

## What Can Carabid Beetles Tell us about Dynamics of Populations?

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**Abstract:** From all-year pitfall sampling in Drenthe at 89 sites (a total of 290 year-samples) reliable data on the fluctuations of numbers in local populations of 64 carabid species were obtained and compared with the expectations from null models (fluctuations occurring at random). From these tests it could be derived that:

1. The frequency distribution of coefficients of net reproduction ( $R$ ) of local carabid populations does not deviate from a lognormal distribution (as expected if fluctuations occur at random).
2. Carabid numbers fluctuate between positive bounds that are generally more widely separated than as expected with random fluctuations.
3. As a corollary of 2: local carabid populations generally die out more frequently than expected.
4. The above conclusions are not restricted to carabid species occupying temporary habitats; they also apply, although less extremely, to inhabitants of permanent habitats.

### 1. Introduction

In their book Andrewartha & Birch (1954) showed that local populations usually do not survive for a very long time, because there is a continuous turnover (extinction and (re)founding) of local populations often accompanied by extension or contraction of the area of distribution. Many ecologists supposed that these phenomena would be restricted to the fringes of distribution of species (e. g. Nicholson, 1958), i. e. in the centre the situation would be more stationary. As carabid beetles

seemed to be suitable objects to study dynamic situations because of observable differences in dispersal power both between populations and between species (wing-dimorphism; Den Boer, 1970), in 1958 I started long-term investigations in Wijster (Drenthe, The Netherlands) into the dynamics of local carabid populations. I considered it an advantage that sampling with pitfalls makes it possible to study a number of (dynamically) different carabid species simultaneously at the same sites, and thus to contribute to a comparative approach to population ecology.

After some years the question arose: Can the pitfall catches also be considered relative estimates of mean density? Therefore, from 1966 onwards a number of extensive mark-recapture experiments with pitfalls were executed (Den Boer, 1979a). The numbers of unmarked individuals caught, which are equivalent to the usual pitfall catches without replacement, were compared with 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  $r = 0.961$ , and 4 species in one site (7-10 years each)  $r = 0.927$  or  $P$  (Spearman) = 0.935 ( $n = 32$ ) (Den Boer, 1979a, Fig. 2). Baars (1979) found the same when, in two species, comparing actual mean densities (by catching and removing all individuals from enclosures) with the summed catches (year-catches) in nearby standard sets of pitfalls:  $r = 0.927$  ( $n = 10$ ) and  $r = 0.957$  ( $n = 9$ ) respectively.

Therefore, it is not surprising that the coefficients of net reproduction ( $R$ ) derived in the mark-recapture experiments (32 pairs of years for 7 species) from the first catches of individuals ( $N_t/N_{t-1}$ ) did not differ from those based on mean population sizes ( $P_t/P_{t-1}$ ): Mann-Whitney U-test (combined; Siegel, 1956)  $z = 0.22$ ,  $p = 0.83$ . Hence,  $R$ -values estimated from summed pitfall catches (year-catches) in two succeeding reproductive seasons (or years) give reliable estimates of the yearly changes in size of local breeding populations (interaction groups in the sense of Den Boer, 1977, 1979b). This opens the possibility of studying the overall dynamics of local carabid populations, and of testing whether or not there are differences in dynamics between species that in the Netherlands are living near the fringes of distribution, and species that are living there in the centre of their area. From 1959 onwards many different sites were sampled uninterruptedly during one or more (up to 12) years with standard sets of pitfalls (cf. Den Boer, 1977, 1c). From these data I will use here the year-catches of the 64 most abundant species from sampling runs obtained until 1981 in 89 different sites.

With the help of these data I will try to get some insight into the generally occurring patterns of fluctuations of local carabid populations, and thus roughly to estimate and compare the chances of survival of local populations.

## 2. The frequency distribution of coefficients of net reproduction

From the 6469 year-catches of the 64 most abundant carabid species, 2893 reliable estimates of net reproduction (R) could be derived, on average 45 per species. The R-values of a single species seemed to be lognormally distributed at first sight. Therefore, for each of the 64 species I estimated the Log Normal Distribution (LND) fitting the R-values, in the following way: let  $M$  be the mean ( $\hat{E}$ ) and  $V^2$  the variance (Var) of the R-values from the field, then the LND  $Y$  fitting these values will have  $\hat{E}(Y) = 2 \ln M - 1/2 \ln(V^2 + M^2)$  and  $\text{Var}(Y) = \ln(V^2 + M^2) - 2 \ln M$  (see: Appendix by Reddingius to Den Boer, 1985). In the 25 species that produced 44 or more R-values the actual distribution was tested against the fitted LND ( $\chi^2$  with 4-8 degrees of freedom). In none of these species did the fitted LND deviate significantly from the actual distribution (some examples in Fig. 1), and the other species seemed to be similar in this respect.

