

Fluctuations of density and survival of carabid populations*

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Summary. Standardized and all-year pitfall-sampling during a number of years gives reliable estimates of the yearly changes in size (year-catches) of the local breeding populations (interaction groups) of carabid species. From sampling runs at 89 sites 2,893 estimates of coefficients of net reproduction (R) of 64 carabid species were obtained. The R -values of all species appeared to be lognormally distributed (LND). For each species realistic fluctuations of density could thus be simulated after estimation of mean and standard deviation of the fitted LND (Appendix). Simulation results were compared with field data in two ways:

1. The range between highest and lowest density (logarithmic range: LR), only for those sampling runs of 4–12 years that are not interrupted by zero year-catches. These LR -values were compared with those from simulated runs at similar catch-levels (n), i.e. runs with the highest catch between $\frac{1}{2} \cdot 3^n$ and $\frac{1}{2} \cdot 3^{n+1}$, if $n=1, 2, \dots, 7$. As the number of uninterrupted (by zero year-catches) time series of catches decreases at lower catch-levels, by which the distribution of LR -values becomes skewed, each sampling run from the field could only be compared with simulations at the same catch-level. It thus appeared, that in the field density usually fluctuated within wider ranges than could be expected from the concerning simulations (where density fluctuated according to R -values drawn at random from the fitted LND). This means, that in the field the succession of R -values generally is less favourable than at random. This was especially evident for species with high powers of dispersal (T-species; glossary). In species with low powers of dispersal (L-species) the density range (LR) of field populations only at higher catch-levels agreed well with the expected values from the simulations.

2. The number of zero year-catches in sampling runs of 4–12 years taking into account the catch-level. In the field very low densities as a cause of zero year-catches cannot be distinguished from extinction and/or (re) founding (turnover). In the simulations the density level (start density) can be chosen such that only very low densities can still be a cause of zero year-catches (pseudo-turnover), the chance of which is higher the lower the catch-level. Correcting the field data for pseudo-turnover for each species gives estimates of the actual turnover. Local populations of carabid species thus appear to survive for only restricted periods, in T-species around 10 years, in L-species around 40 years. This fits in well with previous findings on differ-

ences in the Distribution of Population Sizes (DPS; glossary) between species (Den Boer 1977).

The survival times of local populations are not so much determined by the instability of the habitat, but more by the instability of the populations themselves. The low survival times of local populations of T-species seem directly to result from the high level of dispersal.

1. Introduction

To independently judge the controversies around the book of Andrewartha and Birch (1954) in 1958 I started long-term field investigations in Wijster (Drenthe, the Netherlands) into the dynamics of carabid populations. Another reason was that the forces driving the dynamics of polyphagous arthropods were virtually unknown then. A number of carabid species could be simultaneously sampled with the same sets of pitfalls, and I hoped that a way could be found to stimulate the development of comparative population ecology. In my opinion the latter would be necessary to remove the controversies about the processes governing the dynamics of populations.

A number of more or less natural sites in Drenthe were sampled continuously during one or more years with standard sets of pitfalls (Den Boer 1977, Ic), in order to get the indispensable comparative knowledge on pattern and constancy of habitat relations of the more abundant species. However, can the pitfall catches also be considered relative estimates of mean density? To answer this question a number of extensive mark-recapture experiments with pitfalls were executed from 1966 onwards (Den Boer 1979a) for different species, in different years and at different sites. This enabled me to compare the numbers of still unmarked individuals (equivalent to the usual pitfall catches without replacement) with the estimates of population size according to Jolly's stochastic model (1965). These first catches of individuals summed over the reproductive season (or over the whole year) appeared to be highly correlated with the average of the population sizes estimated for the same period; 8 species in 3 sites (34 breeding seasons) gave r (product-moment corr. coeff.) = 0.961, and 4 species in one site (7–10 years each) $r = 0.927$ or ρ (Spearman's rank corr. coeff.) = 0.935 ($n = 32$): (Den Boer 1979a, Fig. 2). In most cases the mean population size predicted for year t from that in year $t-1$ by means of the ratio first catches in year

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t /first catches in year $t-1$ fell within the confidence (minimax)-interval of the average of the Jolly-estimates for year t . It is therefore not surprising that the coefficients of net reproduction derived from these experiments (32 pairs of years for 7 species) based on the first catches of individuals (N_t/N_{t-1}) were in good agreement with those based on mean population sizes (P_t/P_{t-1}): combination of 7 Mann-Whitney U -tests, $z=0.22$; $P=0.83$ (Siegel 1956). Moreover, the small differences between these two estimates of net reproduction (R) did not show any systematic trend: in 4 species (7–10 years each) $P \rightarrow 1.0$, $P=0.81$, $P \rightarrow 1.0$ and $P=0.58$ respectively (Wilcoxon's test for symmetry: Van Eeden & Benard 1956; or Wilcoxon's matched-pairs signed-ranks test: Siegel 1956), and can thus be considered to be errors of estimation only. This fits in nicely with results obtained by Baars (1979) who, in two species, correlated actual mean densities with the summed catches in nearby standard sets of pitfalls: $r=0.927$ ($n=10$) and $r=0.957$ ($n=9$) respectively.

Hence, R -values (coeff. of net reproduction) estimated from pitfall catches in two successive reproductive seasons give reliable estimates of the yearly changes in size of the local breeding population (interaction group in the sense of Den Boer 1977, 1979b), and this opens the possibility to study the long-term dynamics of carabid populations. Over the last 26 years we have sampled 92 sites in Drenthe during one or more years resulting in a total of 311 year-samples (glossary), from local carabid faunas (with 10–60 species each). Of these I will use here the sampling runs obtained through 1981 (290 year-samples from 89 sites) on the 64 most abundant species, i.e. 6,469 estimates of relative densities in total. The goal of this paper is to get some insight into the dominating features of the fluctuations in numbers of local carabid populations in general, that is, those features that will enable us to roughly estimate the chance of survival of local populations. Data on the separate species will be published elsewhere.

