

## **Density limits and survival of local populations in 64 carabid species with different powers of dispersal**

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### **Abstract**

Patterns of density fluctuations and survival times were estimated for the 64 most abundant carabid species, sampled continuously over 23 years with pitfalls in 89 sites in Drenthe (The Netherlands). I show that for most carabid populations density fluctuated between years, either randomly or between wider bounds than expected with random fluctuations. This was true for all groups, not just those occupying temporary habitats. I discuss the selective processes connected with dispersal (flight) abilities inside and outside populations of species occupying different kinds of habitat, and conclude that under natural conditions the powers of dispersal usually favour an optimal chance of survival of the species; this fits Wright's shifting balance model. Under cultivation, stable habitats have been drastically reduced and fragmented, so that local populations have become highly isolated and the risk of extinction is no longer spread over local groups. This has accelerated selection against dispersal features in isolated populations, so that species with low powers of dispersal apparently can no longer compensate for population extinctions by (re)foundings. Without adequate measures such species are doomed in these areas. Our work leads us to the conclusion that the current ideas on regulation of numbers and on group selection do not adequately describe the situation.

### **Introduction**

Because population biology could benefit from knowledge of expected survival times of natural populations this paper summarizes my findings on the long-term

population dynamics of 64 carabid species. The results of our comparative studies of the fluctuation patterns of numbers in many local carabid populations in diverse habitats, both of the same and of different species, are spread over a series of articles in different journals. It is now desirable to present the synthesis of many years of long-term experiments and field observations on many species. As the results of this synthesis generally confirmed the more speculative conclusions drawn previously (den Boer, 1968; 1970; 1971), 30 years of research by our group at the Biological Station Wijster allow us to draw rather definite conclusions on the processes governing the turnover of local populations. Therefore, our present knowledge of the dynamics and survival of carabid populations (den Boer, 1981; 1985; 1986a; Van Dijk, 1986), and of the evolution of dispersal abilities by flight in carabid beetles (den Boer et al., 1980), might also contribute to the resolution of two major controversies in population biology:

A) The lingering question of whether or not population numbers are regulated (Itó, 1980) would become less urgent if as a rule the population units, in which the "regulating" interactions are supposed to operate, persisted for only a small number of generations (den Boer, 1985).

B) If the time scale of selective processes within and between groups were commensurate, group selection (Wilson, 1983) could be represented as a variation on a general common model that expresses the total gene frequency change as the sum of two covariance components (Wade, 1985).

Moreover, as a more direct corollary of our work we can elucidate another, increasingly urgent problem:

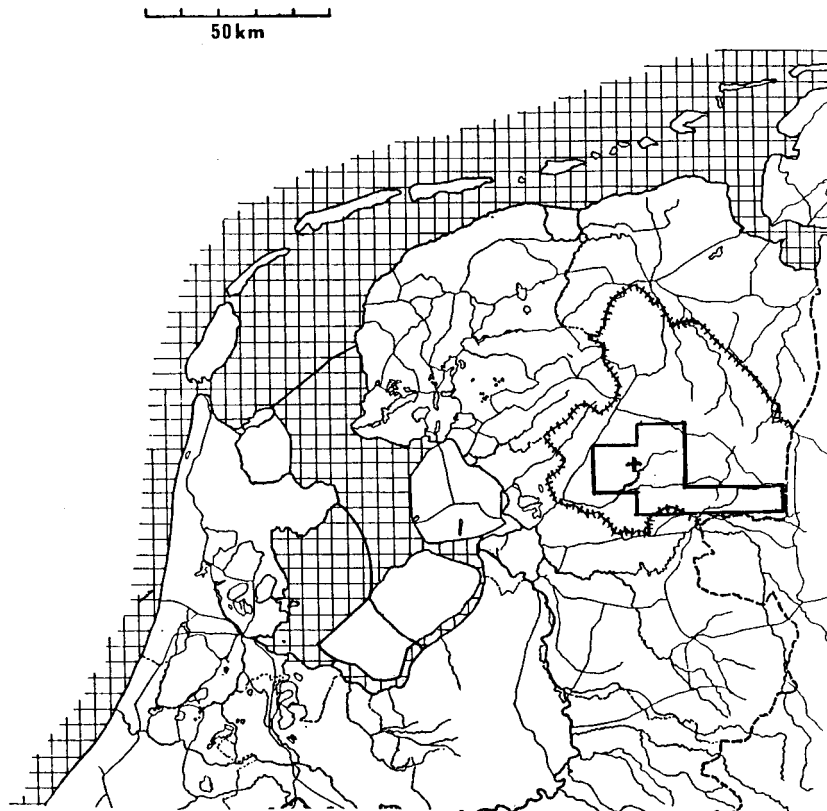
C) As soon as (re)founding of population units no longer compensates for extinction – e. g. because of rapid habitat destruction and fragmentation (Wilcox and Murphy, 1985) – the species concerned will be doomed in that area (den Boer, 1977; 1979a; Turin and den Boer, 1988).

In the following I will try to present the relevant results of our work in such a way that the principal conclusions are shown in a logical sequence, after which I will return to the above statements, to see how far they are supported. To stay within the boundaries of a journal paper the presentation of published results will necessarily be very concise, and details will have to be looked up in the cited papers. Data and results that have not yet been published elsewhere, and in particular the continuous thread through the story, will be treated more thoroughly.

## **Materials and methods**

### *1. Area and sampling sites*

Our sampling sites were situated in the central and southern parts of the province of Drenthe (Fig. 1), The Netherlands. This area, which has a poor sandy soil, was occupied by man thousands of years ago. At that time it was mainly covered by oak-birch forest and surrounded by huge peat moors. By the end of the Middle Ages most of the forest had been cut or burned down and was transformed into



**Fig. 1.** The northern part of The Netherlands with the area of investigation (framed) within the province of Drenthe (barbed boundary); +: the geographical position of the Biological Station Wijster.

heath. Because of overgrazing the dryer parts of the heath eventually changed into blowing sand, which for some hundred years has been partly fixed by planting it with pines. Some 200–100 years ago the remaining forest was reduced to small, isolated patches. Until the general use of artificial fertilizer began, cultivation was restricted to areas around the villages. The systematic reclamation of the heath and peat moor areas started about a century ago, and was only stopped in about 1962. Nowadays, the area is nearly completely cultivated. Forest, heath, peat moor and blown sand are found in small, isolated areas, except for a single heath (1600 ha) and some peat moor (70–1700 ha) reserves, and a few blown sand areas that are used for recreation. More information in den Boer (1977).

Within the framed area shown in Fig. 1, during 23 years (1959–1981), we sampled 22 deciduous forest sites, 10 coniferous plantations, 8 blown sand areas (partly fixed by vegetation again), 10 peat moor sites, 17 sites in heath, 12 grassy sites, and 10 cultivated sites; 89 sites in all. About 25 sites were unstable; either they were

inundated irregularly, or sometimes covered by blowing sand, or changed rapidly (within 20 years), or were arable land. In den Boer (1977) a representative set of 73 of these sites are described (with photographs). Sampling is still continuing.

## 2. *The sampling of carabid beetles*

Carabid beetles are most effectively sampled with the help of pitfalls, because these beetles move about randomly over the surface of the soil. By placing a standard set of pitfalls in the centre of a study site we sample it continuously the whole year round during one or more years (den Boer, 1977). Each week the beetles are collected from the pitfalls. By studying walking patterns in the field – by means of following radioactively marked beetles – and then simulating these patterns (Baars, 1979b), the pitfall catches could be quantitatively mimicked satisfactorily (Baars, 1979a). With the same walking patterns, which were tested again in extensive field experiments, it could be established in what area around the pitfalls ninety percent of the beetles currently caught in a year (*year-catch*, i.e. the sum of 52 week-catches) were moving about. This area varied among species from 0.05 ha for very small individuals (2–3 mm) to more than 200 ha for big individuals (about 20 mm), varying with the way of life and body size of the individuals (e.g. Baars and Van Dijk, 1984).

By using different methods Baars (1979a) as well as den Boer (1979b) could independently show that a year-catch of some carabid species in a standard set of pitfalls gives a surprisingly reliable (relative) estimate of mean density of the reproducing adults moving around the pitfalls. Carabid beetles are univoltine and do not have home ranges, which means that differences in walking activity, both between beetles and in time, are sufficiently levelled out in the course of the breeding season (some months); the more so, since mortality is usually low during the breeding season, and in most species many individuals survive for 2 or 3 years. Such a local group of beetles of a particular species is called an *interaction group*, because only these individuals have the potential to meet and thus to interact.

In this way we have collected many estimates of relative density of interaction groups of the 64 (out of more than 170) more abundant and widespread carabid species in the surroundings of Wijster: den Boer (1977, 1985). In our area, in particular interaction groups of middle-sized carabid beetles (7–12 mm, viz. about half of the species) usually coincide with quite natural habitat units of 1 to 12 ha that can easily be recognized physiognomically. Therefore, in most cases interaction groups in fact are local populations, which at the same time are the most suitable population units to study. The beetles moving around are feeding, copulating and laying eggs (usually one by one) into the soil. The larvae have a much smaller radius of action than the adults (in most species they live in the soil), so that the vast majority grow up within the radius of the group. By definition (Wright, 1969) an interaction group is thus comparable either to a *deme* – if isolated from other groups – or to a *neighbourhood*, if part of a continuum (being a subpopulation): for any carabid beetle caught in a standard set of pitfalls there is a high chance that

its parents were also living within the radius of the group sampled by the pitfalls.

The size of the interaction group, both in numbers and in space occupied, can be dependently estimated with the help of recaptures from high numbers of brand-marked individuals (Baars, 1979b; den Boer, 1979b). Interaction groups of most of the 64 carabid species studied appear to consist of a few hundred up to more than 200,000 individuals. Fewer than 0.1% up to a few percent (varying with the species) of these individuals are accumulated in a year-catch.