I thus concluded that in each of the 64 species the general distribution of R-values can be characterized by the expectation estimate ( $\hat{E}$ ) and standard deviation (S) of the LND fitting the field collection of R-values. As 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) -  $\hat{E}(\ln R)$ ,  $\hat{E}(\ln R)^*$ ;  $r = 0.922$  ( $P = 0.938$ );  $S(\ln R)^*$ ,  $S(\ln R)^*$ ;  $r = 0.760$  ( $P = 0.721$ ) - R-values from the fitted LND could be used to simulate realistic fluctuation patterns for each of the 64 carabid species. As the succession of R-values in the field did not generally deviate fundamentally from random sequences<sup>+</sup>, the R-values in the simulation were taken randomly from the fitted LND. The simulations thus act as null models.

## 3. Density limits in field populations: Logarithmic Range

To compare the fluctuation patterns of density in different populations Reddingius & Den Boer (1970) and Den Boer (1971) especially recommended the use of "Logarithmic Range" (LR):  $\ln(\text{highest density})$  minus  $\ln(\text{lowest density})$ , which gives the bounds between which density has been fluctuating during the observation period. To test hypotheses that predict an influence of particular processes on density limits, for each of the 64 species and for each run of (at least 4) years during which

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<sup>+</sup> It must be noted, however, that in most (relatively short) sampling runs this could hardly be tested. Therefore, we could only assume that in these cases also R-values succeeded each other randomly. But compare with section 4.

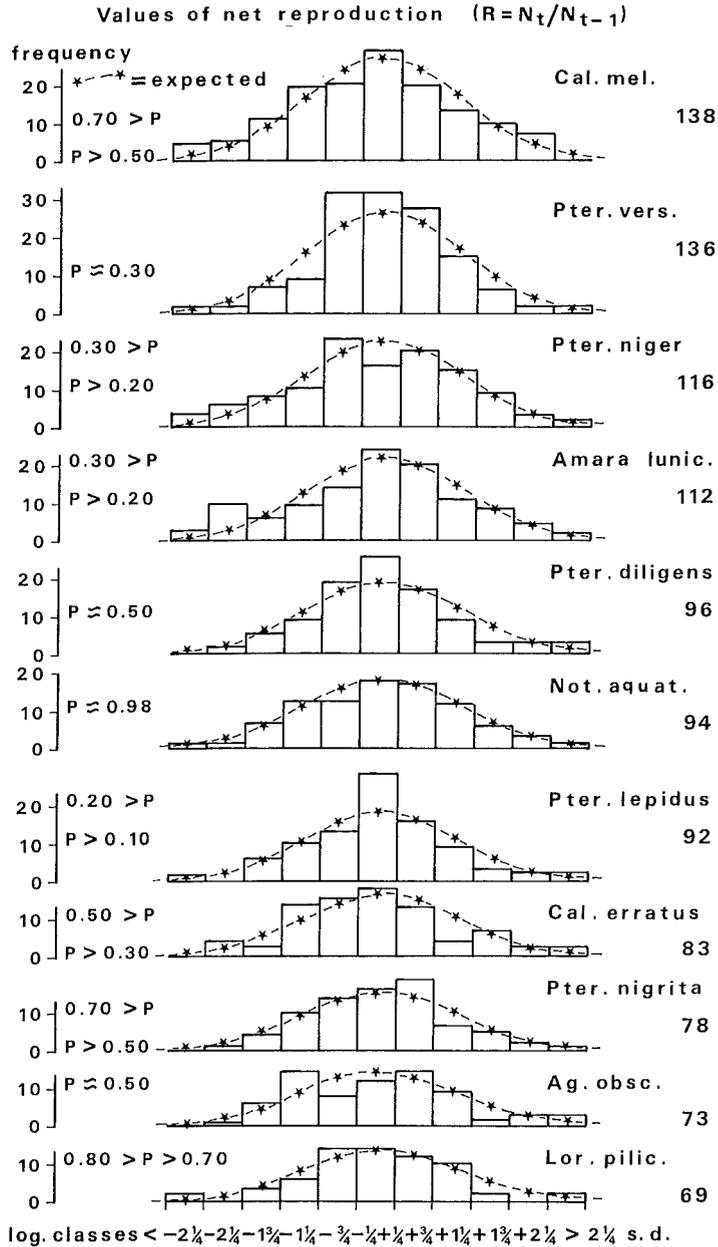


Fig. 1: Frequency distribution of the values of net reproduction ( $R$ ) of the most abundant carabid species as compared with the fitted lognormal distribution (broken line between stars); class-width =  $1/2$  standard deviation (below). At left: probability - from a  $\chi^2$ -comparison - that the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