The methods exposed in the following will probably meet with some resistance because these are only developed on the base of net reproduction ($=R$), which in fact is a "black box". This "black box" contains natality, mortality, immigration and emigration, each of which, however, is a smaller "black box" again consisting of a variety of different more or less interrelated influences in different stages of the life cycle. Our insight in population processes significantly increases, of course, from analyzing e.g. total mortality into its components, as it is done in key-factor analysis (see e.g. Varley et al. 1973). But total mortality itself – as well as its influence on the changes of population numbers – cannot be affected by such an analysis. In the same way analyzing net reproduction into its components would indeed highly increase our insight in population processes but it leaves the fluctuations of numbers unaltered. Although we know a lot about factors (among which density) influencing egg production, mortality, walking patterns, flight activities, etc. of carabid beetles in this paper we intentionally keep a distance to better concentrate upon the relationship between density fluctuations and survival. In following papers, however, we will discuss which of the processes underlying the density fluctuations observed appeared to be most significant. Some indications on the relations between density level and dispersal both in the centre and at the fringes of distribution can already be found in Den Boer (1977) (see also Den Boer 1979b). But

again, the density fluctuations themselves – and with it the conclusions drawn in this paper – cannot be basically changed by such an analysis. At this place I also like to warn against the opposite tendency: if some special population process – e.g. a density-dependent one – has been found to be quantitatively important (e.g. pupal predation, k_s , in the winter-moth: Varley et al. 1973) nothing can be concluded about density fluctuations, density limits or survival without placing back these special effects into the original context, i.e. into the values of net reproduction. I hope to illustrate this in some future papers.

2. The frequency distribution of coefficients of net reproduction

The 64 most abundant carabid species produced 2,893 estimates of coefficients of net reproduction (R), an average of 45 per species. As in most species the R -values apparently are lognormally distributed, for each of the 64 species a lognormal distribution (LND) was fitted to the R -values (see Appendix). In the 25 species with 44 or more R -values (max. 138; 1,876 values in total; mean = 75) the actual distribution was tested against the fitted LND (χ^2 with 4–8 degrees of freedom) with the result that in none of these 25 species the actual distribution deviated significantly from the fitted LND (see some examples in Fig. 1). Nor did these 25 distributions show any sign of asymmetry: Wilcoxon's test for symmetry applied to the summed frequencies in the 3 extreme classes at the left and the right side respectively ($P=0.30$).

In each of the 64 species the general distribution of R -values can thus be characterized by estimates of the two parameters of the fitted LND, i.e. the expectation value (\hat{E}) and standard deviation (S). The 64 values of both $\hat{E}(\ln R)$ and $S(\ln R)$ as directly estimated from the field data are highly correlated, of course, with the corresponding estimates of the fitted LND's, ($\hat{E}(\ln R)^*$ and $S(\ln R)^*$ respectively): $\hat{E}(\ln R)$, $\hat{E}(\ln R)^*$: $r=0.922$ ($\rho=0.938$); $S(\ln R)$, $S(\ln R)^*$: $r=0.760$ ($\rho=0.721$). However, neither $\hat{E}(\ln R)$ and $S(\ln R)$ ($r=0.04$, n.s.), nor $\hat{E}(\ln R)^*$ and $S(\ln R)^*$ ($r=0.08$, n.s.), for the separate species are correlated among each other. Hence, the possible (upward or downward) trend of numbers is independent of the magnitude of the yearly density changes.

The R -values from the fitted LND can thus be used to simulate realistic fluctuation patterns for each of the 64 carabid species. In only 3 species, and only at the sample sites where they are most abundant and were studied for many years, the R -values showed significant autocorrelations in time which had to be taken into account in the concerning simulations (cf. Den Boer 1981). In other species the succession of R -values in time could not be distinguished from random sequences, which may mean either that the population numbers indeed fluctuated at random, or that most sampling runs were too short to trace significant deviations from random (section 3).

3. The bounds of population numbers: logarithmic range

To compare the patterns of density fluctuations of different populations Reddingius and Den Boer (1970) and Den Boer (1971) recommended to make use of $S(\ln R)$ (or variance $\ln R$) and $\hat{E}(\ln R)$ (or average $\ln R$), and to especially establish the "logarithmic range" (LR), i.e. the bounds between which the numbers have been fluctuating: $\ln(\text{greatest den-}$

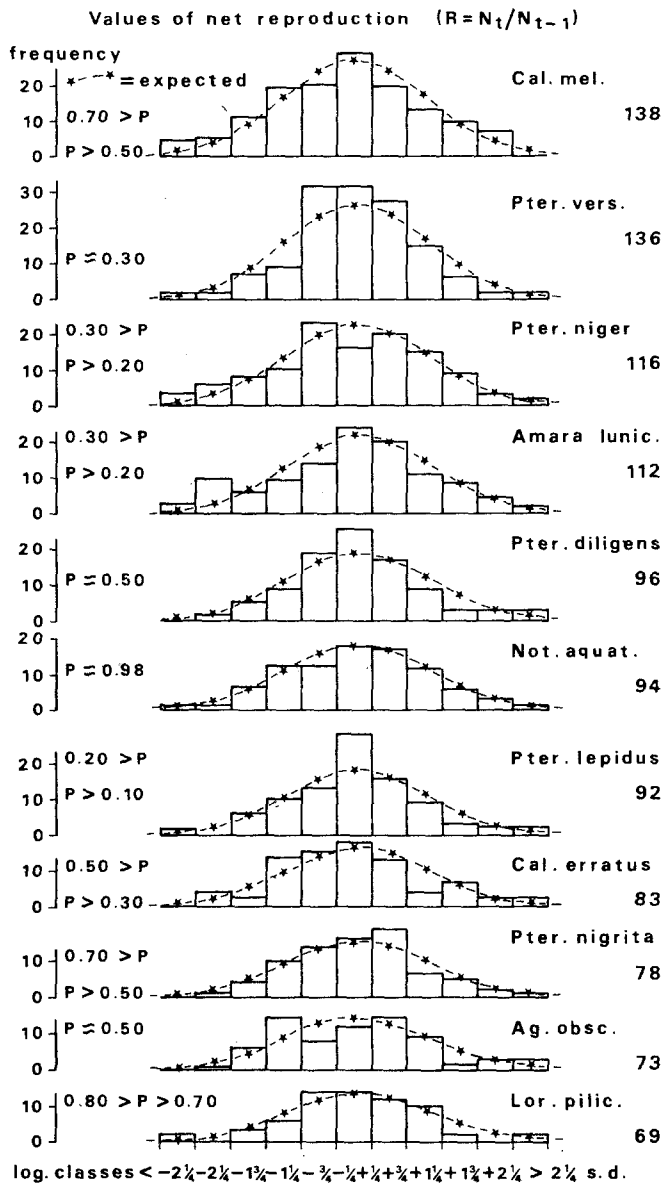


Fig. 1. Frequency distribution of the values of net reproduction (R) of the most abundant carabid species as compared with the fitted lognormal distribution (broken line between stars); class-width = $\frac{1}{2}$ standard deviation (below). At left: probability – from a χ^2 -comparison – that the differences between the two distributions are due to chance deviations only. At right: number of R -values used for the χ^2 -test

