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ENVIRONMENTAL HETEROGENEITY AND THE SURVIVAL OF NATURAL
POPULATIONS

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Abstract. Natural populations consist of different parts under different conditions with movements of individuals between; they are **multipartite**. At the Heath of Kralo and Dwingeloo the multipartite populations of two carabid species, Pterostichus versicolor and Calathus melanocephalus were studied for more than 20 years. In P. versicolor density usually fluctuates differently in different subpopulations, by which in the entire population (7-14 units) density changes are greatly levelled (spreading of risk in space). With differently fluctuating subpopulations the expected survival time increases 9-15 times (1000-3000 years) as compared with similarly fluctuating units. In C. melanocephalus in different subpopulations density fluctuates in parallel, and expected survival time will not exceed 100 years. The dynamics of field populations can only be understood if a number of adequate population units are studied and compared. Because of being deprived of spreading of risk in space isolated units of carabid species in small reserves are expected usually to survive less than 100 years. Therefore, a few large reserves will eventually save more species than a high number of small reserves.

1. Introduction: the multipartite population

Generally, natural habitats more or less continuously extent over large areas; think of rainforest and savannah, of taiga and tundra, of prairie and peat bog. Therefore, natural populations of many species will occupy relatively large areas. As such areas will show local differences of soil, elevation, exposition, drainage, resources, and possibly even climate, a natural population will consist of a number of local populations, or subpopulations, at particular sites, or parts of localities. A natural population is a **multipartite population** (Andrewartha & Birch, 1984). Since effective environmental conditions will not always be similar in different parts of the population area, density in local populations or subpopulations will not always change in a similar way. Many parts of such multipartite population will be linked by individuals moving from one to another local group, and frequently this exchange of individuals will partly level again the differences in density between subpopulations. This state of affairs, which significantly differs from the traditional, theoretical ideas of "population", may have important consequences for the chance of survival of natural populations, and of multipartite populations in general.

2. The Heath of Kralo and Dwingeloo

The comparative studies into the population dynamics of carabid beetles, that were started in 1959 in the surroundings of Wijster (The Netherlands), favoured investigations into the demographic consequences of the possibly multipartite structure of some of these populations. Among the habitats sampled with the help of standard sets of pitfalls (cf. Den

Boer, 1977: Ic) were some sites at the Heath of Kralo and Dwingeloo, an old heath area of 1200 ha in which, in addition to the areas covered with heather (Calluna and/or Erica), differently structured parts can be recognized, such as grassy sites, more mosaicly structured vegetations, wet sites with Molinia-tussocks, etc. After several years we discovered, that in some species the fluctuations of (catch) numbers in the different sample sites did not always run in parallel, and we realized that this might importantly influence the chance of survival of the population as a whole.

Therefore, we gradually changed our program of investigation such that, in addition to sampling a greater number of the differently structured sites in the heath area, and concentrating upon the more abundant species, we eventually should be able to answer following questions:

- (1) To what degree can standardized pitfall catches be considered estimates of mean density?
- (2) What group of beetles around the pitfalls is sampled, i.e. what is the size, both in space and in numbers, of the "interaction group" (Den Boer, 1977)?
- (3) What are the most important causes of the differences between the fluctuation patterns observed?

The first question was answered by Baars (1979a) and by Den Boer (1979). Den Boer during ten years performed mark-recapture experiments in populations of four carabid species of forest. Because the numbers of recaptures were very high the stochastic model of Jolly (1965) could be applied well. Pitfall catches without replacement, when summed over the whole reproduction period, gave very reliable estimates of mean density (see also Den Boer, 1971: Table 2). Baars, in several years and in different places at the Heath of Kralo, caught away all individuals of the two most abundant species, Calathus melanocephalus and Pterostichus versicolor (= coerulescens), from enclosures that were erected before the start of the activity season, and compared these direct measurements of mean density with the summed catches in nearby pitfall sets (Fig. 1). The correlations were almost perfect. Less elaborate studies on still other species confirmed these results, so that in general standardized pitfall catches of some carabid species, when at least summed over the whole breeding season, or over the whole year (year-catch), gives a reliable relative estimate of mean density of that species at that site over that period (see also Den Boer, 1985, 1986a).

The second question was also answered by Baars (1979b). By radioactively marking individual beetles of the above two species, and daily recording the places where these were found again, he could reconstruct the walking pattern, simulate it with the computer, and thus derive the distances that are usually covered in the field during one or more seasons (Fig. 2). These predictions were tested again in field experiments with high numbers of brand-marked beetles. It thus appeared that 90% of the individuals of C. melanocephalus, caught during one year, originated from an area of 1-2 ha around the set of pitfalls (from a subpopulation with a possible size between 10,000 and 200,000 individuals), and 90% of the individuals of P. versicolor caught, from an area of 7-13 ha around the set of pitfalls (from a subpopulation of about 30,000 to 130,000 beetles) (Baars & Van Dijk, 1984a). This means, that most pitfall sets used in the course of years (Fig. 3) sampled separate "interaction groups" (subpopulations) of these species.

