

50 years of carabid investigations at
Uthalo heath, Drenthe, the Netherlands
by Piet den Boer

I passed a greater part of my active life in Wjster at the Biological Station, which was founded in the thirties by the naturalist Willem Beyersinck. The subjects studied in Wjster were already initiated in Leiden where I studied biology and was the first assistant of Don Huener, the first professor of ecology in the Netherlands.

Some times we "assistant and promovendi" came together at Huener's home to discuss current ecological problems. One of these problems was the way of which Carl Lindroth used wingdimorphic carabid beetles to reconstruct the faunal history after the last ice time in Scandinavia.

In Wjster I checked all carabid beetles caught on the development of wings. After some years we decided to erect window traps on the experimental field of the Biological Station. My assistant, Taco van Huizen dissected the females caught and found that a greater part of these females were already inseminated in the habitat of origin. This means that these females could found new populations without the help of males. In this way wing-dimorphism could be an adaptation. But Maartje Nelemans, who studied *Nebria brevicollis*, an always fully winged species, never found a specimen in the window traps. I asked her to tell me why? The answer was quite simple: she told me that for flying you not only need developed wings, but also wing muscles. And the wing muscles *Nebria brevicollis* only developed under optimal

feeding conditions, which were apparently not present in our experimental fields. If you took specimens to the laboratory and fed them there optimally, they developed wing muscles and were ready to fly. As she repeatedly demonstrated me.

The same phenomenon was found in the winged morph of *Calathus melanocephalus* by Berend Aulema: also only there wing muscles are developed under optimal feeding conditions. These phenomena point to wing dimorphism as a gradual degeneration ending after many generations in wingless carabid beetles. Curiously enough a closely related species, *Calathus csikii*, which is hardly to separate from *Calathus melanocephalus* is mostly winged and is under natural conditions generally able to fly.

I tried to give a picture of the significance of dispersal by DPS (Distribution of Population Sizes) values. This is the frequency distribution of the year samples as percentages at probability scale. This year samples contain two sets: one set of the settled populations and a final set of the beetles that arrived somewhere by dispersal and after reproduced for a short time. Between this two sets the frequency distribution percentages often shows a remarkable unimodal, which means that the percentages of the few dispersing specimens filled the last part of the probability plot.

Another subject that was discussed at Huenens home, when I was an assistant of him, was the regulation of animal numbers by Nicholson.

I always opposed to this idea, because I brought forward that not only possible density-dependent processes might influence the processes of population numbers but also many local factors, such as in carabid beetles: structural vegetation, micro weather, soil conditions, spacial distribution of prey etc.

I plant this investigation in Wjster. In 1959 I placed two sets of pitfalls at the heath of Kralo and found indeed that after a year the fluctuations of numbers were quite different in all species sampled. Thus I placed more sets of pitfalls at Kralo heath to check this phenomenon. I found that in all cases the yearly catches fluctuated differently in all species. This confirmed my hypothesis that local factors influenced the fluctuation of numbers more than some overall density-dependent processes.

Around each set of pitfalls was an area from which I caught 80-90% of the individuals of each species in a year catch. I called this an interaction group of which the situation in the field was only determined by a set of pitfalls. This area was different in different species: 2 hectares for small species like *Calathus melanocephalus*, *Pterostichus diligens* and others; and for greater species like *Poecilus coenulescens* and *P. lepidus* about 10-12 hectares.

If you take these interaction groups (as in the graphs shown) together as a measure of the

population as a whole (the graphic on top) you see that the fluctuations of this mean interaction group is much smaller than in separated interaction groups.

I called this phenomenon: stabilisation by Spreading of Risk. Which in my opinion is more important than the "regulating" effect of density-dependent processes.

Moreover you see that if the total area is much decreased and this smaller area will only contained a few interaction groups you understand that the total fluctuations of numbers are much higher than in the example given. This means that the chance of extinction of this smaller population is increased.

In fact the graphs shown is a picture of a stochastic population, this is a population of which the netto reproduction values form a normal distribution. if enough reproduction values are known you can estimate mean and s.d. of this distribution and you can also take other netto reproduction values from this distribution and continue the pattern of fluctuations of the mean interaction group continued in future. In this way you may simulate the possible moment of extinction of this population.