a site was uninterruptedly sampled with a standard set of pitfalls (26 sites), I simulated 500 fluctuation patterns (section 3), and determined the corresponding values of LR. For each species and each run of years the relevant collection of LR-estimates thus gives a fair picture of the possibilities under the null hypothesis: random fluctuations of numbers according to the fitted LND. It can then be estimated how many of the LR-values of the sampling runs from the field deviate positively or negatively from the predicted mean LR-value. The frequency of deviations below zero (limits narrower than expected) as compared with those above zero (limits wider than expected) can then be tested ( $\chi^2$ ) against the expected frequencies of deviations under the null hypothesis. However, the chance of obtaining a zero year-catch for a species (not a single specimen caught during a whole year) during an uninterrupted sampling run of a number of years will differ (both in the field and in the simulations) between different numerical levels of the catches, being higher at a low level than at a high level of the catches. As sampling runs with zero year-catches cannot be used (no LR-value) the testing described above had to be executed separately for different "catch-levels". The "catch-level" is considered to be the range within which the highest catch of that sampling run occurs, and I fixed this range by  $n$  between the bounds  $1/2 \cdot 3^n$  and  $1/2 \cdot 3^{n+1}$  ( $n = 1, 2, 3, \dots, 7$ ), i. e. at "catch-level" I the highest catch was between  $1 \frac{1}{2}$  and  $4 \frac{1}{2}$ , at "catch-level" II between  $4 \frac{1}{2}$  and  $13 \frac{1}{2}$ , etc. More details of this method can be found in Den Boer (1985). For the present discussion we only need to know that it is possible now to test whether the ranges of density of local populations of the 64 carabid species are narrower or wider than would be expected with random fluctuations according to the fitted LND of R-values (section 3).

In most species the number of positive deviations from the expected mean LR appeared to be greater than predicted by the null model (and the number of negative deviations smaller, of course); this means that in most local carabid populations numbers fluctuated between bounds wider apart than expected under the null model. This general trend is very convincing indeed: all 64 species together give  $\chi^2 = 78.5$  (d. f. = 1), whereas only 4 species showed significantly too narrow ranges against 22 species with significantly too wide ranges of density. Though this general trend already supports the observations of Andrewartha & Birch (1954), it is still more interesting in this connection to compare species with high powers of dispersal, T-species (do these live in Drenthe at the fringes of distribution?) with species showing low powers of dispersal, L-species (do these live in Drenthe in the centre of distribution?). Discrimination between L- and T-species depends on their values of DPS, as will be explained now.

The Distribution of Population Sizes, DPS (estimated as year-catches, see section 2) 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 recently greatly altered areas, such as our cultivated countrysides. In fact, DPS estimates the degree of Realization of Population Replacement (RPR): if this realization is complete (local extinctions are currently compensated by local (re)foundings) the

distribution of year-catches will be about lognormal and can thus be represented by a straight cumulation line on log-probability paper (see e. g. Southwood, 1966), but if it is incomplete this line will be broken. A distribution-free estimate of DPS was obtained by the expression:

$$1 - \frac{\sum_{i=1}^j \ln(n_i+1)}{j \cdot \ln(N+j)} \quad (n_i: \text{number of ind. in year-catch } i; j = \text{number of year-catches available; } N = \sum_{i=1}^j n_i).$$

More details are given in Den Boer (1977, 1979b). For the present it suffices to mention that the cumulation lines for the different species can be arranged along a scale according to the corresponding values of this expression for DPS: Fig. 2. This collection of lines in Fig. 2 can be divided into three approximately equal portions, T-species with high values of DPS ( $> 0.753$ ), L-species with low values of DPS ( $< 0.715$ ), and an intermediate group<sup>+</sup>. Fig. 2 nicely illustrates that high values of DPS (T-species) go with straight cumulation lines and low values of DPS (L-species) with broken lines. Hence, T-species should still be able currently to compensate local extinctions by (re)foundings (complete RPR). This is corroborated by frequent catches of flying individuals in window traps (van Huizen, 1979), by which can be shown that nearly all T-species possess high powers of dispersal. On the other hand, L-species are expected no longer to be able to compensate local extinctions sufficiently by (re)foundings (incomplete RPR). The powers of dispersal of these species are too low (many species are unwinged or wing-dimorphic with less than 1% of winged specimens) to bridge frequently enough the greatly enlarged distances between the remnants of suitable habitat that remain in our cultivated countryside. It is therefore not surprising that most T-species are opportunistic inhabitants of temporary or instable habitats, and often also occupy man-made sites like agricultural fields, gardens, etc., whereas most L-species are adapted to the vast and permanent habitats (mainly deciduous forest and peat-moor) that originally dominated these areas.

