

The Significance of Dispersal Power for the Survival of Species, with Special Reference to the Carabid Beetles in a Cultivated Countryside¹

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Summary

To be able to evaluate the significance of density governing reactions for the persistence of populations the frequency of natural population extinctions should be known. Long-term data on the distribution and abundance of 74 carabid species in a cultivated countryside could be used to show that extinction of local populations is a common phenomenon, not only for species inhabiting unstable or temporary sites, but also for species living in more stable or permanent natural environments. An amount of dispersal sufficient to ultimately compensate extinctions by (re)foundations is therefore assumed to be a necessary condition for the survival of each species. The relationships between the powers of dispersal of different groups of carabid species and the changes in the rate of replacement of local populations as a consequence of the taking into cultivation of a natural area are shown and discussed. A first trial is made to understand how in different animals the necessary amount and frequency of dispersal is reached.

1. Introduction²

Until recently population dynamics has been very much concerned with the existence of processes that are able to bring about the persistence of populations. This concentration of interest resulted for a long time in the almost total neglect of the counterpart problem, the rate of natural population extinctions. Even though ANDREWARTHA and BIRCH showed as early as 1954 that populations may become extinct quite frequently, it took several years before some population ecologists became interested in population extinctions. NICHOLSON in 1958, at the time I started the present investigations, still tried to explain the known examples of natural population extinctions as phenomena only occurring near the fringes of distribution of a species, where «density-governing reactions must be slight and inconspicuous», whereas in the centre of distribution «density-governing reaction permits a species to persist indefinitely in all favourable places».

After the book of ANDREWARTHA and BIRCH (1954) was published I wondered what would eventually be considered more important for the survival of a species: either an adequate *turnover of populations* – that is population (re)foundation ultimately compensating for extinctions – or the general occurrence of *density-governing processes* (regulation of numbers). Considering both these phenomena, I expect that the higher the rate of population extinctions is, the smaller the supposed survival-favouring influence of density-governing reactions will be. In any case, density-governing processes cannot be of importance for the survival of species living in unstable or temporary habitats where the

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² I thank Mrs. J. C. NICHOLLS for correcting the English text.

turnover of populations is necessarily very high, often occurring annually. In order to maintain such a turnover the powers of dispersal, that is the ability to span large distances, should be considerable, and consequently it is to be expected that they will generally be the greater the more unstable the habitat. This relationship between dispersal, or «migratory», power and the degree of instability of the habitat was recognized by SOUTHWOOD (1962) after collecting together the literature on this subject. However, just like the entomologists he cites and later authors on «insect migration» (see e.g. JOHNSON, 1969; DINGLE, 1972), SOUTHWOOD thus only concentrated upon «migratory insects», that are insects that, because they are living under rather unstable conditions, traverse remarkable distances often displaying a special kind of behaviour.

But what about the populations of those species which live in more stable environments? Would they indeed «be permitted to persist indefinitely in all favourable places by the occurrence of density-governing reactions», as NICHOLSON said in 1958? Or would they only differ from species living in unstable habitats by having a relatively lower rate of population extinctions? If the latter was the case, even species of permanent habitats would necessarily have to disperse to some extent in order to compensate for the extinctions by (re)founding populations, and thereby survive.

To summarize, ignoring the slight possibility that there are populations that would *never* become extinct (I think even NICHOLSON would not have gone that far) we can make the evident statement: *the ultimate survival of all species will depend on the degree to which the rate of population (re)foundation eventually keeps pace with the rate of population extinction.* And we can add: This rate of population replacement, in turn, will depend on the dispersal power of the particular species. The real importance of these statements will depend very much, of course, on the actual rate of population extinctions in species inhabiting more stable environments. For two reasons this could not be elucidated from data available in the literature.

One reason was that far too few long-term population studies have been carried out. Consequently one cannot expect that the natural extinction of a population in some permanent habitat has been recorded directly very often, let alone that we should be able to estimate the rate of natural extinctions in any of such species. Also because large and dense

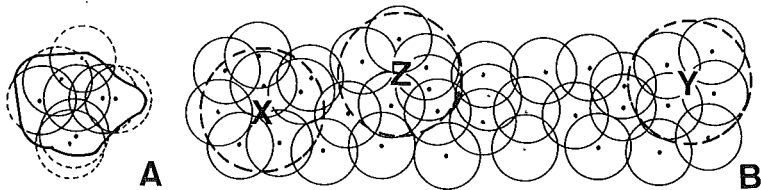


Fig. 1: Diagram of interaction groups. Each dot represents a place where an individual is supposed to have been born, and is the centre of a circle delimiting the maximum distances that can be covered by that individual in the normal patterns of activity, during its lifetime. Only a few of the individuals are pictured, of course.

- A. A separate interaction group at a more or less isolated site of about the right dimensions. Such a group of individuals represents an example of a «simple population» which is the most correct use of the concept «population».
- B. A continuum of interaction groups. Starting from each point an interaction group can be defined (dotted circles), e.g. starting from the points X, Y or Z. Although often such «sub-populations» cannot be independently separated from other ones, in many investigations it is useful to distinguish between different «sub-populations» living under different local conditions, and being parts of a composite population.

populations are generally those under study, the near absence of data on extinctions in the literature indicates little about the occurrence of natural extinctions under more stable conditions. The highly interesting studies about extinctions on islands carried out during the last decades (see e.g. MAC ARTHUR and WILSON, 1967; SIMBERLOFF, 1974; CARLQUIST, 1974; DIAMOND, 1975) were not yet published at the time I solved the present problem. However, I suppose that they would not have helped me very much, because one expects many islands – especially oceanic ones – to be colonized mostly by «migratory animals» (see above). But I will have to study the relevant literature more closely.