### 3. Dispersal in carabid beetles

Because of their walking pattern (previous section and Baars, 1979b) carabid beetles easily move out of the preferred sites, especially when these are small and are surrounded by agricultural areas (den Boer, 1970; 1977; 1979a). After some time such beetles will either return, if they are able to orientate themselves (e. g. Rijnsdorp, 1980), or change over to an extreme kind of directed walk in an arbitrary direction (Baars, 1979b), or climb the vegetation and fly away. Of course, flying can only occur when not only are large hind wings present, but also the wing muscles are fully developed. As the development of both wings and wing muscles is highly variable among carabid beetles (den Boer et al., 1980) the possibilities of dispersing by flight not only differ between species but also in time and in some species even in space (e. g. den Boer et al., 1980: Table 7). Since 1969 we have been recording the frequency of flight of the carabid species of Drenthe with the help of window traps (Southwood, 1966). Up to and including 1984, 13,630 carabid beetles belonging to 93 species were caught in window traps.

Therefore, we can discriminate between (A) species that disperse over short distances only; no wings at all, brachypterous, or only incidentally winged, wing-di(poly)morphic with a frequency of full-winged specimens below 1% and usually no catches in window traps, and (B) species that disperse well, also over great distances; each year multiple catches in window traps occur. In the (A)-species dispersal will principally occur by walking, which means that, even if no insurmountable barriers (roads, canals) are met, the distances covered within that season will only exceptionally exceed a few hundred metres (den Boer, 1970; Baars, 1979b; Rijnsdorp, 1980). Although in most well-dispersing (B)-species the majority of flight activities occur just before, and sometimes also after, the breeding season, usually there is no separation between a dispersal period and a reproductive period. In most species the development of ripe eggs in the ovaries overlaps with the gradual reduction of wing muscles (Van Huizen, 1979), and in some species the latter process is even independent of reproduction (e. g. Nelemans, 1987a). Up till now distinct migration was only observed by us in a single carabid species, *Amara plebeja*, which shows an obligatory change of habitat that is connected with an evident physiological change from flight towards reproduction without wing muscles (oogenesis-flight syndrome: Johnson, 1969), and the reverse process after reproduction (Van Huizen, 1977). There are doubtless more such carabids, especially among riparian and agricultural species, but in the present context they do

not play a part. Therefore, each departure of carabid beetles from one habitat, whether or not it is followed by colonization of another site, is called *dispersal*, though a few transitions to migration will thus be included.

#### 4. The Distribution of Population Sizes (DPS)

Within the 23 years of pitfall sampling each species could have been represented by a maximum of 290 year-catches, the total number of sampling years at 89 sites (Methods: 2). As for every species many year-catches contained zero specimens, only 6469 of the 18,560 possible year-catches of the 64 more abundant species counted one or more specimens. It appeared likely to be highly informative to study and compare the frequency distributions of the mean densities that were estimated from the year-catches of each of the 64 species (Methods: 2) over the 290 possible positions. Concerning the form of these density distributions two groups of species could be distinguished; (i) species with an approximately lognormal distribution of the 290 year-catches, i. e. species in which the zero year-catches fitted the distribution of the positive year-catches, and (ii) species with a left-truncated distribution of the 290 year-catches, i. e. species in which the frequencies in the lower non-zero classes are too low for a lognormal distribution, which means that the frequencies in the zero class are too high. Species of the first group usually disperse well, which mostly results from a high frequency – in comparison with abundance – of flight activities, these are B-species (Methods: 3). However, in a few cases a lognormal distribution is connected with extreme eurytopy; an example is given in Fig. 2. Species of the second group usually have relatively low powers of dispersal (A-species), owing to the coincidence of flight activities occurring only incidentally, or never, with a rather restricted habitat selection (stenotopic); an example is given in Fig. 3.

For each species the frequency distribution of the 290 year-catches over logarithmic classes (in this case  $\times 3$ -classes, see Williams, 1963) can be cumulated and plotted on probability paper (e. g. Southwood, 1966) as a *cumulation line*. Species of the first group (B) will show a straight cumulation line (as in Fig. 2), species of the second group (A) a clearly broken one (as in Fig. 3). See also: den Boer (1977, 1987).

To show that this marked difference between two kinds of cumulation lines does not merely result from the fraction of zero year-catches, the frequency distribution of mean densities, with zeroes excluded, was quantified by the expression:

$$\text{DPS (Distribution of Population Sizes)} = 1 - \frac{\sum \ln(n_i + 1)}{j * \ln(N + j)},$$

in which  $n_i$  = number of individuals of that species in year-catch  $i$ ;  $j$  = number of non-zero year-catches available from all years and all sites;  $N = \sum_{i=1}^j n_i$ . More information on this expression for DPS is given in den Boer (1977), to which Reddingius added a mathematical justification of this equation by analyzing its properties (Appendix to den Boer, 1977).

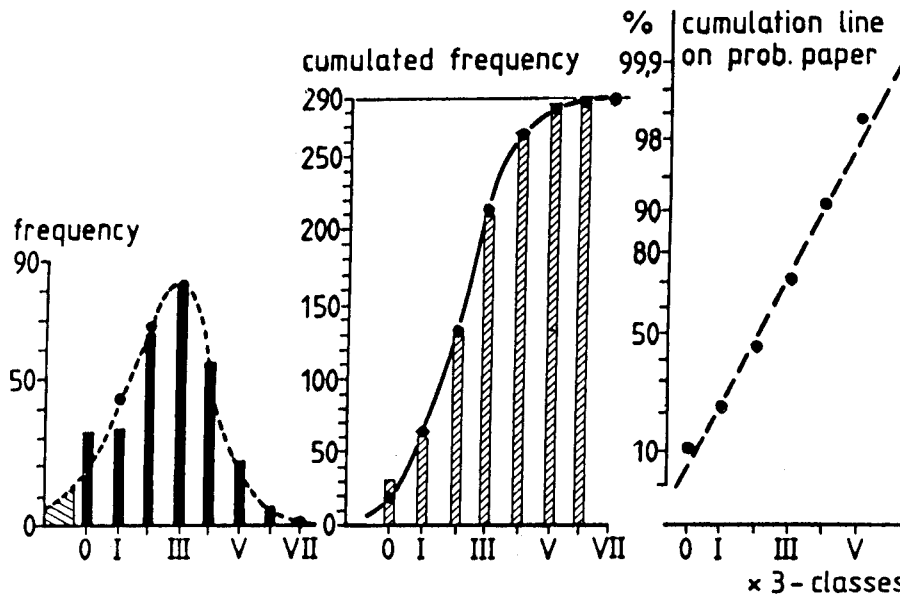


Fig. 2. Distribution of Population Sizes (year-catches cumulated from 290 sampling years at 89 sites) of *Pterostichus niger* Schall over  $\times 3$ -classes of catch-level (32 zero year-catches included), e. g. in class I: year-catches between  $\frac{1}{2}$  and  $1\frac{1}{2}$  (one ind.); in class III those between  $4\frac{1}{2}$  and  $13\frac{1}{2}$  (5–13 ind.), etc. At left: actual frequencies (filled bars) with fitted lognormal distribution (dots and broken line). Centre: cumulated frequencies (hatched bars) with cumulated lognormal (dots and line). At right: cumulated frequencies (as % of 290 "year-catches") plotted on probability paper with fitted cumulation line (by eye). *P. niger* has high powers of dispersal because it breeds well in nearly all kinds of habitat in our cultivated countryside, which means that suitable habitats can easily be reached by walking (it does not show flight activities); it is extremely eurytopic.

To separate the above (A) and (B)-species as distinctly as possible the 64 species were divided into three groups of about equal size: 1) 23 species with  $DPS > 0.753$ , which largely coincide with the above (B)-species and will be called T-species; they have high to very high powers of dispersal; 2) 21 species with  $DPS < 0.715$ , which largely coincide with the above (A)-species and will be called L-species; they generally show (L)ow powers of dispersal; 3) 20 species with  $DPS$  between 0.715 and 0.753, among which are found the less extreme cases of the former (A) and (B) groups; this group was inserted in order to separate the L- from the T-species more distinctly. Although this division into three groups is, of course, arbitrary, it is also unbiased, and most distinctly separates two extreme groups with respect to powers of dispersal.