Returning to the comparison of limits of density with the expectations under the null hypothesis the significance of the information given in Fig. 3 will now be evident. At all catch-levels T-species fluctuate between much too wide bounds when compared with random fluctuations ( $\chi^2 = 72.56$ ,  $df = 1$ ; at the individual catch-levels II to VII  $\chi^2$  lies between 17.4 and 47.0,  $df = 1$ ,  $p < 0.001$ ). In contrast, L-species, at the higher catch-levels (III to VII) show approximately random fluctuations of numbers ( $\chi^2 = 0.006$ ,  $df = 1$ ,  $p \approx 0.95$ ). At the lower catch-levels

<sup>+</sup> As compared with Den Boer (1977) all DPS-values were recomputed, covering now all year-catches until 1981. As already predicted by Den Boer (1977, 5. 4. 4 and 6. 2) these greater sample sizes resulted mainly in an overall increase of the values of DPS without changing appreciably any of the other relations with DPS (as discussed in Den Boer, 1977). Accordingly, the correlation between the old values of DPS (year-catches until 1967: Den Boer, 1977) and these new ones is almost perfect:  $P = 0.94$ .

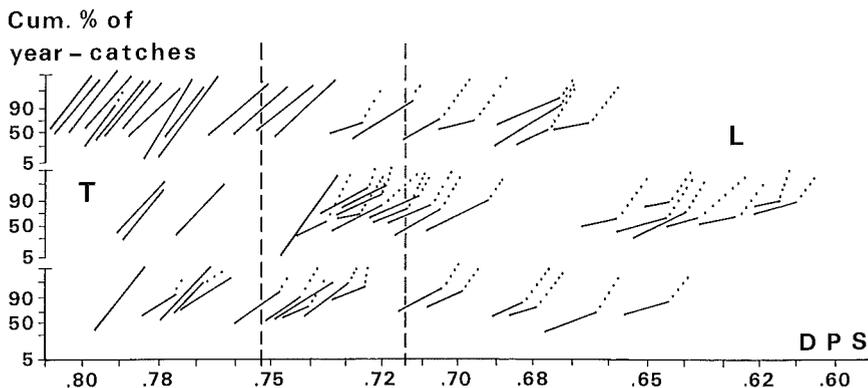


Fig. 2: Cumulation lines (= cumulative frequencies (%)) of year-catches over log-classes - the zero-class included - plotted on a probit scale) of the 64 most abundant carabid species in Drenthe arranged (in 3 groups) along a scale of DPS-values (further explanation in the text, and in Den Boer, 1977). The 64 lines are divided in three approximately equal groups: T-species with  $DPS > 0.753$ , an intermediate group with DPS-values between 0.753 and 0.715 and L-species with  $DPS < 0.715$ . For clarity the upper parts of the broken cumulation lines are stippled.

(I and II) not only T- but also L-species fluctuate more widely than random ( $X^2 = 21.5$  and  $12.0$ ,  $p < 0.001$  ( $df = 1$ ) respectively). In both groups of species the latter data were mainly derived from marginal habitats. In the case of L-species these habitats were usually close to more favourable ones where denser populations of these species are found, so that the small and short-lived populations in the marginal habitats can be refounded repeatedly in spite of low powers of dispersal. Other rather small and/or sparse populations of L-species will for the greater part have disappeared already from the area without sufficient compensation, and this phenomenon is supposed to cause the bends in the cumulation lines of Fig. 2 (see further: Den Boer, 1977).

It is interesting to note that only 4 of the T-species are living in the Netherlands at the fringes of their distributional area, whereas this is true for 8 of the L-species. Hence, this gives no support to the supposition that the dynamics of populations at the fringes of the geographical distribution of species are fundamentally different from those in the centre (see further: Den Boer, 1977, 8.2).

Apparently, geographically marginal does not necessarily imply ecologically marginal, i. e. opportunistic as in T-species.