When I retired in 1991 the sampling was continued at first by Theo v. Dijk and later (since 1998) after closing the Biological Station) by my last promovenus Rikjan Vermeulen with whom I formed

ESTIMATION OF SURVIVAL TIMES AND TURNOVER FREQUENCIES OF POPULATIONS

P.J.den Boer

For a long time most biologists thought that populations and species would mainly become extinct as a result of intervention by man: direct killing of animals, destruction of habitats, poisoning of food, etc. Possibly Andrewartha & Birch (1954) were the first to show that also under natural conditions local populations may disappear rather frequently. But in general, their data were overlooked by population ecologists. Thirteen years later MacArthur & Wilson (1967) succeeded where Andrewartha and Birch had failed: they convinced biologists from the fact that the numbers of species on islands are the result of colonization and extinction. From that time on the extinction of island populations became common knowledge among biologists, especially among nature conservationists. During the following decades the discussion often shifted to the question whether or not isolated habitats on the mainland could be considered **islands**, and whether the numbers of species in such 'island-habitats' would also be the result of colonization and extinction. Therefore, conservationists concentrated more and more upon the effects of fragmentation of habitats for **biodiversity**.

As it is difficult to directly observe the extinction of a population, most work on the effects of fragmentation of habitats was theoretical. Geneticists concentrated upon the unfavourable effects of inbreeding, and mainly disagreed about the critical population size below which inbreeding can be expected to accelerate extinction. Pimm et al. (1988) tried to find data from the field that might be connected with the turnover -extinction and refounding- of island populations of birds in Great Britain, and thus to test the theoretical models developed. To be able to predict the risk of extinction, i.e. the number of years a population can be expected to survive, they thought the coefficient of variation of population size (CV) over a sufficient number of years to be the best estimate. To test these ideas they used a data base of short-term survivals of 355 populations of land birds belonging to 100 species on 16 islands. In fact, they had only sufficient data to calculate reliable CV-values for 39 of these species.

They concluded that the risk of extinction increases with CV.

Many years before publication of the paper of Pimm et al. (1988) I was already engaged in building a data base that might allow me to estimate survival times of populations. From 1959 onwards I sampled carabid beetles with the help of standardized pitfall sets to develop a **comparative population ecology**. With such pitfalls, which were emptied each week the whole year round, at each site between 7 and 40 carabid species could be sampled at the same time. First of all we had to establish the relationship between these catches and population density. Baars (1979a) in different years and at different sites of our main study area, the Heath of Kralo, installed a number of enclosures and caught all beetles present within the enclosure with small pitfalls at the inner edge. These direct density estimates appeared to correlate nicely with the total catch in a year (**year-catch**) of that species in a nearby standard set of pitfalls (in all cases r was greater than 0.9). I myself (1979) compared year-catches of a number of carabid species of forest with the population sizes estimated with the help of extensive mark-recapture experiments, and also found a correlation above 0.9. We concluded that year-catches of the same species in the same standard set of pitfalls but in different years are reliable but relative estimates of mean density around the pitfalls. To know the actual value of density it was necessary to make extensive mark-recapture experiments, which was done for a number of abundant species. We had also to know the surface around the pitfalls from which the year-catch was obtained. This problem was solved by Baars (1979b) for some species. By marking some individuals radioactively and each day looking up these with an advanced Geiger counter and marking the place, he was able to reconstruct the walking patterns in day-distances of a lot of individuals in different stages (young, male, female with and without eggs, etc.) and of different species. Next this stochastic walking pattern could be simulated for a great number of individuals of each species and the area covered by the individuals in a year-catch of a standard set of pitfalls could be estimated. I called such a group of beetles from which a year-catch is obtained an **interaction group** (den Boer, 1977). For example, in the carabid *Calathus melanocephalus* 90% of the individuals in such an interaction group lives at an area of 2 ha and in *Pterostichus versicolor* at 12 ha. With standard sets of pitfalls we sampled all kinds of more or less natural

habitats in Drenthe, the Netherlands, both remnants of forest and peat moor as well as smaller and larger heath areas.