##### 5. Density changes and density limits

As the year-catches of each of the 64 more abundant species, accumulated in the course of the 23 sampling years, can be considered relative estimates of mean

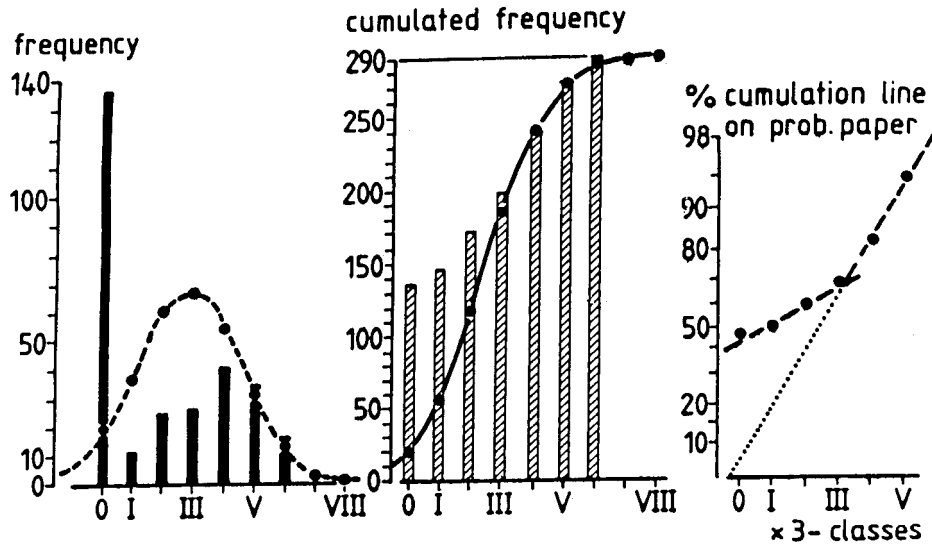


Fig. 3. Distribution of Population Sizes (year-catches) of *Pterostichus lepidus* Leske over  $\times 3$ -classes (136 zero year-catches included). For further explanation see Fig. 2. *P. lepidus* is a brachypterous (unwinged) species of dry, sandy heath areas. This kind of habitat, which covered large areas in The Netherlands some 150 years ago, has been reduced to about 5% (Turin and den Boer, 1988), which mainly includes small, isolated fragments of formerly large heath areas. Therefore, at present it has low powers of dispersal.

density (Methods: 2), for each of these species we could also obtain a set of estimates of the coefficients of net reproduction,  $R = n_t/n_{t-1}$ , in which  $n$  = estimate of mean density (year-catch), and  $t = 2, 3, \dots$ , marks succeeding breeding seasons (years), during which the species has been uninterruptedly sampled at some site without zero year-catches. In most cases, singletons were also excluded, so that the  $R$ -values will actually give estimates of the magnitude of the density changes from year to year in that species. For each of the 64 species the many net reproduction values thus collected appear to satisfy a lognormal distribution. The data on the 25 most abundant species are given in Table 1. The moments of such a distribution can be estimated according to:  $\text{mean}(Y) = 2 * \ln M - \frac{1}{2} * \ln(V^2 + M^2)$  and  $\text{Var}(Y) = \ln(V^2 + M^2) - 2 * \ln M$ , in which  $M$  and  $V^2$  are mean and variance of the set of  $R$ -values estimated from the available field data (columns B and C), whereas  $Y$  is the lognormal distribution fitted to these data (columns F and G), the moments of which can be compared to mean and standard deviation of the set of  $\ln R$ -estimates from the field (columns D and E) with a Chi-square test (columns H and I). In the Appendix to den Boer (1985) Reddingius showed the derivation of this procedure. Such a fitted lognormal distribution of  $R$ -values thus gives the frequencies in which differently sized density changes from year to year are expected to occur in the species concerned.

For every site that was uninterruptedly sampled during a number of years we could next estimate for each species with a sequence of positive year-catches of 4



**Table 1.** Data on the fluctuation pattern of numbers in local populations of the 25 carabid species most abundantly and/or frequently occurring in the surroundings of Wijster, Drenthe (The Netherlands) between 1959 and 1981.

Species	number of <i>R</i> -values	field data			field data			fitted			$\chi^2$ of comparison		d.f.
		<i>M</i> = mean <i>R</i>	$V^2$ = Var <i>R</i>	mean ln <i>R</i>	<i>S.d.</i> ln <i>R</i>	mean ln <i>R</i>	<i>S.D.</i> ln <i>R</i>	mean ln <i>R</i>	<i>S.D.</i> ln <i>R</i>	<i>F</i>	<i>G</i>	<i>H</i>	
<i>Notiophilus aquaticus</i> L.	94	2.253	10.996	.211	1.111	.236	1.074	1.162*	6				
<i>Trichocellus cognatus</i> Gyll.	56	2.100	8.518	.134	1.169	.204	1.037	10.028	6				
<i>Bradyellus ruficollis</i> Steph.	63	1.974	5.177	.186	1.039	.257	0.919	9.605	6				
<i>Loricera pilicornis</i> F.	69	2.004	10.521	.023	1.188	.052	1.134	3.329*	6				
<i>Dyschirius globosus</i> Herbst	59	1.874	3.354	.192	0.993	.293	0.819	5.364*	6				
<i>Amara lunicollis</i> Schiödte	112	2.045	9.408	.046	1.117	.126	1.086	8.046	6				
<i>Bradyellus harpalinus</i> Serv.	63	1.887	4.983	.133	1.025	.197	0.936	3.236*	6				
<i>Metabletus foreatus</i> Fourcr.	44	1.874	3.513	.174	0.977	.282	0.833	2.849*	4				
<i>Calathus erratus</i> Sahlberg	83	1.593	4.052	-.073	1.007	-.012	0.977	6.599	6				
<i>Nebria brevicollis</i> F.	51	1.427	3.084	-.098	0.953	-.105	0.960	2.868*	6				
<i>Amara plebeja</i> Gyll.	66	1.172	1.268	-.188	0.859	-.168	0.809	8.261	6				
<i>Agonum obscurum</i> Herbst	73	1.595	3.775	-.036	1.002	.012	0.954	5.731*	6				
<i>Calathus melanocephalus</i> L.	138	1.234	1.117	-.115	0.857	-.065	0.742	6.742*	8				
<i>Amara communis</i> Panz.	63	1.326	1.881	-.106	0.856	-.082	0.853	5.365*	6				
<i>Notiophilus biguttatus</i> F.	52	1.564	1.990	.115	0.830	.150	0.772	4.017*	6				
<i>Clinina fossor</i> L.	45	1.067	0.574	-.171	0.730	-.139	0.639	5.202	4				
<i>Pterostichus lepidus</i> Leske	92	1.289	1.612	-.054	0.813	-.085	0.823	9.042	6				
<i>Pterostichus nigrita</i> Payk.	78	1.344	2.061	-.042	0.804	-.085	0.873	4.685*	6				
<i>Pterostichus niger</i> Schaller	116	1.351	1.281	.008	0.838	.035	0.729	10.361	8				
<i>Olishopus rotundatus</i> Payk.	44	1.396	1.960	.024	0.798	-.014	0.834	6.101	4				
<i>Pterostichus diligens</i> Sturm	96	1.267	1.478	-.059	0.736	-.090	0.808	5.157*	6				
<i>Pterostichus versicolor</i> Sturm	136	1.341	1.328	.047	0.694	.017	0.744	9.892	8				
<i>Carabus problematicus</i> Herbst	58	1.352	1.424	.046	0.681	.014	0.759	7.729	6				
<i>Harpalus latus</i> L.	59	1.236	1.322	.004	0.607	-.100	0.790	10.495	6				
<i>Pterostichus oblongopunctatus</i> F.	66	1.164	0.379	.025	0.517	.029	0.497	4.197*	6				

Column A: *R* = coefficient of net reproduction = (year-catch of year *t*)/(year-catch of year *t* - 1), see text.

Columns B and C: *M* and  $V^2$  are mean and variance of the distribution of *R*-values estimated from the year-catches.

Columns D and E: mean and standard deviation of ln *R* (natural logarithms of *R*).

Columns F and G: mean and standard deviation of the fitted lognormal; see text.

Column H: Difference between the empirical (D, E) and the fitted (F, G) distribution of ln *R*;

\*:  $p > 0.50$ , in all other cases  $p > 0.10$ ; d.f. = degrees of freedom (column I).

Note: the species have been ranked according to decreasing values of [*S.d.* ln *R* + |mean ln *R*|] (columns E and D), which predicts the trend in numbers, and thus is highly correlated with LR (see Table 3).

years or more the range between the highest and lowest density recorded. This range is expressed as *Logarithmic Range* (LR) =  $\ln(\text{highest density}) - \ln(\text{lowest density})$  (den Boer, 1971; Reddingius and den Boer, 1970). From the many sites that were continuously sampled during 4 or more years we could thus get a fair impression of the limits between which density fluctuated during 4 or 5 or 6 . . . or 12 (23) years in the more favourable habitats, i. e. where zero year-catches do not often occur.

With only a few exceptions (den Boer, 1981) density fluctuations from many years of field sampling cannot be distinguished from randomly occurring fluctuations, which are easily simulated. Therefore, as a first approximation, for each of the 64 species realistic fluctuations of mean density could be obtained by multiplying a reasonable starting density with a series of randomly succeeding *R*-values that are taken from the lognormal distribution, the mean and variance of which were estimated from the field data (den Boer, 1985): Table 1 (B, C); (F, G). In the few populations in which *R*-values showed significant autocorrelations in time this was taken into account in the simulations. In connection with the following it is important to note that in these few cases the ranges within which density fluctuated were either about the same as, or wider than, those with randomly succeeding *R*-values (compare: den Boer, 1981).

For each species and for each number of uninterrupted sampling years at some site (4, 5, 6, and so on) we separately simulated 500 sets of density fluctuations, in such a way – by starting from a sufficiently high “initial density” – that these 500 simulated populations “persisted” (= lowest density > 1) during at least that number of sampling years. From each set of 500 simulations 500 LR-values were thus obtained, from which were computed mean and standard deviation of the expected density ranges (*random-range models*), and this was repeated for each number of sampling runs of 4, 5, . . . 12 (23) years, just as these were carried out in the field.

## 6. Turnover of local populations

Apart from uninterrupted sequences of positive year-catches (previous section), for all species we frequently recorded zero year-catches that interrupted our sampling runs (e. g. den Boer, 1977: Table 9). Such zero year-catches may give us a first impression of the *turnover* of local populations, i. e. of the frequency of extinctions and/or (re)foundings of interaction groups (Methods: 2). In accordance with the usage in island biogeography (e. g. Diamond, 1969; Schoener, 1983) turnover will be expressed as the frequency of (sub)population extinction or (re)founding during a number of long-term population surveys of some species, given here as a percentage of the total number of years the species was present at the study sites during these surveys (see further: den Boer, 1985). Hence, a turnover of 4% means that, on average, among 100 positive year-catches of that species in different sites, we recorded four cases of either “disappearances” (followed by a zero year-catch) or “appearances” (preceded by a zero year-catch) of the species.