Secondly, the concept «population» should be standardized before comparisons of rates of population extinctions are possible. Depending on the problems under study, groups of animals ranging in size from small local groups up to all members of a species on a whole continent have been considered «populations». Because we should also take into account the possibility that density-governing processes may be preventing population extinction, within each species the «population» should be of such a size that its members should have a reasonable chance to (directly or indirectly) interact. Hence, here a «population» is defined by an «*interaction group*», where a group of individuals lives on a site having spatial dimensions which do not substantially exceed the average distances covered by the individual members during their normal patterns of activity (see further: DEN BOER, 1977). In those cases where the site is sufficiently isolated and of the right – or less – dimensions it should be possible (at least in principle) to accurately estimate the overall quantitative influence of interactions between individuals on the pattern of fluctuations of numbers in a population, and so to deduce the probability of extinction of the group (see Fig. 1A).

However, when the dimensions of the inhabited site greatly exceed the distances normally covered by the individuals, matters become more complicated: Over this area from each point of observation we can now define an «*interaction group*» which will gradually merge into other ones (see Fig. 1B). Thus, around different points that are sufficiently far apart, population processes – also density-governing ones – will act independently. This may result in the fluctuation patterns of the numbers of individuals at these places being quite different from each other, through the influence of local conditions. Taking such a composite population as a whole, the pattern of numerical fluctuations will thus be the resultant of both the overall effects of the spatial heterogeneity in density relations (e.g. different degrees of clustering of individuals) as well as in many other local conditions, and of the rate of exchange of individuals between the different interaction groups. Therefore, to study such populations we have to involve a spatial *spreading of risks* in our considerations. For further reading on this subject, see: DEN BOER (1968, 1971a, 1973); REDDINGIUS and DEN BOER (1970).

Considering the turnover of populations an interaction group within a composite population, which I call a subpopulation, will have both a lower chance of extinction and a higher chance to be refounded, than a comparable, but isolated interaction group (simple population). In the following, where the rate of replacement of interaction groups of different species is compared, it should thus be kept in mind that some species will mainly live in our area as isolated interaction groups and other ones mainly as subpopulations of composite populations.

Suppose, we have sampled in many sites and in many years in such a way that we know the sizes of the interaction groups of a number of species. For each species we can now arrange these values in a frequency distribution (over logarithmic classes) and compare these distributions for different species.

Especially when the permanent habitat of a large and highly composite population has been taken into cultivation, so that only some small and isolated parts of the original habitat remain, many of the populations in these remnants will have approached isolated

interaction groups. In such a situation, the chance of extinction of an interaction group will possibly have increased, because of a reduced probability of immigration. On the other hand the chance of refoundation will have severely decreased, because the powers of dispersal were adapted to quite different conditions and one would expect them to be too low now to cope with the new situation. Also, the chance of refounding a population will not only have been reduced by the resulting difficulty of spanning the much greater distances, but as a consequence of cultivation by the direct disappearance of the majority of the interaction groups as well, because the number of potential founders will have dramatically fallen off.

There is generally a greater risk of a species dying out in sparse populations than in comparable dense ones (other things being equal). It follows that, especially concerning sparse populations of species living in permanent habitats, that have become isolated, the rate of refounding of populations will no longer be sufficient to compensate for the extinctions. When this occurs, the frequency distribution of the sizes of those interaction groups still remaining in that area (in the following abbreviated as DPS: frequency *Distribution of Population Sizes*) will change with time, in such a way that the smaller and/or sparser populations will become comparatively more and more underrepresented.

In an area of cultivated land, where remnants of the original countryside still exist, if it were possible to estimate DPS there for a number of comparable species, among which both species occupying more stable and species inhabiting unstable remnants were represented, *the cultivation of this natural area could thus be considered to have been a critical experiment concerning the rate of natural extinctions in species occupying more stable or permanent habitats*. If the rate of natural extinction in these species were high, as compared to the rate of disappearance of habitats through cultivation, the DPS of these species would already be expected to be distinctly different from those of species of unstable or temporary habitats, by showing only a few interaction groups that are relatively small and/or sparse. If, however, the rate of natural population extinction in the species of permanent or stable habitats were low, then after a century has passed (say), there are no strong reasons to expect already marked differences between the DPS' of species of permanent habitats and those of more unstable environments.

Especially when the rate of natural extinction is high, the results of this «experiment of cultivation» highly depends on the efficiency of the different species' means of dispersal under the changed conditions. In those species which originally occupied large and permanent habitats, the powers of dispersal would now be expected to be inadequate, but still sufficient in species also originally living in small and often widely separated, unstable habitats. In a cultivated countryside, because the turnover of populations is very high in species of unstable or temporary habitats, only those of these species which have a power of dispersal which is still sufficient to compensate for the, often annual, disappearance of populations, will be found.

