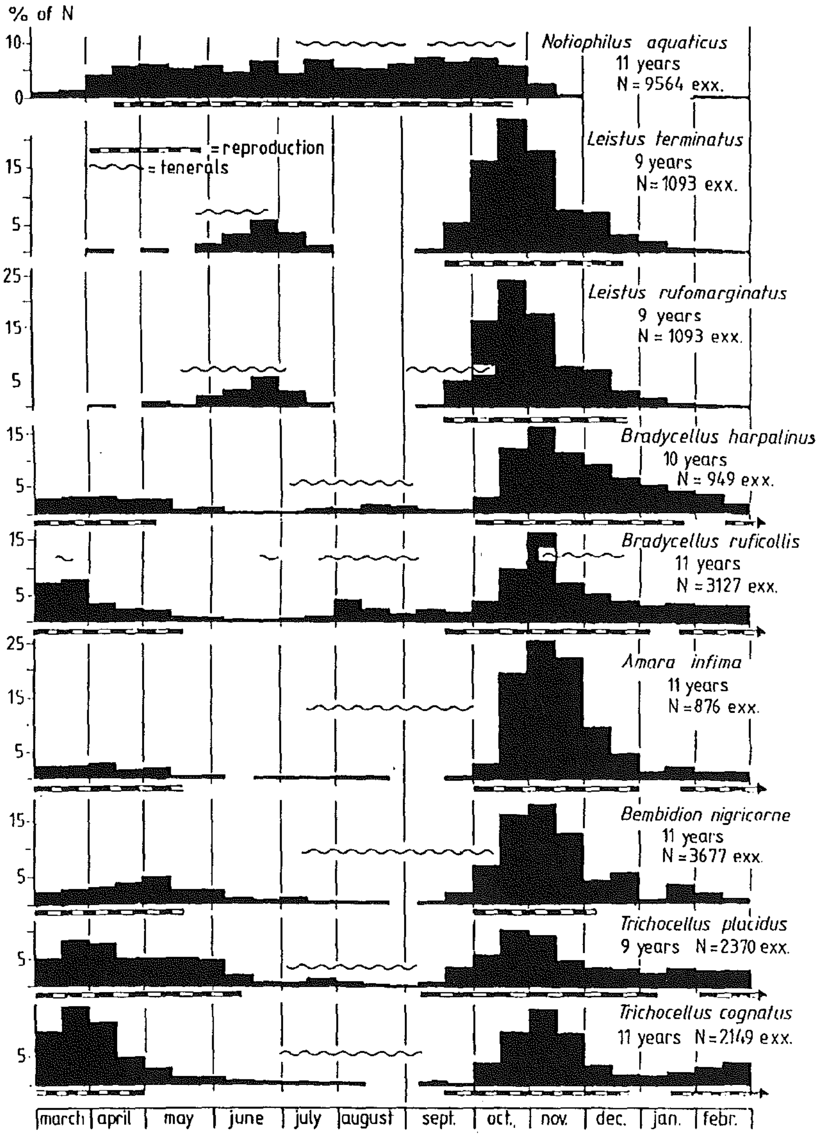

Figure 3. Activity periods of some carabid species of Drenthe (The Netherlands), derived from weekly pitfall-catches in many sampling sites during a number of years (at right). Further explanations in the text.