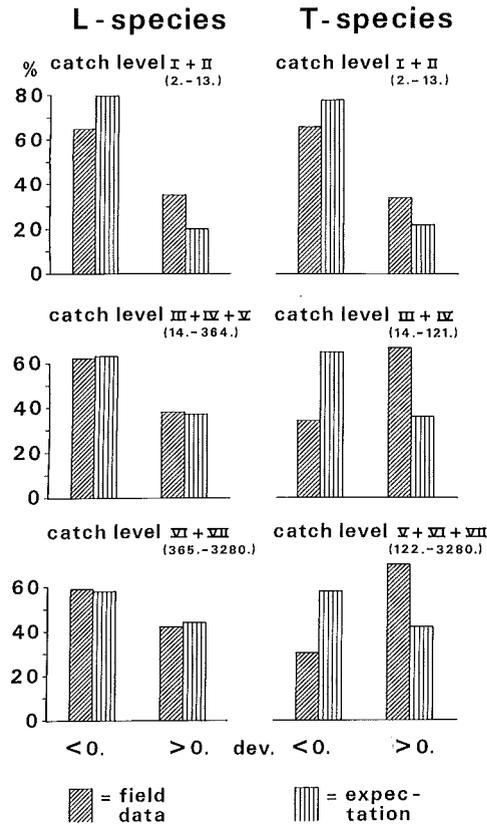


Fig. 3: Percentage of the LR (Logarithmic Range)-values deviating negatively (<0.) or positively (>0.) from the mean LR-values predicted by the relevant null models (from 500 simulations of each case). The deviations of the field data are compared separately with the expected deviations for L-species (DPS < 0.715) and T-species (DPS > 0.753) at different catch-levels.

#### 4. On the turnover of local carabid populations

The analysis in section 4 leads to the surprising conclusion that, from the point of view of the survival time of local populations, randomly fluctuating numbers are the best we can expect to meet in the field, at least as far as carabid beetles are concerned: the simulation models, which were based on random fluctuations, predict narrower limits of density than were actually found in the field in most cases. This seems not to favour the assumption that as a rule populations would be kept

within limits by regulating processes (Varley et al., 1973: 19, 112; Begin & Mortimer, 1981: 18, 162), or it shows that regulating processes need not result in bounds that are significantly narrower than those 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), though it would support the ideas of Andrewartha & Birch (1954). It was therefore necessary to test this expectation. A minor modification of the simulations used in section 4 enabled this.

In the field, very low densities which cause zero year-catches in uninterrupted sampling runs cannot be distinguished from actual turnover (extinction and/or (re)founding) of the local populations concerned.<sup>+</sup> In the simulated "populations", however, the density level can be adapted such that "survival" during 12 years (or less) is ensured. These computer populations can then be "sampled" with different intensities resulting in simulated sampling runs at different catch-levels (section 4). Zero "year-catches" in such simulated sampling runs can then only be due to very low densities, and will thus represent a kind of "pseudo-turnover". These estimates of pseudo-turnover can be used to correct the (gross) turnover as suggested by zero year-catches in sampling runs from the field. To cover all possible cases where correction for pseudo-turnover was necessary, I had to simulate 4032 sets of estimates each based on 500 simulations, i. e. for each species at each catch-level (between 1 and 7) and for each run of sampling years (between 4 and 12) separately (64\*7\*9). More details of this method are given in Den Boer (1985). For the present discussion it suffices to remark that in this way all uninterrupted sampling runs from the field of all 64 species could be corrected for the expected pseudo-turnover (zero year-catches because of very low densities only) at the adequate catch-level.

As a result, pseudo-turnover appeared to be very important, so much so that initially I doubted whether any part of the gross turnover in our relatively short sampling runs could still be attributed to local extinction and/or (re)founding. However, in only 4 species was mean pseudo-turnover higher than the overall gross turnover from the field data. In all other species there were distinct indications of a restricted survival time (the reverse of corrected turnover) of local populations, in spite of the great variability of the field data and of the high variance of pseudo-turnover itself (with standard deviation and average of about the same value). In Fig. 4 the mean values for corrected turnover (as the arc sine values of the square root) of all 64 species are plotted against DPS (section 4). The value of DPS of a certain species appears to be negatively correlated with the expected mean survival time of its

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<sup>+</sup> Turnover is conceived to be the frequency of (sub)population extinctions or (re)foundings in a number of long-term population samplings with standard sets of pitfalls (Den Boer, 1977, Ic) expressed as a percentage of the total number of years the species continued its presence during these samplings.

local populations:  $r = 0.526$ ,  $p < 0.01$ ;  $p = 0.597$ ,  $p < 0.00003$ ). This means that low values of DPS (L-species with low powers of dispersal: section 4) go with relatively favourable mean survival times (around 40 years) of local populations, whereas high values of DPS (T-species with high powers of dispersal: section 4) are associated with low mean survival times (around 10 years) of local populations.