2. The object of study and the estimation of DPS

From 1959 onwards we studied different aspects of the population ecology of carabid beetles by continually sampling with standard sets of pitfalls in different habitats for periods of one or more years. It was realized that, in this way, we were actually sampling interaction groups, because the frequency by which individuals happen upon the fixed site of a pitfall – that is, the number caught – may be expected to be about proportional to the «chance to interact». It was assumed that the catches in such a standard set of pitfalls, totalled over the whole period of activity (hereafter called: *year-sample*), would give a reasonable estimate of the relative size of the particular interaction group. Since different

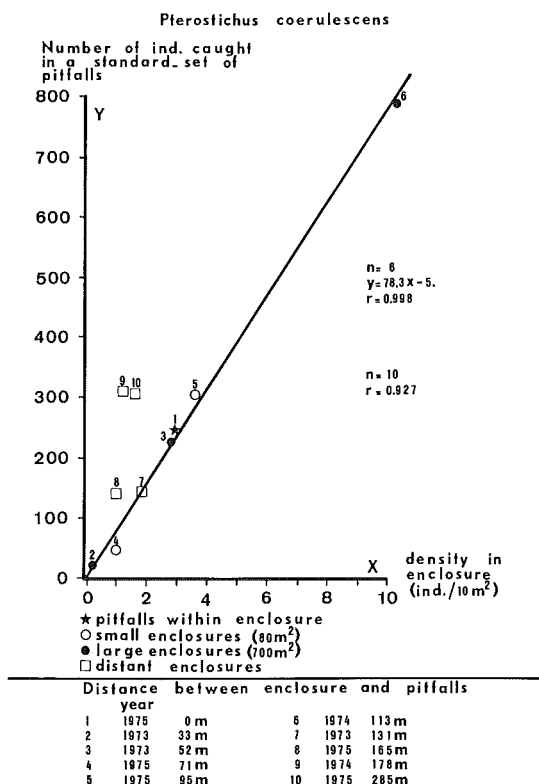


Fig. 2: Relationship between the mean density within an enclosure and the value of the nearby year-sample – i.e. number of individuals caught in a standard set of pitfalls during a whole season (from data of BAARS, 1979).

interaction groups of a particular species may be expected to occupy roughly similar surface areas in our study area, the value of the year-sample should also give a relative estimate of mean density. BAARS (1979) showed this assumption to be correct to a surprisingly accurate degree for the two species he studied. In different localities on Kralo Heath, in different years, he trapped all the individuals present within a fenced site and compared these numbers with the values of that season's year-samples of the same species obtained with nearby (20–120 m distant) standard sets of pitfalls. The data for one of the species are given in Fig. 2; those for the other are similar. The above conclusion has been confirmed for ten other species with the help of intensive and long-term capture-recapture experiments (some of these data are already given in DEN BOER, 1971a: Table 2). The accuracy of the year-sample as an estimate of the mean density of the interaction group is in agreement with other findings of BAARS (in prep.), who has studied the walking pattern of two species in the field in sufficient detail to enable him to simulate it in a computer model, from which he was able to predict pitfall-catches in accordance with our results. It is relevant here to give some idea of the scale on which we are working: an interaction group of one of the two carabid species, which has individuals of 6–8 mm in length, covers an area of about 1½ ha and that of the other species, which has individuals of 10–12 mm, covers an area of about 15 ha.

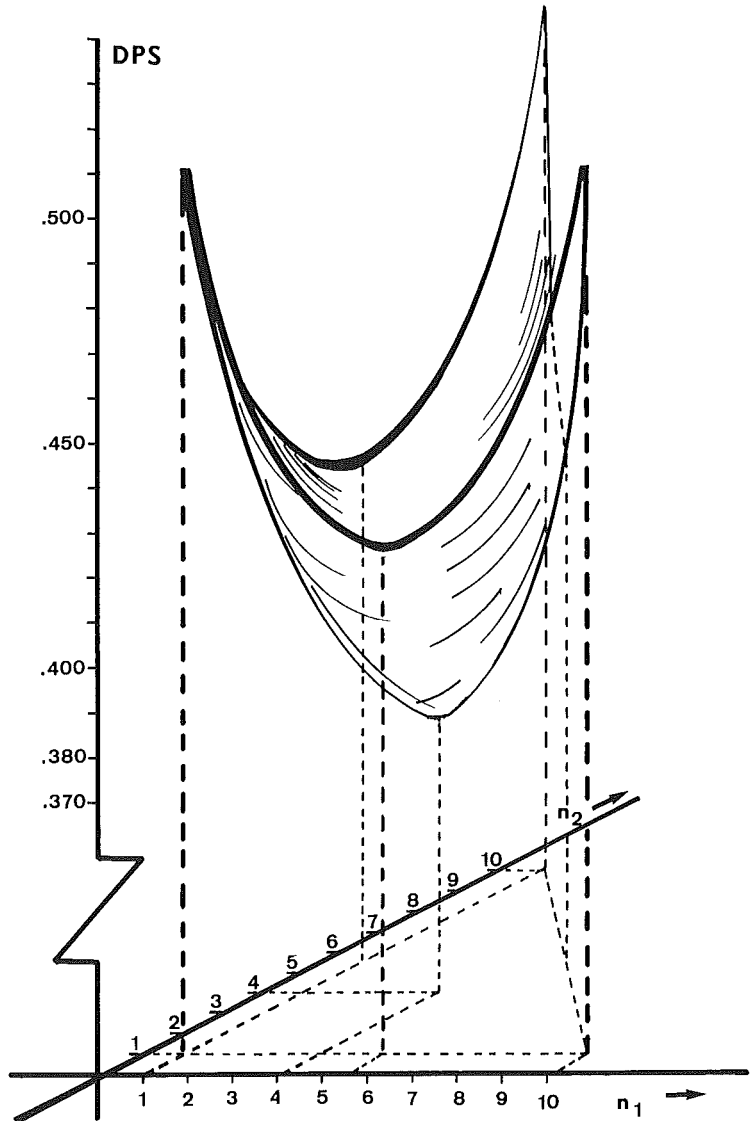


Fig. 3: Graph of DPS as a function of n_1 and n_2 for $j = 3$, $N = 12$. Note that DPS is at its minimum when $n_1 = n_2 (= n_3) = 12/3 = 4$; given e.g. that $n_2 = 1$ DPS is at its minimum when $n_1 = n_3 = 11/2 = 5.5$ and so on; maxima occur where one n_i is equal to 10 and the others are equal to 1.

