

Recruitment and summer diapause in the dynamics of a population of *Nebria brevicollis* (Coleoptera: Carabidae)

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We studied the population dynamics of the carabid *Nebria brevicollis* (F.) by conducting a capture-recapture experiment between 1968 and 1978. We used 30 pitfalls, emptied (almost) daily and marked individually 11521 beetles. A part of the experimental area was fenced in 1976 and 1977 (about 360 m²). We used key-factor analysis to analyze the life cycle of this beetle. Density fluctuated heavily in the population investigated. The species is almost completely semelparous; on average only 1.3% of the old beetles reproduced again in following years. The most important factors influencing variation in population size are the number of eggs laid and the survival of the preadult stages. It is not yet possible to decide which of these varies most in the field. There is an indication that a negative correlation exists between recruitment and number of parent females, but this could also be related to differential survival of larvae. Larval mortality is highly affected by the amount and quality of food as well as by predation and parasitism. Previous research suggests that in our area conditions during larval development are suboptimal. Larval mortality appears to vary within a much wider range than egg production. Therefore, we consider variation in survival of the preadult stages as more influential.

Young beetles need to increase their hatching weight by 50–60% before entering summer diapause. Although on average one third of these beetles died before or during summer diapause, this could not be considered to be a key-factor. Young adults were more mobile than reproducing beetles, often leaving the hatching site. The pattern of catchability of marked beetles deviated from the expected Poisson distribution. Too many beetles were either caught only once or four or more times. This might explain why estimations of population sizes according to Jolly were lower than the number of beetles actually marked. Calculations based on models of Craig yielded a better fit. His second model rightly predicted population size when the area was fenced off. In our area *N. brevicollis* is widespread and often abundantly present. In our opinion the success of *N. brevicollis* is presumably based on high mobility of (young) adults, which favours reaching new suitable sites, together with plasticity in developmental mode of the larvae, which enables them to make the best of an ever changing food situation, and which influences both the quality and quantity of adults.

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Introduction

Population dynamics aims to study the causes and consequences of fluctuation of population sizes and of variation in mean abundance between areas. To get reliable data it is necessary to collect quantitative information on all stages of the life-cycle. The key-factor method

(initiated by Morris, 1959, and extended by Varley and Gradwell, 1960) has been found useful for a first analysis (especially in insect populations, Southwood 1978). It usually is difficult to get quantitative data on the preadult stages in carabids, because they generally show only restricted mobility and thus are difficult to sample with the usual techniques (Thiele 1977). Therefore most

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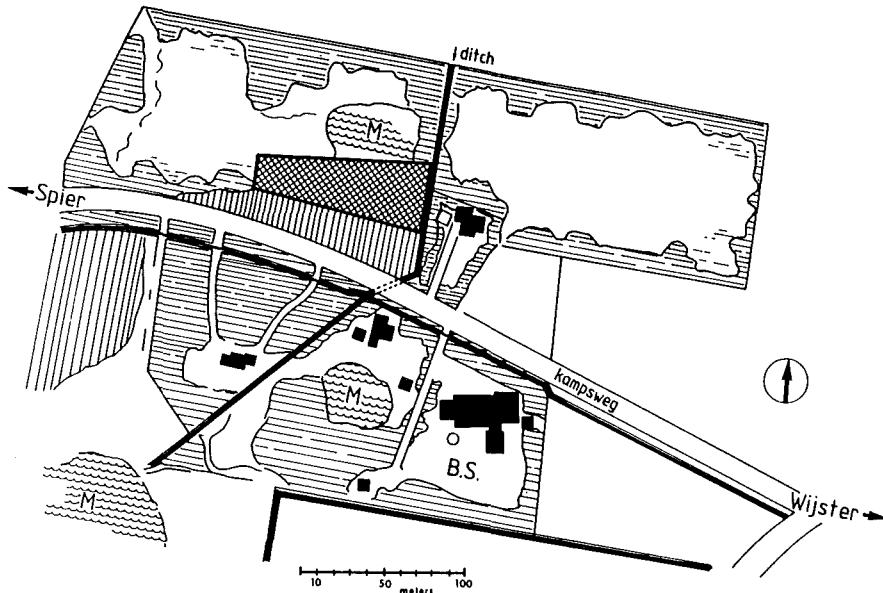


Fig. 1. Study area. Location: Wijster, Province of Drenthe, The Netherlands. Symbols: horizontally hatched: deciduous trees; vertically hatched: coniferous forest; white (except around the buildings): area with patches of *Erica spec.*, *Calluna spec.* and *Molinia* vegetation; M = shallow moorland pools; B.S. = buildings of the Biological Station. The mark-recapture experiment was done in the doubly hatched area (deciduous forest).

population dynamical research on carabids is restricted to adult stages: (sub)population fluctuations are related to 'factors', such as weather, dispersal, food, individual variability, adult survival, egg production, density, etc. There are a few exceptions: Heessen (1981), Heessen and Brunsting (1981) and Brunsting and Heessen (1984) demonstrated the influence of mortality of eggs and of larvae on the fluctuations of adult numbers with field experiments. Grüm (1975) found that in the period of egg incubation, prepupation and pupation, mortality seems to be close to zero. Nelemans (1988) indicated that vicissitudes experienced during larval stages may significantly affect the quantity and quality of adults.

The carabid beetle *Nebria brevicollis* (F.) appears to be more suitable for population dynamical research than many other carabid species, because its larvae are surface active and can thus be sampled by pitfalls (Nelemans 1986). The species is an atypical autumn breeder (Larsson 1939) because the young adults pass through a summer diapause before they start reproducing (Thiele 1969, Penney 1969). Although publications on its life history, emphasizing the adult stages (Greenslade 1964, Penney 1966, 1969, Jørum 1976) are available, only a few refer to the larvae (Manga 1972, Critchley 1973, Nelemans 1988). In addition, data from research on the population dynamics of *N. brevicollis* are available at the Biological Station Wijster (Drenthe, The Netherlands). In this investigation we recorded fluctuations of a local population both in an open experimental area and in a fenced off part of the same area. The experiments cover the years 1968 until 1979 (see also Den Boer 1979). Therefore, although these data also mainly concern adults, in the present paper we attempt to give a more detailed outline of the population dynamics of

this beetle. First of all we will try to determine the key-factor(s) in the life history of *N. brevicollis*. We consider also mortality of young adults during summer diapause in addition to the factors normally studied in carabids such as egg numbers, egg mortality, mortality of larvae and pupae (taken together), survival to following years, male/female ratio and yearly catches of adults. Data are available both from the field and from laboratory experiments.

