



International Association for Ecology

The Life Histories and Population Dynamics of Two Carabid Species on a Dutch Heathland. 1.
Fecundity and the Mortality of Immature Stages

Author(s): Th. S. van Dijk and P. J. den Boer

Source: *Oecologia*, Vol. 90, No. 3 (1992), pp. 340-352

Published by: [Springer](#) in cooperation with [International Association for Ecology](#)

Stable URL: <http://www.jstor.org/stable/4219983>

Accessed: 24/10/2014 04:49

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer and International Association for Ecology are collaborating with JSTOR to digitize, preserve and extend access to Oecologia.

<http://www.jstor.org>

The life histories and population dynamics of two carabid species on a Dutch heathland*

1. Fecundity and the mortality of immature stages

Th.S. van Dijk and P.J. den Boer

Biological Station LUW, Kampsweg 27, NL-9418 PD Wijster, The Netherlands

Received October 30, 1991 / Accepted in revised form January 22, 1992

Summary. We deal with the causes of the synchronously fluctuating numbers of subpopulations of the carabid species *Calathus melanocephalus* as compared with the asynchronously fluctuating numbers of subpopulations of the carabid *Pterostichus versicolor*. Both species continuously occupy a large heath area, Dwingelder Veld (1600 ha), in The Netherlands, and are studied there in the same localities with the same methods. Of the adults of *C. melanocephalus*, 90% do not cover more than 2 ha during the entire reproductive season, while 90% of adults of *P. versicolor* cover no more than 12 ha. In *C. melanocephalus* egg production in the field is usually similar to that under optimal feeding conditions in the laboratory, but in *P. versicolor* egg production seems to be much lower in the field. In the field 70–80% of the eggs most probably are killed by eelworms, followed by more than 90% mortality among the remaining larvae. Comparing mortality of developmental stages in laboratory experiments with that in field experiments in enclosures, it appears that mortality of larvae is not density-dependent, even when density in the experiments is much higher than it ever is in the field. Larval mortality mainly results from the poor ability of the larvae to find prey, even when in field experiments prey density is increased far above natural densities. We discuss why these poor prey-finding abilities are not improved by natural selection. In the spring breeder *P. versicolor* differences between localities both in abiotic factors, soil moisture and surface temperature, and biotic factors, reactions of prey species to abiotic factors, in spring and summer when the larvae are maturing contribute to the asynchronous fluctuations of numbers between subpopulations. In the autumn breeder *C. melanocephalus* possible differences in biotic factors between sites are outnumbered by the effects of winters with a higher or lower than normal amount of precipitation respectively. During a wet winter mortality among the larvae is much higher than during a dry winter. As these winter conditions are similar over large areas (many

km²) the fluctuations of numbers between subpopulations are synchronous.

Key words: Life histories – Prey-finding ability – Larval mortality – Abiotic factors – Subpopulations

Population dynamics aims to explain the fluctuations in number of individuals in a population. In practice this boils down to studying the principal variables that in each generation determine the amount of reproduction and mortality in different stages within the population. If possible, this is completed with estimates of dispersal out and into the population. However, to usefully study population dynamics, first of all one has to demarcate one's object of study, the *population*. According to Bakker (1971), "A population is a biological unit for study, with a number of varying statistics (e.g. number, density, birth rate, death rate, sex ratio, age distribution) and which derives a *biological* meaning from the fact that some direct or indirect interactions among its members are more important than those between its members and members of other populations". If the members of a population are only able during their life-time to cover a restricted part of the area continuously occupied by the species these important interactions are also restricted to a space the size of which depends on the movement pattern of the individuals. According to the above definition, in such a situation the area as a whole is not occupied by a "population", but by a complex of (sub)populations that mutually merge into one another. Andrewartha and Birch (1984: 8.5) call such a complex of interconnected subpopulations a *multipartite population*. We differentiate between this situation where an area is continuously occupied by a complex of subpopulations of the same species and that where discrete habitat fragments are occupied by subpopulations with dispersal between, and which is generally called a *metapopulation* (see contributions to Gilpin and Hanski 1991). The dif-

* Communication No. 443 of The Biological Station, Wijster
Correspondence to: Th.S. van Dijk

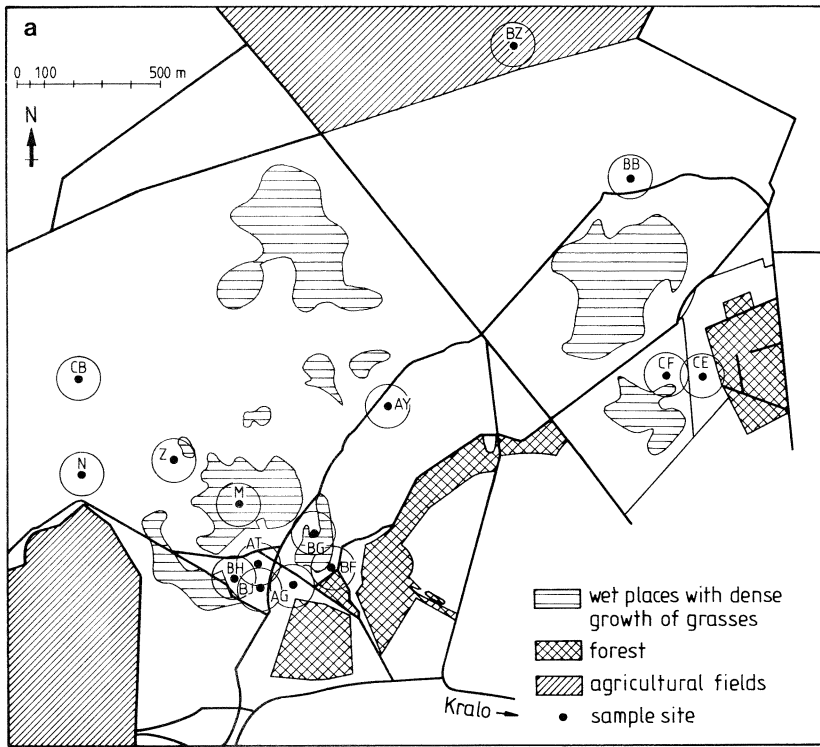
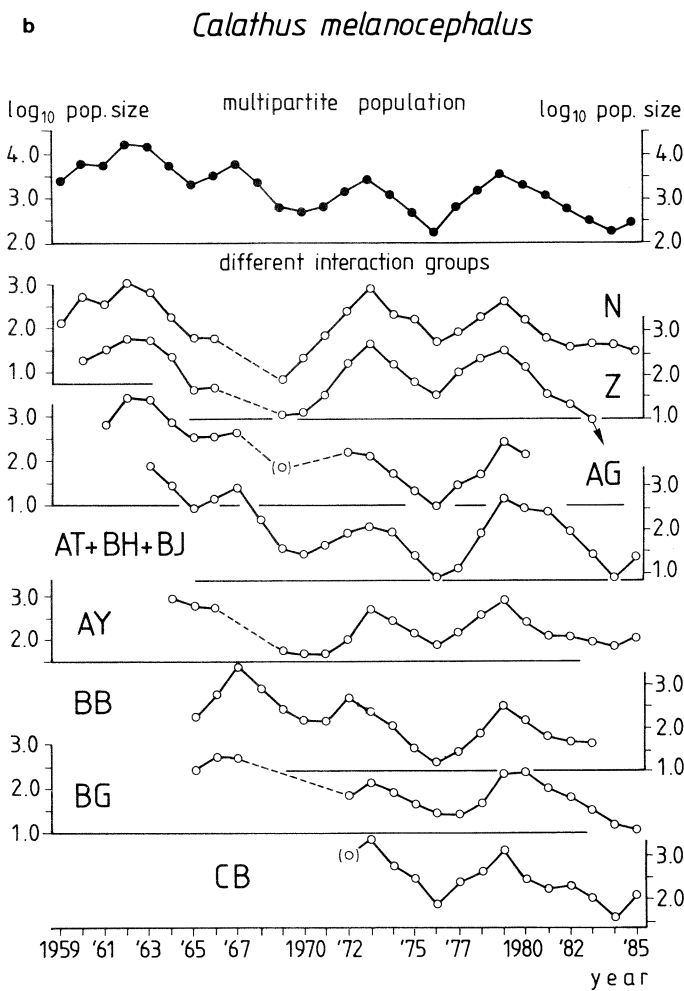


Fig. 1. a Areas of 2 ha around standard sets of pitfalls from which 90% of a year-catch of the carabid species *Calathus melanocephalus* is obtained in the eastern part of Dwingelder Veld (Drenthe, The Netherlands). **b** fluctuation patterns of year-catches from the different interaction groups (subpopulations) and from the multipartite population composed of these interaction groups



ferent parts of a multipartite population are either more or less predetermined by dissimilarities in the environment or fixed by the investigator observing and/or sampling in a restricted locality. The group of individuals in such a locality, among which the important interactions occur, is called an *interaction group* by Den Boer (1977, 1979, 1981). Within an interaction group the effects of spatial heterogeneity are largely evened out by the movements of the individuals, so that following the changes of mean density from generation to generation gives a fair idea of the dynamics of the interaction group (subpopulation), our biological unit of study.