From 1959 to 1968 we sampled 73 sites in this way for periods of one to eight years, which give a total of 175 set-years. These data should enable us to compare the frequency distributions of year-samples - i.e. the DPS' - of at least the more abundant carabid species; 74 species were eventually used for that, being that half of the species, which were caught most abundantly. We were especially interested in the relationship between the

numbers of year-samples with low and higher values, sampled from sparse and denser interaction groups respectively. We therefore looked for a statistic that would adequately express this relationship. After some trial and error the simple and standardized (between 0 and 1) expression:

$$\text{DPS} = 1 - \frac{\sum \ln(n_i + 1)}{j \cdot \ln(N + j)}$$

appeared to satisfy our requirements.

[n_i is the value of the year-sample; j is the number of year-samples with catches; N is the total number of specimens of a particular species caught during the nine years of study.] The features of this expression are amply discussed in DEN BOER (1977: ch. 5) and its use is mathematically supported by REDDINGIUS in an Appendix to that paper.

Here we suffice by showing in Fig. 3, a case with $j = 3$ and $N = 12$, that DPS is at its minimum when all n_i 's are equal and reaches maxima when all except one of the n_i 's are 1. In more general terms, the maximum values DPS may take on for a fixed value of N is an increasing function of j , increasing from zero, when $j = 1$, to $\ln N / \ln(2N)$, when $j = N$. If the ratio of N to j is kept fixed the maximum value of DPS is also an increasing function of j , and hence also of N . The same statements are true with respect to the minimum value of DPS, when j is decreasing from very high values down to 1. It is also important to note, that for a given distribution sequence of year-samples and with j at a fixed value, DPS is the lower the higher the value of N , that is the total number of individuals caught. Hence, in all respects DPS adequately measures the degree to which sparser populations of the particular species were met with in our study area as compared with more abundant ones found.

3. Population replacement in permanent habitats

We considered those sampling sites which were situated in localities that were known to have been in existence for more than a century, and which showed no major changes during our nine years of study, as permanent or stable, and all other sampling sites as temporary or unstable. Thus, remnants of deciduous forest, blown sand for a long time already fixed by vegetation (mainly heather), old heathland and peat-bog represented permanent habitats. Temporary or unstable habitats were found in some parts of the heathland which are either flooded quite often or gradually overgrown by young trees, partly floating bog vegetations, and recently disturbed sites. By rigorously applying some criteria based on the kind of habitat where the majority of the individuals of a particular species were caught (cf. DEN BOER, 1977: 4.3) we were able to classify most of the species as either *D-species* (in remnants of deciduous forest), or *E-species* (in sites with fixed blown sand), or *F-species* (on old heathland and peat-bog), or *G-species* (in unstable habitats). Those species to which our criteria could not be applied, were called *H-species*. These are more eurytopic than the other species and usually inhabit both unstable habitats and certain kinds of more stable habitat. In most respects, especially those concerning the powers of dispersal, the *H-species* resemble the *G-species*.

After such categorization, it became evident that the DPS-values of both the *G-* and *H-species* are much higher than those of any of the groups of species living in permanent habitats, as is shown in Fig. 4. This implies – and I will also show this later on in another way – that among species of permanent habitats sparse interaction groups are severely underrepresented relative to the denser ones. The more large-scale cultivation of our area, especially in the heath, peat-bog and blown sand areas, was only started some 50–100 years ago. This gives considerable support to the supposition that the rate of population extinctions must also be relatively high under more stable conditions.

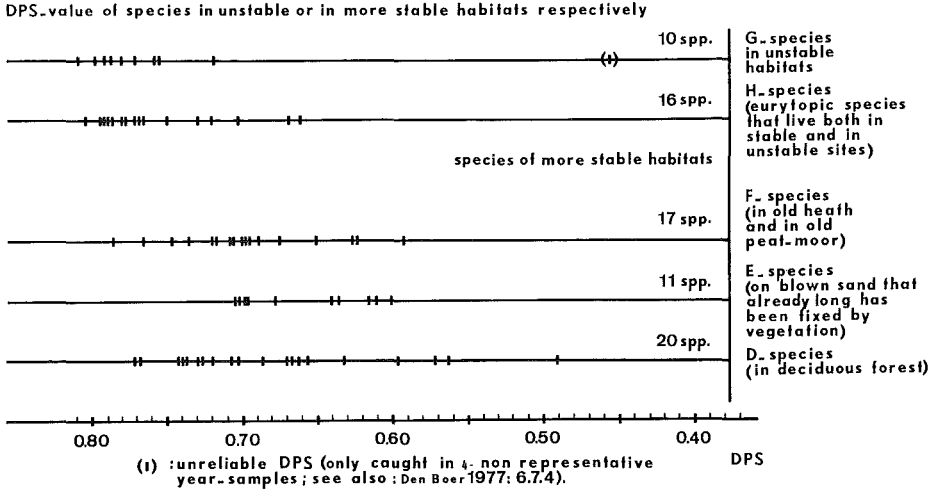


Fig. 4: The DPS-values of different groups of carabid species to show the general differences between species of unstable environments – i.e. G- and H-species, and species of permanent habitats – i.e. D-, E- and F-species.