This paper is part of a comprehensive study of the population ecology of *N. brevicollis* (Nelemans 1983, 1986, 1987a, b, c, 1988).

Material and methods

The species

Nebria brevicollis is a common West-Palaearctic carabid species that is most abundant at edges of deciduous woodland (Lindroth 1945), but can also be found in more open, but still somewhat shaded areas. The reproduction period covers the end of August till December and larvae are present from October till May. Since the species is virtually semelparous (Thiele 1969) hibernation occurs almost exclusively in larval stages. In the second part of May young beetles hatch almost synchronously. They are very active during a short period and then disappear into summer diapause. Activity starts again in the second part of August.

Yearly catches

From 1968 through 1978 *N. brevicollis* was sampled continuously in a small deciduous forest close to the

Tab. 1. Mark-recapture experiment. In the right part estimates of the size of the reproducing population are presented. In 1976 and 1977 the area was fenced in.

* for explanation, see Material and Methods.

Year	total number	total number	estimated*	estimations of population size		
	of marked ind.	of catches		Craig I	Craig II	Jolly
1968	517	945	268	545	696	193
1969	658	1216	341	672	878	220
1970	460	1052	238	398	534	167
1971	1513	3592	784	1296	1729	585
1972	765	1588	396	737	936	431
1973	1165	2377	604	1130	1444	436
1974	1208	2382	626	1213	1532	541
1975	3168	6792	1641	2932	3808	1264
1976	461	3090	1281	353	467	232
1977	362	1719	1006	263	374	148
1978	1244	2732	645	1394	1610	592

Biological Station at Wijster. This area (mostly oaks, about 1700 m²) is on the four sides bordered by a small area of pine forest, by a shallow moorland-pool, by a ditch and by some heathland (Fig. 1). Thirty pitfalls were placed at about equal distances of 3 m in 4 rows 4 m apart. The pitfalls, circular time-sorting pitfalls with an effective circumference of 48.7 cm and a depth of about 30 cm, were emptied either daily or every second (or third) day all year round. Each trap was equipped with a perspex roof to keep out litter and rain (see Den Boer 1979). In these capture-recapture experiments beetles were sexed, individually brand-marked (Schjøtz-Christensen 1965) and released along a line of about 20 m in the centre of the study area. During 1976 and 1977 the central part of the study area was fenced in, and extra pitfalls were placed just inside the perimeter of the fence. Estimations of population sizes were made according to Jolly and to Craig (Southwood 1978). Craig offers two mathematical estimation-equations based on the Poisson distribution; both are computed here. Both spring and autumn catches were used. To mitigate disturbance resulting from capturing, handling and marking the beetles, in the calculations with the model of Jolly-Seber (Seber 1973) recaptures within the same week were rejected. Population density was estimated for the reproduction period only.

We estimated also numbers of beetles per 1000 m² to be able to include 1976 and 1977 in the fluctuation pattern over the years, and to be able to compare, if necessary, key-factor analysis for all years. First, the sum of beetles caught in the years 1976 + 1977 is divided by the sum of beetles in the adjacent years 1975 and 1978. This gives an estimate of the fraction of the population that was enclosed in 1976 and 1977, which was 0.186. The enclosed area was about 360 m², thus the area from which the beetles were caught and marked, when not fenced was about 1930 m². From this the numbers per 1000 m² could be calculated for all years.

Fig. 1 shows that, besides the 1700 m² oakland, the surroundings (pineforest, heathland and some wet areas) were of restricted significance to *N. brevicollis*. Available data from the adjacent pine forest indicate a much lower frequency of catches in this habitat. Therefore an effective area of 1930 m² in use by this local population seems reliable.

Frequency and distribution of recaptures; mobility of adults

All years of the mark-recapture experiment are evaluated and supplemented by laboratory data. The frequencies of recaptures in both the spring period (young beetles) and the autumn period (reproduction) were recorded separately. The catches were classed according to the number of times an individual was recaptured (0x, 1x, 2x..., when possible up to 5 and more times). The enclosed populations (in 1976 and 1977) gave information on the rate and intensity of catching of young beetles in spring.

The tendency of young and reproducing beetles to leave the area was assessed by comparing data from an open area with those from an enclosed area, as well as by a laboratory experiment with newly hatched individuals, in which the relationship between weight increase and start of summer diapause was investigated. The latter data enabled us to distinguish between beetles leaving the study area and entering summer diapause. During 36 days two groups of 23 young beetles each were kept separately at 15°C, with blowfly maggots in abundance, added twice or three times a week. The beetles were weighed each time before their next meal. One group consisted of laboratory bred beetles with a mean starting weight of 46.6 mg (full description in Nelemans 1987b); the other group contained beetles captured as young as possible in a woodland area near the Biological Station (mean starting weight 45.7 mg).