In the course of years I more and more concentrated our sampling efforts in a large heath area, the Heath of Kralo, because it is possible to compare there different interaction groups of the same **multipartite population** (Andrewartha & Birch, 1984: 8, 9.1). By sampling the same site during many years I got an impression of the pattern of density fluctuations of each species at that site. This pattern is determined by the successive values of **net reproduction (R)**: N_{t+1}/N_t . In most species these fluctuations of numbers did not occur synchronously in the different interaction groups sampled at the Heath of Kralo. Nevertheless, the frequency distributions of R-values of interaction groups sampled between 12 and 23 years did not differ significantly (Mann-Whitney), which means that the pattern of density fluctuations -though often running asynchronously- was essentially the same in each interaction group at this Heath area. Therefore, I could add the R-values of the different interaction groups into the same frequency distribution. These frequency distributions highly resembled log-normal distributions, so that we could fit a log-normal to the field distribution of each species. When V^2 and M are Variance and Mean of the field distribution of R-values respectively, the fitted log-normal (Y) has $\text{mean}(Y) = 2 * \ln M - 1/2 * \ln(V^2 + M^2)$ and $\text{Var}(Y) = \ln(V^2 + M^2) - 2 * \ln M$ (see Appendix by Reddingius to den Boer, 1985). When also adding R-values from sampling series in other areas than the Heath of Kralo, where the species was abundant, the fitted log-normal did not change fundamentally. From these data we concluded that the pattern of density fluctuations -at least within the same climatic region- is a species characteristic that can be formulated by mean and variance of the log-normal fitted to the frequency distribution of R-values collected from all sites sampled, and of course, the more R-values (between 12 and 138 per species) are available to fit a log-normal the better this will characterize the pattern of density fluctuations.

In this way I could construct reliable log-normal distributions of R-values for the 65 more abundant carabid species of my area (Drenthe). For none of these species the field distribution of R-values differed significantly from the fitted log-normal (X^2). This was a great advantage, because it made it possible for me to extrapolate density fluctuations

beyond the sampling periods in the field. But all these R-values originated from year-catches, and though year-catches appeared to be reliable estimates of densities of the interaction groups concerned, and thus will represent the fluctuation pattern of densities dependably, for most species the actual densities were unknown. As a series of succeeding year-catches faithfully represents the pattern of density fluctuations of that interaction group during these years, it was possible to estimate the density range, i.e. the **Logarithmic Range (LR)**, being the logarithm of the highest density (year-catch) minus the logarithm of the lowest density (year-catch) of that series of year-catches, which is independent of the actual densities.

Now it became interesting to compare the LR-value of some series of positive year-catches from the field with the LR-values of simulations over the same number of years when randomly taking R-values from the log-normal of R-values of that species. For each number of years such simulations were repeated 500 times, and it was estimated how many simulation runs had LR-values below and how many LR-values above the mean of the 500 simulations for that number of years. Also the deviation of the LR of the concerning field series from that mean (rankits) was established. For each species this procedure was repeated for each run with positive year-catches from the field that was 4 years or longer. To summarize these results for each species separately we first had to know whether or not short series differed from long series as well as series at a high level of catches from series at a low level of catches, but without zero year-catches. Significant differences were only incidentally found, so that it was again confirmed that the pattern of density fluctuations is characteristic for the species and not for the habitats where the species was sampled and only slightly for the density levels at which it was realized. Therefore, it appeared possible for each of the 64 more abundant species to add the results for all field series and to establish how many LR-values were lower and how many higher than the mean LR from the simulations for that species. These frequencies could be compared with the expected frequencies when the year-catches of that species would have fluctuated randomly. It then appeared that in 38 of 64 species these frequencies did not differ significantly from those of random series (χ^2). In 22 of these species significantly more LR-values were greater than expected for random

fluctuations, and in only 4 species significantly more LR-values were lower than expected.