sity) minus \ln (smallest density). As a null model, for each of the 64 species and for each run of years (minimum 4) during which a habitat was uninterruptedly sampled (26 sites) a great number of fluctuation patterns (500) was simulated (cf. section 2), and the corresponding values of LR were determined. For each species and each run of years this collection of 500 LR -estimates ("population"- LR 's) thus gives a fair picture of the possibilities under the null hypothesis: random fluctuations of numbers according to the fitted LND. But having assumed that the fluctuations are random we cannot expect that all field or simulated populations will survive during a large number of years, so that in the latter not all 500 LR -values would be available. Survival time will depend, of course, on initial density and on the particular sequence of R -values realized

in that case. In our simulations cases of "extinction" within a restricted number of years (between 4 and 12, the most frequent sampling runs in the field), would mean the loss of potentially high LR -values (which are especially proper to populations with a downward trend), and this would influence the probability distribution of LR -values of the above null model ("population"- LR 's). By choosing sufficiently high start values we could almost completely avoid this complication.

The above complication, i.e. the occurrence of zero values in a time series (the logarithm of which does not exist, so that no LR -values can be estimated) becomes very important in the field data, because from the field year-catches (glossary), are obtained that are 100 to 1,000 times smaller than relevant population sizes. Because of that, zero year-catches occur rather frequently – especially in runs with overall low catches, of course – by which many LR -values are lost and the distributions of the remaining values are skew. To "adapt" our simulations to the field situation we had thus to "sample" the computer populations at a number of different levels of intensity. This resulted in "catches" at different (*3) catch-levels: at level I the highest "year-catch" of that "sampling run" was between 2 and 4 ($1\frac{1}{2}$ and $3*1\frac{1}{2}$), at level II between 5 and 13 ($4\frac{1}{2}$ and $3*4\frac{1}{2}$), at III between 14 and 40, at IV between 41 and 121, at V between 122 and 364, at VI between 365 and 1,093, and at VII between 1,094 and 3,280, in general between $\frac{1}{2} \cdot 3^n$ and $\frac{1}{2} \cdot 3^{n+1}$ ($n=1, 2, \dots, 7$). It will be clear, that the lower the catch-level the higher the chance that zero year-catches will occur in the sampling runs (especially in the longer ones) and the more deviating from the $\hat{E}(LR)$ of the above "population"- LR 's – i.e. smaller – will be the average of the LR -values that can still be established, because with a decreasing catch-level also the range of still possible LR -values is progressively restricted (from above), e.g. at catch-level I LR can maximally reach $(\ln 4 - \ln 1) = 1.3863$, at catch-level II maximally $(\ln 13 - \ln 1) = 2.565$, at level III maximally $(\ln 40 - \ln 1) = 3.689$, etc.

Hence, from the 500 "population" simulations of each species we had to produce for each run of sampling years and for each catch-level separately those logarithmic ranges that can be expected for runs of catches that are not interrupted by zero year-catches, after which for each of the different catch-levels separately these LR -values must be compared with the "population"- $\hat{E}(LR)$ of that species. This comparison boils down to computing a kind of "rankits" of the "catch" LR , i.e. the standardized deviations from the "population"- $\hat{E}(LR)$ concerned: [$\text{"catch"}LR - \hat{E}(LR)$] divided by $S(LR)$ (see Table 1). If no zero year-catches occur in any of the "sampling" runs the relevant rankits will be distributed symmetrically around zero with a standard deviation of one. The occurrence of zero year-catches, however, results in the biased withdrawal of a number of potentially high LR -values, by which the distribution of rankits will become predominated by negative values. After having studied for some time the frequency distributions of rankits thus produced it became evident that the necessary information could still be saved by only considering the numbers of rankits below and those above zero (see Table 1).

Next, for all uninterrupted sampling runs from the field we can likewise establish the LR -values and the rankits of LR for that species. For all catch-levels the numbers of rankits below zero and that above zero can be tested

now against the relevant expectations (χ^2 test) (Table 1). As rankits are standardized deviations their numbers can be added in different combinations in order to make possible all kinds of comparisons we are interested in.

In most species the number of positive rankits appeared to be greater than expected (and the number of negative rankits smaller, of course), which means that in the field population numbers fluctuated between bounds that were generally more widely apart than could be expected with random fluctuations. For all 64 species taken together this phenomenon is very convincing indeed ($\chi^2 = 78.5$; $df = 1$), but in the separate species it is often not significant, though there is a clear tendency: in 22 species the bounds are significantly too wide, and in only 4 species significantly too narrow.