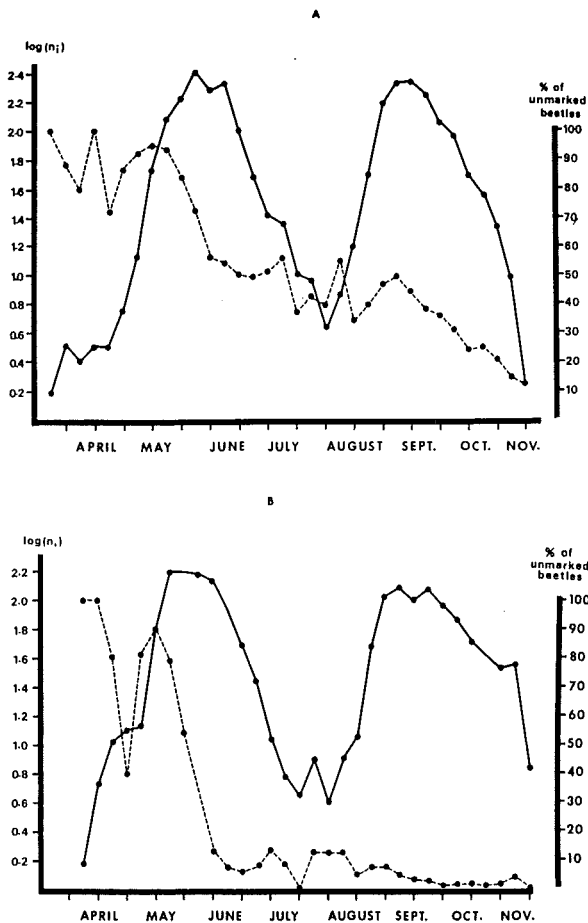


Fig. 2. Mean weekly catches of a population of *Nebria brevicollis*. ●—● = % unmarked beetles in the catches
A: Open experiment. Years 1968 till 1975, and 1978
B: Enclosed experiment. Years 1976 and 1977.

Start of summer diapause was related to a consistent refusal of beetles to eat.

Mortality of young adults

Data from the mark-recapture experiment were applied as follows: Each year the number of beetles, marked in spring and recaptured in autumn was multiplied by the inverse of the recapture chance of newly marked beetles during that autumn (recapture chance was calculated as follows: the number of beetles recaptured was divided by the sum of beetles captured during the whole (chosen) period). The result is an estimate of the number of spring beetles still alive in the study area in autumn, and can thus be compared with the total number of young adults caught in spring.

Survival to (the) following year(s)

Data of yearly catches were used as follows: The number of marked beetles in year t recaptured in the next year ($t+1$) was multiplied by the inverse of the recapture chance of beetles in year $t+1$. The resulting figure is an estimate of the survival to year $t+1$. The same calculation was used for beetles surviving to year $t+2$ (see also Den Boer 1979: Tab. 1).

Egg numbers

In 1982, 38 ♂♂ + 38 ♀♀ were kept in an outside insectary and were fed with maggots in abundance. During summer diapause they were sampled by hand near the Biological Station. The eggs of each pair were collected once a week and the experiment was continued until all females stopped ovipositing and the ovaries regressed ("spent") (fully described in Nelemans 1987b). Also, in 1977, 1980, 1981 and 1982 weekly or fortnightly from May till December female beetles were sampled in the same area. They were dissected and the numbers of full-grown eggs were counted.

Egg mortality

Egg mortality was estimated for beetles collected outside near the Biological Station, and kept in the laboratory for experiments on egg production (Nelemans 1987b). Each week 100 or 200 eggs from randomly chosen females (each accompanied by a male) were collected and kept individually in an incubator (12°C). The eggs were observed for ten weeks and checked for hatching.

Mortality of larvae and pupae

Mortality rates of the immature stages were investigated in laboratory experiments with various temperatures and different quantities and qualities of food (Nelemans 1987b). The beetles were fed and checked once a week in all experiments. One group of 150 first instar larvae was kept in an outside insectary with blowfly maggots in excess. Two other groups of 150 first stage larvae each were bred in incubators with a different temperature regime (Larva I and II at 12°C; larva III at 5°C during 5 wk and thereafter at 12°C; pupa at 12°C). Food (blowfly maggots of different sizes according to the size of the larva) was provided in different quantities: in one group each larva got about 4 maggots per week, in another group 1–2 maggots per week. In addition, 265 larvae were fed weekly with about 10–12 larvae of *Drosophila melanogaster*, and 75 larvae with about 40 individuals of the collembolan *Orchesella cincta* weekly, each (conditions in the incubators were the same as mentioned above). Finally, 150 third instar larvae were collected near the Biological Station from February till April 1982. They were reared in the laboratory, with maggots

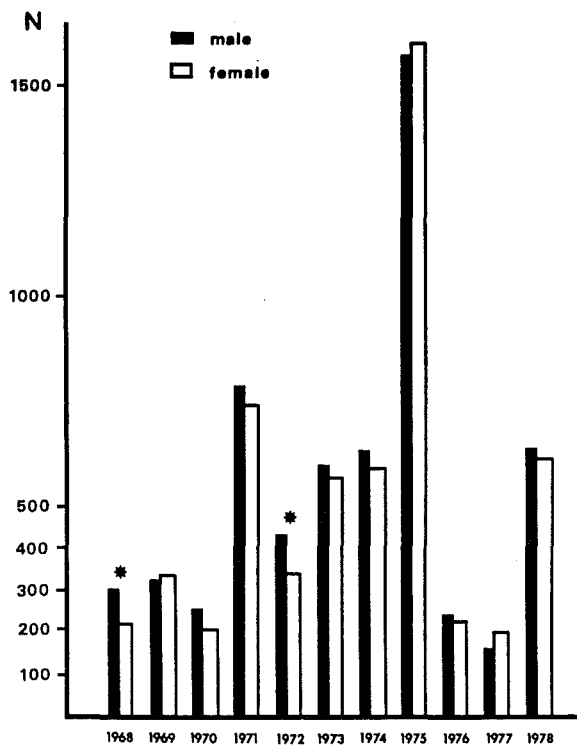


Fig. 3. Number of males and females in the mark-recapture experiment.
* = significant at $P = 0.01$.

in excess and under the same temperatures as mentioned above.

Life tables and key-factor analysis

The calculations were made according to Varley and Gradwell (1960) and Southwood (1978). The numbers of individuals are based on the results of field and laboratory experiments. Only the data of the years with the open experimental area are used. The results of the enclosed area are available for comparison.

Life tables are presented on adult to adult basis. The total generation mortality (K) is found by subtracting the logarithm (to the base 10) of the number of adults entering the reproductive stage from the log (maximum potential natality) of the previous generation (i.e. number of reproducing females \times maximum natality). The series of age-specific mortalities is calculated by subtracting each \log_{10} (population estimate) from that of the previous age interval (k_1, k_2, k_3 , etc.). In this way we could test which stage contributes most to the pattern of density fluctuations. A high k -value means a strong decrease of numbers during that stage. However, we also have to consider the standard deviation, because a high k -value with a low standard deviation will only have a slight influence on variation of population size.