Although frequent turnover is indeed suggested by the regular occurrence of zero year-catches, in the field exceptionally low densities cannot be distinguished from actual turnover as a cause. In the simulations, however, the density level of each species was chosen in such a way that “persistence” during that run of sampling years is ensured. Just as in the field, also the computer populations of that species can be “sampled”, in this case with different intensities. This means that different percentages of the “beetles” are “taken away” as “catches”, resulting in sampling-runs at different “catch-levels” ( $q$ ), i. e. runs with the highest catch between  $\frac{1}{2} \cdot 3^q$  and  $\frac{1}{2} \cdot 3^{q+1}$  ( $q = 1, 2, 3, \dots, 7$ ). Zero “year-catches” (values  $< 1$ ) in such simulated sampling-runs thus indicate “exceptionally low densities”; they measure “pseudo-turnover” in the sense of Nilsson & Nilsson (1983). For each species, for each run of sampling years between 4 and 12 (23), and for each catch-level (between 1 and 7), the expected pseudo-turnover (%) – and its variance, from 500 simulations – was thus computed.

Of course, each sampling run from the field also occurred at a definite catch-level, and its gross turnover could thus be adequately corrected for the expected pseudo-turnover. Because of the high level of variation both in the field data and in the simulations only the overall results per species were reliable and thus interesting (den Boer, 1985). Within the restrictions of area (Drenthe) and time (23 years of research), corrected turnover now estimates the chance (% $T$ ) that in some year one or other local population of that species will become extinct or will be (re)founded. The reciprocal of corrected turnover, times 100, thus gives the expected mean survival in number of years of an average interaction group (local population) of that species. An example of this procedure is given in Table 2.

As we estimated Logarithmic Ranges (LR's) from uninterrupted sequences of positive year-catches it could be expected that extreme  $R$ -values (previous section) might be relatively underrepresented in the frequency distributions, which might also affect our simulations and the resulting estimates of pseudo-turnover. Therefore, as far as possible, we compared both the  $R$ - and the LR-values derived from series at a high catch-level (taken from favourable habitats) with those from series at a lower catch-level (from less favourable or marginal habitats) of the same species. Such comparisons were possible for 32 of the 64 species: in 21 species no difference could be found between fluctuation patterns at different levels (3 to 7 per species); in 6 species density fluctuated less heavily at high than at lower catch-levels, and in 5 species just the reverse was observed. Hence, considered over all species we need not expect systematic estimation errors in our values of corrected turnover, though in a minority of the species these estimates may either be somewhat too high or somewhat too low. We carried out a similar procedure to compare short (4 or 5 years) with long (8 or more years) sequences of positive year-catches, and reached the same kind of results; no systematic deviations, but in some species there were higher LR- and more extreme  $R$ -values in short series than in long ones, or, in other species, the reverse was found. We thus have good reasons to expect that our estimates of mean survival times of local populations are of the right magnitude, and can be used as long as we do not ask for an exact value for one particular species.

**Table 2.** Estimation of average turnover of local populations by correcting (gross) turnover for the pseudo-turnover at the correct catch-level (see text) in *Bradycellus ruficalis* Steph., an L-species in which the LR-values of the field series do not deviate from those predicted by simulations with random fluctuations of numbers ( $\chi^2 = 0.492$ ,  $df = 2$ ). Direct extrapolation of these simulations gives survival times for local groups between 30.4 and 43.1 years (initial population size between 400 and 10,000 individuals). Catch-levels are brought into  $\times 3$ -classes; compare legend to Fig. 2. Only sampling runs with the highest year-catch  $> 2$  (catch-level  $I = \frac{3}{2} - 1\frac{1}{2}$  is excluded) are included. For each run of year-catches 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 (or equal to) unity ( $a$ ), after which  $\frac{1}{2}(a + d)$  is weighted against the total number of years in the run with positive catches ( $y$ ); then uncorrected turnover =  $\frac{1}{2}(a + d)/y$ . 100%

Sampling site	recorded run of year-catches	run of ... years	catch-level	a	d	y	Uncorrected turnover (%)	estimates of pseudo-turnover (%)	estimates of corrected turnover (%)	imperfect estimates of survival times
N	90, 53, 54, 80, 27, 62, 37, 12, 4, 3, 45, 64	12	V	0	0	12	0.0	1.9127	-1.913	??
Z	458, 311, 72, 24, 97, 30, 26, 11, 44, 87, 69	11	VII	0	0	11	0.0	0.3570	-0.357	??
CF	25, 2, 12, 21, 29, 10, 11, 33	8	IV	0	0	8	0.0	2.9082	-2.908	??
AT	-, 4, 1, 4, 1, -, -, -	8	II	1	1	4	25.0	26.0291	-1.029	??
AU	36, 10, 11, 12, 21, -, 4, 14	8	IV	1	1	7	14.3	2.9082	11.392	8.78
AV	8, 10, 4, 8, 23, -, 1, 5	8	IV	1	1	7	14.3	2.9082	11.392	8.78
M	-, -, 1, 2, 1, -, -, 3	8	II	2	1	4	37.5	26.0291	11.471	8.72
AG	13, 16, 12, 34, 37, 120, 43	7	V	0	0	7	0.0	0.6636	-0.664	??
AZ	-, -, 7, 11, 1, 1, 6	7	III	1	0	5	10.0	7.3429	2.657	37.64
BJ	4, 4, 2, -, -, -	6	II	0	1	3	16.7	24.5000	-7.800	??
BB	3, 16, 82, -, 30, 85	6	V	1	1	5	20.0	0.4399	19.560	5.11
AE	2, 2, -, 1, -, 1	6	II	2	2	4	50.0	24.5000	25.500	3.92
AY	59, 85, 251, 4, 13	5	VI	0	0	5	0.0	0.0409	-0.041	??
P	1, -, -, 2, -	5	II	1	2	2	75.0	20.2030	54.797	1.82
AM	-, -, 3, -, 1	5	II	2	1	2	75.0	20.2030	54.797	1.82
O	14, 13, 4, 8	4	IV	0	0	4	0.0	0.6421	-0.642	??

16 sampling sites with 114 sampling years result in:  $\Sigma a = 12$ ,  $\Sigma d = 11$ ,  $\Sigma y = 90$ , and in a mean pseudo-turnover of 10.099%. Gross turnover is  $\frac{1}{2}(12 + 11)/90$ . 100% = 12.78%, by which corrected turnover would be 2.68%. The mean survival time of a local population of this species is thus estimated at 37.33 (37) years, which fits the estimates from direct extrapolation of the random-range models (see headlines).

## Results

### 1. Logarithmic Ranges in the field and in random-range models

When considering the Logarithmic Ranges (LR, Methods: 5) of sampling runs, without zero year-catches, of 4, 5, . . . 12 (23) years in the field, in a particular species, as a rule the mean density of the local population appeared to fluctuate between wider bounds than was predicted from the pertinent random-range models. Some technical complications are passed over here; see also den Boer 1985: Table 1). This means that, in the field, time series fluctuating more heavily than a random walk appear to occur more frequently than less fluctuating series, which implies that many of these series, especially those at low density-levels, will not persist very long. This is a remarkable result, because in the separate field runs the fluctuations could not be distinguished from randomly occurring ones; apparently, the deviations from randomness are too subtle to appear directly from the current sampling runs (these should be longer than 12 years for that). In total, there were only 4 out of 64 species, in which, in the field, significantly more runs with Logarithmic Ranges (LR) narrower than was predicted by the random-range models occurred; on the other hand in 22 species, in the field, there were significantly fewer LR's narrower than predicted, and in the remaining 38 species the numbers of narrower and wider LR's of the field runs fitted the predictions from the random-range models reasonably well ( $p > 0.10$ ). Compare Table 3, where data for the 25 most abundant species are presented.

As the species in Table 3, just as in Table 1, are ranked according to decreasing values of  $[S.d. \ln R + |\text{mean} \ln R|]$  we may expect that this sequence, which predicts a decreasing time trend in the population numbers, will be correlated with the corresponding density ranges (LR in last column). This expectation is answered:  $r_s$  (Spearman) = +0.73 ( $p = 0.0003$ , 2-sided) for columns E + |D| of Table 1, and  $r_s = +0.65$  ( $p = 0.002$ , 2-sided) for columns G + |F| of Table 1, which supports the reliability of our methods.

### 2. Population replacement

During the last century most local populations of the poorly-dispersing species (usually L-species: Methods: 4) have become isolated in remnants of their old habitats. At present, they show relatively high densities there, because they have mainly survived in the more favourable sites. These latter populations generally satisfy the random-range models (Methods: 5) in that, on average, density indeed fluctuated randomly within the expected bounds (den Boer, 1985: Fig. 2): Table 3, e. g. the L-species *Notiophilus aquaticus*, *Calathus erratus*, *N. biguttatus*, *Pterostichus lepidus*. As randomly fluctuating numbers are apparently the best from the point of view of survival times that can be expected to occur in the field it is no coincidence that especially local populations of L-species show this pattern: it is mainly these populations that have been able to persist up to now. However, because of the

**Table 3.** Numbers of sampling runs in the field that show narrower (na) or wider (wi) density ranges than the mean Logarithmic Ranges (LR) from simulations under the assumption of randomly succeeding *R*-values (see Table 1), as compared with the expected frequencies of deviations according to these random-range models. The data concern the same 25 species in the same ranking as in Table 1. Some mean LR-values are added in the last column.