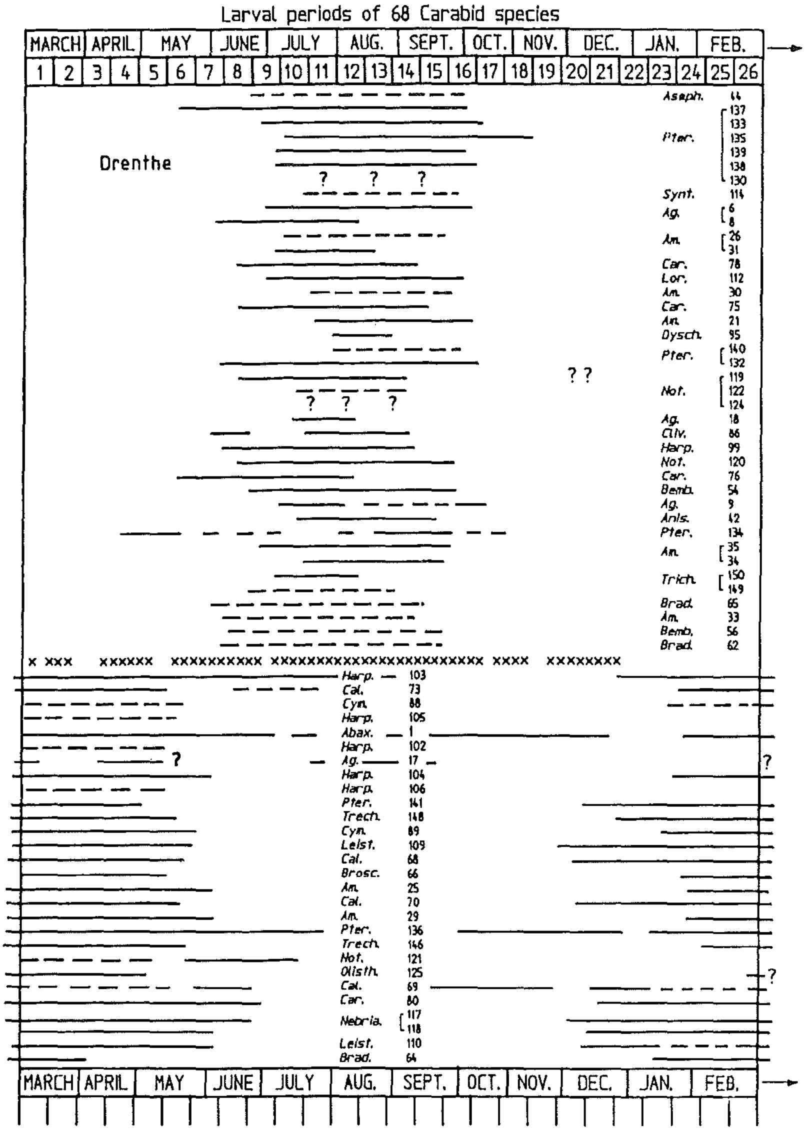

Figure 4. Periods of larval development of the 68 most abundant carabid species of Drenthe (The Netherlands) as these were established from data available at the Biological Station Wijster, supplemented by data from Larsson (1939) and Lindroth (1945). The species could be divided into two groups: 40 species with summer larvae (above), and 28 species with winter (and early spring) larvae (cf. Table 1). Broken lines indicate uncertain periods, either because the few data do not agree with each other or because hardly any data are available. ? points to the absence of direct data on larval development.

Table 1. Division of 68 carabid species from Drenthe (The Netherlands) according to the period of larval development.

Summer larvae	Winter larvae
6. *Agonum assimile* Payk.	1. *Abax parallelepipedus* P. & M.
8. *A. ericeti* Panz.	
9. *A. fuliginosum* Panz.	17. *Agonum obscurum* Hbst. ?
18. *A. sexpunctatum* L.	
21. *Amara aenea* de Geer	25. *Amara brunnea* Gyll.
26. *A. communis* Panz.	29. *A. equestris* Dfts.
30. *A. famelica* Zimm.	
31. *A. infima* Dfts.	
34. *A. lunicollis* Schiödte	
35. *A. plebeja* Gyll.	
42. *Anisodactylus binotatus* Fabr.	
44. *Asaphidion flavipes* L.	
54. *Bembidion lampros* Hbst.	
56. *B. nigricorne* Gyll.	
62. *Bradycellus caucasicus* Chaud.	64. *Bradycellus harpalinus* Serv.
65. *B. ruficollis* Steph.	66. *Broscus cephalotes* L.
	68. *Calathus erratus* Sahlb.
	69. *C. fuscipes* Goeze
75. *Carabus arvensis* Hbst.	70. *C. melanocephalus* L.
76. *C. cancellatus* Illig.	73. *C. rotundicollis* Dej.
78. *C. nemoralis* Müll.	80. *Carabus problematicus* Hbst.
86. *Clivina fossor* L.	88. *Cymindis macularis* F.v.W.
95. *Dyschirius globosus* Hbst.	89. *C. vaporariorum* L.
99. *Harpalus affinis* Schrank	102. *Harpalus solitaris* Dej.
	103. *H. latus* L.
	104. *H. rufipes* de Geer
	105. *H. quadripunctatus* Dej.
	106. *H. rufipalpis* Sturm
	109. *Leistus terminatus* Hellw.
	110. *L. rufomarginatus* Dfts.
112. *Loricera pilicornis* Fabr.	117. *Nebria brevicollis* Fabr.
114. *Syntomus foveatus* Fourcr.	118. *N. salina* Fairm. & Lab.
119. *Notiophilus aquaticus* L. ?	
120. *N. biguttatus* Fabr.	121. *Notiophilus germinyi* Fauvel
122. *N. palustris* Dfts.	
124. *N. refipes* Curtis	125. *Olisthopus rotundatus* Payk.
130. *Pterostichus quadrifoveatus* Letzner ?	
132. *P. versicolor* Sturm	
133. *P. diligens* Sturm	
134. *P. lepidus* Leske	
135. *P. minor* Gyll.	136. *Pterostichus niger* Schall.
137. *P. rhaeticus* Heer (+ *nigrita* Payk.)	
138. *P. oblongopunctatus* Fabr.	
139. *P. strenuus*Panz.	
140. *P. vernalis* Panz.	141. *Pterostichus melanarius* Illig.
149. *Trichocellus cognatus* Gyll.	146 *Trechus obtusus* Er.
150. *T. placidus* Gyll.	148. *Trechus (Epaphius) secalis* Payk.

between 25 evident spring breeders and 19 evident autumn breeders there occur 17 species with a less clear status, and seven more species mainly reproduce in winter. The division of Lindroth (1949) into adult hibernators and larval hibernators does not work either because, apart from *Nebria* and possibly *Leistus* species, '*larval hibernators*' most probably also overwinter as old adults. From the considerations about the reproductive cycles pictured in the Figs 2 and 3 it can be derived that another division into two groups is possible: species with *summer larvae* and species with *winter larvae*. To test this we collected data on the time of development of the larvae of the 68 species pictured in Fig. 1, mainly from Larsson (1939) and Lindroth (1945), but also from observations done at the Biological Station Wijster. Although there are many uncertainties, it was indeed possible roughly to classify our 68 most abundant carabid species under these two headings (Fig. 4). Therefore, exactly 50 years after the division proposed by Larsson (1939) we present another dichotomy of carabid species: summer developers and winter developers (Table 1). For the moment this division is only based on the carabid species occurring in Drenthe, though data on larval periods in Denmark and Fennoscandia are taken into account.

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