Tab. 2. Distribution of spring and autumn catches; between brackets the estimates according to the Poisson distribution. All values differ significantly from the Poisson values (χ^2 -test).

No. of re-capt. for each individual	Spring catches											
	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	
0	200(191)	243(225)	117(92)	466(399)	302(262)	499(439)	476(411)	1317(1050)	107 (48)	122 (67)	477(440)	
1	59 (73)	100(124)	57(83)	212(292)	117(160)	183(261)	167(247)	562(853)	73(106)	67(107)	169(223)	
2	16 (14)	29 (34)	28(38)	98(107)	31 (49)	69 (78)	60 (74)	264 (346)	79(116)	57 (86)	63 (56)	
3	4 (2)	16 (6)	14(11)	29 (26)	20 (10)	30 (15)	29 (15)	113 (94)	52 (85)	28 (46)	12 (10)	
4	1 (0)	2 (1)	4 (3)	13 (5)	8 (2)	12 (2)	13 (2)	54 (19)	45 (46)	20 (18)	6 (1)	
5 or more	0 (0)	0 (0)	7 (0)	12 (1)	5 (0)	3 (1)	5 (1)	55 (3)	76 (31)	37 (7)	3 (0)	
N	280	390	227	830	483	796	750	2365	432	331	730	
recapture-chance	0.29	0.38	0.48	0.44	0.37	0.37	0.37	0.44	0.75	0.63	0.35	
	Autumn catches											
0	175(136)	202(161)	147(109)	425(288)	257(207)	305(249)	398(324)	756(621)	53 (13)	57 (17)	379(283)	
1	70(110)	80(121)	72(110)	227(342)	104(161)	153(214)	156(238)	342(490)	33 (39)	20 (41)	212(291)	
2	28 (44)	30 (45)	43 (56)	126(203)	51 (62)	76 (92)	64 (88)	145(193)	26 (60)	26 (50)	93(149)	
3	14 (12)	11 (11)	14 (19)	76 (80)	18 (16)	33 (26)	30 (22)	70 (51)	17 (61)	20 (40)	42 (51)	
4	11 (2)	8 (2)	16 (5)	35 (24)	11 (3)	8 (6)	16 (4)	34 (10)	24 (47)	11 (25)	33 (13)	
5 or more	7 (1)	10 (1)	8 (1)	55 (7)	9 (1)	14 (2)	12 (1)	20 (2)	121 (54)	58 (19)	31 (3)	
N	305	341	300	944	450	589	676	1367	274	192	790	
recapture-chance	0.43	0.41	0.51	0.55	0.43	0.48	0.41	0.45	0.81	0.70	0.52	

Results

Year-catches

Catches of adults were averaged over the years 1968 till 1975 and 1978 when the area was open (Fig. 2A) and for the enclosed area of the years 1976 and 1977 (Fig. 2B). Initially there was low activity of a few individuals. As can be seen from dissected females these are old beetles that hibernated as adults. The first activity peak was caused by young beetles hatching in May and June. Then activity declined until the beetles had disappeared almost completely and entered the summer diapause. The second activity peak resulted from reproducing beetles. Total catches (including recaptures) in both periods were of about the same size (Fig. 2A: 10071 and 9439 catches respectively) but the spring peak is made up of more individuals (6852 as compared to 5762 in autumn).

In the second part of the reproduction period most beetles were marked (Fig. 2A); apparently even in the open experiment the total area from which beetles were caught is rather restricted.

In all but two years the male/female ratio (number of individuals) is about unity (Fig. 3): χ^2 -tests are not significant, except in 1968 ($\chi^2 = 13.38$; $N = 515$) and 1972 ($\chi^2 = 10.88$; $N = 761$). In both years the percentage of males was higher than that of females.

Population sizes during reproduction were estimated according to Jolly and to Craig I and II (Tab. 1). Although Craig's models both consider the population enclosed (which was only the case in the years 1976 and 1977) and all capture-recapture models assume a Poisson distribution of catches (which is not the case, see below) Craig's estimates are much better than those of Jolly. In the open situation Craig I appears to give about the size of the marked population; in the years with fenced populations Craig II seems to be the best fitting (because then almost all individuals were marked and the model rightly predicted population sizes). Note that estimations of the spring population only revealed smaller differences between Craig I and II (e.g. 1976: 470 (I) and 478 (II); 1977: 352 and 392). Moreover, they indicate that estimations based on spring catches alone apparently give maximum values of the size of the population. On the other hand estimations based on autumn catches alone, are about 35–45% lower than in Tab. 1 (e.g. 1976: 233 (I) and 277 (II); 1977: 167 and 202).

Frequency and distribution of recaptures; mobility of the adults

In all cases the distribution of recaptures deviates significantly from those predicted by a Poisson distribution (Tab. 2). Both the frequencies of beetles not recaptured and those of beetles recaptured 3 or more times are too high; the latter especially in the open populations.

In most years the frequency distributions of spring and autumn catches also differ significantly (χ^2 -tests). In autumn individuals are recaptured more often than in spring. There are also significant between-year differences in recapture chances both with regard to spring and autumn catches.

The frequency of recaptures in the enclosed population demonstrates the high mobility of young adults (including also a high trapping chance caused by the presence of a fence, which intensified encounters with the traps). Over 90% of the beetles marked by the end of the year were already captured in spring (cf. Fig. 2). Within the enclosed area it took about one month to capture the majority of the locally hatched beetles (Fig. 2B). After that month in the open area the unmarked specimens in the weekly catches (about 40%) will mainly indicate that these arrived from the outside (dispersal); this figure could be biased by the difference in trapping chance between an enclosed population and an open one.

In the enclosed population on average 30% of the marked beetles were not recaptured in spring, but in the open population this averaged at 60%. In autumn these numbers were 24% and 53%, respectively. Clearly (cf. Tab. 1), the traps caught beetles from a wider area than the fenced part (see previous section). Distances covered by the beetles in the reproduction period are still high, as is shown by an average of about 30% of unmarked beetles in the autumn catches in the open population. This mobility is presumably related to reproduction activities, whereas spring mobility is highly associated with the gathering of food, as was shown by Penney (1969).