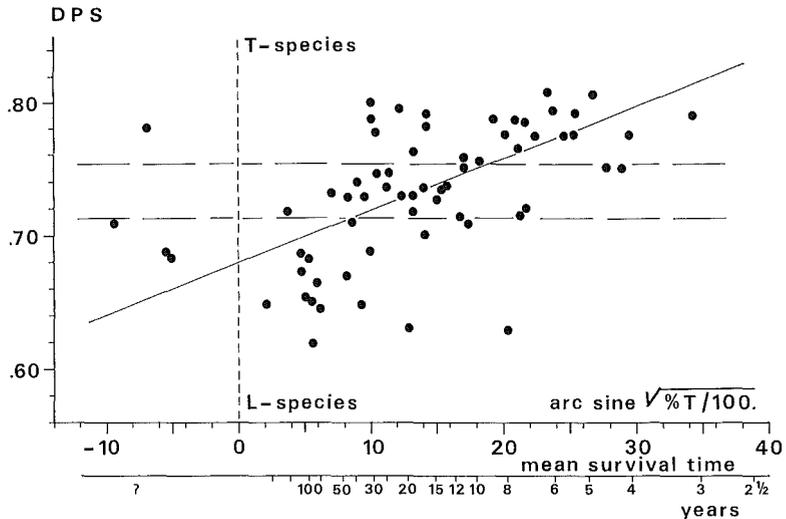


Fig. 4: Relationship between the corrected turnover (plotted as the arc sine values of the square root, with a scale of mean survival times added) and the Distribution of Population Sizes (DPS) in 64 carabid species of Drenthe (The Netherlands). Line of least squares (Bartlett):  $y = 0.679 + 0.00386(x)$ . Note the difference between L-species (DPS  $< 0.715$ ) and T-species (DPS  $> 0.753$ ).

The mean survival times that were estimated for the L-species fit in well with the conclusion of Den Boer (1977), that the DPS would give an estimate of the degree of Realization of Population Replacement (RPR) in a cultivated countryside. The great acceleration of cultivation and thus the major destruction of the large areas with natural (forest, peat-moor) and semi-natural (heath, blown-sand areas), rather stable habitats started at least 100 years ago (Den Boer, 1977, 8.1). This means that many local populations (especially the sparser and smaller ones) of the species inhabiting the nowadays generally isolated remnants of these permanent natural and semi-natural areas (L-species) will already have become extinct during this period in which the possibility to compensate by (re)foundings has rapidly decreased. This increasing "selection" of local populations during the last 100-200 years will thus have led to a gradual increase of the expected mean survival time of the local populations present simultaneously, and in most species this

agrees well with the magnitude of the values estimated. Note that the local populations still persisting at present are not merely those with higher densities (catches at higher catch-levels: Fig. 3), but also the only ones with random fluctuations of numbers (Fig. 3). Fig. 5 shows that these randomly fluctuating local populations of L-species are indeed those among the local populations with the best expectations of survival. Again, this does not favour the assumption that the survival of populations would benefit from special (regulating) processes.

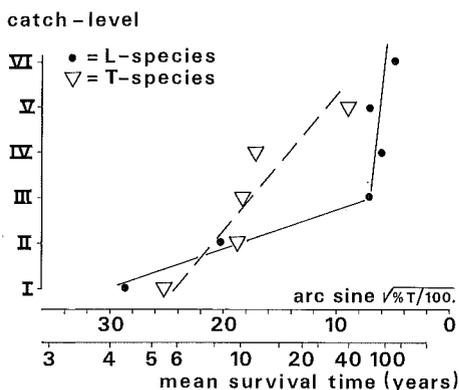


Fig. 5: Corrected turnover (and mean survival time) of local carabid populations with different density levels (indicated by the catch-level: section 4). T-species (high powers of dispersal) are compared with L-species (low powers of dispersal). No turnover could be estimated for catch-level VII in L-species and for catch-levels VI + VII in T-species, because too few local populations were available at these levels.