The third question cannot yet be answered. We know that temperature as well as food (both quality and quantity) highly influence egg production

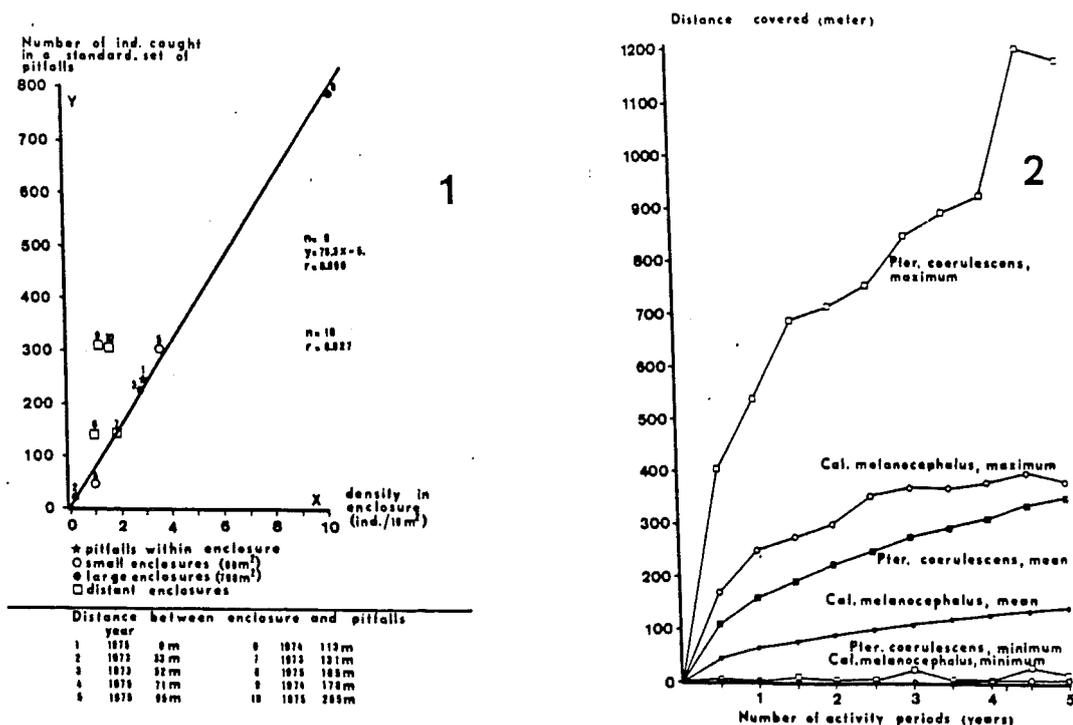


Fig. 1: Relationship between mean density of the carabid beetle *Pterostichus versicolor* within an enclosure (all individuals were caught away) and the number of individuals caught in a nearby standard set of pitfalls during the whole season (from data of Baars, 1979a).

Fig. 2: Distances covered at the Heath of Kralo by individuals of *Pterostichus versicolor* (= *coerulescens*) and of *Calathus melanocephalus* during a number of seasons. The data were obtained from simulations of the walking pattern as it was observed in the field by Baars (1979b). One activity period was in *P. versicolor* estimated at 90 days, and in *C. melanocephalus* at 60 days.

(Van Dijk, 1983, 1986). But we also know, that the yearly variation in larval mortality as well as that in adult survival is much greater than the yearly variation in egg production (Baars & Van Dijk, 1984b; Den Boer, 1986b). For the moment I am therefore inclined to suppose that physical factors during development will have major effects on the fluctuation pattern of numbers, and will thus also result in both differences and similarities of density changes between sites. Independent of our knowledge on the causes of the fluctuation patterns found, however, we can try to estimate the consequences of these patterns for the survival of the populations concerned.

The Heath of Kralo and Dwingeloo, though man-made in origin, is both large and heterogeneous enough for carabid beetles to present all features of a natural area. *C. melanocephalus* and *P. versicolor* more or less continuously occupy the entire area of 1200 ha, so that the natural populations of these species consist of many hundreds of mutually connected interaction groups. By comparing the fluctuation patterns of numbers in a representative sample of these interaction groups (subpopulations) we hoped to be able to quantify the survival value of the multipartite structure of natural populations.