Apart from this unexpected overall trend there was found another interesting relationship: populations of the 21 species with low values of DPS^1 (< 0.715), L-species, at the higher catch-levels (III–VII) showed about random fluctuations of numbers (not significantly deviating from the expectations: $\chi^2 = 0.006$; $df = 1$), whereas populations of the 23 species with high values of DPS^1 (> 0.753), T-species, at all catch-levels fluctuated between much too wide bounds as compared with random fluctuations ($\chi^2 = 72.56$; $df = 1$; at the individual levels II to VII χ^2 lies between 17.4 and 47.0; $df = 1$, $P < 0.001$) (Fig. 2). At the lowest catch-levels (I and II) not only T- but also L-species fluctuated more heavily than random ($\chi^2 = 21.5$ and 12.0 ($P < 0.001$) $df = 1$, respectively); these latter data were mainly derived (in both groups of species) from marginal habitats. The above relationship on the one hand suggests, that well dispersing species (T-species) often settle down in sites where the chance to survive will be lower than expected with randomly fluctuating numbers, probably because of environmental instability. On the other hand it suggests, that in our cultivated countryside, where suitable and more stable habitats (habitats where at least during the 25 years of our investigations the species, that prefer these habitats, could reproduce each year – though with varying success, of course; see Den Boer 1977) generally have become more widely separated than in a natural area, short-living populations of species with low powers of dispersal (L-species) will now be extinct; only a few small populations in some marginal habitats that can still be refounded repeatedly from nearby favourable sites (catch-levels I and II in Fig. 2), may be met with. The longer living – and denser – populations of L-species, that still survive in part of the more stable halbitats, are obviously those that nicely fit our null

¹ DPS (Distribution of Population Sizes) was shown by Den Boer (1977) to give a reliable indication of the powers of dispersal – especially in relation to the chance to (re)found populations – in a recently greatly altered (e.g. cultivated) countryside, by which in fact it is an estimate of RPR (degree of Realization of Population Replacement). $DPS = 1 - \frac{\sum \ln(n_i + 1)}{j \cdot \ln(N + j)}$; n_i : year-catch, as an estimate of population size (section 1); j : number of year-catches; $N = \sum n_i$. Note that high values of DPS go with high powers of dispersal (T-species), whereas low values of DPS go with powers of dispersal that are generally insufficient to replace extinct populations in our cultivated countryside (L-species). For the present analysis all DPS -values were computed anew, covering now the year-catches of 1959 until and including 1981. Whether using the old (1959 until and including 1967; Den Boer 1977) or these new values of DPS does not influence any of our conclusions: correlation old/new DPS : $p = 0.94$

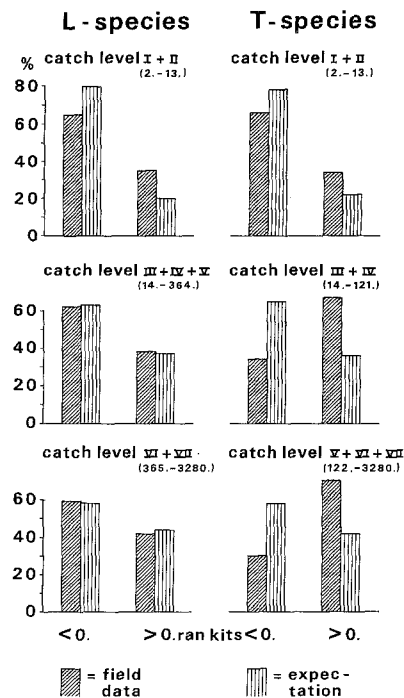


Fig. 2. Percentage of the rankits of LR below and above zero for field populations at different catch-levels (corresponding highest catch-numbers between brackets) in two groups of carabid species: L-species (with DPS -values < 0.715) and T-species (with DPS -values > 0.753), as compared with the expectations. Further explanation in the text

models by showing near random fluctuations of numbers. Note that this means that from the point of view of survival times randomly fluctuating population numbers generally are the best we can expect to meet in the field. Obviously, in most populations R -values succeed each other in time less favourably than at random.

4. The turnover of local populations

Even within the restrictions of our null models, i.e. R -values taken at random from fitted LND's, most carabid populations could have been fluctuating within a narrower range than they happen to do in the field (section 3). This seems not to favour the assumption that as a rule populations would be kept within limits by regulating processes (Varley et al. 1973, p. 19, 112; Begon and Mortimer 1981, p. 18, 162), or it shows that even regulating processes need not result in ranges that are significantly narrower than without such processes. As a consequence it may be expected that local populations of carabid species do become extinct rather frequently, which is not in agreement with the main stream of the literature on population dynamics (see Itô 1980). Therefore, it is necessary to test this expectation. A minor modification of the simulations used for section 3 made this possible.

I noted before that zero year-catches occur rather frequently in sampling runs of many years. I had to know how many of the disappearances (d) – year-catches changing from positive (≥ 1) to zero – refer to extinction, and how many of the appearances (a) – year-catches changing from zero to positive (1 or more) – refer to (re)founding of a local population. If this is known the corrected value

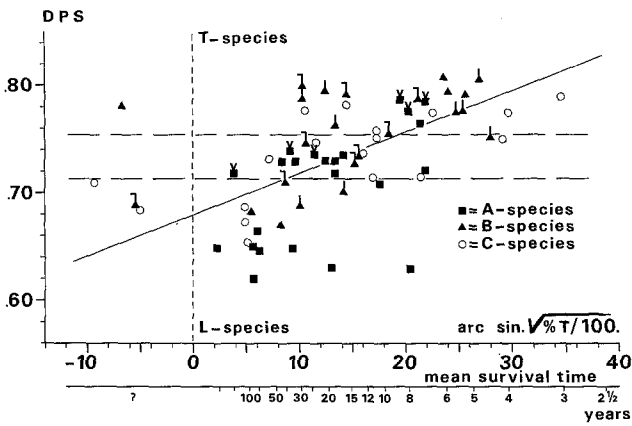


Fig. 3. Relationship between the corrected turnover of local populations (plotted as the arcsine values of the square root, and with an added scale of mean survival times) and DPS in 64 carabid species; *solid squares*: A-species (with v : big individuals that walk very well); *solid triangles*: B-species (in 9 years caught in window traps: *simple triangles*, ≤ 5 ind.; with bar, 6–60 ind.; with hook, > 60 ind.); *open circles*: C-species. *Solid line*: least squares (Bartlett, cf. Sokal and Rohlf 1969) for all 64 species: $y = 0.6790 + 0.00386(x)$; limits of confidence (95%): $0.6590 + 0.005328(x)$; $0.6968 + 0.002545(x)$. *Least squares* (Bartlett) for B-species only: $y = 0.7093 + 0.00308(x)$. L-species = DPS < 0.715 ; T-species = DPS > 0.753). Further explanation in the text

of $\frac{1}{2}(a+d)$ divided by the number of years with positive catches (y) would give an estimate of “turnover” (compare Schoener 1983), i.e. an estimate of the chance that in a given year a local population of that species will disappear or be (re)founded, whereas the inverse of this value, $2y/(a+d)$ estimates the mean survival time in years of an average local population (see Table 2). It seems reasonable, however, to suppose that many – if not all – disappearances and appearances in the year-catches are caused by very low densities only, i.e. not by real extinctions, but by what may be called “pseudo-turnover”. The gross turnover that is directly derived from the field data thus needs correction for “pseudo-turnover” to become an estimate of the actual turnover.