For many years fluctuations of numbers of different interaction groups within multipartite populations of the carabid beetle species *Calathus melanocephalus* and *Pterostichus versicolor* have been studied in a large heath area, Dwingelder Veld, in the Dutch province of Drenthe. By continuously sampling with standard sets of pitfalls (Den Boer 1977: 1c) in 4–14 different localities in this heath area the fluctuations of numbers in different parts of the multipartite populations of these species could be compared. It has been shown already by Baars (1979a) that the catches of these univoltine species in a standard set of pitfalls, summed over the whole reproductive season of 3–4 months – or over the whole year (*year-catch*) – give a reliable estimate of mean density of the reproducing interaction group (subpopulation) in that year. Moreover, by daily recovering radioactively marked individuals of these species Baars (1979b) could reconstruct the walking pattern of the beetles as well as determine the space occupied by an interaction group. Baars and Van Dijk (1984a) found that 90% of the year-catch in a standard set of pitfalls originated from an

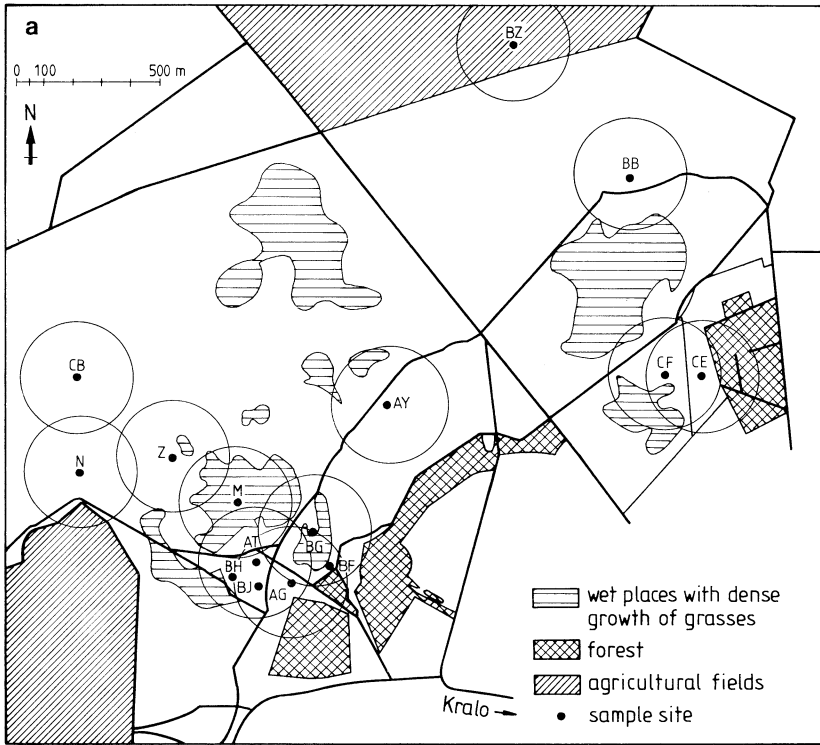
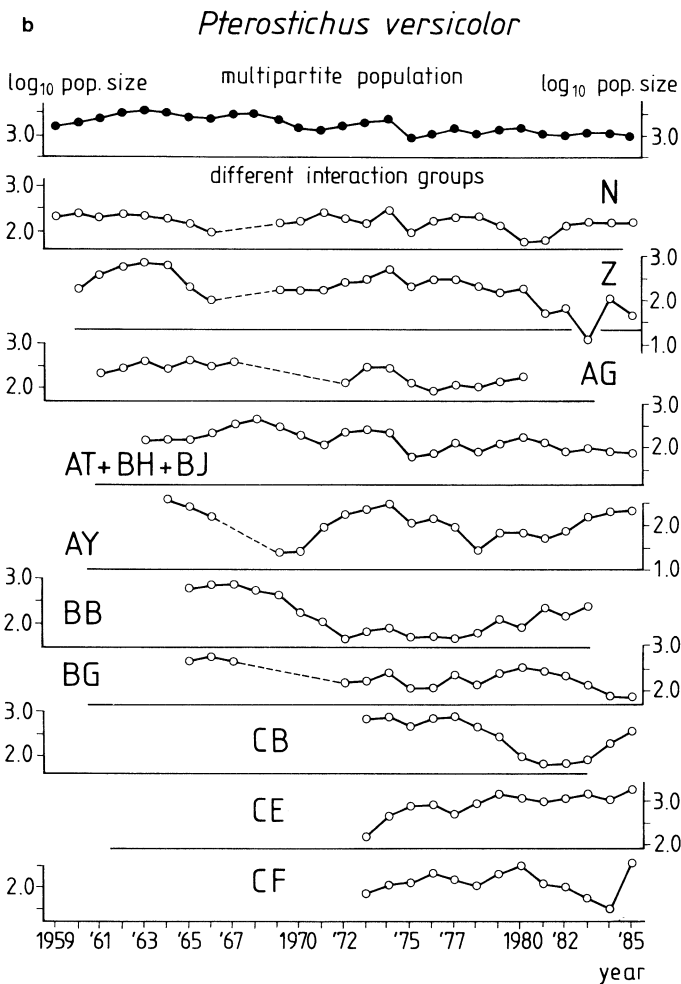


Fig. 2. a Areas of 12 ha around standard sets of pitfalls from which 90% of a year-catch of the carabid species *Pterostichus versicolor* is obtained in the eastern part of Dwingelder Veld (Drenthe, The Netherlands). **b** Fluctuation patterns of year-catches from the different interaction groups (subpopulations) and from the multipartite population composed of these interaction groups



area around the pitfalls of about 2 ha (radius 80 m) in *C. melanocephalus* and of about 12 ha (radius almost 200 m) in *P. versicolor*. The maps of the different sample sites (Figs. 1a and 2a) show the areas from which 90% of the year-catches were obtained. It will be evident from Fig. 1 that at each sample site a separate interaction group of *C. melanocephalus* has been sampled, although we considered that the pitfall sets AT, BH and BJ sampled the same subpopulation, partly due to the high degree of structural uniformity of that site. Figure 2, on the other hand, shows that in *P. versicolor* some interaction groups overlap, e.g. CE with CF, AG with AT + BH + BJ and with BG, so that year-catches from these subpopulations cannot be completely independent.

Den Boer (1981) showed that in different interaction groups of *C. melanocephalus* numbers fluctuate more or less synchronously from year to year, so in a multipartite population composed of these interaction groups numbers fluctuate as much as in an average subpopulation (Fig. 1b). He also showed that in *P. versicolor* numbers fluctuate largely asynchronously between interaction groups, by which the risk of extinction of the multipartite population is spread over all the subpopulations, and thus reduced (Den Boer 1968; Reddingius and Den Boer 1970) (Fig. 2b). Simulations demonstrate that in *P. versicolor* this spreading of the risk of extinction can result in a prolongation of the survival time of the multipartite population by a factor 4–10 as compared with a group of similar subpopulations, whereas in *C. melanocephalus* such an effect cannot be shown (Den Boer 1981; Tables 2 and 3). In *P. versicolor* synchronization is a function of distance between interaction groups: r_s (Spearman) = -0.622 ($P < 0.047$), Y (degree of synchronization) =

0.507–0.39X (X = distance in km), whereas in *C. melanocephalus* distance does not play a significant part: $r_s = -0.30$ ($P = 0.06$).

What causes the synchronously fluctuating numbers of different subpopulations in *C. melanocephalus* (Fig. 1b), on the one hand, and the asynchronously fluctuating numbers of *P. versicolor* (Fig. 2b), on the other? Baars and Van Dijk (1984a) found that the pattern of synchronous fluctuations of *C. melanocephalus*, studied at two sites (AT + BH + BJ and CB), was highly correlated with weather factors during reproduction (August–September) and in spring when development is finished. The correlations with weather factors they found for *P. versicolor* (at the same two sites) are inconclusive, however, because of the asynchronous fluctuation of numbers between sites. Baars and Van Dijk (1984b) also found a significant negative correlation between mean density (year-catch) and total number of eggs in ovaries of both species. But Den Boer (1986a) showed that the range of variation of egg density is only 1–2% of the total range of variation of numbers in *C. melanocephalus*, and only 2–7% of total variation in *P. versicolor*, so that this relationship cannot significantly contribute to the patterns of fluctuation of numbers seen in Figs. 1b and 2b. Moreover, Van Dijk (1986a) showed that, especially in *P. versicolor*, the numbers of eggs in ovaries gives an unreliable estimate of eggs actually laid, because both egg production and egg laying are continuous processes with different temperature relations, in which sometimes egg production is running faster than egg laying and eggs accumulate in the oviduct.