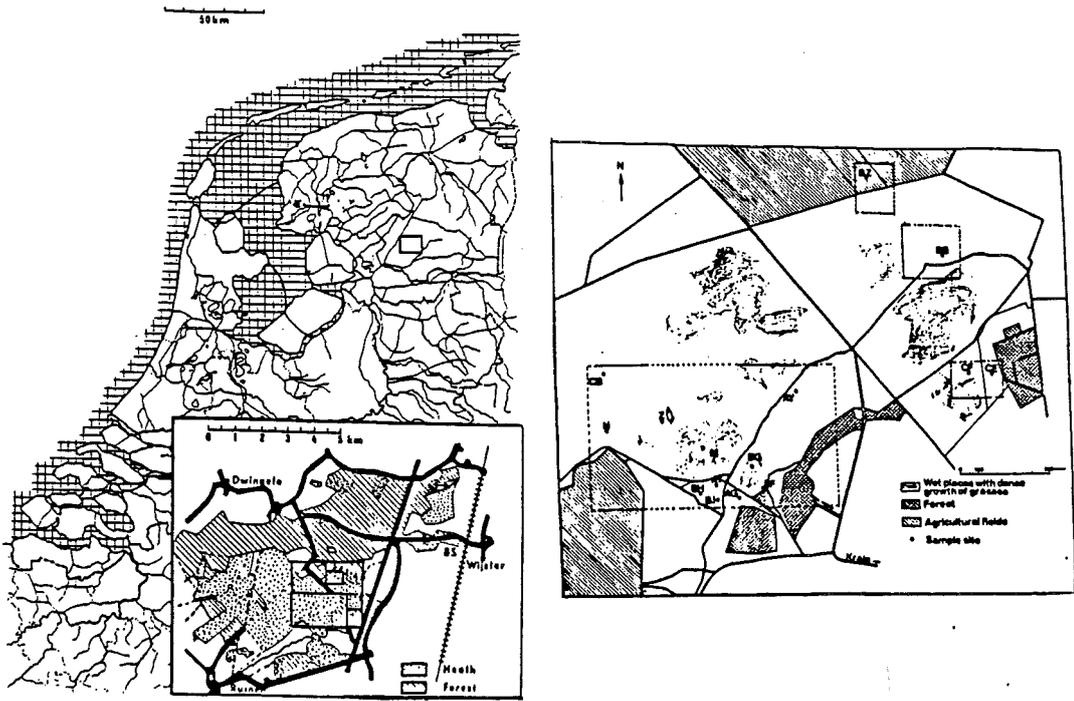


Fig. 3: At left: geographical situation of the study area in The Netherlands (framed, and enlarged below). At right: part of Kralo Heath (enlarged from framed part left below) with indications of the sample sites (capitals) the year-catches of which are plotted in Fig.'s 4 and 5.