The validity of this assumption has been tested by artificially introducing a D-species (*Abax parallelepipedus*) and an F-species (*Calathus melanocephalus*) into respectively suitable sites where they had been found to be absent. Both species settled without difficulties, and they have already persisted for a number of years.

The powers of dispersal of most species of permanent habitats have apparently become insufficient to enable them to replace natural extinctions. However, this also means that in

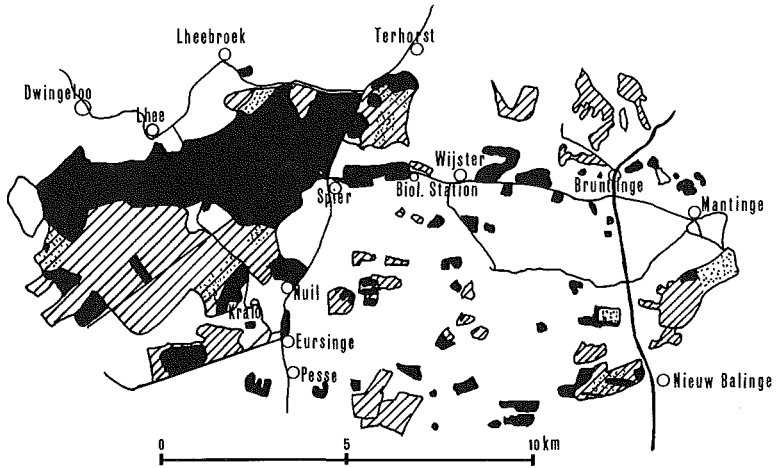


Fig. 5: The study area (the sampling sites in peat bogs in the southern part of Drenthe are not shown). Black: woodland. Hatched: heathland. Stippled: blown sand. At the left: Kralo and Dwingeloo Heath. Note: the extensive woodland area between Spier and Lhee, above the Kralo and Dwingeloo Heath, a former blowing sand, is nowadays almost completely planted with conifers as are about half of the smaller woodland localities.

some past, more natural situation, these powers of dispersal, although rather low, were adequate, for otherwise these species would have long been absent from our study area.

Fortunately, one of our groups of species, the F-species, was sampled mainly in sites situated in the vast nature reserve of Kralo and Dwingeloo Heath, which has an area of about 1200 ha, and which can be taken as sufficiently representative of this past situation (Fig. 5). Here, therefore many F-species will have been sampled as subpopulations of large and composite populations of the kind shown in Fig. 1B. This indicates that part of the population replacement in many F-species will have been less incomplete than in, for example, most D-species. These will have been predominantly sampled in small and highly isolated remnants of forest, thus approaching the size of isolated interaction groups of the kind shown in Fig. 1 A. It could indeed be shown by a suitable test (cf. DEN BOER, 1977: 6.5) that the DPS-values of the F-species are significantly higher than those of the D-species, in spite of the fact that the powers of dispersal of the F-species are *not*, as expected, higher than those of the D-species – in fact they are lower.

Further it could be estimated that 14% more of the interaction groups of an average D-species must have disappeared unreplaced than those of an average F-species, and that this resulted exclusively from the increasing insular distribution of the remnants of natural habitat that has occurred during the last century. This process has been more radical for our D-species than for our F-species. Even when direct losses of the majority of natural areas by cultivation are not considered this is thought to be an underestimation.

By thus comparing F- and D-species we not only demonstrated that species which live naturally in more stable environments also show a rather high rate of population replacement, but we also reconstructed, so to say, the historical events by which our species of these remnants of permanent habitat entered a process of gradual extinction.

These findings do not support the supposition that, at least in permanent habitats, density-governing processes would prevent a population (interaction group) from becoming extinct. However, this does not imply that density reactions may not occur in carabid populations, but only that their possible effect on the number in a population does not differ substantially from that of other influences as regards the delay in population extinction. In other words: such density reactions do not significantly regulate numbers.

4. Dispersal power and population replacement

In the previous section we assumed that there should be a close relationship between the powers of dispersal and the value of DPS. Among carabid species the capabilities for dispersal are very diverse indeed, ranging from entirely unwinged, brachypterous, species, via wing-dimorphic species, to entirely fullwinged, macropterous, species. It can hardly be expected that brachypterous species – with the possible exception of those few with large individuals, for example *Carabus* (cf. DEN BOER, 1970) – are able to span the present distances between the remnants of natural habitat to a sufficient extent. Hence, they have low powers of dispersal and it is expected that their DPS-values should also be low. In some other species the capabilities to disperse cannot be much better, as for example in those wing-dimorphic species with a very low frequency – say less than 1% – of fullwinged individuals.

Together we could thus separate 25 species with very low expected powers of dispersal: *A-species*.

Because observations on flying carabid beetles were scarce we were less sure about the dispersal power of other dimorphic and the macropterous species. Therefore, in 1969 we started sampling flying carabids using window traps (cf. DEN BOER, 1971b, p. 128). After five years we could thus classify 26 of our 74 species by their ability to disperse by flight,

although in some species this apparently occurs only very occasionally. We tentatively assumed that most of these 26 species would therefore have powers of dispersal which would still be adequate to keep up a more or less sufficient replacement of populations, and that their DPS-values should thus be relatively high: *B-species*.