Den Boer's (1986a) analysis shows that in both species more than 90% of the variation in numbers from year to year is caused by variation in the recruitment of young beetles from eggs and by variation in survival of old adults. The former is generally more important than the latter, at least in the longest series of year-catches from site AT + BH + BJ, in which young and old adults were distinguished (and eggs in ovaries estimated) over 18 years (*C. melanocephalus*) and 13 years (*P. versicolor*) respectively. When results of rearing carabid beetles are also taken into account, circumstantial evidence accumulates suggesting that abiotic factors, especially temperature and soil moisture, largely determine the survival of larvae through the three larval stages. In this paper we will test this hypothesis. As *P. versicolor* is a spring-breeder its larvae mature during summer, when variations of soil moisture and temperature between sites can be pronounced. *C. melanocephalus* is an autumn-breeder, so its larvae mature during autumn and winter, a period with lower temperatures and high soil moisture. Hence, we will compare mortality during development between the two species under different conditions of temperature and moisture. In a following paper we will complete the picture by presenting data on mortality of adults after reproduction.

Material and methods

Species and sites

Both species are univoltine polyphagous predators with a broad range of prey (Hengeveld 1980), including ants, spiders, aphids, all kinds of larvae, mites and small flies. For 3 to 4 months the adults move around on the surface of the soil, hunting prey, males looking for females, and females laying their eggs. *P. versicolor* usually lays eggs one at a time, but often two or even three together, in the upper layer of the soil. *C. melanocephalus* lays eggs singly on the surface of the soil. The entire development from egg to young adult occurs in the soil from October to June in *C. melanocephalus*, and May to August in *P. versicolor*. The production and laying of eggs continues during April to July in *P. versicolor* and July to September in *C. melanocephalus* (Van Dijk 1972). After reproduction the adults of both species enter diapause and a varying number (about 50% on average) survive to reproduce again in the next year (Van Dijk 1979a; Baars and Van Dijk 1984a: Appendix). In *P. versicolor* only adults, both young and old, overwinter, but in *C. melanocephalus* the larvae, the majority in the third stage, also overwinter.

Both species belong to the five most abundant species in our area and occupy the entire heath area Dwingelder Veld almost uninterrupted, and often reach higher numbers than in other areas in Drenthe (Den Boer 1977: 149, 165). For *C. melanocephalus* the heath area seems to represent one of the most favourable kinds of habitat, but we are less sure about this for *P. versicolor*. In spite of the sometimes very high numbers on the heath *P. versicolor* have reached still higher numbers in an abandoned agricultural field bordering the heath area (Van Dijk 1986b: Table V). Moreover, in the latter habitat (CE) the beetles are bigger and lay more eggs. Nevertheless, even if the heath area does not represent the optimal habitat type for *P. versicolor*, it is one of the better habitats. Although the larvae of both species actively hunt smaller invertebrates in the soil and frequently come to the surface in doing so, the distances covered during development are small. Although we did not accurately estimate the "area of discovery" of this kind of carabid larvae, we are sure that they will not move through more than a few dm³ of soil during their development. The activities of the adults are also restricted.

In our area winged specimens of the wing-dimorphic *C. melanocephalus* are very rare: about 2 of 1000 beetles (Den Boer 1977: Table 3). So changes in numbers from individuals flying in or out of the area are negligible. *P. versicolor* is macropterous, but the wings are only rarely large enough to enable flight (Den Boer et al. 1980: Table 3). In the course of 20 years (1969–1988) only 10 specimens were caught in window traps (during flight) against more than 45,000 in pitfalls in 20 years (1959–1978). The majority of these pitfall samples were from interaction groups at Dwingelder Veld. Therefore, changes in numbers of this species from individuals flying in or out are also negligible. In a year beetles, walking around in any direction, cannot move outside an area of 8 ha (90% not outside 2 ha) in *C. melanocephalus*, and not outside an area of 48 ha (90% not outside 12 ha) in *P. versicolor*: Baars (1979b).

Our study area, Dwingelder Veld (1600 ha), is quite heterogeneous, and we tried to sample the most representative elements: Z and CF are moist heath sites (mainly *Calluna*) on sand with a highly fluctuating water table, which, especially late in winter and in early spring, can rise above the surface; N is a moist to wet *Erica-Calluna* vegetation on a loamy soil; AY and BB have dry *Calluna-Empetrum* vegetation with some grass patches and open spots at blown sand ridges; AT + BH + BJ is a grassy vegetation of *Festuca* and *Nardus* with large patches of *Empetrum* on a flat, sandy plateau about 1 m above the surrounding area; AG, BG and CB are moist mosaics of patches of *Erica*, *Calluna*, *Festuca*, *Deschampsia*, *Nardus*, *Molinia*, and *Empetrum* with open spots between; CE is a dry cornfield that was abandoned in 1972. This field is mowed each year in August, and the plant material is removed. This will cause the vegetation to gradually change into a heath vegetation (Van Dijk 1986b). Photographs of N (photo 8), AG (13), AT (21) and AY (24) can be found in Den Boer (1977).

Determination of egg-laying period and egg production

To estimate the length of the egg-laying period and egg production under optimal feeding conditions at the start of the breeding season of 1979, females of *P. versicolor* were collected at Dwingelder Veld, placed individually in Petri-dishes with fine ground peat-dust, and kept at field temperatures in an outdoor insectary. Three times a week the beetles were fed with an excess of blowfly maggots (optimal food), and every 3 days a male was added to each female for 24 h. Once a week or each day all eggs laid were collected and counted (for methods see Mols et al. 1981), and this was continued until no more eggs were laid. In 1982 and 1983 similar experiments were done with *C. melanocephalus*, but with different feeding levels; in 1982 two groups got, respectively 4 and 8 mg of food a day, in 1983 three groups got either 4, 8 or 16 mg (excess) of food daily (see also Van Dijk 1986a).

To estimate egg production in the field in 1983 and again in 1986 each week 10 females of *P. versicolor* were taken from Dwingelder Veld and within a few hours individually put into Petri-dishes in the outdoor insectary (above). Without food they do not lay any eggs, so they were fed with red-coloured blowfly maggots to separate eggs produced from food taken in the field (white) from those produced from the blowfly maggots (red). Maggots were coloured by staining their food with a red dye (tradename "oil red tax", soluble in oil; colour-index = solvent-red-24, colour-index number is 26105). The first red eggs appeared after about 5 days (Van Dijk 1986b). Until the end of the breeding season each week the females were returned to the field and replaced by newly collected ones. In 1979–1986 similar experiments were done with *C. melanocephalus*, but females of this species were kept without food (they do not need the feeding stimulus to lay eggs that *P. versicolor* does) for only 3 days, after which 80–90% of the females had laid all ripe eggs, and were then replaced by newly collected ones. After 4 days without food egg resorption starts (Van Dijk 1979b, 1986a).

Under constant feeding conditions egg production is highly temperature-dependent (Van Dijk 1979a, b, 1983). As there are indications that females show some preference for certain sites to lay their eggs we experimented with substrates with different moisture contents. By adding measured quantities of water to oven-dried quantities of peat-dust we obtained substrates with, respectively 45, 65 and 85% by weight of water. Dried peat-dust is highly hygroscopic, so that a moisture level of 45% is a rather dry substrate, whereas 85% gives a wet, but still compact, substrate. These three levels are called dry, medium and wet respectively, and for each of these substrates egg production and the length of the egg-laying period were determined at 19° C (cf. Van Dijk 1983).

Mortality during development

In the laboratory both *C. melanocephalus* and *P. versicolor* were reared at five constant temperatures and at the three levels of soil moisture (above). Each of the 15 combinations was started with 70 eggs (*P. versicolor*) or 30–40 eggs (*C. melanocephalus*) that were 2–3 days old. The mortality in each developmental stage was then checked twice a week under different combinations of temperature and soil moisture (Table 1A).