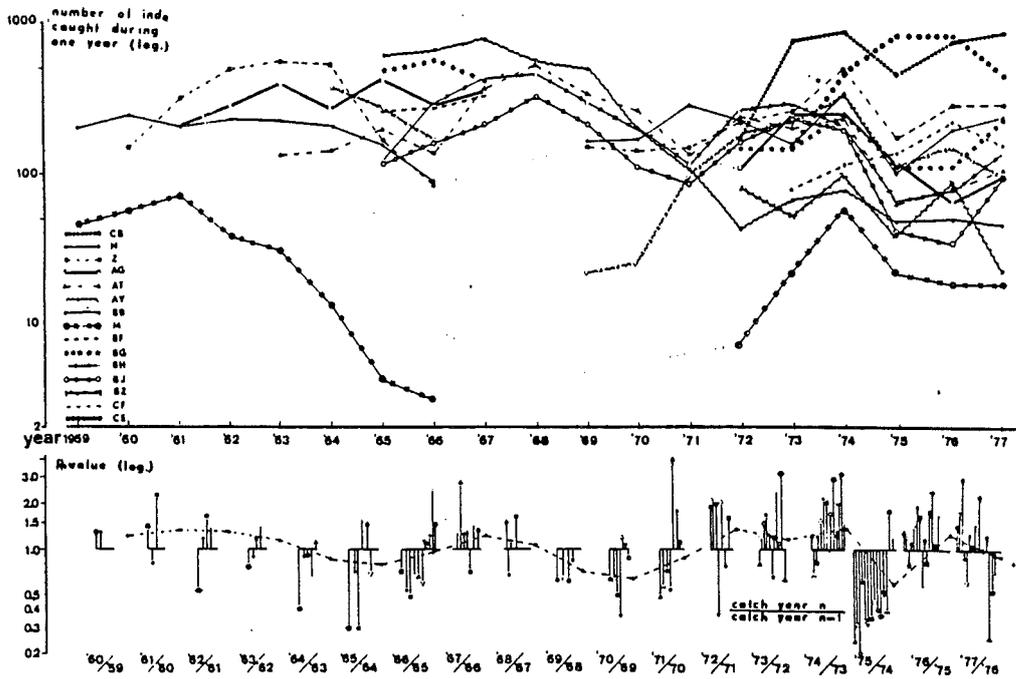


Fig. 4: Year-catches from different interaction groups (subpopulations), as estimates of (relative) mean densities, of *Pterostichus versicolor* at Kralo Heath. The sample sites (indicated by capitals) were situated as in Fig. 3. In the lower part: values of net reproduction (R) in the different subpopulations (vertical bars), and in the multipartite population (dots connected by broken lines) respectively.

3. The survival value of environmental heterogeneity

Fig. 4 shows that in most years the fluctuations of numbers (year-catches) of *P. versicolor* do not run in parallel at all sample sites. This is most obviously shown in the lower part of Fig. 4, where the values of $R = \text{net reproduction (year-catch in year } n / \text{year-catch in year } n-1)$ of the different subpopulations are plotted: in most years density decreased only in part of the sample sites, and increased in others. This is quite different in *C. melanocephalus*, where in most years at all sample sites density either increased or decreased simultaneously: Fig. 5. Apparently, *P. versicolor* responds to the environmental heterogeneity in the heath area, but *C. melanocephalus* does not.

As all localities in the heath area, whether sampled or not, are linked up by a considerable exchange of individuals, locally favourable as well as unfavourable density changes are gradually spread over neighbouring localities, and thus diminished. Because this continuous spreading of density changes occurs everywhere in the area, in fact the risk of extinction of the multipartite population is spread over all the different parts composing the population (Den Boer, 1968). Therefore, we can consider the subpopulations sampled to represent a single multipartite population, which in the case of *C. melanocephalus* would occupy 15-25 ha, and