“Sampling” of the computer populations for each species and each run of sampling years – resulting in “catches” at the different (*3) catch-levels as it occurred for the data discussed in section 3 – can also tell us how many times at each catch-level a simulated year-catch from a persisting “population” crosses the value of one individual from above (d) or from below (a), which would give the desired estimate of “pseudo-turnover” (see Table 2). I thus calculated how much “pseudo-turnover” could be expected to occur in the field data (runs of 4 years or more with a highest year-catch of two or more), and for each run this was subtracted from the (gross) turnover actually observed in that field data (Table 2).

Pseudo-turnover indeed occurs frequently, but surprisingly in only 4 species mean pseudo-turnover appeared to be higher than the overall (gross) turnover from the field data². In all other species we got distinct indications of a restricted survival time of local populations, in spite of the great variability of the field data and the high variance

² These 4 species are all different from the 4 species with significantly to narrow bounds mentioned in section 3

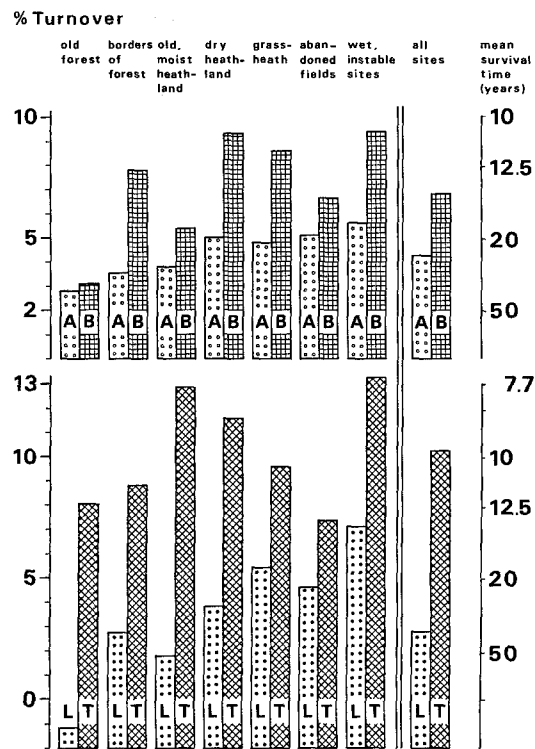


Fig. 4. Corrected turnover in different kinds of carabid species if only local populations are compared that occur together at the same sites. From left to right: very stable to highly unstable sites. *Above*: comparison according to directly observable powers of dispersal: A-species (*low*) and B-species (*high*). *Below*: comparison according to values of DPS (as an estimate of RPR: the degree of Realization of Population Replacement): L-species (*low*) and T-species (*high*)

of pseudo-turnover itself (with standard deviation and average of about the same value). Because of this variation with a probability of about 80% survival times of local populations of individual species will be within a range of 0.25–2.0 (and corrected turnover within 0.5–4.0) times the expected values that were estimated with the above procedure, and which are plotted in Fig. 3. Here I will only make a few comparisons that are quite insensitive to this high level of variability; data on some abundant species will be published separately.

Figure 3 shows, that the corrected turnover of individual species is distinctly correlated with DPS³ ($r = 0.526$; $P \leq 0.01$; $\rho = 0.597$; $P < 0.00003$; $n = 64$). This means that low values of DPS (L-species: section 3) are associated both with relatively favourable mean survival times (around 40 years) of local populations and with low powers of dispersal (mainly A-species⁴) whereas high values of DPS⁵ (T-species; section 3) are associated both with low mean survival times (around 10 years) and with high powers of dispersal (mainly B-species⁴). As some A-species disperse better than expected at first (big individuals that can cover rather great distances by walking), and some B-species less

³ See footnote 1

⁴ A-species are unwinged or wing-dimorphic with less than 1% of winged individuals. B-species are winged or wing-dimorphic with much more winged individuals, and can be captured in window traps (during the act of flying): the powers of dispersal of C-species are unknown (Den Boer 1977)

⁵ See footnote 1

Table 1. Species 70 (*Calathus melanocephalus*) as an example of the comparison of logarithmic ranges (LR) of uninterrupted sampling runs in the field with the expectations derived from simulation of sampling runs by taking values of net reproduction (R) from the LND (lognormal distribution) fitted to the 138 R -values estimated from actual year-catches. The fitted LND has $\hat{E}(\ln R)^* = -0.0646$ and $S(\ln R)^* = 0.7417$, and simulation of 500 "populations", each during 8 years (start density = 2,000), gives 500 values of LR with $\hat{E}(LR) = 2.39103$ and $S(LR) = 1.01395$. *Procedure:* From these 500 "populations" runs of "year-catches" are taken of size 3^{-1} , 3^{-2} , ..., 3^{-10} respectively. Then, each completely positive "sampling" run (i.e. without "catches" < 1) is labeled with the "catch-level" corresponding with the highest "catch", and the "catch" LR is estimated (catch-levels are between $\frac{1}{2} \cdot 3^n$ and $\frac{1}{2} \cdot 3^{n+1}$, $n = 1, 2, \dots, 7$). Next, for each of these simulated "catch" LR 's the rankit is calculated, i.e. ["catch" $LR - \hat{E}(LR) / S(LR)$], in the present case ("catch" $LR - 2.39103) / 1.01395$. At each "catch-level" the relevant rankits are then divided into two groups, rankits < 0 , and rankits > 0 , which are the expected frequencies for sampling runs of that length and at that catch-level from the field