Comparison of figures 3 and 5 suggests that, at least as far as the L-species are concerned, the two tests (density-limits and turnover test) are quantitatively consistent with each other. This is not self-evident, in spite of the fact that both versions of the null models are based on R-values taken at random from the fitted LND's (section 3): in the density-limits test (section 4) sampling runs with zero year-catches could not be taken into account, whereas the turnover test (this section) works exactly with the frequency of zero year-catches. Therefore, it might be enlightening to estimate also expected survival times by extrapolating from the simulated populations of the density-limits model. However, to do this we need to know the absolute density levels of the field populations sampled, and for most species we only know relative densities. But our knowledge is sufficient to warrant the assumption that the majority of the local populations sampled will have had mean sizes between 400 and 10,000 individuals (interaction groups: Den Boer, 1977, 1979b). By simulating for all species at 4 different density levels between these limits, I could estimate for each species a most probable range of survival times and compare this with the relevant mean sur-

vival time from the turnover model. Fortunately, just as in the simulations treated in Den Boer (1981, Fig. 4), survival time appeared to be insensitive to differences in density level: on average the midrange did not differ more than 50% from the extremes. Because of this only slightly restrictive effect of density level, I could ascertain rather robustly that the survival times of the L-species as estimated by extrapolation of the density-limits model did not deviate systematically from those estimated with the turnover model ( $p = 0.98$ ; Wilcoxon's signed-ranks test: Sokal & Rohlf, 1969).

Such a satisfactory result was not reached in the case of the T-species, however: with only a single exception, the survival times obtained by extrapolating from the simulated populations of the density-limits model were all higher than those from the turnover model (Wilcoxon's signed-ranks test:  $p < < 0.01$ ). This was expected, since in T-species population numbers fluctuate less favourably than at random (Fig. 3), so that extrapolation from supposed random fluctuations will give too high survival times. For the same reasons, however, in the turnover model the corrections for pseudo-turnover might be too low which could result again in too low survival times. Nevertheless, I am convinced that in general the survival times of the T-species as estimated by the turnover model - though possibly not very reliable in the separate species - will not be too low. First, as the fluctuations of numbers in T-species are less favourable than random, very low densities (pseudo-turnover) will frequently pass into extinction. This increased chance of extinction is highly facilitated by the frequent downward trend in numbers in local populations of T-species, as indicated by negative values of  $\hat{E}(\ln R)$  in Fig. 6. Second, as high numbers of individuals of T-species participate in dispersal, local populations are readily (re)founded - as has been noted several times - so that actual turnover can not always be associated with zero year-catches, viz. not when rapid extinction is followed by successful refoounding within a year. The latter will occur especially in species that show change of habitat (Van Huizen, 1977), and also in some other species that usually live under highly unpredictable conditions. As it is known that, in at least part of these species, the majority of local populations will not persist for longer than one or two years in the same places, there are good reasons to suppose that the estimates of mean survival times of many T-species - as given in Fig. 4 - are even too high. An additional consideration supporting the latter opinion is, that because of technical restrictions, only three highly unstable habitats (out of 26) were sampled frequently enough to participate in the present analyses. As these 3 sites contributed only for 9% to the 190 year-samples available, the most short-lived local populations of typical T-species will have been severely underrepresented in our sampling runs. On the other hand, most T-species show an increasing tendency to settle down in more stable (especially semi-natural) habitats as well, where local populations could be expected to survive longer, but - interestingly enough - do not nearly reach the survival times of L-species (see: Den Boer, 1985, Fig. 4). The latter is an interesting consequence of the high level of dispersal which results in taking away many potential reproducers, and thus increases the chance of a downward trend in numbers (Fig. 6); see further: Den Boer (1985).

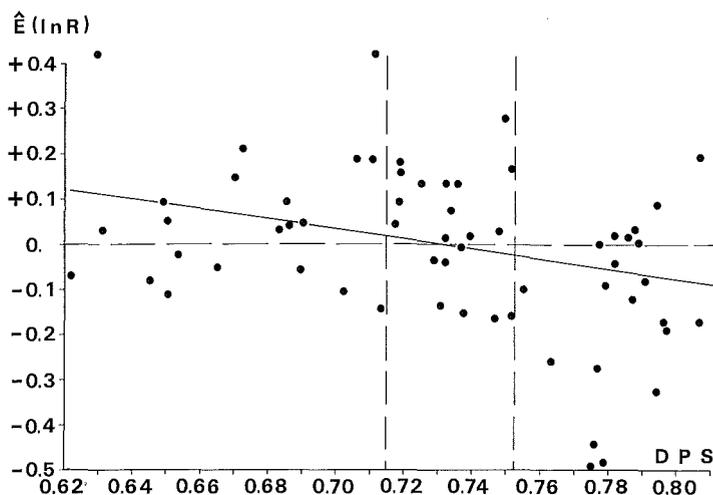


Fig. 6: Relationship between DPS (as an estimate of population replacement) and average  $\ln R$  (as an estimate of the trend in population numbers). At right: T-species ( $DPS > 0.753$ ); at left: L-species ( $DPS < 0.715$ ). A downward trend in population numbers is associated with a high level of population replacement:  $r = -0.339$  ( $p = 0.01$ ),  $r^2 = -0.328$  ( $p = 0.009$ ); least squares (Bartlett):  $y = 7.71 - 10.553(x)$ .