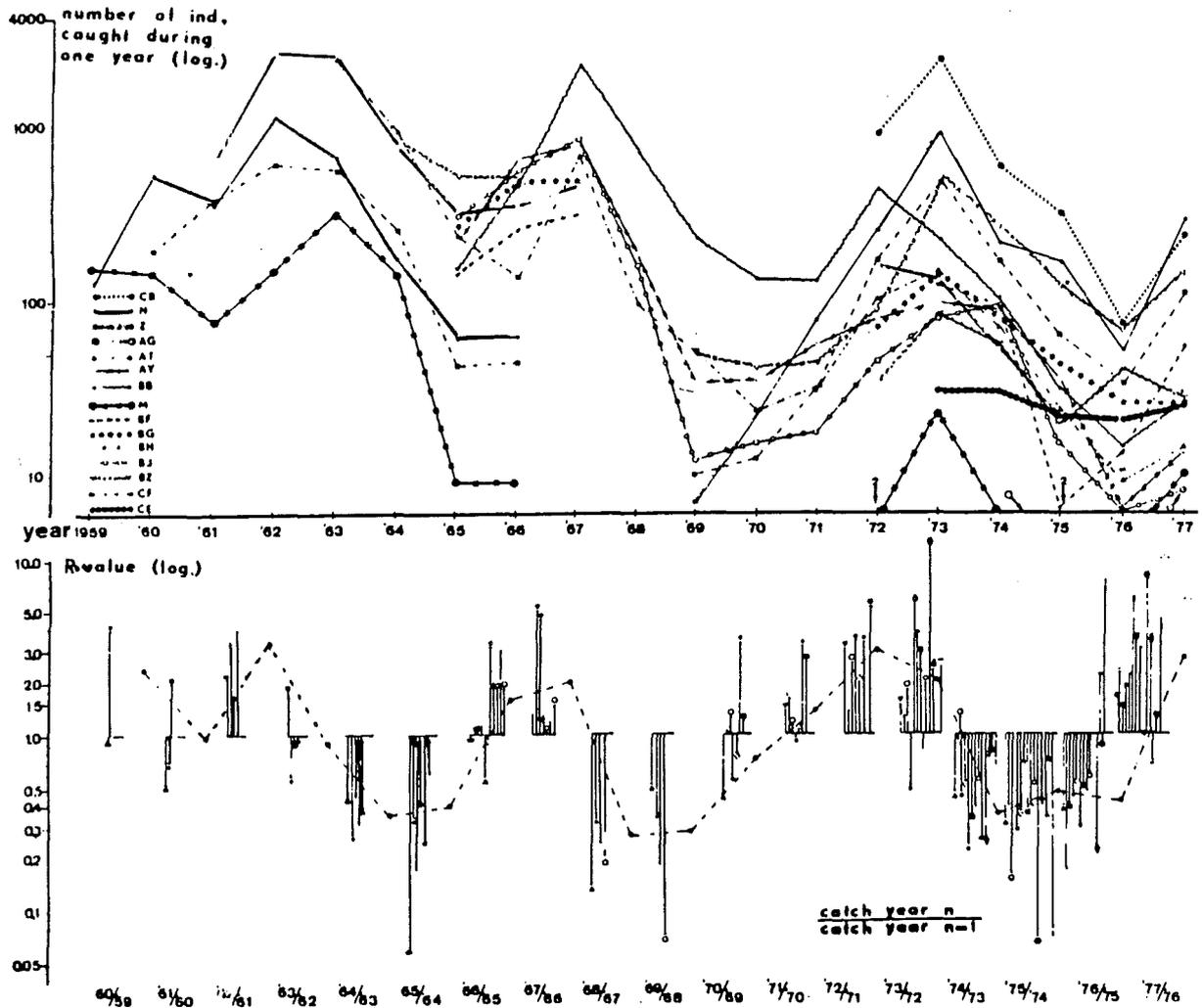


Fig. 5: Year-catches from different interaction groups (subpopulations) of *Calathus melanocephalus* at Kralo Heath. See further text Fig. 4.

in the case of P. versicolor an area of 150-250 ha. By averaging the year-catches over the different sample sites we get estimates of mean density, and thus of the yearly changes of mean density, of the multipartite population. The results are shown in Fig. 6.

By as well as possible simulating the fluctuation patterns shown in Fig. 6 with the help of the computer, and then continuing these fluctuations until "extinction", we get some idea of the chance of survival of such multipartite populations. It then appears that P.versicolor can be expected to survive the next 1000 to 3000 years (ceteris paribus), but C. melanocephalus at best only 100 years (see: Den Boer, 1981: Table 2). If we compare these estimates with the survival times in simulations in which all subpopulations show the same fluctuation pattern (that of the modal subpopulation), it becomes clear that the difference shown in Fig. 6 indeed is the effect of **environmental heterogeneity**: with similar (modal) subpopulations P. versicolor would not survive longer than about

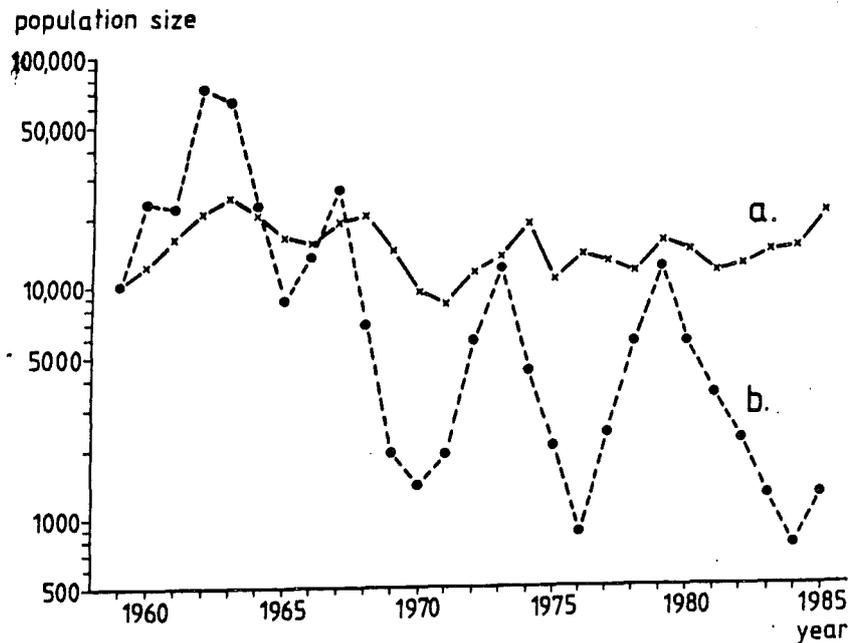


Fig. 6: Fluctuations of numbers in multipartite populations of two carabid species, (a) Pterostichus versicolor (crosses and solid lines), and (b) Calathus melanocephalus (dots and broken lines) at Kralo Heath. The multipartite populations are thought to be composed of the subpopulations plotted in Fig.'s 4 and 5 respectively. To facilitate comparison population size was assumed to have been similar in both species in 1959 (an arbitrary value).