Species 70 for runs of 8 years					Species 70 for all runs					
Catch-level	Expected frequency or rankits		Rankits of field data (sampling site; LR)	Actual frequency of rankits		Frequency of rankits of sampling runs of different length				
	< 0	> 0		< 0	> 0	Length in years	Field data		Expectations	
							< 0	> 0	< 0	> 0
I:	51	0		—	—	4:	11	10	12.7	8.3
II:	215	43		—	—	5:	10	10	12.1	7.9
III:	270	153	-0.25 (CA; 2.140)	2	0	6:	7	11	11.1	6.9
			-0.25 (CD; 2.140)			7:	9	5	8.5	5.5
IV:	276	199	-1.12 (CE; 1.260)	4	0	8:	7	4	6.7	4.3
			-0.73 (AV; 1.6487)			9:	3	3	3.8	2.2
			-0.32 (CF; 2.071)			10:	2	2	2.7	1.3
			-0.50 (BZ; 1.8853)			11:	0	2	1.4	0.6
V:	276	217	+1.17 (M; 3.5773)	1	1	12:	0	1	0.7	0.3
			-1.36 (AV; 1.0133)			Total	49	48	60.9	36.1
VI:	276	222	+1.69 (Z; 4.1043)	0	1	$\chi^2 = 6.248$ (d.f. = 1)				
VII:	252	202	+2.23 (AT; 4.651) ^a	0	2	$\rho \approx 0.01$, too many rankits > 0				
			+0.52 (N; 2.920)			Total	1616	1036	(11 runs)	7
	(6.7)	(4.3)								

^a Highest catch was 2,408 (catch-level VII); rankit = $(4.651 - 2.39103) / 1.01395 = +2.23$

than expected (restricted to small and highly isolated remnants of deciduous forest), the contrast between L-species and T-species appears to represent the contrast of low versus high powers of dispersal better than the difference between A- and B-species, especially as far as the relationship with the frequencies of (re)founding of local populations is concerned. At the same time this supports the conclusion of Den Boer (1977) that in a cultivated countryside DPS would give an estimate of RPR⁵.

An interesting question is whether the low survival times of local populations of T-(or B)-species – which goes with unfavourable LR -values (Fig. 2) – directly result from the degree of instability of the habitats they use to occupy (which coincides with the hypothesis of Southwood 1962), or is caused by the high dispersability itself of this kind of species. As the habitat relations of most of our carabid species are not very strict we can also find local populations both of T-(or B)-species in more stable habitats (sometimes even in high numbers) and of L-(or A)-species in rather unstable habitats; the latter less frequently than the first. Because of this it is possible to compare the turnover of T-(or B)-species with that of L-(or A)-species within the same habitats. Our null hypothesis now is: the turnover of local populations of carabid species does not show any relationship with the level of dispersal of the species; under this hypothesis dispersal is expected mainly to occur in unstable or temporary habitats and then by all species present there (escape from adverse conditions). This null hypothesis must be rejected, however: in each habitat T-species show

a higher (mean) turnover than L-species ($P = 0.0001$, Wilcoxon's test for symmetry; 2-sided), and about the same applies to B-species as compared with A-species ($P = 0.023$; 2-sided) (Fig. 4). The conclusion is, that it is not so much the instability of the habitat occupied that determines the actual survival times of local populations as the instability of the populations themselves. The instability of local populations of T-species may result from the high level of dispersal, because it will take away so many potential reproducers that in most T-species local populations will have an increased chance to show a downward trend in numbers (Fig. 5, at right).

5. On the dynamics of (carabid) populations

From an evolutionary point of view Southwood (1962) is generally right when stating that the level of dispersal ("migratory movement") in any species is geared to the rate of change of its habitat and is highest in species that occupy temporary habitats. Indeed, the "strategy" of individuals of T-species, which results in withdrawing many individuals from still flourishing populations, will not be changed fundamentally as long as the chance to found populations elsewhere is sufficiently high to compensate on the average for the shortened survival times, i.e. under predominantly unstable conditions. As soon as the greater part of the generally occupied habitats becomes more stable (or when populations tend to be founded in more stable habitats) on

Table 2. Species 121 (*Notiophilus germinyi*) as an example of the estimation of the average turnover of local populations by correcting the (gross) turnover, that is derived from the sampling data, for pseudo-turnover (ps.-turn.) resulting from very low densities only

By taking *R*-values from the fitted LND – with $\hat{E}(\ln R)^* = 0.2077$ and $S(\ln R)^* = 0.7830$ – for each run of sampling years (between 4 and 12) 500 “populations” are simulated, which “survive” during that number of years (the adequate start density is 1,000). *Procedure:* From each set of 500 “populations” runs of “year-catches” are taken of size $3^{-1}, 3^{-2}, \dots, 3^{-10}$ respectively, after which each sampling run is labeled with the “catch-level” corresponding with the highest “catch” (catch-levels are between $\frac{1}{2} \cdot 3^n$ and $\frac{1}{2} \cdot 3^{n+1}$, $n = 1, 2, \dots, 7$; sampling runs with the highest catch below 2 are thus discarded). For each run of sampling years (between 4 and 12) and for each catch-level separately it is determined how many times “catches” changed to values below unity (*d*), and how many times from values below unity to values greater than unity (*a*), after which $\frac{1}{2}(a+d)$ is weighed against the total number of years with positive “catches”, i.e. ≥ 1 (*y*) to give: ps.-turn. = $[\frac{1}{2}(a+d)/y] \cdot 100\%$