Therefore, it could be concluded that among the 64 carabid species investigated density fluctuations often occur randomly, but in many situations these may occur between wider limits than expected for random fluctuations, and only in a few cases between narrower limits than expected. Just as in random walks also in the interaction groups studied the limits between which densities -in these cases year-catches- fluctuated become wider in the course of time. It must be noted in passing that the same phenomenon -widening of density limits, i.e. growth of LR-values- occurs in all time series of densities I could find in literature, including in populations that are claimed to be 'regulated', such as the great tit of Kluyver (1951), the pine looper of Klomp (1966), and the winter moth of Varley & Gradwell (1968). Because of this general phenomenon of increasing LR-values with time it must be possible by adequate simulations to estimate how many years it can be expected to take before the population concerned has become extinct or has reached impossible densities. We silently suppose in such cases that the environmental conditions are stationary, i.e. that the fluctuation patterns of environmental variables, such as temperature, do not change in the course of time. However, even under the restriction of stationarity it is necessary to know exact densities to estimate survival times in this way, and as far as carabid beetles are concerned we only knew these for a few species during a restricted number of years. As said before, the relationship between pitfall catches and actual densities is different for each carabid species, and has to be estimated by time-consuming mark-recapture experiments during the whole year. If possible such mark-recapture experiments should be continued during a number of years to check whether this relationship is a constant one or not. Although in the 7 species where the relationship between pitfall catches and densities was estimated in this way during some succeeding years this relationship appeared to be rather constant, I looked for another method to estimate expected survival times under the hypothesis of stationary environmental conditions, in order to be able to include more species.

Apart from uninterrupted sequences of positive year-catches for all species we frequently recorded zero year-catches that interrupted our

sampling series (e.g. den Boer, 1977: Table 9). These zero year-catches, i.e. not a single specimen of that species has been caught during an entire year, as far as these followed or preceded positive year-catches, may give us an impression of the **turnover** of interaction groups, i.e. of the possible frequency of local extinctions whether or not followed by (re)colonization of the site. However, a zero year-catch does not always indicate extinction of the local group; it is also possible that density has become so low that even the chance to catch a single specimen is too low to be realized within a year. I called such false zero year-catches **pseudo-turnover** in the sense of Nilsson & Nilsson (1983). Therefore, I had to find a method to discriminate among the zero year-catches between 'pseudo-turnover' and actual extinction. First of all, for the highest catch in that series I fixed the **catch-level** (n), i.e. the value of n when the highest catch is between $1/2 \cdot 3^n$ and $1/2 \cdot 3^{n+1}$ (n= 1, 2, 3,7). Hence, with n= 1, the highest catch is between 1 1/2 and 4 1/2, with n= 2 between 4 1/2 and 13 1/2, etc. Next, starting with a sufficiently high density I took R-values from the log-normal for that species and simulated a series of densities of the same length as the field series, during which the computer population persisted. Subsequently, such a computer population was sampled at the catch-level of the field series, i.e. an adequate percentage of 'beetles' was taken away from every 'density' as 'year-catches'. Such simulations were repeated 500 times for each case, and mean and variance of the number of 'zero year-catches' per run (catches < 1) were computed. As I only used computer populations that persisted, the number of zero year-catches computed was the expected pseudo-turnover (%). Because of the high level of variation both in the field data and in the simulations of these data only the overall results per species can be expected to be reliable (den Boer, 1985). For all species studied the number of actual zero year-catches in all sites sampled was higher than the computed mean 'pseudo-turnover', so that the number of zero year-catches observed could be corrected for pseudo-turnover. Within the restrictions of area (Drenthe) and time (30 years of research), this **corrected turnover** now estimates the chance (%T) that in some year one or other interaction group of that species will become extinct or will be (re)founded. The reciprocal of corrected turnover (%) times 100 gives the expected mean survival time in number of years of an average interaction group of that species.

The results for 65 more abundant carabid species show survival times between 2 and more than 200 years, the majority between 4 and 60 years. How reliable are these estimates? To get some impression for the 25 most abundant species I also computed survival times by extrapolating from the field series, i.e. by considering the fluctuation patterns random walks of densities that are determined by R-values taken from the log-normal of R-values of that species. But for most species I had no reliable information about population sizes in the field. Therefore, I executed these extrapolations for each species from three initial population sizes, 1000, 10,000 and 100,000, values that are within the range of sizes of interaction groups of some abundant species the densities of which were estimated by extensive mark-recapture experiments. Curiously enough for each of the 25 species the survival times thus estimated did not differ very much between the three density levels. In 9 species survival time increased with increasing density level -as could be expected- though often with a few years only. But in 11 other species survival times decreased with increasing density level, and in the remaining 5 species the highest survival time was with the median initial population size of 10,000. This unexpected result shows that, contrary to most publications on the subject, density level does not seem to be the dominant parameter determining survival time.