To estimate mortality during development under field conditions several experiments were conducted in field enclosures, as follows:

Table 1B (upper part): In each of 400 cylinders (ϕ 10 cm), which were buried 10 cm into the soil of a heathland, but leaving 5 cm above the surface, a single egg or first instar larva of *P. versicolor* was placed. The bottom of each cylinder was closed with micro-mesh gauze through which not even first instar larvae could escape, but which allowed free passage of rainwater. Upon the gauze was placed the undisturbed soil core of about 800 cm³ with the egg or larva in a small hole 3–4 cm below the surface. Each cylinder was closed at the upper side with coarse-meshed gauze to prevent preda-

tion. Once a week during the first 8 weeks the same 20 randomly chosen cylinders were checked for hatching of the eggs. When an egg appeared non-viable it was replaced by a fresh one. In this way 83 eggs were replaced in 20 cylinders, which gives us the null value for egg mortality.

Table 1B (lower part): In May/June of two years eggs from laboratory cultures of *P. versicolor* were brought into enclosures of 4 m² (1975) and 8 m² (1977) at two densities, 25 and 50 eggs per m², which approximated "low" and "average" egg densities in the field (as far as these could be estimated from egg-laying experiments). Mortality during development was determined from the number of young beetles hatching in each enclosure in autumn. In these and the following experiments with enclosures all "wild" adults in the enclosure had been removed by trapping before the experiments were started. Experiments have not been performed with eggs of *C. melanocephalus* in the field.

Table 1C: In some experiments laboratory-cultured larvae of both species were released in a heathland in moist and dry enclosures respectively, and the newly hatched beetles were subsequently collected in pitfalls closely fitting the inner side of the enclosures. We used enclosures of 8 m² and of 4 m²; larvae were released individually or in groups. "Moist" means a high water table (in winter sometimes above the surface); "dry" a low water table. In both species all larval densities were below average field densities.

Table 1D: The possible influence of larval density on mortality was investigated by successively releasing different numbers of larvae in a heathland within enclosures of 4 m² each. Note that a high larval density of *P. versicolor* is 10–20 third instar larvae per m², and in *C. melanocephalus* 24–48 second instar larvae per m².

Table 1E: In *P. versicolor* the structure of the vegetation might significantly influence larval mortality, because in this species development takes place in summer. Therefore, first instar larvae were released in enclosures of 4 m², which were placed respectively in a heath area, in heather more than 10 years old, in heather not older than 3 years, and in areas of the grass *Molinia caerulea*. The development to adults was estimated by catching the newly hatched beetles (see above).

Results

Egg laying period and egg production

In *P. versicolor* individual females lay eggs for no more than 6–7 weeks (Table 2), although most females have ripe eggs in the ovaries for more than 12 weeks (April till mid-July). Apparently, most females neither start nor stop reproduction at the same time (Van Dijk 1979b), which was confirmed by observing marked beetles inside enclosures. Egg development starts at lower temperatures (below 13° C) than egg-laying (at mean day temperatures above 13° C, Van Dijk 1979b), so that in many years egg development had already started before the females became active. Therefore, neither the number of eggs in the ovaries in the course of the season, nor the mean number of eggs laid per female per week multiplied by the number of weeks of the breeding season, gives a reliable estimate of egg production in the field. The latter must be based on the performances of individual females, as in our experiments (Table 2).

Under field conditions the mean period of egg laying is slightly longer in *C. melanocephalus* than in *P. ver-*

Table 1. Scheme of field and laboratory experiments on mortality of immature stages of *Pterostichus versicolor* and *Calathus melanocephalus*

A	Mortality of all stages at 5 temperatures at 3 levels of soil-moisture	<i>P. vers.</i> :	Temp. 12°, 15.5°, 19°, 22.5° and 19°/12° C (12 h each) ± 70 eggs at each temp.
B	Mortality during development from egg till adult in the field	<i>C. mel.</i> :	temp. 5°, 8.5°, 12°, 15.5° and 22.5° C 30–40 eggs at each temp.
C	Mortality in the field under moist and dry conditions	<i>P. vers.</i> :	one egg/cylinder Ø 10 cm: 100 with food, 181 without food one larva 1/cylinder Ø 10 cm: 55 with food, 44 without food control group for egg hatching: 20 cylinders
		<i>P. vers.</i> :	large enclosures } 4 enclosures 4 m ² with 100 or 200 eggs each } 7 enclosures 8 m ² with 200 or 400 eggs each } in 1974 moist } 2 enclosures dry } 2 enclosures } 1975 and 1976 1 st larvae } 3 enclosures } 3 rd larvae } 3 enclosures } 2 nd larvae } 2 enclosures } in 1974 1 st larvae } 3 enclosures } 1975 and 1976
D	Relationship between density and mortality	<i>P. vers.</i> :	2.5/m ² , 5/m ² , 10/m ² , 20/m ² , 40/m ² and 80/m ²
		<i>C. mel.</i> :	6/m ² , 12/m ² , 24/m ² and 48/m ²
E	Mortality in fields with different vegetations or with different ages	<i>P. vers.</i> :	4 encl. old heather 4 encl. young heather 4 encl. <i>Molinia</i>

Table 2. Mean number of weeks of egg-laying and mean number of eggs laid per ♀ per week in *Pterostichus versicolor* and *Calathus melanocephalus* at field temperatures in an outdoors insectary and in the field, (with SD in parentheses)

Year	<i>Pterostichus versicolor</i>			<i>Calathus melanocephalus</i>						
	Reproduction period	# ♀♀	Length of the individual egg-laying period (weeks) mean	Number of eggs laid per week mean	Actually laid in the field per week mean	Reproduction period	# ♀♀	Length of the individual egg-laying period (weeks) mean	Number of eggs laid per week mean	Actually laid in the field per week mean
1978	21/4–27/7	27	7.33 (2.77)	8.21 (8.28)	8.21 (8.28)	19/7–5/10	20	8.25 (2.20)	not counted individually	not counted individually
1979	22/4–25/7	25 ^a	6.00 (2.22)	8.44 (10.54)	8.44 (10.54)	30/7–5/10	22	8.64 (1.68)	31.93 (20.32)	15.61
1979	22/4–25/7	28	6.79 (3.24)	11.66 (14.38)	11.66 (14.38)	8/8–10/10	20 ^b	7.55 (1.88)	34.67 (21.94)	
1979						8/8–10/10	20 ^c	8.15 (1.09)	33.04 (19.83)	
1982	19/4–19/7	20	6.31 (1.76)	23.83 (17.50)	23.83 (17.50)	4/8–13/10	11 ^d	8.27 (1.10)	15.82 (9.86)	48.7
1982						4/8–13/10	11 ^e	9.00 (0.77)	26.09 (12.70)	
1982						4/8–13/10	10 ^f	9.30 (0.95)	36.83 (16.87)	
1983						9/8–11/10	11 ^d	8.85 (1.10)	14.50 (11.88)	
1985						9/8–11/10	11 ^d	8.72 (0.90)	24.20 (19.00)	53.3
1986	30/4–22/7	8	9.25 (1.58)	15.08 (16.21)	15.08 (16.21)					37.11
										15.03

^a Only these ♀♀ were collected at a heathland, other ♀♀ were from a grassland (previous arable field: CE); # = number of; ^b first-year beetles; ^c second or more years old beetles; ^d 4 mg food (maggots of blowfly) per ♀ per day; ^e 8 mg food per ♀ per day; ^f 16 mg food per ♀ per day (excess). In other experiments the beetles were supplied excess of food

Table 3. Number of eggs laid per female and the length of the egg-laying period in weeks at different temperatures; mean and SD (in parentheses)

<i>Pterostichus versicolor</i> (10 ♀♀ per experiment)	Temperature				
	8.5° C	15° C	20° C	25° C	30° C
Length of egg-laying period (in weeks)	0.7 (1.34) ^a	5.9 (2.02) ^b	5.7 (2.36) ^b	4.4 (2.74) ^{a, b}	4.9 (2.0) ^{a, b}
Number of eggs per ♀ per week	1.1 (1.83) ^a	8.4 (6.53) ^b	17.2 (11.98) ^c	19.3 (14.19) ^{c, d}	11.6 (11.9) ^b
Total number of eggs per female	1.6 (2.95) ^a	49.6 (22.4) ^b	98.1 (66.46) ^b	85.5 (70.52) ^b	56.6 (49.7) ^b

<i>Calathus melanocephalus</i> (20 ♀♀ per experiment)	Temperature					
	5° C	8.5° C	12° C	15.5° C	19° C	22.5° C
Length of egg-laying period (in weeks)	2.9 (2.91) ^a	5.6 (1.92) ^b	7.9 (1.59) ^c	10.4 (1.18) ^d	14.1 (3.66) ^e	15.3 (3.50) ^e
Number of eggs per ♀ per week	3.1 (3.99) ^a	9.4 (7.02) ^b	23.0 (12.74) ^c	39.5 (21.12) ^d	49.4 (32.60) ^e	37.4 (33.33) ^{d, f}
Total number of eggs per female	9.1 (11.72) ^a	52.7 (34.53) ^b	181.9 (63.19) ^c	410.8 (155.17) ^d	694.9 (283.16) ^e	572.4 (213.05) ^{d, e}

Values followed by different letters differ significantly ($P < 0.05$) according to the Mann-Whitney test

sicolor (Mann-Whitney for means: $P = 0.03$): Table 2. As soon as ripe eggs are present in the ovaries *C. melanocephalus* starts egg-laying. Therefore, in this species the length of the egg-laying period of individual females approaches that of the breeding season of the population. Also, the number of eggs laid per female per week is much higher in *C. melanocephalus* than in *P. versicolor* (Table 2). For the whole season the mean number of eggs per female ranged from 128 (in 1983) to 275 eggs (in 1979) in *C. melanocephalus*, and from 60 (in 1978) to 150 eggs (in 1982) in *P. versicolor*.