Species	in the field		expected		$\chi^2$ of comparison	ranges of field runs usually are:	mean LR of 8-year series (n)
	na	wi	na	wi			
<i>Notiophilus aquaticus</i> L.	41	20	45.6	15.4	1.838		2.846 ( 6)
<i>Trichocellus cognatus</i> Gyll.	18	17	25.1	9.9	7.100***	too wide	3.694 ( 4)
<i>Bradycellus ruficollis</i> Steph.	25	12	26.9	10.1	0.492		3.053 ( 5)
<i>Loricera pilicornis</i> F.	24	13	28.9	8.1	3.795*	too wide	3.135 ( 7)
<i>Dyschirius globosus</i> Herbst	22	16	27.7	10.9	3.346*	too wide	3.120 ( 6)
<i>Amara lunicollis</i> Schiedte	50	29	54.4	26.6	1.084		2.229 (12)
<i>Bradycellus harpalinus</i> Serv.	22	16	30.6	7.4	12.417***	too wide	2.743 ( 7)
<i>Metabletus foveatus</i> Fourc.	7	13	13.6	6.4	10.010***	too wide	3.689 ( 6)
<i>Calathus erratus</i> Sahlberg	35	17	34.8	17.2	0.004		1.947 ( 5)
<i>Nebria brevicollis</i> F.	23	13	24.5	11.5	0.288		3.084 ( 7)
<i>Amara plebeja</i> Gyll.	24	30	34.7	19.3	9.232***	too wide	3.157 (12)
<i>Agonum obscurum</i> Herbst	34	20	37.5	16.5	1.069		2.708 ( 8)
<i>Calathus melanocephalus</i> L.	49	48	60.9	36.1	6.248***	too wide	2.492 (11)
<i>Amara communis</i> Panz.	22	25	30.0	17.0	5.898**	too wide	2.908 (10)
<i>Notiophilus biguttatus</i> F.	21	12	21.8	11.2	0.087		2.607 ( 5)
<i>Clivina fossor</i> L.	15	20	23.3	11.7	8.845***	too wide	2.742 ( 6)
<i>Pterostichus lepidus</i> Leske	39	25	43.1	20.9	1.194		2.061 ( 6)
<i>Pterostichus nigrita</i> Payk.	43	9	41.5	10.5	0.269		1.902 ( 5)
<i>Pterostichus niger</i> Schaller	41	41	57.3	24.7	15.394***	too wide	2.520 (10)
<i>Olisthopus rotundatus</i> Payk.	23	8	21.9	9.1	0.188		2.200 ( 4)
<i>Pterostichus atligens</i> Sturm	37	23	40.4	19.6	0.876		2.263 ( 6)
<i>Pterostichus versicolor</i> Sturm	68	28	60.8	35.2	2.325		1.911 (12)
<i>Carabus problematicus</i> Herbst	30	8	24.8	13.2	3.139*	too narrow	1.688 ( 6)
<i>Harpalus latus</i> L.	36	9	29.8	15.2	3.819*	too narrow	2.464 ( 6)
<i>Pterostichus oblongopunctatus</i> F.	20	25	26.6	18.4	4.005**	too wide	1.484 (10)

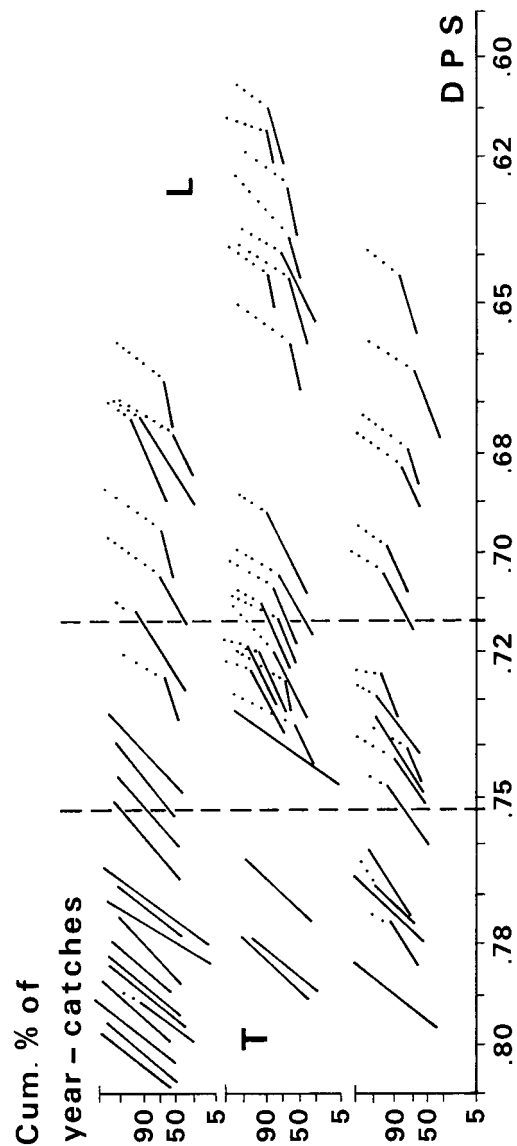
Last column: mean of the Logarithmic Range (LR)-values for uninterrupted sampling runs in the field during 8 years (the most generally occurring run-length); between brackets the number of runs. LR estimates the limits between which density has been fluctuating (here: during 8 years).

\* = 0.10 > *p* > 0.05    \*\* = 0.05 > *p* > 0.01    \*\*\* = *p* < 0.01    in all other cases *p* > 0.10

highly increased distances between habitable sites, we can be sure (see also den Boer, 1977) that it is unlikely that these poorly-dispersing species can still compensate for the extinction of local populations by (re)foundings. Because of this incomplete population replacement, at present these species rarely occur in more-or-less isolated, marginal habitats, and thus in low densities. Because of that, such species tend to show broken cumulation lines and low DPS-values (Methods: 4): e. g. Fig. 3. The few marginal groups (with low densities) of these poorly-dispersing species which are still observed "behave" just as do all the local populations of most of the well-dispersing species (T-species), in that they fluctuate more frequently than predicted between wider density bounds than would be expected according to the above random-range models (den Boer, 1985: Fig. 2); compare e. g. the T-species *Clivina fossor*, *Loricera pilicornis*, *Amara plebeja* (Table 3).

As DPS expresses the same feature as the cumulation lines, the degree of incompleteness of population replacement, in Fig. 4 we could quantitatively discriminate between well-dispersing and poorly-dispersing species by arranging the cumulation lines according to the corresponding DPS-values. This figure convincingly shows the remarkable difference between the frequency distributions of population sizes of T- and L-species respectively. In Table 4 we ranked the 25 most abundant species in the same way as all 64 species in Fig. 4, i. e. according to decreasing DPS-values, and added the relevant data on dispersal (Methods: 3) and turnover (Methods: 6).

Most L-species (12 out of 21) were never caught in window traps, and 5 more species only incidentally (<10 catches in 15 years). This means that 4 L-species still show some dispersal by flight, but, apparently, this does not suffice to compensate for extinctions by (re)foundings. In two of these four species this can be understood as a consequence of stenotopy, *Bradycellus ruficollis* (Table 4) being restricted to old *Calluna*-vegetation, and *Trichocellus placidus* Gyll. (not in the table) to deciduous forest; because of this, the chance to colonize new suitable habitats to a sufficient degree may well be too low. *Pterostichus diligens* (Table 4) is less stenotopically restricted to grassy moor vegetation, but it is much more hampered in finding suitable habitats than e. g. the eurytopic T-species *Nebria brevicollis*, which has about the same relationship between window trap and pitfall catches (0.0014 and 0.0019 respectively). *Amara lunicollis* is a special case, and in this respect a confusing one, since it is involved in a rapid evolutionary process from a T- towards an L-species (see den Boer et al., 1980, and Discussion: 1), resulting in great differences in dispersal power between populations. Nevertheless, the catches in window traps of the 21 L-species are highly significantly lower than those of the 23 T-species (Mann-Whitney  $p = 0.0015$ , one-sided), in spite of the many times higher population densities in L-species than in T-species (Table 4: column P divided by L). It should be noted that the window trap catches of *Amara plebeja* are exceptional in that it is a migratory species (Methods: 3). We have sound indications that the same applies to *Bradycellus harpalinus*, though up till now this has not yet been supported by the necessary studies.



**Fig. 4.** Cumulative frequencies of year-catches (1959-'81) in log-classes (at base 3; compare Figs. 2 and 3, zero class included), for the 64 most abundant carabid species in Drenthe, first plotted as individual "cumulation lines" on a probability scale, and then arranged according to the corresponding DPS-values: Methods: 4, and den Boer (1977). The vertical dashed lines divide the species into three groups of about equal size: 23 T-species with DPS > 0.753, 20 species with DPS between 0.753 and 0.715, and 21 L-species with DPS < 0.715. The upper parts of the broken cumulation lines are stippled for clarity only.



**Table 4.** Data on the Distribution of Population Sizes (DPS), dispersal and turnover of local populations of the 25 carabid species most abundantly and/or frequently occurring in the surroundings of Wijster, Drenthe (The Netherlands) between 1959 and 1981.