The remaining 23 species, which could not be placed unambiguously as either A- or B-species, were called *C-species*. In many respects these C-species have appeared to resemble the A-species. See further: DEN BOER (1977). When all the year-samples – that is zero values included – of some B-species with high catches in the window-traps are considered, these 175 set-years appeared to show an approximately log-normal distribution. It could thus be expected that species with low powers of dispersal would show a specific deviation from such a distribution, and have a smaller number of year-samples in the lower classes and a consequently higher number of zero year-samples. When such a frequency distribution of year-samples is plotted cumulatively on log-probability paper, the resulting *cumulation-lines* for the above B-species will thus be straight (B-type). However, for species with insufficient powers of dispersal these cumulation lines should be bent,

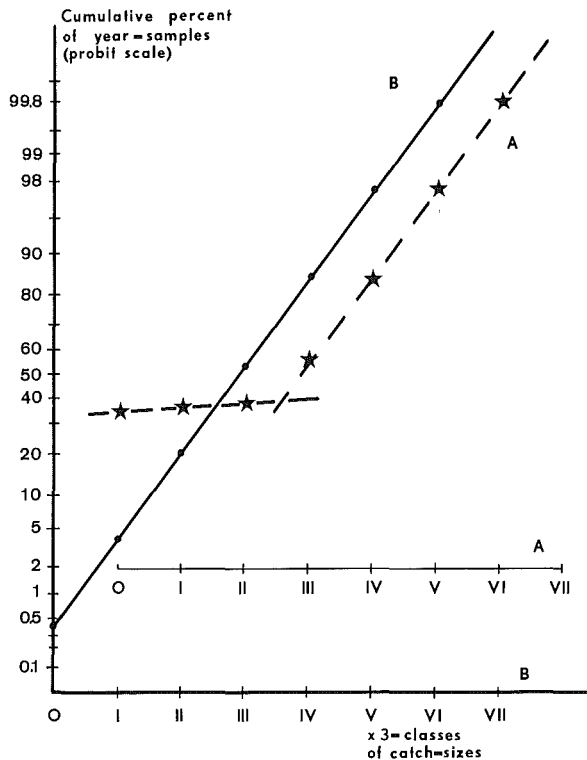


Fig. 6: Cumulated distribution of year-samples over x 3-classes, plotted as the percentage of the total number of year-samples on a probability scale, for two model species: a species with an approximately complete replacement of those populations which have disappeared (B-species), and a species without significant population replacement and a chance of extinction of local groups of $P_n = \lambda^n$ (A-species); n : number of specimens in a year-sample; $\lambda = 0.92$ (arbitrary). Note, that for the sake of clarity the scale of classes for the A-species is moved one class to the right. ●: B-species; ★: A-species.

showing a high start in the zero class followed by a line that rises slowly over the lower geometric classes, changing abruptly into a more steeply rising line over the higher classes (A-type): Fig. 6 gives examples of this (further: DEN BOER, 1977).

In Fig. 7 we arranged the cumulation lines of B-, A- and C-species respectively according to their DPS values, that is from high to low. This figure shows nicely that low values of DPS do indeed coincide with an underrepresentation of the more sparse interaction groups. It is also evident that this phenomenon is strongly connected with differences in dispersal power. This becomes even more convincing when we look more closely at those few A- and B-species that seem to show exceptions to such relationships. Nearly all B-species with an approximately straight cumulation line are indeed either G-species living exclusively in unstable habitats or H-species living also in unstable sites. The few B-species with a bent cumulation-line – and lower DPS-values – however, live under more stable conditions, and accordingly will have suffered comparatively more than other B-species from «the experiment of cultivation» by the severe reduction of inhabitable area and thus by an important decline in the production of potential population founders. Most A-species occupy permanent habitats and show bent cumulation lines; the few exceptions with an approximately straight cumulation line – and higher DPS-values – have large individuals (more than 15 mm) and are generally more eurytopic. The C-species also fit this pattern, the few species with high DPS-values and approximately straight cumulation lines living in unstable environments or being eurytopic, and the species with lower DPS-values and bent cumulation lines occupying permanent habitats.

It can therefore indeed be concluded that *the survival of each species is highly dependent on the degree to which its powers of dispersal enable it to maintain a rate of population (re)foundation that keeps pace with the rate of population extinction*. This is not only true for species of unstable environments such as migrating insects (cf. SOUTHWOOD, 1962), but – most importantly – also for species living in permanent habitats.

Just as a population cannot survive without a rate of reproduction that eventually compensates for the rate of mortality and emigration, so a species cannot survive without a rate of dispersal that is ultimately sufficient to result in the replacement of extinct populations.

Hence, such an adequate amount of dispersal is a *necessary condition* for the survival of all species, which by *increasing the possibility to (re)found populations*, must be considered the *general significance of dispersal*. I emphasize this point, because on the one hand, studies on «migratory insects» have led to the consideration of «the possibility to escape from currently adverse conditions» – analogous to diapause – as the predominant significance of dispersal (see e.g. JOHNSON, 1969); and on the other hand, the concentration of interest on density-governing processes has led to the consideration of «a relieve of the pressure from too high densities» to be the most important effect of dispersal (see e.g. DEMPSTER, 1975). Although, of course, both these aspects will be relevant for the survival of certain populations – and we may also add that the exchange of genes between interaction groups is another very important effect of dispersal – in general terms, neither can be a *sufficient condition for the survival of a species*. In my 1977 paper I treated these different points of view as hypotheses which could be opposed, and thus tested. In this way I was able to show that the «*founding hypothesis of dispersal*», put forward above, can best explain all the relevant data on carabid beetles we found (DEN BOER, 1977).