Our laboratory experiment demonstrated a rapid weight increase after hatching for about two weeks; thereafter the beetles almost stopped feeding. They had added about 50–60% of the starting weight after fifteen days, and apparently this is a signal to stop feeding activities and to enter diapause. Beetles that were fed parsimoniously during six weeks continued eating during the whole period (experiments described in Nelemans 1983). Therefore, in the enclosed area the frequency of beetles that were captured in spring only once, gives information on the availability of food in that area. A low food level will result in a longer activity period, and possibly many recaptures. In spring 1976, 107 beetles out of 432 were captured only once, in 1977 a higher proportion (122 beetles out of 331). In 1976 young beetles were recaptured more often than in 1977 ($\chi^2 = 13.04$; $df = 1$, $N = 763$). Evidently, in 1976 they needed a longer period to gather enough food. In the open experiments the failure to catch many individuals twice or more in spring has to be attributed to changes in beetle behaviour that result in a lower trapping chance. Either walking activities lead into leaving the area around the pitfalls, or entering diapause ceases activity. To distinguish between these two possibilities we will have to weigh beetles repeatedly in the field

Tab. 3. Estimates of loss (mortality and disappearance) of young adults during summer diapause.

Year	marked in spring	recapt. in autumn	new in autumn	recapt. chance*	estimate of spring pop. still alive in autumn	% mortality (disappearance) of spring population	k ₃ (young adults)
1968	280	68	237	0.44	155	44.6	0.2568
1969	390	73	268	0.39	187	52.1	0.3192
1970	227	67	233	0.48	140	38.3	0.2099
1971	830	260	684	0.55	473	43.0	0.2442
1972	483	168	282	0.42	400	17.2	0.0819
1973	796	220	369	0.48	458	42.5	0.2400
1974	750	218	458	0.40	545	27.3	0.1387
1975	2364	566	802	0.45	1258	46.8	0.2740
1976	432	246	28	0.89	276	36.1	0.1946
1977	331	161	31	0.65	248	25.1	0.1254
1978	730	276	514	0.54	511	30.0	0.1549

* = recapture chance of beetles, newly marked in autumn.

during spring, after having estimated hatching weight and size of the elytra (see Nelemans 1988).

Loss of young adults

Estimates of the loss (mortality and dispersal) of young adults during summer diapause are shown in Tab. 3. The most reliable figures are from the years 1976 and 1977 and they point to a mean loss of about 30%. In the open area rough estimates give a mean (mortality + dispersal) in the order of 40%. Compared with the figures of the enclosed population this might imply that on the average about 10% of the beetles that disappeared after spring will have dispersed too far from the pitfalls to be recaptured again in autumn.

Craig's estimates of the size of spring and autumn populations separately (see previous section), indicated a decline of about 35–45% in the autumn populations. As expected, these figures are in the same range as the estimates in Tab. 3.

Survival to following years

A low fraction of the beetles survive hibernation and sometimes even a second winter (Tab. 4). Estimates of survival to the next year vary from 0.8 till 11.7%; survival to the second year varies from 0 till 3.2% (see Den Boer 1979). Laboratory experiments show that old beetles are able to reproduce again, but they only form a very small part of the reproducing population (last column of Tab. 4).

Egg numbers

In the laboratory experiment the mean number of eggs per female in the entire reproduction season was 334.1, with a range of 54–513. The eggs were laid during a period of 16.6 wk on average (range 12–21 wk), with a weekly average of 14.8 eggs per female. Egg mortality is low during the first six weeks (see below). For these six weeks the mean number laid is 176.4 eggs per female, range 24–312.

Tab. 4. Survival of individual *N. brevicollis* to following years; percentage of old beetles during reproductive period.

Year	N year t	recapt. in year t+1	recapt.* chance in year t+1	estimated % survival to year t+1	recapt. in year t+2	recapt. chance in year t+2	estimated % survival to year t+2	% of old beetles in reprod. period
1967	213	6	0.45	6.3	3	0.44	3.2	
1968	517	11	0.44	4.8	2	0.55	0.7	0.8
1969	658	12	0.55	3.3	0	0.57	0	0.6
1970	460	10	0.57	3.8	0	0.52	0	1.1
1971	1513	75	0.52	9.5	3	0.51	0.4	0.3
1972	765	20	0.51	5.1	0	0.50	0	6.5
1973	1165	8	0.50	1.4	5	0.53	0.8	0.8
1974	1208	75	0.53	11.7	3	0.82	0.3	0.5
1975	3168	21	0.82	0.8	0	0.67	0	1.2
1976	461	50	0.67	16.2	1	0.51	0.4	1.5
1977	362	8	0.51	4.3	?	?	?	5.2
1978	1244	?	?	?	?	?	?	0.5

* = recapture chance of beetles newly trapped and marked in year t+1.

Tab. 5. Mean number of eggs in the ovaries of dissected beetles. The females were sampled in a woodland near the Biological Station in Wijster (The Netherlands). Females with undeveloped gonads or with spent ovaries were discarded.

Year	1977	1980	1981	1982
No. females	39	133	56	52
mean no. of eggs	7.2	14.4	16.6	12.9
St. dev.	7.44	8.14	9.85	8.73
range	1-31	1-37	1-37	1-32

Mann-Whitney tests: 1980-81, $Z = 1.18$, 1981-82, $Z = 1.91^*$, 1977-82, $Z = 3.43^*$

* = significant at $P = 0.05$ (one-sided).

In Tab. 5 the mean numbers of full-grown eggs in the ovaries and oviducts of field-collected females are given. The Mann-Whitney test shows variation between the years.

Egg mortality

In the laboratory egg mortality (i.e. non viable eggs) stays at about the same level during the first six weeks of egg laying and amounts to 10-15%. Thereafter the viability sharply declines, and even in the laboratory after 10 wk less than 50% of the eggs hatch; 17 wk after the start of egg laying no viable eggs are produced (Nelemans 1987b: Fig. 3).