150-200 years, whereas the survival time of C. melanocephalus would be about the same as before (Den Boer, 1981), because in the field the subpopulations were already almost similar (Fig. 5). Hence, the differences between the fluctuation patterns of the subpopulations of P. versicolor, as shown in Fig. 4, and which are responses to environmental heterogeneity, prolong the expected survival time of a multipartite population of this species, consisting of only 7-14 interaction groups, 9-15 times! It is interesting to note, that this spectacular effect of spreading of the risk of extinction over subpopulations of P.versicolor is not optimal: there is still more parallelism in the density changes between subpopulations (e.g. in 1974 to 1975: Fig. 4) than could be expected if the changes occurred at random (Den Boer, 1982). This means, that the

importance of environmental heterogeneity for the survival of natural - i.e. multipartite- populations, provided that the animals sufficiently respond to the heterogeneity present, can hardly be overestimated. The more so as the multipartite population of P. versicolor, studied in this case (with not more than 7-14 parts), is an only weak representative of a natural population, if it is compared with the populations that will have occupied the vast natural habitats that once covered large parts of the continents.

It is not yet clear what is the main cause of the curious difference in response to environmental heterogeneity between C. melanocephalus and P. versicolor at the Heath of Kralo and Dwingeloo. It is supposed, that this difference is connected with the time of the year during which the larvae have to grow up. P. versicolor is a spring breeder with summer larvae, and it can easily be imagined that during summer there will be great differences in moisture content and temperature of the (sandy) soil (where the larvae develop) between sites. C. melanocephalus, however, is an autumn breeder with winter larvae, and during winter everywhere in the heath area the soil (where the larvae stay) is moist to wet, which also will level possible local differences in soil temperature. Because of this, in general, no great differences in survival of larvae of C. melanocephalus between sites can be expected. On the other hand, different winters will be very different, which will be fully expressed at every site, and this will initiate great and spatially unlevelled density changes, as these are shown in Fig. 6.

4. Population units

The preceding sections will have demonstrated that the processes, that increase the stability of a natural population, will be discovered only when adequate population units are studied. Much misunderstanding will arise from regarding as an entity a population that occupies a heterogeneous area, where in fact it consists of many different units, i.e. is multipartite. If, for instance, we had considered the entire population of P. versicolor at the Heath of Kralo and Dwingeloo as a homogeneous unit of study, we would have concluded that the differences between the year-catches from different sites were sampling errors, and would have averaged these year-catches. The population studied in this way would have appeared to be exceptionally stable, as shown in Fig. 7 (above). Many population ecologists would have been convinced that this population must be governed by a very powerful "regulation mechanism". But regulation of numbers -and especially "self-regulation" by competition- presupposes that, within each generation anew, the individuals are able to effectively influence one another's chance to survive and reproduce. This is only possible, of course, if they significantly interact, i.e. this will only occur within interaction groups, the population units that are currently sampled by the pitfalls. These interaction groups (Fig. 7, indicated by different capitals), however, are less stable than the population as a whole. Many interaction groups even show a distinct trend in numbers, which does not support the idea of "regulation" around some "equilibrium level". However, whether the numbers in some or even many interaction groups are "regulated" in some way, or are not, the exceptional stability of the population as a whole obviously results from spreading of the risk of extinction over subpopulations, which is brought about by the exchange of individuals between interaction groups (see also Reddingius & Den Boer, 1970).

The carabid populations discussed will have shown, I hope, that, when studying the dynamics of field populations, it will be necessary to find