Species	field data 1959–1981			in window traps 1969–'84	field data % Turnover (corrected)
	j	N	DPS	U	W
T-species					
<i>Amara plebeja</i> Gyll.	182	1,934	.797	3,744	3.28
<i>Clivina fossor</i> L.	129	502	.796	59	4.66
<i>Loricera pilicornis</i> F.	200	1,699	.787	107	3.20
<i>Pterostichus nigrata</i> Payk.	210	1,902	.781	8	?
<i>Nebria brevicollis</i> F.	149	2,122	.754	4	9.16
<i>Olisthopus rotundatus</i> Payk.	89	658	.748	–	4.22
<i>Amara communis</i> Panz.	148	4,503	.747	191	3.41
<i>Pterostichus niger</i> Schaller	254	3,861	.739	–	2.50
<i>Bradycellus harpalinus</i> Serv.	151	1,544	.735	5,345	7.34
<i>Harpalus latus</i> L.	158	5,095	.733	12	5.85
<i>Agonum obscurum</i> Herbst	166	2,674	.730	–	2.12
<i>Trichocellus cognatus</i> Gyll.	126	3,024	.726	83	7.03
<i>Metabletus foveatus</i> Fourcr.	108	1,498	.718	1	13.71
<i>Carabus problematicus</i> Herbst	147	3,187	.716	–	0.42
L-species					
<i>Bradycellus ruficollis</i> Steph.	147	4,123	.710	94	2.68
<i>Dyschirius globosus</i> Herbst	157	12,166	.707	–	8.98
<i>Amara lunicollis</i> Schiødt	212	31,664	.690	182	?
<i>Pterostichus diligens</i> Sturm	202	7,762	.689	11	3.04
<i>Notiophilus aquaticus</i> L.	174	11,687	.673	–	0.73
<i>Notiophilus biguttatus</i> F.	118	4,444	.671	7	2.14
<i>Pterostichus lepidus</i> Leske	154	6,339	.664	–	1.10
<i>Pterostichus versicolor</i> Sturm	233	33,902	.650	7	0.88
<i>Calathus melanocephalus</i> L.	207	35,229	.649	–	0.15
<i>Calathus erratus</i> Sahlberg	137	15,449	.646	–	1.11
<i>Pterostichus oblongopunctatus</i> F.	145	19,511	.631	2	5.03

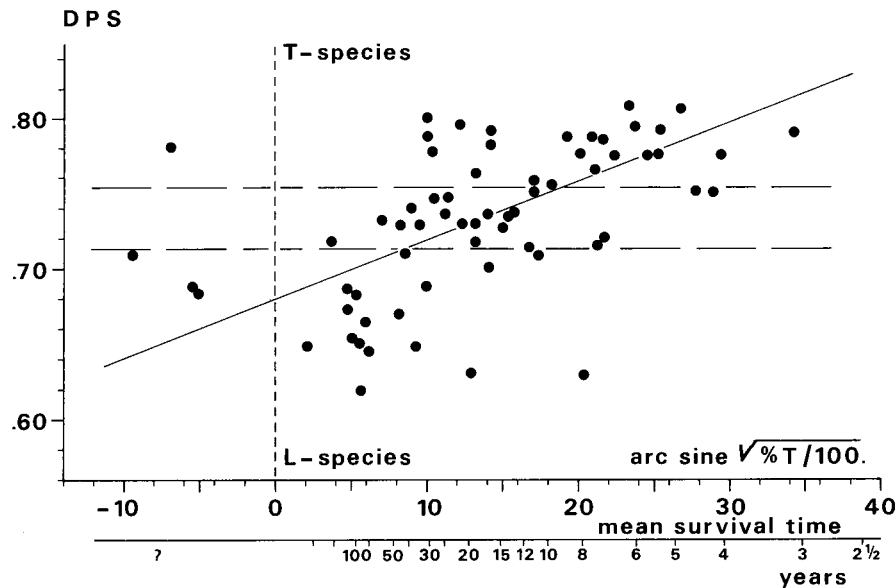
Columns L, P and S: j (number of year-catches) and N (total number of individuals caught) for the computing of DPS (see text).

Column U: number of individuals caught during the act of flying (in window traps, see Den Boer, 1977). Column W: see text; the % Turnover (corrected) is highly correlated with DPS; see Fig. 5.

The species are ranked according to decreasing values of DPS, so that the first 5 species are T-species and the last 11 L-species. The turnover of these T-species is significantly greater than that of the L-species (Mann-Whitney:  $p = 0.027$ ); compare Fig. 5.

### 3. Turnover of local populations and survival times

It is already clear from Table 4 (column W) that the turnover of local populations of L-species is much lower than that of other carabid species, which will be still more evident from Fig. 5. This figure shows that local populations of our 64 carabid species on average appear to survive for rather restricted periods only, in



**Fig. 5.** Relationship between the corrected turnover, plotted as the arcsin-value of the square root of  $\%T/100$ , of local populations (with an added scale of mean survival times) and the Distribution of Population Sizes (DPS) in 64 carabid species of Drenthe (The Netherlands). The relationship is highly significant:  $r$ (product-moment corr.) = +0.526 ( $p \ll 0.01$ ), or  $r_s$ (Spearman) = +0.597 ( $p < 0.00003$ ), and can be described by the least squares line (Bartlett):  $Y(\text{DPS}) = 0.679 + 0.00386(X)$  with limits of confidence (95%):  $0.659 + 0.00533(X)$  and  $0.697 + 0.00255(X)$  respectively. The mean survival time of local populations of L-species (DPS < 0.715, below lower broken line) is highly significantly better than that of T-species (DPS > 0.753, above upper broken line): Mann-Whitney,  $p \ll 0.00006$ . Further explanation in the text.

T-species around 8–10 years, in L-species around 40 years. By comparing the turnover of local populations of T-species with that of L-species that coexist in the same habitats (and are thus sampled by the same pitfalls) it could be shown that the low survival time of such groups of T-species is not so much determined by the degree of instability of the habitats occupied – as might be assumed by Southwood (1962) – but more by the instability of the populations themselves: Table 5. In all kinds of habitat local populations of T-species show an overall similar turnover, but much higher than that of L-species. This instability undoubtedly results from the high level of dispersal (emigration) by flight. These flight activities are especially stimulated by weather conditions favourable for flying (Van Huizen, 1979), and are thus largely independent of habitat conditions. In some years this takes away so many potential reproducers that in most T-species population numbers show a downward trend on average (indicated by a negative mean  $\ln R$ : den Boer (1985: Fig. 5); compare also Tables 4 and 1.

Since in most local populations of L-species numbers fluctuate between similar bounds (LR) as in the matching random-range models (Methods: 5), we could

**Table 5.** Turnover and expected survival time of local populations of L-species (low powers of dispersal) and T-species (high powers of dispersal) respectively, which were sampled in the same habitats (with the same pitfalls). It is demonstrated that independent of the level of stability of the habitats sampled, T-species show a much higher turnover than L-species.

Group of about equally stable sample sites	L or T	number of sites	number of species	$\Sigma z^{11}$	$\Sigma y^{22}$	mean pseudo- turnover	Turnover (%) uncorrected	corrected	mean survival time (years)
old deciduous forest	L	5	16	24	309	5.0090	3.8835	-1.1255	>100 (?)
	T	5	16	87	214	12.3140	20.3271	8.0131	12
borders of forest	L	3	17	40	207	6.8865	9.6618	2.7754	36
	T	3	17	54	148	9.4053	18.2432	8.8380	11
old, moist heathland	L	4	15	46	361	4.5386	6.3712	1.8326	55
	T	4	22	186	361	12.8308	25.7618	12.9310	8
dry heathland, inland dunes	L	4	12	32	261	2.2341	6.1303	3.8961	26
	T	4	19	107	230	11.6944	23.2609	11.5664	9
poor, grassy heathland	L	3	11	33	154	5.2182	10.7143	5.4961	18
	T	3	17	79	170	13.6424	23.2353	9.5929	10
abandoned agricultural fields	L	3	13	38	127	10.2858	14.9606	4.6749	21
	T	3	16	68	261	5.6375	13.0268	7.3893	14
wet, instable sites in heath	L	4	13	41	171	4.8382	11.9883	7.1501	14
	T	4	18	75	164	9.5923	22.8659	13.2735	8

<sup>1)</sup> number of times that a positive year-catch turned into a zero one, or the other way round (= uncorrected number of local disappearances or appearances of catches in a standard set of pitfalls), summed over all species and sites;  $z = a + d$  of Table 2.

<sup>2)</sup> number of years with positive year-catches, summed over all species and sites. Note, that uncorrected turnover is  $[(\Sigma z/2)/(\Sigma y)] \cdot 100\%$ , e. g.  $[(24/2)/309] \cdot 100 = 3.8835$ .

extrapolate these models until “extinction” (starting from initial numbers between 400 and 10 000). We could thus compare the obtained mean survival times with those estimated from corrected turnover (Table 4, Fig. 5). The overall values from both approaches did not differ significantly (Wilcoxon’s signed-ranks test,  $P = 0.90$ ): in 8 species the random-range models gave lower and in 7 species higher survival times than corrected turnover. In 6 species both estimates of survival times covered the same range; Table 2 gives an example of such a species (further den Boer, 1986b). This means that, when working with density limits (Methods: 5) on average the results do not systematically differ from those when working with corrected turnover (Methods: 6). Of course, we could not apply this check of our methods to the T-species, but from other observations (den Boer, 1986b) we know already that the estimated survival times (Table 4; Fig. 5) are more likely to be too high than too low.

We are convinced that the magnitude of this data on turnover and survival does not only apply to these 64 carabid species from Drenthe during the 23 years of study, but is representative for other areas and other periods as well, and is not likely to be a particular feature of carabid beetles. Boycott (1936: 124–126), studied in 1915 and again in 1925 the fresh-water molluscs in 84 separated cattle ponds (in the parish of Aldenham, England), the exchange between which was brought about by ducks. From his data we could estimate a minimum turnover of 4.2 % per year among 200 small local populations (minimum, because turnover of the same species within the same pond between 1915 and 1925 was not recorded). This fits in well with the mean turnover of 6% per year for local groups of our 64 carabid species. It must be noted, however, that the estimated mean survival times of our carabid groups are most probably maximum values, because among the sampled groups of most species – in particular L-species – there were a number of neighbourhoods, which with other neighbourhoods occupied larger habitats. Such neighbourhoods show relatively favourable density fluctuations, by which survival times are substantially prolonged (see den Boer, 1981; 1986a). Nevertheless, together with the data of Boycott it gives us a first idea of the magnitude of mean survival times of more-or-less isolated natural population units of invertebrates.