Mortality of larvae and pupae

Nelemans (1987 b) described mortality of larvae (per instar) and of pupae in breeding experiments. In the following only mortality figures for the whole developmental period, pupae included, will be given (Tab. 6). In the outside insectary this mortality was 26.7%. The experiments in the incubators reveal the importance of food - both its quality and quantity. In the experiment with third instar larvae collected weekly in the field mortality was rather high (48%). The causes of mortality among these larvae differed from those in the laboratory: parasitism and infection by fungi were recognized. Larvae often changed their colour from yellow-brownish into pink-brownish and hardened before dying (cause unknown). This phenomenon has never been recorded during breeding experiments. Critchley (1973) investigated causes of mortality of carabid larvae, including *N. brevicollis*, in two areas. These data are included in Tab. 6. He collected third instar larvae and kept them in the laboratory. In these larvae the degree of parasitism from *Phaenoserphus viator* and *P. pallipes* (Latreille) (Hymenoptera) varied from year to year and between areas but resulted in up to 25% mortality. Critchley mentioned other identifiable causes of death, namely those due to injury and to nematode

parasites. Total mortality varied between the two areas from 55.5% to 68.7%.

Key-factor analysis

The mark-recapture experiment enables us to estimate the yearly values of (1) number of recruits per female and (2) mortality of young adults during summer diapause (Tab. 7 and Tab. 1, column 3). Calculations are based on the years 1968 up to 1975. Data of the years 1976 and 1977 (when the experimental area was fenced in) are also given but have to be considered apart from the remaining years. As the variance of \log_{10} (recruitment/female), 0.0595, is much greater than the variance of k_3 (\log_{10} of adult mortality during summer diapause), which is only 0.0058, recruitment/female must be considered the main key-factor. This conclusion does not change if we compare the coefficients of variation: c.v. (k_3) = 0.346, c.v. (\log_{10} recr./female) = 0.402. k_3 is neither dependent on the number of young adults preceding k_3 (r_s (Spearman) = 0.095, $p = 0.397$, one sided, n.s.), nor correlated with the number of reproducing adults after k_3 ($r_s = 0.024$, $p = 0.467$, one sided, n.s.). When 1976 and 1977 are included in the calculations, we come to the same conclusions (var. \log_{10} recr./female = 0.0631; var. $k_3 = 0.0052$; c.v. $k_3 = 0.353$; c.v. \log_{10} recr./female = 0.459).

There is some indication of a negative correlation between recruitment and the number of reproductive females ($r_s = -0.405$; $p = 0.163$, one-sided; n.s.). If we include all years we find a just significant correlation ($r_s = -0.548$; $p = 0.048$, one sided). We return to this in the discussion.

Discussion

Continuous pitfall catches summed over at least the whole reproductive period of that year (i.e. year-

Tab. 6. Percentage mortality during the preadult development of *Nebria brevicollis* in different experiments.

Breeding condition	experiment started with	Food ¹⁾	Mortality
reared outside	eggs	++	26.7
reared inside	eggs	+	62.9
reared inside	eggs	+/-	97.3
reared inside	eggs	Dros. ²⁾	63.8
reared inside	eggs	Orches. ³⁾	100
Field sampled	larvae III	++	48.0
Critchley, area 1	larvae III	++	68.7
Critchley, area 2	larvae III	++	55.5

++ = food in excess

+ = food sufficient for development but suboptimal

+/- = minimal food

1. Food: blowfly maggots, unless mentioned otherwise

2. Larvae of *Drosophila melanogaster*

3. *Orchesella cincta*

Explanation, see text.

Tab. 7. Key-factor analysis with recruitment per female and mortality of young adults in the mark-recapture experiment. Calculations are based on the years 1968 through 1975. Variance of $k_3 = 0.00584$ (all years: 0.00518). Variance of \log_{10} (recruitment) = 0.0595 (all years: 0.0631). Mean of $k_3 = 0.2206$ (all years: 0.2036). Mean of \log_{10} (recruitment/ \bar{Q}) = 0.6066 (all years: 0.5477).

	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
\log_{10} pop. size per 1000 m ² (number) young	2.4281 (268)	2.5328 (341)	2.3766 (238)	2.8943 (784)	2.5977 (396)	2.7810 (604)	2.7966 (626)	3.2151 (1641)	3.1076 (1281)	3.0026 (1006)	2.8096 (645)
k_3 : mortality of young adults	0.2568	0.3192	0.2099	0.2442	0.0819	0.2400	0.1387	0.2740	0.1946	0.1254	0.1549
\log_{10} pop. size repr. adults (number) repr. ♀♀	2.1733 (74)	2.2136 (82)	2.1667 (73)	2.6501 (223)	2.5158 (164)	2.5410 (174)	2.6579 (227)	2.9411 (437)	2.9129 (409)	2.8772 (377)	2.6547 (226)
\log_{10} repr. ♀♀	1.8703	1.9125	1.8656	2.3491	2.2148	2.2400	2.3568	2.6401	2.6119	2.5762	2.3536
recruitment/ \bar{Q}	(4.60)	(2.91)	(10.68)	(1.77)	(3.68)	(3.60)	(7.22)	(2.93)	(2.46)	(1.71)	
\log_{10} recr.	0.6625	0.4641	1.0287	0.2486	0.5663	0.5566	0.8583	0.4675	0.3907	0.2334	
\log_{10} young adults in next year (number) young	2.5328 (341)	2.3766 (238)	2.8943 (784)	2.5977 (396)	2.7810 (604)	2.7966 (626)	3.2151 (1641)	3.1076 (1281)	3.0026 (1006)	2.8096 (645)	

catches) give a reliable relative measure of the density of local carabid populations (Baars 1979, Den Boer 1979). Therefore, the capture-recapture experiment, as described here, could be used to estimate the size of the local population of *N. brevicollis* (see also Den Boer 1979).

The mark-recapture experiment reveals high between-year fluctuations of numbers in this population of *N. brevicollis*. The most important factors affecting fluctuations of population sizes seem to be the number of eggs laid and survival of the preadult stages. We will return to this later.

At first, we will briefly discuss the model used for estimating population size. Then, we will consider the contribution of the adult stages to the fluctuations (old beetles; young beetles). Next, we will try to discriminate between the influence of the number of eggs laid and survival of the larvae (including pupae). Finally, we will outline the life strategy of this beetle.