It is striking that in *P. versicolor* the number of eggs actually laid in the field is much lower than in our experiments under field conditions (Table 2). Possibly, in the field either the quantity or quality of the food are usually suboptimal for this species (Van Dijk 1986b). In *C. melanocephalus*, however, the numbers of eggs laid in the field are generally as high – or even higher – than those laid in our experiments with an excess of high quality food (Table 2) (see Van Dijk 1986a).

The period of egg laying as well as the number of eggs laid per female per week are affected by temperature (Table 3). Moreover, egg production is significantly influenced by food supply (see Table 2: *C. melanocephalus*) as well as by food quality (Van Dijk 1983). Temperature effects are smaller in *P. versicolor* than in *C. melanocephalus* (Table 3), yet in both species the mean number of eggs produced per female per week with food in excess at (fluctuating) field temperatures are similar to those extrapolated from the values of Table 3 (using daily maximum temperatures, averaged per week, for *P. versicolor*, and mean 24-h temperatures, averaged per week, for *C. melanocephalus*: Van Dijk 1983). This means that within some (adaptive) range all processes determining both the rate of egg production and the period of egg-laying are immediately determined by temperature in an

almost proportional manner. In *P. versicolor* this range is somewhere between 15 and 23° C, in *C. melanocephalus* between 8.5 and 19° C. It is interesting to note that, apparently, these processes are mainly influenced by temperature during activity periods, *P. versicolor* being day-active in spring, especially in the hours around noon, and *C. melanocephalus* being night-active late in summer and early in autumn, particularly in the first hours after twilight (Vlijm et al. 1961). During the day temperature at the surface of the soil will often be very different between sites, so the egg production of females of *P. versicolor* active at the different study sites could have shown great differences. Although females of both species prefer to lay their eggs in moist (to wet) soil rather than in dry soil, in our experiments the moisture condition of the soil hardly affected the number of eggs laid. Only females of *C. melanocephalus* laid significantly more eggs in moist soil than in dryer soil when permanently kept on soil with a constant moisture content.

Survival of eggs and mortality during development

The majority of eggs laid in the field do not hatch; they are preyed upon and/or parasitized. In the experiment with eggs in cylinders, and thus protected from arthropod predators (Table 1B: upper part), 77% of the eggs in the 20 control cylinders did not produce larvae, which fits the results of similar experiments by Heessen (1981), who found 83% egg mortality, mainly because of predation by small nematodes (eelworms), which are always present in the soil. When the cylinders were not provided with food not a single adult was produced, whereas by adding food to eggs adults emerged in 3 out of 100 cylinders, and when first instar larvae were provided with food 11 out of 55 cylinders produced adults. The percen-

Table 4. Mortality during the development from egg (or larval stages) to adult in field enclosures: mean + SD in parentheses (see Table 1B (lower part) and 1C)

Stage	<i>P. versicolor</i>		<i>C. melanocephalus</i>	
	density	% mortality	density	% mortality
Egg	25/m ²	97.9 (1.94)		
Egg	50/m ²	99.4 (0.73)		
Larvae 1	25/m ²	98.8 (0.51)		
Larvae 1 ^a	22.5–25 m ²	97.7 (2.28)	38–125/m ² ^c	92.09 (11.38)
Larvae 1 ^b	22.5–25 m ²	93.2 (6.92)	39–165/m ² ^d	98.04 (2.00)
Larvae 2	12/m ²	84.0		
Larvae 3	12/m ²	83.1 (7.94)	12/m ²	80.6

^a without food added

^b with food added

^c dry soil conditions

^d wet soil conditions

tage of unfertilized eggs depends on temperature, and is lowest at 19° C (6.5%) in *P. versicolor*, and at 15.5° C (2.4%) in *C. melanocephalus*.

Table 4 shows that in the field mortality during development is very high in both species, 98.9% on average in *P. versicolor*, and 95% on average in *C. melanocephalus*. When eggs (or larvae) were individually put into small holes in the soil mortality was equally as high as when they were released in groups on the surface. The range of mortality during development in different enclosure experiments is especially great when releasing first instar larvae; 76.7–100% in *P. versicolor*, and 65.4–99.8% in *C. melanocephalus*. But even when third instar larvae were released in enclosures mortality during their development to adult was still above 80% in both species (Table 4). Mortality during development can be very

different between years, but is not significantly different under moist or dry conditions, mainly because the variability of the results is very great. For instance, the lowest mortality (65.4%) ever found in experiments with *C. melanocephalus* (in 1977) contributes to the high mean mortality under wet soil conditions in this species (Table 4). In both species larval density shows no correlation with mortality rate (Table 5), though densities of 20–80 third instar larvae of *P. versicolor* per m² are far higher than ever found in the field. Supplying the enclosures with additional food (blowfly maggots three times per week) significantly reduces mortality in *P. versicolor* (Table 5; Student's *t*-test: $P < 0.0005$), though it remains very high. The mortality of *P. versicolor* during development was significantly lower in young heather than in old heather or in *Molinia* (Table 6; Student's *t*-test: $P < 0.0005$), but in all types of vegetation it was still very high. Providing the larvae with extra food indeed decreased mortality significantly (Table 6; Student's *t*-test: $P < 0.0005$), but not below 90%, even though the amount of food added (blowfly larvae three times per week) significantly raised the normal feeding level in the field. Hence, although in the field mortality during development can vary greatly, it is always very high: both when eggs or larvae are kept separately and when they are released in groups, both when larval density is high and when it is low; both without and with extra food; both under moist and dry conditions.

Mortality during development under laboratory conditions

In the laboratory extreme moisture conditions of the soil (dry or wet peat-dust) appear to be unfavourable to the

Table 5. Relationship between density of larvae released in enclosures in the field and mortality during development (see Table 1D)

Stage	<i>P. versicolor</i>		Stage	<i>C. melanocephalus</i>	
	Density	% Mortality		Density	% Mortality
Larvae 3	2.5/m ²	100.0	larvae 2	6/m ²	95.8
Larvae 3	5/m ²	85.0	larvae 2	12/m ²	97.8
Larvae 3	10/m ²	92.5	larvae 2	24/m ²	92.7
Larvae 3	20/m ²	88.8	larvae 2	48/m ²	90.1
Larvae 3	40/m ²	96.2	larvae 2	48/m ²	90.1
Larvae 3	80/m ²	99.4			
correlation between density and mortality				$r_s = -0.80$ ($P = 0.334$)	
r_s (Spearman) = +0.086 ($P = 0.8$)					

Table 6. Mortality during the development of *P. versicolor* from first stage larvae to adults in fields with different vegetations or with a different age of the heather. Standard deviation between brackets (see Table 1E)

Field	No. of enclosures	No. of years studied	Mortality during development		
			Density	Without food	With food
<i>Molinia</i>	4	3	23–25/m ²	99.1 (1.60)	95.9 (3.12)
Old heather	4	3	23–25/m ²	98.3 (1.20)	94.9 (5.88)
> 10 years old					
Young heather	4	3	23–25/m ²	94.6 (2.12)	84.0 (8.30)
< 3 years old					