5. The phenomenon of dispersal

So far we put a value on dispersal which is not shared by all ecologists. Therefore, we will have a look at some aspects of the phenomenon of dispersal as it presents itself in the

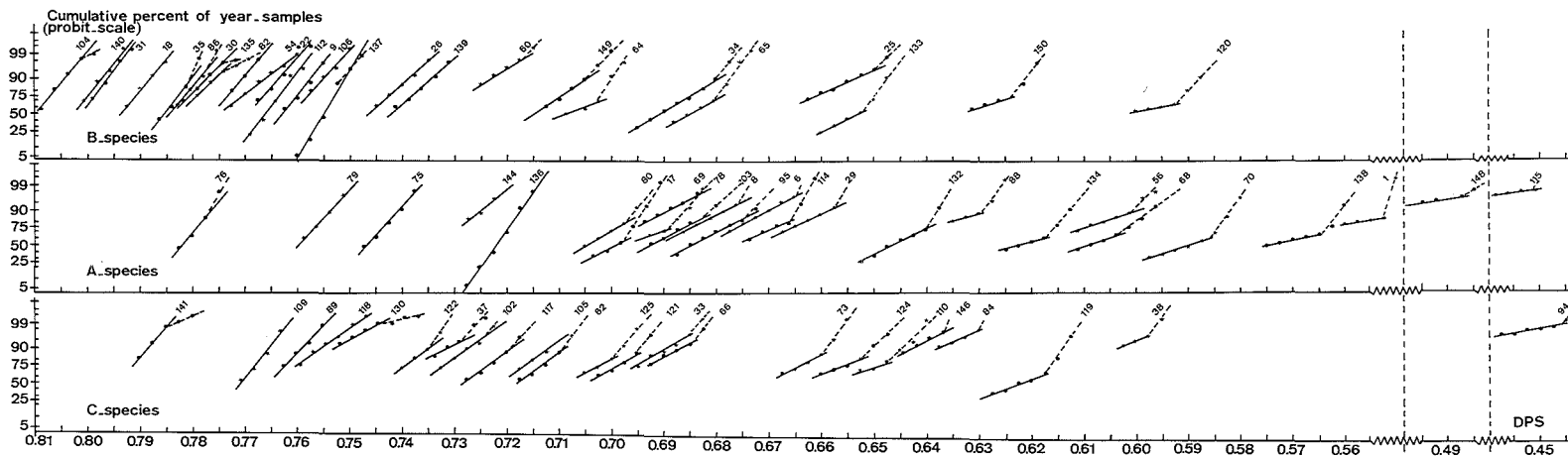


Fig. 7: Cumulation-lines (compare Fig. 6) for 74 carabid species (divided into B-, A- and C-species respectively) arranged according to the corresponding DPS-values, which appear on the abscissa.

field and supports our point of view. During a small symposium at Wijster on the dispersal of carabid beetles (DEN BOER, 1971c) a major point of controversy was: Because it can hardly be favourable to an individual to leave a locality where its life and reproduction are not threatened, that is where conditions have not turned adverse and/or density has not grown too high, it is difficult to understand, why it would still go away. Nevertheless, in many cases it is necessary for this to occur to keep up a sufficient replacement of populations. Moreover, as conditions are not always favourable for a successful settlement, dispersal should occur regularly – e.g. annually – in order to sufficiently increase the chance of (re)foundation of populations. It should not, therefore, depend too much on incidental events such as, for example, a density that exceeds the «capacity» of the habitat through some unusual combination of «factors».

We were able to establish how the conditions necessary for determining the amount and frequency of dispersal in carabid beetles are satisfied in nature. BAARS (in prep.) discovered that, within their normal habitat, the walking pattern of carabid beetles is composed of two elements, the random walk and the directed movement.

These alternate on average each 3 to 7 days, the random walk being made in random directions over short day-distances, and the directed movement in about the same, randomly chosen, direction over longer day-distances. Especially during a directed movement an individual may now and then leave its habitat. BAARS was able to establish that they can *not* avoid this, and that only after just one or two days there is a change to an extreme kind of directed movement during an increased number of days. This kind of behaviour will either take them rapidly back to their habitat, or drive them to dispersal, thus giving the possibility to reach another suitable site. Under favourable conditions many forest carabids are then able to direct their movements towards a forest silhouette (LAUTERBACH, 1964, NEUMANN, 1971).

We have some indications that individuals that have left their habitat in this way and possess both suitable wings and functional flight muscles, may after some time show an increased tendency to fly. This situation can easily be simulated in the laboratory. Fine weather conditions such as sun, an air temperature of above 17 °C and not too much wind, encourage dispersal by flight (VAN HUIZEN, 1977), and that to such an extent that weather forecasts can be used to predict the flying of carabid beetles. The same relationship between weather conditions and aeronautic behaviour was found in the ballooning of wolf spiders by RICHTER (1971) and apparently applies to many other arthropods (see e.g. DINGLE, 1972). In many insects – especially the «migratory» ones – the flight muscles are only functional during one or two short periods of the year (cf. JOHNSON, 1969). Generally this functional period only occurs during some weeks just before the start of reproduction, although in some cases the wing muscles are rebuilt after reproduction has taken place. VAN HUIZEN (1977) gives an example of this in a carabid species. However, a different situation has recently been found mainly among macropterous and dimorphic carabid species occupying permanent habitats. Many individuals *never* have functional flight muscles, although they have suitable wings. Other individuals which have functional wing muscles often keep them during reproduction as well, and in some, perhaps most, species show an increased tendency to leave the habitat. In some species fertilized females with developing eggs have indeed been observed in flight. Although it may be expected that other variations will be discovered, some degree of regularly occurring dispersal either by walking or by flight or by both is obviously certain to occur in all species.