1. All capture-recapture models for estimating population sizes start from the assumption of constant catchability. Both the recaptures of spring and autumn beetles in the mark-recapture experiment distinctly show that multiple catches are not normally distributed, and this is independent of the kind of experiment (enclosed or open area). There are too many individuals that are recaptured not at all, and also too many that are recaptured three or more times. Apparently the chance to be recaptured is not the same for each marked beetle, as reported before by Southwood (1978) and Den Boer (1979). Applying these models to carabid beetles therefore might lead to serious errors.

This paper revealed great differences between the results from the model of Jolly and those of Craig. The

estimates of Jolly systematically are much too low, even lower than the total numbers of marked beetles. The models of Craig (in the enclosed population especially his second model) give much better fitting results, although they too assume a constant probability of capture. However, in his models the chance to be caught need not be the same for all individuals, if only the deviations from the average capture chance show random distribution. Apparently, the model of Jolly is much more sensitive to deviations from the expected frequencies of captures. Not only in *N. brevicollis*, but also in other carabid species (Den Boer 1979) the estimates according to Jolly lead to underestimates; other authors, such as Cormack (1972), Carothers (1973) and Gilbert (1973) reported discrepancies in the same direction. Apart from this Craig also considered the population as closed (there are no births or deaths and the animals stay within their habitat). In accordance with that the estimates for 1976 and 1977 (enclosed population) narrowly fit the numbers of beetles actually marked and which will indeed have covered almost the entire population.

2. Since the percentage of old beetles (that have passed already one reproductive cycle) in the reproductive period is 1.3% on average (the species is virtually semelparous), this population lacks a possible stabilizing effect by changes in age composition over years. This is in contrast to most other carabid species, where sometimes even the majority of the beetles may be old (Baars and van Dijk 1984: Appendix), and where variation in the fraction of old beetles damps the fluctuations of numbers as a whole (van Dijk 1982).

3. Mortality of young adults before and during diapause can amount to at least 36%. Young adults are

highly mobile which often results in them leaving the local hatching sites, as is shown not only by the mark-recapture experiments but also by other observations. This mobility could result in (re)founding populations. Walking activities in spring will be connected with the gathering of food.

4. It is not yet possible to decide whether the variation in the size of the egg production or in survival of the preadult stages will be the most influential factor in the fluctuations of population numbers of *N. brevicollis*, because (among others) data on the amount of eggs laid in the field are still lacking. Dissection data revealed yearly differences in the number of mature eggs present in the ovaries. This could imply a yearly difference in batch actually laid (van Dijk 1979b, Baars and van Dijk 1984). Still, we are inclined to suppose that differences in larval survival are more influential, and next we defend this opinion.

We start with data from laboratory experiments only. We calculated supposed numbers of recruits per female after different levels of egg production and mortality of developmental stages. These calculations made clear that variation in egg production was not sufficient to account for the variation in recruitment observed in the mark-recapture experiment. Also, larval mortality, compared with egg production, appeared to vary within a much wider range (difference in effects: 20–25 times to 7 times).

Both egg production and survival of the preadult stages are influenced by food supply in the field (Mols 1979, 1988, Heessen 1981, van Dijk 1983, Ernsting and Huyer 1984, Nelemans 1987b, 1988). In general this food supply is not optimal, but in most years rather suboptimal (see e.g. White 1978, Pearson and Knisley 1985, Lenski 1984, van Dijk 1986, Nelemans 1987a). White even proposed that for many animals the single most important factor limiting their abundance is a relative shortage of nitrogenous food for the very young. In our area we found that larvae of *N. brevicollis* experience suboptimal field conditions. Although we do not have reliable figures on the actual level of food present in the field we could equate poor conditions with a relatively low attainability of adequate food. In the larval stages food can therefore be considered a major factor (Nelemans 1987a, b, 1988). Since both the food level in the field and the attainability of food for poikilothermic animals will be highly influenced by abiotic conditions, weather may be more important than is often supposed.

Since in some other carabids a correlation between number of recruits and egg production of the previous year has been recorded (e.g. Baars and van Dijk 1984), we looked for this in *N. brevicollis*. The results of years with the open experiments did not indicate such a phenomenon. However, when including the results of both the open and enclosed experiments, we found a negative correlation between the size of recruitment and the number of females. This could point to two phenomena:

(1) a highly negative correlation between density of reproducing beetles and egg production at high densities will result in a lower number of eggs and (assuming a 'constant' survival of the larvae) in a smaller recruitment (compare Baars and van Dijk 1984). (2) egg production is less or not at all density-dependent, but larval mortality is higher at high than at low densities. Mortality causes are among others predation (within the species and between species), and parasitism. The latter indeed is variable between years and places and can amount to 25% (Critchley 1973). Predation could be density-related, too, because of the high mobility of the larvae. Also intraspecific competition for food cannot be excluded at high densities, although there are no observations to support this.

There are almost no data on larval mortality of carabids in field populations. Nelemans (1974, internal report) estimated population sizes of both third instar larvae and of the following spring population of young adults in the same area. According to the population estimate derived from Craig II the larval population amounted to 545, the adult population to 208. This would imply a larval (and pupal) mortality of 61.8%, which agrees quite well with Critchley's data (cf. Tab. 6).

Anyway, the variation in density of adult beetles over all years (the 11-year data set) does not confirm an overall density dependence of population numbers when calculated according to the Pollard et al. (1987) randomization test ($p = 0.359$, for details see Den Boer and Reddingius 1989).

In two other carabid species Baars and van Dijk (1984) recorded a significant positive correlation between the number of recruits and egg production of the previous year. They suggested that recruitment is almost completely determined by the amount of eggs, and survival of larvae and pupae were therefore held constant in their model. However, Den Boer (1986) showed that in the same data the variance of egg production over years was much smaller than that of recruitment from eggs, which contrasts with that conclusion.

In these discussions it is assumed that egg viability will be about constant between years. Mortality of eggs laid in the field was investigated by Heessen (1981) on eggs of the carabid *Pterostichus oblongopunctatus* (F.). He found a mean egg mortality of 70% when eggs were deposited in an undisturbed soil sample, most probably accounted for by predation. Van Dijk (pers. comm.) found a similar high mortality of eggs laid in the field by *P. versicolor*, mainly because of predation by nematodes.