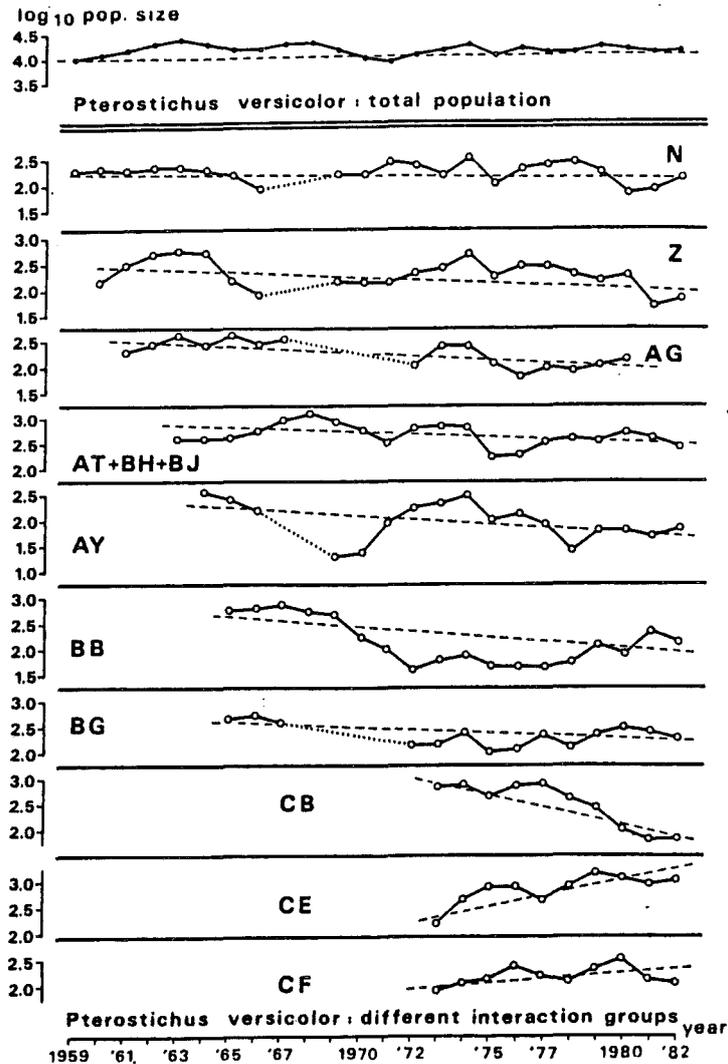


Fig. 7: Fluctuations and trends of numbers in the more important interaction groups of *Pterostichus versicolor* at Kralo Heath (compare Fig.'s 3 and 4), as compared with fluctuation and trend of numbers of the multipartite population composed of these subpopulations (above).

out what are adequate population units. Only after having separately studied a number of such units for some time we will know whether our population is effectively multipartite, such as *P. versicolor*, or is not effectively so, such as *C. melanocephalus*. This knowledge will not only affect the sampling program, but also the working up and interpretation of the population data. This was already realized by Andrewartha & Birch (1954), and in their new book (Andrewartha & Birch, 1984) this is worked out more consistently in the concept of the multipartite population, which is based again on the possibilities of spreading the risk (Den Boer, 1968).

5. Isolation of population units

The above data on *P. versicolor* may also help to enlighten the discussion on size, form and distribution of nature reserves. Simberloff & Abele (1976, 1982) are of the opinion that more species would eventually be saved from extinction by many small reserves than by a few large reserves with the same joint surface. This opinion is especially violently attacked by Wilcox & Murphy (1985), who among others refer for that to the

data on carabid species at the Heath of Kralo and Dwingeloo (Den Boer, 1981).

In section 3 of this paper we saw that a population of *P. versicolor* consisting of (7-14) similar subpopulations would not survive very long (150-200 years). The same applies, of course, to an isolated interaction group. This means, that in a suitable but isolated heath reserve of about 10 ha *P. versicolor* is not expected to survive longer than some 100 years. It must be noted, however, that *P. versicolor* is a rather favourable case: Fig. 8 shows that separate interaction groups of most carabid

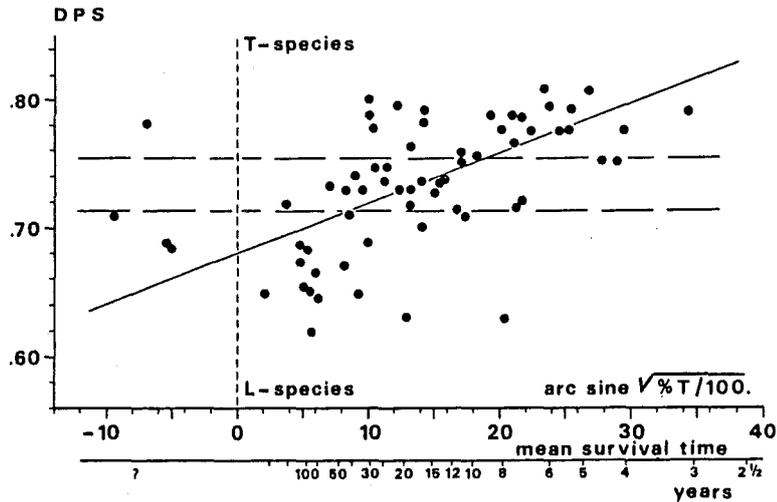


Fig. 8: Relationship between the average turnover (expressed as arcsine value of the square root, and with an added scale of mean survival times) - as an estimate of the frequency of extinctions/(re)foundings- of interaction groups in the 64 more abundant carabid species of Drenthe (Den Boer, 1985) and DPS (Distribution of Population Samples), as an estimate of the overall powers of dispersal (Den Boer, 1977, 1985, 1986a). T-species (DPS > 0.753) have high powers of dispersal (usually by flight), L-species (DPS < 0.715) have low powers of dispersal (usually by walking). The powers of dispersal of the species with DPS between 0.715 and 0.753 are generally more like those of L-species than like those of T-species.

species will survive much shorter than 100 years (see further Den Boer, 1985, 1986a). As the dispersal abilities of *P. versicolor* are almost completely restricted to walking, and the distances covered within a season will not exceed a few hundred meters (Fig. 2), *P. versicolor* will not be helped by a high number of small heath reserves, if mutual distances are more than 200 meters (say). A safe reserve for *P. versicolor* should be an uninterrupted and effectively heterogeneous heath area of at least 150-250 ha (see section 3).