## Discussion

### *1. Selection against dispersal*

Within isolated populations individual selection against properties favouring dispersal by flight will nearly inevitably occur, because emigrating individuals will both take away dispersal features from the group and will have a lowered chance of surviving (den Boer, 1970; Van Valen, 1971). Therefore, averaged over many local populations, fewer individuals will immigrate into more-or-less isolated populations than emigrate from these. Even if immigration on average amounts to only a few percent of numbers it may still sufficiently influence the dynamics of the population to increase the chance of survival (Van der Eijk, 1987, Ch. 7).

Nevertheless, in species with little emigration this number of immigrants will usually be too low to increase net reproduction – except possibly in a few sparse (marginal) populations – in the sense of Kuno (1981) and Metz et al. (1983). On the other hand, each (re)founding will give a new run of multiplication of dispersal features. Only in groups of T-species, because of the high turnover, will individual selection against dispersal features usually not have time to restrict dispersal abilities substantially, although such a selection can often be expected to prolong survival of the group (L-species: Fig. 5).

This balance between opposite kinds of selection on a similar time scale is very unstable, however. As soon as the majority of the less stable habitats, normally occupied by some species, become more stable (or when populations are increasingly founded in more stable habitats), individual selection within these populations will favour reduction of dispersal abilities, because of the already existing dominance of emigration over immigration. This can be illustrated by the probably recent reduction of both relative wing size and flight-muscle development in *Amara lunicollis* as a consequence of the long-term lowering of the water table in most of its habitats, which were formerly periodically inundated, and thus unstable (den Boer et al., 1980): Fig. 6. In the full-winged species *Nebria brevicollis*, in which comparable processes apparently started earlier, at present flight-muscles only develop if the third stage larvae grow up under optimal conditions of food and temperature (Nelemans 1987a). Interestingly enough, flight occurs only rarely in the field, which indicates that such optimal conditions (Nelemans 1987b) are infrequent (Table 4, compare columns P and U; see also: den Boer et al., 1980, Table 4). Nevertheless, the species thrives well, because of its preference for shaded man-made sites (Nelemans 1987b). In the wing-polymorphic carabid *Pogonus chalceus* Marsh., where wing size is genetically fixed (Desender, 1989), the progress of wing reduction could be distinctly related to the different ages of 3 isolated populations: Desender (1989: Table 2). It will be clear that, if such selective processes are allowed to continue (see den Boer et al., 1980), for many species a point of no return may eventually be reached – followed by a positive feedback – i. e. a situation in which the numbers of dispersers increasingly become insufficient constantly to compensate for extinction by (re)founding. The species will have become an L-species; a species that, because the powers of dispersal are no longer adequate, will not be able to maintain itself in the long run in a rapidly altering area (*ceteris paribus*).

We expect that about half of our carabid species will eventually share such a fate, but not primarily because of the above processes. Most of the species we now call L-species had already suffered a substantial reduction of flight abilities under primary natural conditions (most carabid species occupying old, stable habitats are either brachypterous or wingdimorphic with a very low fraction of full-winged specimens: den Boer, 1977), but they had not reached the point of no return. On the contrary, under natural conditions, more-or-less suitable habitats were sufficiently large to contain a high number of gradually merging subpopulations (neighbourhoods). Because of a continuous exchange of walking individuals between neighbourhoods (cf. Baars, 1979b) the population as a whole was often favoured by *spreading of risk* (den Boer, 1968; Reddingius and den Boer, 1970; see also: Kuno,

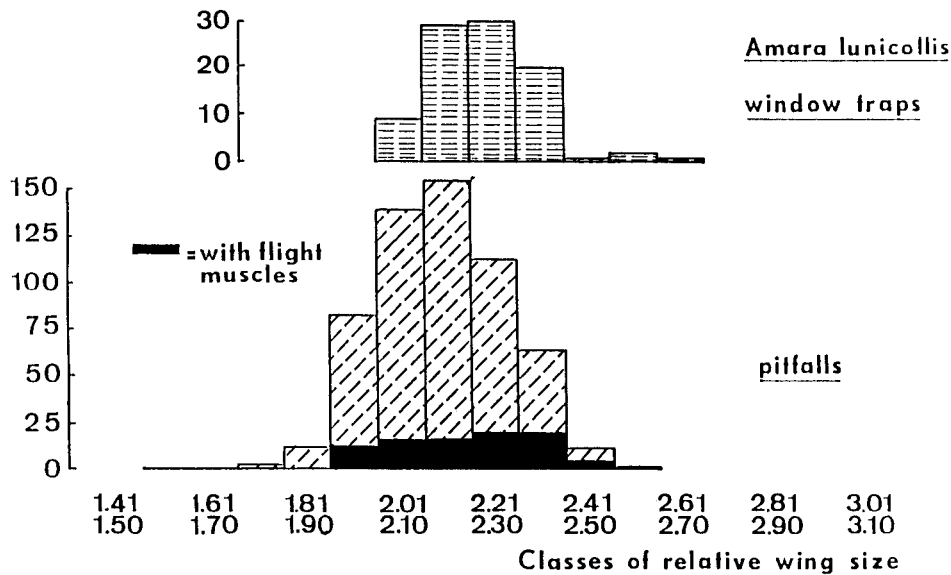


Fig. 6. Frequency distributions of relative wing sizes (surface of wing/surface of elytron) in *Amara lunicollis*. Below: wings of individuals caught in pitfalls; above: wings of individuals caught in window traps (during flight); difference:  $\chi^2 = 50.56$  ( $p \ll 0.001$ ). Many specimens in local populations are no longer capable of flight, in most cases because they have lost the ability to develop flight muscles; even in the dispersal period (early spring) only 16% of individuals show fully developed flight muscles (Van Huizen, 1979). The connected reduction of wing sizes has already progressed substantially: individuals with flight muscles have significantly larger wings than those without (lower graph):  $\chi^2 = 20.11$  ( $0.01 > p > 0.001$ ). If relative wing size has been reduced below 2.00 the wings of carabid beetles become increasingly unsuitable for flight (den Boer et al., 1980).

1981; and Metz et al., 1983). This spreading of the risk of extinction over neighbourhoods not only very much delayed the moment of extinction of local groups, but in particular it substantially decreased and levelled density fluctuations in the population as a whole, which could thus survive for thousands of years. This crucial phenomenon could be distinctly demonstrated in *Pterostichus versicolor* in the heath area of Kralo and Dwingeloo, which is still large enough (1600 ha) to resemble a natural habitat (den Boer, 1981; 1986a).

Hence, under natural conditions the present low powers of dispersal of L-species were adequate. Population replacement, which, because of significant (more than a few percent) exchange of individuals between groups, occurred only infrequently (Van der Eijk, 1987), will usually have been complete (i. e. DPS-values will have been high). In some of the present L-species the potential for flight is more-or-less preserved at a very low frequency, either because the wings are only occasionally large enough for flying, e. g. in *P. versicolor* (Table 4: columns P and U; see also den Boer et al., 1980; Table 3), or because the expression of the gene "full-winged" in wingdimorphic species (where the possession of wings is mono-factorially inherited) is under environmental control. The latter was found to occur in *Calathus*

*melanocephalus*, in which the (generally low) expression of “full-winged” is favoured under optimal conditions of food and temperature (Aukema, 1986; compare *N. brevicollis*, above). In spite of the very low frequency of macropterous specimens (usually less than 1%) full-winged individuals of *Calathus melanocephalus* were able to found populations in the Dutch IJsselmeer-polders (den Boer, 1970). Contrary to the opinion of Darlington (1943) full-winged specimens of this species, and of the closely related *C. erythroderus*, appear to show a higher fitness (greater egg production over a longer period) than short-winged individuals (Aukema, 1986; 1987). Thus, full-winged specimens are well adapted for founding. Under the present conditions, in particular *Pterostichus niger* (Table 4) occurs in our area in a situation that resembles a natural one; individuals are unable to fly, but – also because of their large body size (about 20 mm) – can cover reasonable distances by walking; moreover, they are able to feed, reproduce and develop nearly everywhere in our cultivated countryside: Fig. 2. This section has shown that under natural conditions carabid species will generally fit the population structure required for Wright’s shifting balance model (Wright, 1931); in the often mutually differing effective environments of different interaction groups – with restricted exchange between them – natural selection may reach different adaptive peaks, by which the adaptive possibilities of the species as a whole in that area may be appreciably broadened. These favourable conditions are largely lost in a cultivated countryside.