Since food can be considered a vital resource in larval stages, and both the availability and the attainability of adequate food will significantly vary between years we believe it unlikely that larval survival will be constant. Of course, we do not exclude a possible influence of the size of egg production on population size, but since we,

just as Den Boer (1986), also found that larval mortality appears to vary within a much wider range than egg production, for the moment we consider variation in survival of the larvae (and pupae) a more influential factor.

5. Both Thiele (1969, 1977) and Penney (1969) investigated the ecological significance of summer diapause in *N. brevicollis*, and they supplement each other very well. Penney showed that the cessation of locomotory activity was connected with the amount of food taken up. Starved beetles remained active during summer months, independent of the photoperiod.

These results are in agreement with our experiments. To be able to survive summer diapause young beetles have to accumulate large fat reserves. We could demonstrate that in spring they will stay active until they have added 50 to 60% of their hatching weight. The length of this activity period will be an indication of the food level in that area, and we found differences between years. Penney suggested that summer diapause is obligatory for the species because food supply generally is low in British woodlands during summer. A large part of the diet of the adults is formed by microarthropods, such as springtails, woodlice, mites and small flies (Evans 1965, Penney 1969, Hengeveld 1980). During summer months (and winter months) in the Netherlands springtails are far less numerous than in other seasons (Ernsting 1978) and in our area there may be a more general scarcity of the usual food for the adults. In addition to Penney, Thiele could show that long-day conditions and high temperatures prevented maturation of the gonads. The main factor, which could terminate diapause, was a sufficiently long period of short-day conditions (about 2–3 months) together with a temperature below 20°C.

Thiele emphasized the importance to this species of preventing reproduction in spring (immediately after emergence of the beetles), when temperatures are too high for the development of the larvae. In his breeding experiments he demonstrated the low tolerance of especially first instar larvae for high temperature and suggested an obligatory temperature of 2–4°C from the first instar on. It must be noted however, that the food he administered (chopped meat) was not very suited to the needs of the larvae, which could have influenced the mortality rate.

In our experiments mortality caused by insufficient food was higher at high temperatures than at low ones. In contradiction to Thiele, we generally found a quite good tolerance of larvae of "high" temperatures (up to 12°C). This could also be expected, when looking at the field temperatures during larval development, although even in the warmest winter recorded in The Netherlands, mean temperature was only 5.5°C. Conditions must be sufficiently moist, however, because larvae are very sensitive to desiccation. In our area both the hypothesis of Thiele and that of Penney thus seem quite plausible.

6. Muggleton (1969) suggested that *Nebria* beetles

can have two hatching peaks: in spring and in autumn. Muggleton supports his evidence with three kinds of data, of which the most conclusive is the capture of lightly coloured adults in autumn. The time needed to achieve a black and hard dorsal integument is given as twenty days (Greenslade 1965). We found a positive correlation between the amount of food and the time young beetles needed to harden out. At 15°C and with a minimal amount of food even after ten weeks beetles were still soft. The presence of callow beetles in autumn could therefore also be caused by the food level in the field. Besides, as mentioned above, larvae will have only a small chance to survive summer conditions. We therefore believe this hypothesis to be wrong.

7. To a certain extent it is now possible to outline the life strategy of *N. brevicollis*. In our area, *N. brevicollis* is widely spread and often abundantly present. Therefore, the species can be considered highly successful in spite of several drawbacks: the species is virtually semelparous, and therefore population size is entirely dependent on recruitment each year; hibernation occurs in the larval stages, and the larvae are surface active (with relatively high risk of predation and parasitism); field conditions for this species generally are suboptimal during winter (at least in our area, Nelemans 1987a); young adults undergo summer diapause, with risks of desiccation, predation and starvation.

In our opinion the unquestionable success of *N. brevicollis* is based on two points: firstly, the (young) adults are very mobile and show a rather high dispersal rate (although only very few beetles are able to fly; Nelemans 1987a) – the walking abilities enable the species to continuously reach suitable places, which are numerous since the beetles do not require very specific habitat conditions. Secondly, the larvae have adopted a strategy of life which may be very successful for the species. The high surface activity, which will result in both encounters with food patches and with suitable habitat conditions might be sufficient to compensate for the high predation risk. The larvae are able to deal with a relative shortage of food (quantitatively or/and qualitatively) by curtailing growth and reaching the reproductive stage at a smaller size (Nelemans 1987b).

Furthermore, under favourable conditions larvae easily are able to collect adequate food; the resulting beetles will develop flight muscles and eventually can fly away (provided flight conditions are favourable). Even if they do not use their flight muscles for flight, they can still resorb them as a source of energy. Such beetles are bigger and (if female) will lay more eggs than smaller ones (Nelemans 1987a, b). The vicissitudes of the larvae therefore have consequences for both the quality and the abundance of the adults.

In addition, it may be important that most species of the genus *Nebria* are montane or submontane. *N. brevicollis*, together with *N. salina* and *N. livida* belong to the few species that live in lowland habitats. Loser

(1972, in Thiele 1977) could demonstrate that the distribution of montane carabids towards the lowlands is limited by soil moisture and humidity of air near the ground; both have to be high. In our area the life strategy of *N. brevicollis* will ensure a sufficient humidity level during the larval stages, because these susceptible stages are only present in autumn and winter. The adults are protected by a period with complete cessation of locomotory activity during summer months. This strategy of life will not prevent local extinction of *N. brevicollis*. The mark-recapture experiment showed that the area from which the beetles were captured was restricted, so that we apparently dealt with a rather isolated local population.

Founding or refounding populations is concentrated in the young adult stage but to a lesser extent also occurs in the reproductive phase, thus spreading possibilities of dispersal, both in time and in mode (dispersal occurs both by walking and flying). Den Boer (in press) estimated the survival time of isolated local populations of *Nebria brevicollis* in general at 5–88 (mean 11) yr. A rough guess for the present population resulted in values around 30–60 yr.

Still, the species will always be present at enough other sites in the vicinity to give a reasonably high chance of (re)foundings and it thus will enjoy a long term persistence.

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