In many other animals as well, under natural conditions the normal activities will result in sufficient dispersal, such as was observed for the woodlouse *Porcellio scaber* in a natural dune area by DEN BOER (1961). However, in a number of species, more specialized processes may be expected to join in the maintenance of an adequate amount of dispersal.

A very nice example of this, described by WELLINGTON et al. (1975), is found in the «Western Tent Caterpillar» (*Malacosoma californicum pluviale*). The female of this Lepidopteran lays all her eggs at one time. The first eggs to be laid always have a generous supply of yolk, and from these very active larvae emerge that grow rapidly, becoming very active moths that usually disperse by flight over great distances. However, the later eggs that are laid contain less and less yolk, and the larvae and moths that result from them are progressively less active. Hence, in each batch of eggs some eventual dispersal is ensured. THOMPSON et al. (1976) showed that this regular occurring dispersal indeed determined the survival of this species, in which the turnover of interaction groups is high. A different process was indicated by OOSTERHOFF (1977) in the landsnail *Cepaea nemoralis* in which the mucus secreted by the crawling snails affects their level of activity. Fast growing and active snails especially are stimulated to disperse by traversing a rather high density of mucus trails. It seems, therefore, that in this case the density of mucus trails can be considered a regularly repeating «signal» for dispersal. It is of note that both in the «Western Tent Caterpillar» and in this landsnail, individuals that are the best, also in their reproductive capacity, will leave the population. However, with these qualities, they will also be the most successful founders (compare: DINGLE, 1972)!

It may also be useful to consider territoriality from the dispersal aspect. Territorial behaviour will regularly force a number of individuals to look elsewhere for a place to settle. In many cases one may wonder if it is the restriction of density resulting from territorial behaviour, or the stimulation to settle in other localities which is more important for the survival of the species.

6. Natural selection and the survival of carabid species in a cultivated countryside

Generally, an individual that is dispersing, especially if doing so by flight, will have a much lower chance of survival than an individual remaining in the population. Therefore, ultimately many of the genetic characters connected with dispersal can only be maintained if they are repeatedly reproduced in newly (re)founded populations. Especially in more or less isolated populations the rate of emigration is usually higher than the rate of immigration resulting in a gradual decrease in the frequency of many genetic characters connected with dispersal, so that in older populations their frequencies will be much lower than in young ones. This phenomenon has already been extensively documented for many wing-dimorphic carabid species by e.g. DARLINGTON (1943) and LINDROTH (1949). This also implies that this decrease will be the more accelerated the less complete the replacement of populations becomes. Hence, in a cultivated countryside many species of permanent habitats will undergo a continuous reduction of dispersal power, resulting in a decline of population replacement. In my opinion, because of the opportunistic nature of natural selection, there is hardly any possibility that the powers of dispersal of such species will adapt to the new situation. Only if such a species increases its ability to reproduce in some of the highly accessible man-made sites as well, will it perhaps restore its powers of dispersal significantly. In some species such a process seems to be taking place. We have also observed that two dimorphic species of permanent habitats with very low frequencies (0.11% and 0.06%) of fullwinged specimens were nevertheless able to colonize the new IJsselmeerpolder of Oostelijk Flevoland. There they produced populations with much higher frequencies (48% and 34% resp.) of fullwinged individuals (DEN BOER, 1970). On the other hand, it is possible that some species of unstable habitats will gradually also penetrate into our impoverished remnants of more stable habitat. We already obtained indications of this occurring. This is especially expected of species of arable land, which are

already highly favoured by an enormous extension of the inhabitable area and are thus generally enlarging their area of distribution with the help of increasing numbers of potential founders (see also: DEN BOER, 1970). It may be expected that in the long run this will greatly stimulate speciation.

We conclude this paper with a speculation: If we project the above processes onto a large – geological – time-scale, we will possibly get some idea of how major environmental changes – which occurred repeatedly during the history of life – ultimately resulted in an accelerated replacement of «old» by «new» taxa. In contrast to the common opinion that this phenomenon should result from «competitive exclusion» of «old» species by «new» and more efficient ones (see e.g. the different contributions to CODY and DIAMOND: Ecology and evolution of communities, 1975), merely as a kind of mental exercise it may now be suggested that a great part of the «old species» had already developed low, although still adequate, powers of dispersal during a period of little environmental change. However, the occurrence of a radical change in the environment over vast areas – which may be compared with the cultivation of a natural region – may have meant that the population replacement in these species became increasingly insufficient and their extinction will have been thus accelerated. On the other hand, the new conditions might have been so favourable to a number of species which still possessed high powers of dispersal, that they were increasingly able to settle in these changing areas, there to eventually evolve into a number of new taxa.

Given enough time the «experiment of cultivation» will probably also lead to the development of new taxa. We observe phenomena that do suggest that some new taxa are already making an appearance.

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