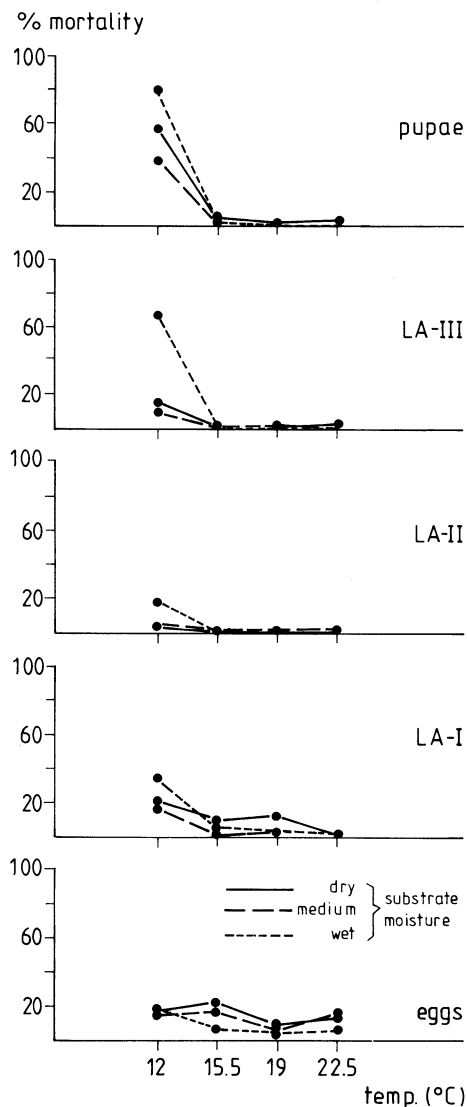


Fig. 3. *P. versicolor*: % mortality of the different developmental stages at three substrate moisture levels and at different temperatures

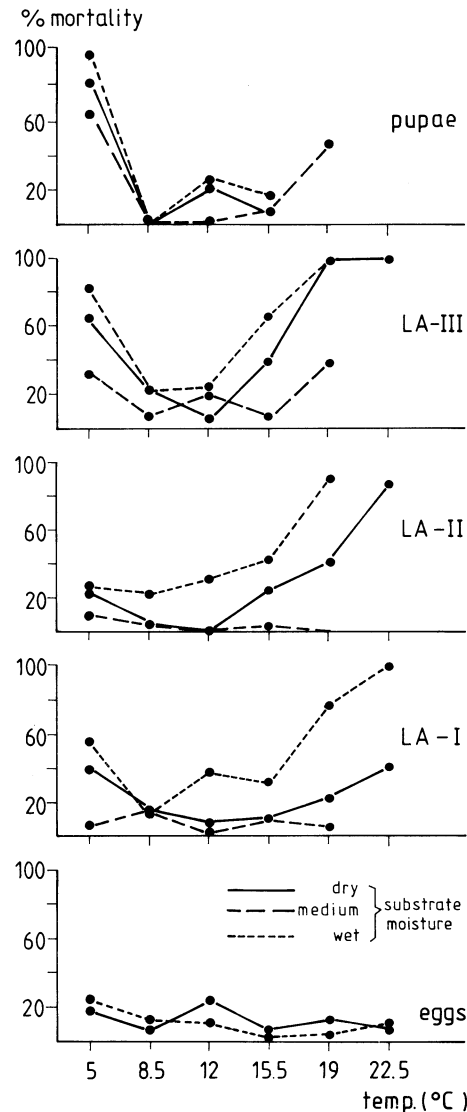


Fig. 4. *C. melanocephalus*: % mortality of the different developmental stages at three substrate moisture levels and at different temperatures (no experiments were done with eggs at medium substrate moisture and with larvae at 22.5° C and medium substrate)

survival of larvae and pupae of *P. versicolor* only at low temperatures, 12° C or lower (Fig. 3), but across a wide range of temperatures in *C. melanocephalus* (Fig. 4). Especially under wet conditions third instar larvae and pupae of *P. versicolor* show a high mortality at 12° C. Total mortality in *P. versicolor* during development decreases sharply at higher temperatures at all substrate moistures (Fig. 5).

In contrast to *P. versicolor*, in most developmental stages of *C. melanocephalus* mortality is rather low between 8.5 and 15.5° C (Fig. 4), but increases significantly at higher and lower temperatures, except for eggs. Particularly third instar larvae and pupae are highly sensitive to temperatures below 8.5° C. Total mortality during development is much higher in *C. melanocephalus* than in *P. versicolor* under all conditions of temperature and substrate moisture, but most pronouncedly so under

wet conditions (Fig. 5). Hence, the larvae of *C. melanocephalus* survive best under medium moisture conditions in the substrate combined with relatively low temperatures (Figs. 4 and 5). *P. versicolor*, on the other hand, survives best during development at relatively high temperatures combined with medium or wet moisture conditions of the soil (Fig. 5).

In all experiments food was always easily accessible, and the larvae were reared individually without mortality factors other than abiotic and possibly phenotypic ones, so mortalities were much lower than in the field. Especially in *P. versicolor* in the field accessibility of food seems to be the most important limiting factor for the survival of larvae (Tables 4 and 6), abiotic conditions being usually favourable for this species in our area. Important limiting factors for the survival of larvae of *C. melanocephalus* are warm and dry (or wet) weather in Septem-

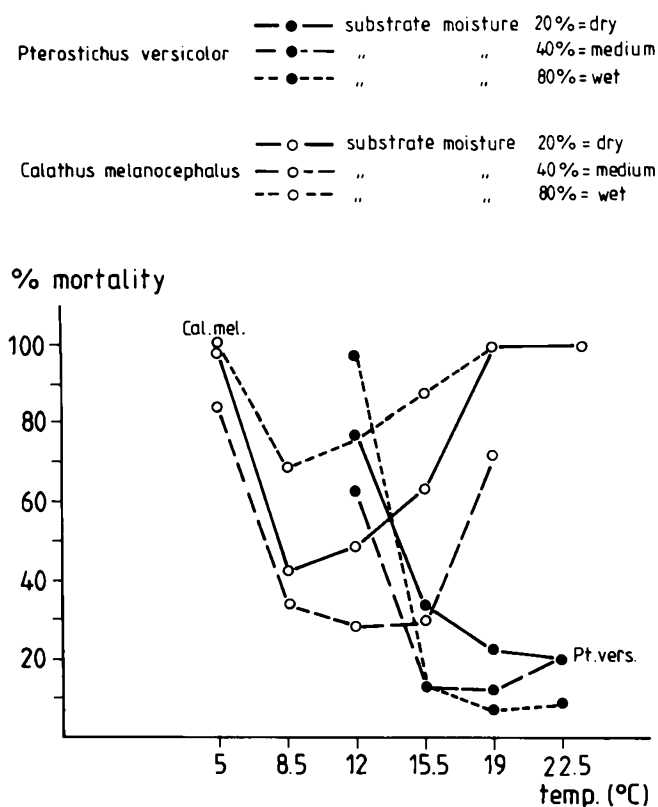


Fig. 5. *P. versicolor* and *C. melanocephalus*: Percentage mortality during development from egg to adult

ber/October, and cold and wet weather in winter. We have no conclusive data about the availability of food for the larvae of this species under field conditions.

Discussion

In agreement with the findings of Grüm (1984) for other carabid species, the fecundity of the autumn breeder *C. melanocephalus*, with a relatively long period of larval development, is much higher than that of the spring breeder *P. versicolor*, with a much shorter period of larval development. Apparently, in *C. melanocephalus* the higher risk of larval mortality during 8–10 months of development is compensated by a high fecundity. However, the variation in numbers of eggs laid per female is similar in both species; only the mean is different. Apart from individual differences between females (Van Dijk 1979a), and temperature (Table 3), both the quality and the quantity of food will contribute considerably to this variation (Van Dijk 1983, 1986a; Lenski 1984; Mols 1988; Sota 1985). Mols (1988) could satisfactorily simulate egg production of *P. versicolor* under different feeding conditions in the field. As most carabids, including the present two species, are extremely polyphagous (Hengeveld 1980), it is very difficult to estimate the quantities of food that they take in the field. So far, it has only been demonstrated that the accessibility of high quality food is limited under field conditions (Van Dijk 1983, 1986a; Mols 1988). This seems to limit egg production in

P. versicolor (but see below), but only incidentally so in *C. melanocephalus* (Table 2).

It is not yet clear whether or not the negative relationship between density and the numbers of eggs in the ovaries of *C. melanocephalus*, as found by Baars and Van Dijk (1984b), actually points to a shortage of food at high densities of beetles. Van Dijk (1986a) showed that a better measure for egg production is the number of eggs actually laid per female per unit of time. In years with low densities of *C. melanocephalus* the mean number of eggs laid per female per week is about 3–4 times higher than the mean number of ripe eggs in the ovaries of dissected females, whereas in high density years this ratio does not differ appreciably from unity. Hence, this reinforces the negative relationship with density (Baars and Van Dijk, 1984b). For instance, 1982 and 1983 were low density years and 1979 was a high density year (compare Fig. 1) (Table 2). Nevertheless, even taking into account this reinforcement of the negative relationship with density does not raise the share of variation in egg production between years above 6–10% of the fluctuation in numbers (compare Den Boer 1986a). There are indications that this density effect is more connected with the quality of the food, which differs between high and low density years, than with the quantities of food available (Den Boer 1986b). These indications came from experiments in which it appeared that very different numbers of eggs are produced when the females are fed with only one of the different kinds of prey that are all readily taken in the field. Be this as it may, variation in the mortality of developmental stages is much more important in limiting numbers than the variation in numbers of eggs produced (see Introduction).