Sampling runs of species 121 from the field with highest catch ≥ 2

Sam- pling site	Year catches	Run of ... years	Catch- level	<i>a</i>	<i>d</i>	<i>y</i>	Uncor- rected turnover (%)	Expected ps.- turn. (%)	Cor- rected turnover (%)	Esti- mated survival time
N	1, 2, 1, 5, 12, 1, 12, 5, 1, -, -, 1	12	II	1	1	10	10.0	8.4534	1.5466	64.66
Z	-, 9, 6, 6, 1, -, -, -, -, 2, -	11	II	2	2	5	40.0	8.1281	31.872	3.14
AT	1, -, -, 1, -, -, 2, -	8	I	2	3	3	83.33	16.9421	66.39	1.5
BH	-, 6, 3, -, -, -	6	II	1	1	2	50.0	2.5926	47.407	2.11
BJ	1, -, 3, -, -, -	6	I	1	2	2	75.0	15.2174	59.78	1.7
AG	14, 3, 5, 3, 1, -, 2	7	III	1	1	6	16.66	0.9619	15.7	6.37
AU	36, 23, 49, 22, 38, -, 7, 24	8	IV	1	1	7	14.285	0.1402	14.145	7.07
AV	33, 46, 60, 27, 55, -, 4, 18	8	IV	1	1	7	14.285	0.1402	14.145	7.07
AZ	4, 24, 15, 45, -, 3, 18	7	IV	1	1	6	16.66	0.1319	16.535	6.04
BB	6, 9, 19, -, -, -	6	III	0	1	3	16.66	0.7152	15.95	6.3
AY	1, 4, 4, -, 3	5	I	1	1	4	25.0	16.8342	8.166	12.25
O	1, 2, -, -	4	I	0	1	2	25.0	11.5789	13.42	7.45
X	1, 2, 1, -, -, -, -	7	I	0	1	3	16.66	17.6554	-0.99	??
AE	26, 30, 16, 15, 20, 9	6	III	0	0	6	0.0	0.7152	-0.715	??

14 sampling sites with 101 sampling years: $\sum a = 12, \sum d = 17, \sum y = 66$ ps. turn. = 100.2067 (mean = 7.1576). Gross turnover = $\frac{1}{2}(12+17)/66 \times 100\% = 21.97\%$; corrected turnover = 14.812%. The mean survival time of a local population of species 121 is thus estimated at 6.75 (i.e. 7) years, and also taking into account the great variance of ps.-turn. with a chance of about 80% it will lie between 2 and 14

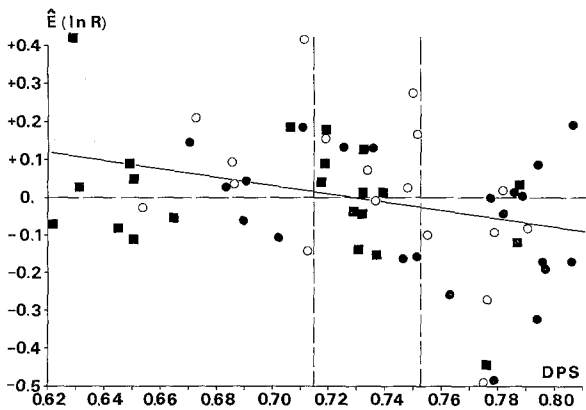


Fig. 5. Relationship between DPS (as an estimate of population replacement) and average $\ln R$ (as an estimate of the trend in population numbers). At right: T-species (DPS > 0.753); at left: L-species (DPS < 0.715). Solid quadrats: A-species; solid circles: B-species; open circles: C-species. A downward trend in population numbers is associated with an increase in population replacement: $r = -0.339$ ($P = 0.01$), $\rho = -0.328$ ($P = 0.009$); least squares (Bartlett): $y = 7.71 - 10.553(x)$

the average natural selection will favour individuals that stay behind in the population, and the (carabid) species concerned will have entered the evolutionary processes that are described by Den Boer et al. (1980). Because of a decrease of dispersal losses the latter processes will be accom-

panied by an overall increase of the survival time of local populations: in Fig. 3 the species will “shift” from right above to left below, roughly as is indicated by the line of least squares. This process can continue until the numbers of the more abundant local populations fluctuate about randomly, i.e. until the species has become an L-species (Fig. 2). The reverse process under the hypothesis of Southwood (1962), however, the way back from L- to T-species, when the generally occupied habitats become temporary or more unstable, in many cases will be very difficult, if not impossible (e.g. because the species has become apterous), at least in carabid beetles. Hence, rapid and large-scale changes in the environment, such as brought about by man, will favour a lot of T-(or B)-species, in general: opportunistic species, whereas most L-(or A)-species will gradually die out – possibly about half of our carabid species –, not always in the first place because of the disappearance of many suitable sites, but more because they are unable to reach in time the now widely separated remnants of suitable habitat, by which population replacement (RPR) becomes increasingly insufficient (and which is indicated by low DPS-values; see further Den Boer 1977, 1979b). These processes, of course, are not restricted to carabid species.

It seems surprising that even among species inhabiting permanent habitats (like old forest) the fluctuations of numbers are generally not better than random (Fig. 2). Apparently mean survival times of local populations only rarely exceed 100 years and in most species are only some de-

cedes (Fig. 3). This is not a statistical artefact of adding together the rankits of local populations with quite different density levels (i.e. populations in marginal and in more optimal habitats respectively). In the 32 most abundant of the 64 species I could compare the fluctuations of numbers in populations with different (at least 3) catch(density)-levels (section 3). Though there was much variation – as could be expected – in only 11 species local populations at some density level(s) clearly deviated from the general species pattern: in 5 species the range was significantly too wide and in 6 species too narrow (in only 4 significantly so) in the more dense populations as compared with local populations at lower density levels. This could be expected in the null case: the high level of variation increases the chance that fluctuations in numbers are different at different catch-levels, but such differences should in different species be about equally frequent in each direction, and this was shown to occur. Note that the magnitude of the survival times estimated, especially for the L-species, fits in well with the hypothesis on DPS⁶, and which was based on the reclamation history of the study area Drenthe (Den Boer 1977).

When looking again at Fig. 5 one may even wonder what should be the main question of population dynamics: “How to keep high population numbers down?” or: “How to compensate sufficiently for disappearing local populations (how to keep up RPR)?” There will always be found some populations with fluctuation patterns that favour persistence (by chance, or by the influence of density-dependent processes?) I will return to this question in following papers, but at least in carabid beetles the *general* picture is different, and agrees well with the overall picture of population ecology that is given by Andrewartha and Birch (1954, 1984).