For many species the point of no return in the individual selection against dispersal abilities appeared to be far surpassed after reclamation of the area by man. Not only was the amount of habitable area drastically reduced, which meant that risk-spreading over neighbourhoods was destroyed, and many populations were reduced to single interaction groups, but also the distances that had to be covered to achieve compensating (re)foundings were dramatically enlarged (den Boer, 1977; 1979a). Moreover, these distances are interrupted by many barriers for walking beetles (roads, ditches, canals), which, judging by experiments with marked individuals, appear to be highly effective. Species have thus become L-species. *Pterostichus lepidus* (Fig. 3) clearly illustrates the fate of L-species in cultivated areas. More than a century ago the wholesale afforestation with conifers of dry heathland, the habitat of *P. lepidus*, was started (Turin and den Boer, 1988). When relating this to the mean turnover rate of the species (about 1 %, Table 4: W), and thus to a mean survival time of local populations of about 100 years, it can be expected that many local groups in still suitable, but isolated, sites will have disappeared already without replacement. Indeed, this phenomenon accounts for the disproportionately high number of zero year-catches in Fig. 3. These zero catches cannot only have come from unsuitable habitats (in that case the cumulation line would not have been broken, but would only have started from a rather high percentage), but must also include many suitable places where the species appeared to have been absent during the sampling years. In fact, the decrease of occurrences of this species in The Netherlands started in the second decade of this century, and has clearly continued ever since (Turin and Peters, 1986, Figs. 3 and 4; Turin and den Boer, 1988, Table 6B). Recently (1988), De Vries (in prep.) showed the disappearance of all three populations of *Agonum ericeti* Panz., an unwinged and stenotopic species of

peat-moor, from small (<5 ha), isolated, but not altered habitats, where its presence was recorded in 1959-'62. In larger peat-moor areas (>30 until 1700 ha) it was still present. These findings fit our estimates of expected survival times of isolated interaction groups (at 2-4 ha) of this species: 7-44 (mean 19) years. We fear that these prospects apply not just to carabid beetles. They are a general consequence of the fragmentation of natural habitats (Wright and Hubbell, 1983; Wilcox and Murphy, 1985).

## *2. Regulation of numbers and group selection*

We now return to the Introduction to see how far our findings on the dynamics of carabid populations support the statements made there.

A) Regulation (governing) concerns the hypothesis that population densities neither increase indefinitely nor decline to zero; instead, they would be expected to fluctuate around an equilibrium level under the influence of density-dependent (governing) factors; see Reddingius (1971). In other words, densities would be kept within positive bounds that show a definite relationship to environmental conditions (carrying capacity). To sufficiently lower the chance of the otherwise inevitable "random walk" to extinction, or the reaching of pest densities, a necessary corollary of this hypothesis is that density fluctuations must be "better" than random, i. e. density is expected generally to fluctuate within a narrower range than with randomly succeeding density changes. As shown, local populations of carabids do not generally support such a model; see Table 3. Also, the rather short survival times of most carabid interaction groups (Fig. 5) hardly give scope for significantly regulating processes. This does not mean, of course, that I would exclude the possibility that in some or even many (carabid) populations - especially in dense populations of L-species - density governing processes would be operating. But there are no coercive reasons why in the field such processes in the long run would keep density within positive bounds (see den Boer, 1981). Recently Reddingius and den Boer (1989), and den Boer and Reddingius (1989) showed that regulating processes cannot be expected to contribute significantly to such keeping of density within positive bounds.

B) As long as (re)foundings compensate for extinction of local groups the powers of dispersal will generally be sufficient also to result in a significant immigration of dispersers into existing groups. This will not only increase net reproduction (Kuno, 1981; Metz et al., 1983), and level density fluctuations (Van der Eijk, 1987), but also slow down the individual selection against dispersal features. In fact, spatially separated groups with still significant immigration only differ in degree from gradually merging neighbourhoods, in that the selection against dispersal features by loss of dispersers is partly compensated by immigration of dispersers. In my opinion, the same can be said about the difference between individual selection against dispersal features within groups, and the more-or-less opposite selection between groups (culminating in extinction and founding of groups), as long as these operate on a similar time scale. These differently directed



kinds of selection will increasingly diverge as soon as the powers of dispersal have become insufficient for extinction of groups generally to be compensated by (re)founding. In that situation also the immigration of dispersers into existing groups will increasingly decline, which will lead to spatially separated groups becoming more and more isolated. This growing isolation will accelerate selection against dispersal features within these groups. Initially this will prolong survival times, as in many of the present L-species pictured in Fig. 5, from which only the better groups, showing random fluctuations of numbers, have survived so far. However, under the present rapidly changing environmental conditions, in the long run this kind of "group selection" (extinction without or with insufficient replacement) will result in the species concerned being doomed in large parts of its distribution area. When environmental changes occur less rapidly, however, as during past geological periods, the turnover of whole populations may be one of the major aspects of evolution. This was clearly formulated by Darlington (1959): "... effective evolution – general adaptation – is correlated with number of populations and occurs partly by selection of whole populations, with continual extinctions, replacements, and movements (spreadings) of evolving populations" (p. 509; see also p. 507), which is in general accordance with Wright's shifting balance model (Wright, 1931). Therefore, for the moment I do not see urgent reasons to distinguish group selection from individual selection (see also Wade, 1985).

### 3. Extinction of species

About the increasingly urgent problem of the extinction of species we can now conclude:

C) As the survival times of most interaction groups of L-species are still too long (Fig. 5) to allow a single population ecologist directly to observe many extinctions (but see Ehrlich et al., 1980, and *Agonum ereceti* in Discussion), the expected doom of the L-species in our cultivated countryside cannot yet be proved beyond all doubt. But if we look again at Fig. 4, where the cumulative frequencies of the year-catches (zero catches included) of the 64 carabid species are arranged as "cumulation lines" according to the corresponding DPS-values, we hardly escape the suggestion that all L-species are indeed on the way to disappearing from the remnants of suitable habitats (mostly nature reserves) left in cultivated areas; compare *P. lepidus* (Fig. 3). Most of the less dense interaction groups have already died out without sufficient compensation during the last century of accelerated cultivation and overall fragmentation of suitable habitats. Because of this, the frequency of zero year-catches has increased disproportionately and the cumulation lines have become broken (Fig. 4; see further den Boer, 1970; 1977). In fact, our data support – even to a dramatic extent – the point of view expounded by Wilcox and Murphy (1985); see also Turin and den Boer (1988). I expect that, unless adequate measures are taken (see den Boer, 1970; 1977; 1986b), nearly all local populations of L-species remaining in smaller fragments of the old habitat (smaller than 30–200 ha, say) will disappear in the course of the next two centuries, and for

many of these species this will be equivalent to complete disappearance from the area. This extinction of species by fragmentation of habitats adds to the many other causes of extinction, mentioned by Paul and Anne Ehrlich (1981), and makes it urgent for us to reconsider carefully the minimum sizes of nature reserves. For instance, the data of Willis (1974) and Karr (1982) show that the surface of Barro Colorado Island (17 km<sup>2</sup>) is much too small permanently to house many bird species that lived there before the creation of the Panama Canal (1914).

### Summary

The continuous thread through this paper can be summarized as follows:

1) The population units of carabid beetles (which are univoltine), when continuously sampled by standardized pitfall sets, are comparable either to demes or to neighbourhoods; they are called *interaction groups*.

2) A non-zero *year-catch* from pitfalls of a particular species gives a relative estimate of the mean density of the interaction group (local population) during that breeding season.

3) The many coefficients of net reproduction [ $R = \text{year-catch}(t)/\text{year-catch}(t - 1)$ , zero year-catches excluded] of each of the 64 more abundant species, sampled at many sites during many years, satisfy a lognormal distribution, the moments of which can be estimated.

4) Realistic density fluctuations can be simulated by randomly taking  $R$ -values from the fitted lognormal distribution concerned. From these simulated populations "year-catches" can be taken, just as in the field.

5) From each run of non-zero year-catches of each species at each site the range between the highest and lowest mean density reached, expressed as *Logarithmic Range* (LR), estimates the expected density bounds, both for the field samplings and for the simulations to match.

6) When the LR-values from field samplings are compared with those from the relevant simulations, some species appear to show ranges as with random density fluctuations, others fluctuate between wider bounds.

7) For each species, from the available year-catches, the frequency Distribution of Population Sizes (DPS) is estimated, and measured with a formula (between 0 and 1). This quantity indicates the *shortage* (from the expected lognormal distribution) of samples from sparse local populations (occupying marginal habitats), and thus the possible (in)completeness of population replacement.

8) DPS is distinctly connected with both the powers of dispersal (usually by flight) and the pattern of density fluctuations of the species concerned.

9) Two groups of species can thus be distinguished, L-species with low powers of dispersal (no or hardly any flight activities), incomplete population replacement (left-truncated distribution of samples), ranges as with random density fluctuations, and  $\text{DPS} < 0.715$ ; T-species with high powers of dispersal, complete population replacement (high turnover), wider ranges than with random density fluctuations, and  $\text{DPS} > 0.753$ .

10) From the frequency of zero year-catches in long series of samples for each species a maximum value of the turnover of local populations can be estimated (i. e. all zero year-catches are assumed to result from extinctions).

11) From the “pitfall sampling” in the simulations an estimate can be made of how many zero year-catches cannot concern extinctions, but must be expected to result from temporarily exceptionally low densities: *pseudo-turnover*.

12) Gross turnover can be corrected for pseudo-turnover.

13) Corrected turnover is correlated with DPS, and the expected mean survival times of local populations of L- and T-species can thus be compared: local groups of T-species appear to survive for a much shorter time (a few years only) than those of L-species (some decades).

14) *Turnover* and DPS are associated with individual selection against dispersal features: isolation of local groups accelerates this kind of selection and thus promotes extinction without replacement.

15) The consequences of selection against dispersal features are made worse by the rapid destruction and fragmentation of natural habitats in our cultivated countryside: risk-spreading over neighbourhoods is destroyed, and extinction of local groups is thus highly accelerated.

From these 15 points it can be concluded that:

A) Because fluctuation patterns are only exceptionally “better” than random, and survival times of local populations are concordantly short, *regulation* of population numbers is not expected to play a significant part in the persistence of local populations.

B) Because under natural conditions selection processes within and between local populations will generally be commensurate, *group selection* cannot be distinguished from individual selection, but will at best be a special kind of gene frequency change; the latter especially when isolated population units become extinct.

C) As a consequence of highly accelerated habitat destruction and fragmentation, many species with low powers of dispersal have become isolated in small remnants of their habitat, where they will become extinct rather soon without a reasonable chance of refoundation; this means that unless adequate measures are taken, such species will be doomed in large parts of (or even the entire) area of distribution.

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