Van Dijk (1986a) clearly showed that in *P. versicolor* the number of eggs in ovaries does not correlate with the number of eggs laid in the field, so that we do not know whether or not the low number of eggs laid by this species in the field has something to do with density of beetles. In any case *P. versicolor* spends much more time in looking for an adequate site to lay eggs than *C. melanocephalus*. When such a site is found the female *P. versicolor* crawls into the soil and prepares a small hole for its egg(s) while the ripe eggs descend to the oviduct. Therefore, the egg-laying strategy of *P. versicolor* is more directed towards finding adequate sites than to the production of a high number of eggs. *C. melanocephalus*, on the other hand, simply puts its eggs, covered with humus particles, on the surface of the soil. This difference between the two species is confirmed by the observation that females of *P. versicolor* do not feed when they lay eggs, and do not lay eggs when they are hunting. Because of this alternation of two kinds of behaviour the females are only caught in pitfalls when hunting, which means that they have already laid their ripe eggs (Van Dijk 1986a). Because of this females do not lay eggs when brought to the laboratory. They have to be stimulated by feeding them with red-colored blowfly maggots (Material and methods) before ripe eggs will descend from the ovaries to the oviduct. As a consequence our estimate of the number of eggs laid in the field (as given in Table 2) must be much too low. In fact, we cannot estimate the number of eggs

laid in the field in this species. Therefore, when we add food in our enclosure experiments the females of *P. versicolor* rapidly disappear from the surface (after having fed, of course) to develop and lay eggs, and can only be caught again in the pitfalls at the inner border of the enclosure when they are hungry and start hunting (see also Mols 1988). Females of *C. melanocephalus*, on the contrary, hunt and lay eggs in the same activity bouts.

Table 4 shows that in both species mortality during development is very high, whereas Table 5 demonstrates that density of larvae cannot be a significant cause of that, in spite of the cannibalistic tendencies of the larvae. Even at the unrealistically high density of 80 third-instar larvae of *P. versicolor* per m² the chance that they will meet is only small. As they move through the upper 20 cm of the soil at that density there is an average of only 4 larvae in 1 l of soil (at the highest field densities recorded there is less than one larva per liter of soil). So the chance of encountering an organism other than a congener will usually be higher, but still not great. And it is not the reason for the extremely high rates of mortality in all the field experiments where food was added. We believe that this is mostly due, not to the lack of prey, but to the poor abilities of the larvae to find prey. They are bad hunters; and this was clearly demonstrated in the enclosures to which food was added. The larvae were hardly able to find any of the many blowfly maggots that were placed in the enclosures three times a week. We have seen larvae as well as adults run over or close by prey without recognizing it as such, even when they are hungry. The situation is quite different in the laboratory. When they are placed directly with prey in a small tube or Petri-dish they have no trouble recognizing and eating them, though only after some time. This, we think, accounts for why the mortality of the larvae is so high in the field, while we can rear equivalent larvae in the laboratory with an efficiency of 80% or better. Such inefficient hunting, even at their maximum field densities, would preclude them having any real influence upon the number of their prey. Brüning (1991) came to the same conclusions concerning the effects of *Formica polyctena* on the numbers of spiders. The modest capabilities of the carabids' central nervous system forces these animals to hunt in a simple and rather rigorous (stereotyped) manner, which is far from "optimal foraging". It is not necessarily ineffective however (see further Den Boer 1986b). Moreover, this lack of efficiency at catching prey does not prevent these species being very successful. Sufficient of them still survive for both species to be among the five most abundant carabids of our area (Den Boer 1977: Table 3), and to occupy a considerable part of the available non-forest habitats, both natural and agricultural. This situation of a successful species, the larvae of which generally live under suboptimal feeding conditions, is also found in the carabid *Nebria brevicollis* (Nelemans 1987a, b, 1988), and may be widespread among carabid species.

When we compare the data in Fig. 3 with those in Table 4 we must conclude that in *P. versicolor* temperature and soil moisture can only exceptionally be responsible for the high mortality of developmental stages. Moreover, Table 5 shows that neither can very

high larval densities be the cause, which also excludes the possibility of significant competition for food. As in preceding years other species of predatory beetles were removed before starting the enclosure experiments, so significant predation by larvae of other species can also be excluded as a cause of the high mortalities shown in Table 4. Predation by nematodes is restricted to eggs as far as we know (Results; and Heessen 1981). Hence, these high larval mortalities are most probably due to failure of the larvae to find sufficient food (above). Although spreading 30–50 blowfly maggots three times per week over 4 m² significantly reduced these mortalities (Tables 4 and 6), mortality is still many times higher than in the laboratory, where the larvae are fed with similar blowfly maggots at the same frequency. This brings us back to the poor ability of the larvae to find prey. Apparently, it makes a vast difference whether a blowfly maggot is offered on a smooth surface of 2.5 cm² in a small tube in which the larva is reared in the laboratory, or whether a larva has to find such a maggot in an area of about 1000 cm² and covered with debris in an enclosure. This vast difference in traceability is possibly reinforced by the fact that the maggots soon burrow into the soil, both in the field enclosures and in the tubes with peat-dust. It may seem surprising that natural selection has not improved the ability of carabid larvae to detect prey. We must realize, however, that such an improvement would not so much be a matter of better sense-organs, but more a matter of learning to react adequately to the behaviour and spatial distribution of many different kinds of potential prey, sometimes well beyond the modest capabilities of carabid larvae.

As the traceability of different kinds of prey can well be different at different sites and/or in different years, e.g. because of different degrees of clustering, the asynchronous fluctuations in different interaction groups of *P. versicolor* (Fig. 2) may be caused by differing chances of the larvae finding enough food to complete development (compare Table 6). This would be very difficult to investigate, however. Different temperatures at the soil surface between sites (with differently structured vegetation and different kinds of soil) will lead to dissimilarities in egg production and egg-laying between sites, which will contribute to the asynchronous fluctuation patterns of Fig. 2.

In the case of *C. melanocephalus* the high larval mortalities under field conditions (Table 4) can be explained by the data of Fig. 4. As soon as temperature surpasses 15.5° C, which will frequently occur in the heath in September when first instar larvae hatch, and in April/May when third instar larvae pupate, mortality will be high, especially under wet soil conditions. But also in winter, when temperature often decreases below 8.5° C, mortality will be high, in particular under wet soil conditions. Just as in *P. versicolor* larval density does not negatively affect survival in *C. melanocephalus* (Table 5), so that again competition for food can be excluded. Of course, failure to catch enough food will play some part in this species too, but we do not expect this to be a dominant factor, for then more asynchronously fluctuating numbers would have been observed. Hence, most

Table 7. Relationship between the fluctuation pattern of numbers in three subpopulations of *Calathus melanocephalus* at Kralo Heath and the occurrence of wet (unfavourable for the survival of larvae) or dry winters. Subpopulation numbers increased after winters with low precipitation and decreased after winters with higher than normal precipitation. A wet winter is defined as December–March with precipitation > 10% above the mean over the preceding 30 years; other winters are called “dry”

Year	Numbers caught in a whole year				Increase (+) or decrease (-) in numbers	Dry winter (+) or wet winter (-)	Agreement (+) with hypothesis
	Z ^a	N ^a	CB ^a	Total			
1971	31	73	–	(104)	+	+	+
1972	167	249	978	1394	+	+	+
1973	468	876	2339	3683	+	+	+
1974	152	208	553	913	–	–	+
1975	62	160	306	528	–	–	+
1976	32	50	71	153	–	–	+
1977	104	276	227	607	+	+	+
1978	214	595	395	1204	+	+	+
1979	354	472	1168	1994	+	+	+
1980	147	167	274	588	–	–	+
1981	34	64	165	263	–	–	+
1982	21	42	203	266	±	+	(+)
1983	9	47	101	157	–	–	+
1984	1	47	36	84	–	–	+
1985	0	34	118	152	+	+	+
1986	20	439	300	759	+	–	–
1987	235	249	536	1020	+	–	–

^a Z, N and CB are three sites sampled with a standard set of pitfalls the whole year round

probably in *C. melanocephalus* temperature and soil moisture are responsible for the high mortality of developmental stages.