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Appendix (by J. Reddingius)

A random variable X is said to have a logarithmico-normal distribution, or lognormal distribution, with parameters α , μ , σ^2 , if $Y = \ln(X - \alpha)$ has the normal distribution with expectation μ and variance σ^2 (see Cramér 1946, pp. 219–220). We will compute the expectation and variance of X for the case $\alpha=0$. We show first that for $k=1, 2, \dots$:

$$E(X^k) = \exp(k\mu + \frac{1}{2}k^2\sigma^2).$$

Indeed, as $Y = \ln(X)$, $X = \exp(Y)$, and therefore

$$E(X^k) = E(e^{kY}) = (2\pi\sigma)^{-1} \int_{-\infty}^{\infty} e^{ky - \frac{1}{2}\sigma^{-2}(y-\mu)^2} dy$$

Now we may write

$$\begin{aligned} ky - \frac{1}{2}\sigma^{-2}(y-\mu)^2 &= -\frac{1}{2}\sigma^{-2}[y^2 - 2(\mu + k\sigma^2)y + \mu^2] \\ &= -\frac{1}{2}\sigma^{-2}[(y-\mu-k\sigma^2)^2 - 2\mu k\sigma^2 - k^2\sigma^4] \\ &= -\frac{1}{2}\sigma^{-2}(y-\mu-k\sigma^2)^2 + \mu k + \frac{1}{2}k^2\sigma^2 \end{aligned}$$

Because

$$(2\pi\sigma)^{-1} \exp[-\frac{1}{2}\sigma^{-2}(y-\mu-k\sigma^2)^2]$$

is the probability density of a normal distribution with expectation $\mu + k\sigma^2$ and variance σ^2 , therefore its integral over the real line equals 1, it is seen at once that

$$E(X^k) = \exp(\mu k + \frac{1}{2}k^2\sigma^2)$$

as stated. Substituting $k=1$ and $k=2$, we get

$$E(X) = \exp(\mu + \frac{1}{2}\sigma^2) E(X^2) = \exp(2\mu + 2\sigma^2)$$

and as

$$[E(X)]^2 = \exp(2\mu + \sigma^2)$$

$$\text{var}(X) = E(X^2) - [E(X)]^2 = [\exp(2\mu + \sigma^2)][\exp(\sigma^2) - 1]$$

Conversely, suppose that

$$E(X) = \xi, \text{ var}(X) = \beta^2,$$

and let it be required to find μ and σ^2 . Put $\exp(\mu) = p \cdot \exp(\sigma^2) = q$, then

$$\xi = p \cdot q^{\frac{1}{2}}, \quad \beta^2 = p^2 q(q-1)$$

Solving for p and q , we obtained

$$p = \xi^2 (\xi^2 + \beta^2)^{-\frac{1}{2}}, \quad q = 1 + \beta^2 \xi^{-2}$$

whence

$$\mu = 2 \ln(\xi) - \frac{1}{2} \ln(\xi^2 + \beta^2), \quad \sigma^2 = -2 \ln(\xi) + \ln(\xi^2 + \beta^2).$$

Cramér, H. (1946): *Mathematical Methods of Statistics*, Princeton Univ. Press. 575 pp.

Glossary

- ln: natural logarithm (with base e).
- r : product-moment correlation coefficient.
- ρ : Spearman's rank correlation coefficient.
- z : deviation from the mean of the standardized normal distribution measured in standard deviation units.
- R : coefficient of net reproduction, i.e. estimate of density in year t /estimate of density in year $t-1$.
- LND: lognormal distribution (here of R -values).
- $\hat{E}(\ln R)$: mean (expected value) of the frequency distribution of $\ln R$ -values of that species estimated from the field data.
- $S(\ln R)$: standard deviation of the frequency distribution of $\ln R$ -values from the field data.
- $\hat{E}(\ln R)^*$: $\hat{E}(\ln R)$ of the fitted LND of $\ln R$ -values of that species (see Appendix).
- $S(\ln R)^*$: $S(\ln R)$ of the fitted LND of $\ln R$ -values of that species.
- LR : logarithmic range, i.e. $\ln(\text{greatest density}) - \ln(\text{smallest density})$ of a run of (year)-estimates of population size; it measures the range within which density has been fluctuating.
- year-catch: catches of a certain species in a standard set of pitfalls summed over the whole breeding season (or year) (with year-sample in most cases is indicated the collection of year-catches of different species from the same site in a certain year).
- catch-level: level of the highest catch in a run of year-catches; catch-levels have bounds $\frac{1}{2} \cdot 3^n$ and $\frac{1}{2} \cdot 3^{n+1}$, $n=1, 2, 3, \dots, 7$, i.e. catch-level I between $1\frac{1}{2}$ and $4\frac{1}{2}$; level II between $4\frac{1}{2}$ and $13\frac{1}{2}$, etc.
- rankit: here defined as: deviation (of a “catch” LR) from the “population”- $\hat{E}(LR)$ (mean of the LR -values of 500 simulated population-runs during a certain number

6 See footnote 1

- (4–12) of “years”) measured in standard deviation units of that “population”- $\hat{E}(LR)$ (see further Table 1).
- DPS: frequency Distribution of observed Population Sizes of a certain species. DPS is characterized by the expression $1 - \frac{\sum_j \ln(n_i + 1)}{j \cdot \ln(N + j)}$ (cf. Den Boer 1977: Appendix BII by J. Reddingius), in which:
- n_i : number of individuals of that species in year-catch i , i.e. caught during one year in one standard set of pit-falls.
- j : number of year-samples in which the pertinent species is represented by at least one specimen, and
- N : total number of specimens of one species caught in all year-catches together, i.e. $N = \sum_{i=1}^j n_i$.
- RPR: Realization of Population Replacement, i.e. the degree to which (within a given area) the rate of extinction of populations is currently compensated by the rate of (re)foundings.
- L-species: species with a low value of DPS (< 0.715), i.e. species in which small and/or sparse populations are relatively underrepresented.
- T-species: species with a high value of DPS (> 0.753), i.e. species in which all population sizes (also the small ones) together reasonably fit a lognormal distribution (see further Den Boer 1977).
- A-species: species with a supposed low dispersal power, i.e. no or only very few individuals (less than 70 out of N ind., which at the same time is less than 1% of N ind.) are expected sometimes to be capable of flying, although up till now no individuals are caught in window-traps; most A-species are brachypterous (un-winged).
- B-species: species with a supposed high dispersal power, i.e. at least one individual is caught in a window-trap; most B-species are macropterous (fully winged).
- C-species: species of which no individuals are caught in window-traps, but which cannot unambiguously be considered A-species: the dispersal power in fact is unknown.

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