What is said here about *P. versicolor* applies *mutatis mutandis* to most carabid species of heath, blown sand and peat bog areas, and still more strictly to carabid species of forest, because the majority of these species have only low powers of dispersal (Den Boer, 1977; L-species in Fig. 8). Possibly, (carabid) species with high powers of dispersal (T-species in Fig. 8, usually regular flyers) might be favoured by a high number of small reserves, if these are concentrated in certain (suitable)

regions to reduce dispersal losses. But even then will a high number of small reserves only be better than a few large ones, if the advantages of the (supposed) increase of environmental heterogeneity is not nullified again by increased dispersal losses and decreased exchange of individuals. Moreover, the majority of T-species is hardly endangered, because these are common species of agricultural fields and of related man-made (instable) habitats.

6. Discussion

Reproduction and mortality of insects (and of other arthropods) are generally highly affected by weather conditions (Uvarov, 1931; Andrewartha & Birch, 1954), which often results in violent fluctuations of numbers, not only in temperate and arctic regions, but also in the tropics (Wolda, 1978). These density fluctuations continuously endanger the persistence of local groups. There seem to be three "strategies" to cope with this difficulty:

- (1) Compensating extinctions by sufficient (re)foundings.
- (2) Opposing the density-changing forces by powerful feedback processes.
- (3) Spreading the risk of extinction by sufficient movement of individuals between differently fluctuating groups.

Species of instable habitats usually live according to "strategy" (1), which is necessarily connected with high powers of dispersal. This implies, that in order to about maximize the chance of colonizing unoccupied sites each generation anew high numbers of individuals will have to leave the local populations (with the extreme in which all individuals leave: change of habitat of "migrating" insects, e.g. Van Huizen, 1977). At least among carabid beetles (T-species: Fig. 8) unfavourable, accompanying effects for the parent populations are: numbers that fluctuate more heavily than at random (Den Boer, 1985: 3), and survival times that are importantly shortened as compared with those of coexisting L-species (Den Boer, 1985: Fig. 4). See further Den Boer (in press).

Field populations of arthropods, in which survival time is significantly increased by "strategy" (2), seem to be rare (but see: Oghushi & Sawada, 1985). Apparently, the variation of density as a result of weather conditions and of other "non-reactive" factors (Andrewartha & Birch, 1954) usually is too great to be spanned by the correcting possibilities of the governing (density-dependent) process; see e.g. Den Boer (1986b, 1986c, 1987).

"Strategy" (3) is discussed in this paper, and is supposed to result in the almost indefinite survival of large natural populations. An important condition, apart from sufficient movement of individuals between groups, is, that the weighted mean of the variances of densities over years within groups is about equal to (or even smaller than) the weighted mean of the variances of densities over groups within years. In P. versicolor at the Heath of Kralo and Dwingeloo this condition is indeed answered (Den Boer, 1971: Table 3), which means that effective environmental heterogeneity is sufficient to compensate for the overall effective environmental variability in time. In C. melanocephalus, however, the first (mean variance over years) is much greater than the latter (mean variance over groups): Den Boer (1971: Table 4), which means that the overall effective environmental variability in time is too great to be significantly compensated for by effective environmental heterogeneity (see further section 3).

It can be expected that in many areas environmental heterogeneity will be a function of distance, which would imply that it would decrease with

reduction of the area available for the natural population. I am inclined to conclude from this that, the greater the area that is effectively occupied, i.e. with significant movement of individuals between groups, the greater will be the chance that effective environmental heterogeneity will compensate for the overall environmental variability in time, or, in other words: the greater the chance that spreading of risk in space will result in a satisfactory degree of levelling of density changes in time, as it was found in P. versicolor (Fig. 7). But also -and probable even more, because the function of environmental heterogeneity with distance will not be linear- the smaller the area effectively occupied by the natural population, the greater the chance that spreading of risk in space will not play a decisive part, because effective environmental heterogeneity is too much reduced, as it was found in C. melanocephalus (Fig. 5).

Therefore, I generally agree with Wilcox & Murphy (1985), that reduction and fragmentation of natural habitats in most cases will be unfavourable from the point of view of the conservationist. Not only will the chance of extinction of many species -especially of those with low powers of dispersal- be increased, but because of interdependences between species also many other species will be endangered more indirectly. Probably, only "weedy" and other highly opportunistic species -with high powers of dispersal- will thus be favoured, because of the connected increase of transitional and border habitats with less stable conditions.

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