As mean day-temperatures in January–March are low in our area (1.2–3.9° C), and wet conditions predominate at Dwingelder Veld in winter, because winter rains drain only slowly into the saturated soil, in many winters mortality of larvae of *C. melanocephalus* must be very high during this period. Frost-free but wet winters with only small local differences in temperature and moisture (at a scale of square kilometers) are common in The Netherlands. Such winters will not only cause a low survival of third instar larvae (10–20% or lower) and thus a low recruitment, but such changes in numbers will also run in parallel in different interaction groups. Therefore, it is not surprising that the annual abundance of *C. melanocephalus* at Dwingelder Veld (Fig. 1) is closely correlated with wet-year deviations from the normal amount of precipitation (= average of 30 years) based on December to March records. Subpopulation numbers increased after winters with average or low precipitation, and decreased after winters with higher than normal precipitation (Table 7). More generally, the high mortality risk of carabid larvae during long periods of inundation is connected with the observation that in wet habitats (marshes, bogs, banks, water meadows) less than 5% of carabid species are autumn breeders (Murdoch 1967; Den Boer 1980: Table 3). Hence, in spite of reaching very high numbers in some years (Fig. 1) at Dwingelder Veld, this site might not be the optimal habitat for *C. melanocephalus*. The close relationship of the numbers of *C. melanocephalus* with the moisture conditions in winter were absent in only the last two years of observations (1986, 1987). This could have resulted from increasing pollution (by nitrogen) of the area, which causes heather to disappear and grasses to increase over large areas. Also the introduction of large scale machine-cutting of grass may have caused differentiation of survival chances between

the sampling sites. Most carabid species responded in numbers to these large-scale changes.

Summarizing, we conclude that the striking difference between the subpopulation fluctuations of *C. melanocephalus* (Fig. 1) and *P. versicolor* (Fig. 2) at Dwingelder Veld most probably arises from the different life histories of these species. *C. melanocephalus*, being an autumn breeder, has larvae that have to pass winters with either favourable or unfavourable abiotic conditions which are the same over large areas, so that the numbers in different interaction groups change synchronously. *P. versicolor*, on the other hand, being a spring breeder, has larvae that mature in summer, when there is a high chance of local differences in both biotic (accessibility of food) and abiotic (temperature) conditions. In this species we expect biotic differentiation between sites to be the most important of the two.

Acknowledgments. We are greatly indebted to Arnold Spee, for without his daily and intensive assistance it would not have been possible to get so many data to base this work upon. Many thanks are due to Tom White (Australia), Martin Luff (UK) and Graeme White (New Zealand) for valuable critical remarks and for improving the English text, to Yde Jongema for his assistance during practical work, to Marian Stevens for typing tables.

References

- Andrewartha HG, Birch LC (1984) The ecological web. More on the distribution and abundance of animals. Chicago Univ Press, Chicago London
- Baars MA (1979a) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41: 25–46
- Baars MA (1979b) Patterns of movement of radio-active carabid beetles. *Oecologia* 44: 125–144
- Baars MA, Van Dijk ThS (1984a) Population dynamics of two carabid beetles at a Dutch heathland. I. Subpopulation fluctuations in relation to dispersal. *J Anim Ecol* 53: 375–388
- Baars MA, Van Dijk ThS (1984b) Population dynamics of two

- carabid beetles at a Dutch heathland. II. Egg production and survival in relation to density. *J Anim Ecol* 53:389–400
- Bakker K (1971) Some general remarks on the concepts "population" and "regulation". In: Den Boer PJ, Gradwell GR (eds) Dynamics of populations. PUDOC, Wageningen, pp 565–567
- Brüning A (1991) The effects of a single colony of the red woodant, *Formica polyctena*, on the spider fauna (Araneae) of a beech forest floor. *Oecologia* 86:478–483
- Den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheor Leiden XVIII*: 165–194
- Den Boer PJ (1977) Dispersal power and survival. Carabids in a cultivated countryside. *Misc Pap Landbouwhogeschool Wageningen* 14:1–190
- Den Boer PJ (1979) The significance of dispersal power for the survival of species, with special reference to the carabid beetles of a cultivated countryside. *Fortschr Zool* 25:79–94
- Den Boer PJ (1980) Exclusion or coexistence and the taxonomic relationship between species. *Neth J Zool* 30:278–306
- Den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50:39–45
- Den Boer PJ (1986a) Population dynamics of two carabid beetles at a Dutch heathland. The significance of density-related egg production. In: Den Boer PJ, Luff ML, Mossakowski D, Weber F (eds) Carabid beetles, their adaptations and dynamics. Gustav Fischer, Stuttgart New York, pp 361–370
- Den Boer PJ (1986b) Facts, hypotheses and models on the part played by food in the dynamics of carabid populations. In: Den Boer PJ, Grüm L, Szyszko J (eds) Feeding behaviour and accessibility of food for carabid beetles. Warsaw Agr Univ Press, Warsaw, pp 81–96
- Den Boer PJ, Van Huizen THP, Den Boer-Daanje W, Aukema B, Den Bieman CPM (1980) Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera, Carabidae). *Entomol Gen* 6:107–134
- Gilpin M, Hanski I (eds) (1991) Metapopulation dynamics. Special volume of *Biol J Linn Soc* 42:3–323
- Grüm L (1984) Carabid fecundity as affected by extrinsic and intrinsic factors. *Oecologia* 65:114–121
- Heessen HJL (1981) Egg mortality in *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae). *Oecologia* 50:233–235
- Hengeveld R (1980) Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). *Neth J Zool* 30:564–584
- Lenski R (1984) Food limitation and competition: a field experiment with two carabid species. *J Anim Ecol* 53:203–216
- Mols PJM (1988) Simulation of hunger, feeding and egg production in the carabid beetle *Pterostichus coeruleus* L. (= *Poecilus versicolor* Sturm). *Agric Univ Wageningen Pap* 88:1–99
- Mols PJM, Van Dijk ThS, Jongema Y (1981) Two laboratory techniques to separate eggs of carabids from a substrate. *Pedobiol* 21:500–501
- Murdoch WW (1967) Life history patterns of some British Carabidae (Coleoptera) and their ecological significance. *Oikos* 18:25–32
- Nelemans MNE (1987a) Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.). The importance of food during larval growth. *Oecologia* 72:502–509
- Nelemans MNE (1987b) On the life-history of the carabid beetle *Nebria brevicollis* (F.). Egg production and larval growth under experimental conditions. *Neth J Zool* 37:26–42
- Nelemans MNE (1988) Surface activity and growth of larvae of *Nebria brevicollis* (F.) (Coleoptera, Carabidae). *Neth J Zool* 38:74–95
- Reddingius J, Den Boer PJ (1970) Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5:240–284
- Sota T (1985) Limitation of reproduction by feeding condition in a carabid beetle *Carabus yaconimus*. *Res Popul Ecol* 27:171–184
- Van Dijk ThS (1972) The significance of the diversity in age composition of *Calathus melanocephalus* L. (Col., Carabidae) in space and time at Schiermonnikoog. *Oecologia* 10:111–136
- Van Dijk ThS (1979a) On the relationship between reproduction, age and survival in two carabid beetles: *Calathus melanocephalus* L. and *Pterostichus coeruleus* L. *Oecologia* 40:63–80
- Van Dijk ThS (1979b) Reproduction of young and old females in two carabid beetles and the relationship between the number of eggs in the ovaries and the number of eggs laid. In: Den Boer PJ, Thiele HU, Weber F (eds) On the evolution of behaviour in carabid beetles. *Misc Pap Landbouwhogeschool Wageningen* 18:167–183
- Van Dijk ThS (1983) The influence of food and temperature on the amount of reproduction in carabid beetles. How to translate the results of laboratory experiments into the reality of the field? In: Brandmayr P, Den Boer PJ, Weber F (eds) The synthesis of field study and laboratory experiment. PUDOC, Wageningen, pp 105–123
- Van Dijk ThS (1986a) How to estimate the level of food availability in field populations of carabid beetles? In: Den Boer PJ, Luff ML, Mossakowski D, Weber F (eds) Carabid beetles, their adaptations and dynamics. Gustav Fischer, Stuttgart New York, pp 371–384
- Van Dijk ThS (1986b) On the relationship between availability of food and fecundity in carabid beetles: How far is the number of eggs in the ovaries a measure of the quantities of food in the field? In: Den Boer PJ, Grüm L, Szyszko J (eds) Feeding behaviour and accessibility of food for carabid beetles. Warsaw Agr Univ Press, Warsaw, pp 105–121
- Vlijm L, Hartsuijker L, Richter CJJ (1961) Ecological studies on carabid beetles. I. *Calathus melanocephalus* (Linn.) *Arch Néerl Zool* XIV: 410–422