In summary, Fig. 4 most probably gives a realistic picture of the mean survival times of local populations of 64 carabid species in Drenthe, as long as we do not ask which species is represented by which dot. Also the magnitude of the overall differences in survival time between L- and T-species will not be much off the mark.

## 5. What do carabid beetles tell us about dynamics of populations?

The story told by carabid beetles in the foregoing sections is essentially the same as that told by Andrewartha & Birch (1954, 1984) and Thompson (1956) about a number of quite different animals: Life is a kind of lottery with more blanks than prizes, or in the present case: local populations will usually not survive very long, and the species will thus only persist if in the long run local extinctions are compensated by (re)-foundings. The latter will only occur if the powers of dispersal of the species are such that suitable places can be reached frequently enough. Therefore, dispersal is as essential to the survival of the species as reproduction is to the survival of the population: together they represent the money with which the lottery of life has to be played.

This continuous turnover of local populations is not restricted to the fringes of the geographical distribution of species. The estimated mean survival times of the local populations of the 16 species - among the 64 carabid species studied - that live in the Netherlands at the fringes of their distributional area do not deviate from those of the other species (Mann-Whitney U-test:  $z = 0.256$ ,  $p = 0.80$ ). Everywhere within the area of distribution of a species suitable as well as unsuitable habitats will be found, but - at least in carabid species - the frequency of suitable ones seems to decrease towards the fringes of the area (Den Boer, 1977, 8.2). The dynamics of local populations in suitable habitats, however, and thus mean survival times, will usually be similar at the fringes and in the centre of distribution. Because of the possibly more sparse distribution of suitable habitats at the geographical fringes of a species, the powers of dispersal can often be expected to be better there than nearer the centre. But the latter may also be the case, because the fringes became colonized rather recently. A higher frequency of winged specimens at the distributional fringes of a wing-dimorphic carabid species than in the centre is therefore a somewhat ambiguous finding (compare: Lindroth, 1949).

It may seem surprising that even among species inhabiting old permanent habitats like forest, the fluctuations of numbers are usually not better than random (Fig. 3), so that the survival time of local populations will only rarely exceed 100 years. This phenomenon is not restricted to carabid beetles in temperate regions: Wolda (1978) showed that in the tropics - and even in the tropical rain forest - insect numbers fluctuate as heavily as in temperate regions. As many carabid species of old permanent habitats will have lost, by the evolutionary processes described by Den Boer et al (1980), the capability to fly, the powers of dispersal will only suffice to cover short distances (by walking). Hence, if by cultivation such old permanent habitats become small and highly isolated remnants in an ocean of agricultural fields, within a few centuries all local populations of such species will have died out without compensation.

Only if the area of the habitat is large enough to contain more than a single local population, i. e. if it contains a number of interwoven subpopulations (interaction groups: Den Boer, 1977, 1979b) that show incompletely synchronized fluctuations of numbers, will matters be different. In such cases the risk of extinction of the (composite) population is spread over a number of subpopulations and is thus diminished (Den Boer, 1968). If the numerical fluctuations of the subpopulations are sufficiently different (cf. Den Boer, 1982, p. 225) spreading of risk can lead to an impressive increase of survival time: in the case of Pterostichus versicolor the integration of 10-14 subpopulations - together occupying an area of 100-200 ha - will magnify survival time 10- to 20-fold (Den Boer, 1981, 1982), which will thus reach the millennial scale. Note also that even in this case an average subpopulation fluctuates less favourably than at random (compare "similar subpopulations" of P. versicolor in the tables 2 and 3 (OPEN) in Den Boer, 1981).

It will be evident what we have to do to save the (carabid) species of old permanent habitats that now remain in a number of more or less iso-

lated remnants: make or keep these remnants as large and heterogeneous (from the point of view of carabid beetles) as possible. Further, we must try to diminish the degree of isolation of these habitat remnants as far as possible, for instance by connecting different remnants by corridors of a suitable type and/or by laying out "stepping stones". If, in spite of adequate measures the number of local populations continues to decrease, we will have to consider increasing the lowered chance of refounding by supplementing the insufficient powers of dispersal with our travelling abilities. Thus we will have to study the ecology of (re)founding and to practise it in (carabid) species that disappeared from remnants of stable habitat by providing reintroductions (see also: Den Boer, 1970).

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