I had already detected this phenomenon when simulating survival times for the two most abundant species at the Heath of Kralo (den Boer, 1981) under many different conditions, such as separate versus combined interaction groups, whether or not density-dependence density-dependence between succeeding densities, whether or not exchange of individuals between groups, etc. In all these cases it appeared necessary to multiply density level with a factor between 80 and 2000 to only double survival time.

For 22 of the 25 most abundant species the survival times from the extrapolation models were higher than those from the zero year-catches model. This may be the result of the fact that for most carabid species at most sites the adequate random walks of densities fluctuate between narrower limits than the actual densities in the field, so that continuation of such random walks until extinction (population size < 1) can be expected to give too optimistic survival times. On the other hand, in the zero year-catches model the percentage pseudo-turnover was also

estimated with the help of random walks, though very short ones. Therefore, it can not be excluded that the corrections for pseudo-turnover in the zero year-catches model often will have been too low, which resulted in too low survival times. However, I expect that the short random walks of densities (mostly between 4 and 12 years) usually will have been closer to reality than the much longer random walks used in the extrapolation models (often more than 100 years). Moreover, some well dispersing species occupying very unstable habitats cannot have survived there for many decades as is suggested by the extrapolation models (some T-species).

In the only case in which we could compare actual survival times directly estimated from field observations with the survival time estimated with the zero year-catches model the latter gave realistic values. This case concerns *Agonum ericeti* that at 3 small sites was present in normal densities in 1961-'62, but appeared to have become extinct there in 1988. This gives an expected survival time of less than 26 years, whereas the zero year-catches model estimated 7-44 years (mean 19 years), a satisfactory fit with the field observations.

The insensitivity of random walks of densities for the density level strikingly contrasts with the high sensitivity for the two parameters of the log-normal of R-values, especially for mean $\ln R$. For the 25 most abundant species survival times estimated with extrapolation models correlate highly significantly with mean $\ln R$: for density level 1000 $r_s = -0.902$ ($P < 0.0^{435}$), for level 10,000 $r_s = -0.926$ ($P < 0.0^{435}$), for level 100,000 $r_s = -0.815$ ($P = 0.0^{435}$). The dominant position of mean $\ln R$ is less evident in the zero year-catches model: $r_s = -0.503$ ($P = 0.007$). Mean $\ln R$ predetermines the trend of numbers over time by establishing the ratio between the numbers of R-values above and below zero. Also Var $\ln R$ has an important effect on survival times, though less than mean $\ln R$. For the 25 most abundant species we found: at density-level 1000 $r_s = -0.380$ ($P = 0.03$), for level 10,000 $r_s = -0.463$ ($P = 0.012$), for level 100,000 $r_s = -0.572$ ($P = 0.0025$). Curiously enough survival times according to the zero year-catches model are not correlated with Var $\ln R$ for the 25 most abundant species: $r_s = +0.076$ (n.s.).

To illustrate the dominant effect of mean $\ln R$ for survival times of random walks of densities for 31 values of mean $\ln R$ between 0.4 and -0.4, which is the range of mean $\ln R$ for 62 more abundant carabid species, from

each the 31 log-normals, all with the same Var lnR (the average Var lnR of the 62 species) I simulated 500 random walks of densities for each of the density levels 10^2 , 10^3 , 10^4 , 10^5 and 10^6 , and estimated mean survival times. As expected the highest survival times concentrated around mean lnR=0 and decreased rapidly the more mean lnR values deviated from zero, which goes with decreasing differences in survival times between density levels. The frequency distribution of the mean lnR of the 62 carabid species appeared to be about similar to that of the 'survival times' computed for the random walk models (χ^2 between 2.76 and 7.66, P between 0.30 and 0.90). Hence, if time series of densities from the field could be considered random walks of densities the survival times of such random walks would be highly determined by mean lnR with only a significant effect of density level for series with mean lnR close to zero. However, at least for carabid beetles, time series of densities from the field usually fluctuate less favourably than random walks, so that a model with mean lnR as an estimator of survival times does not seem adequate. Moreover, for a reliable estimate of mean lnR many lnR-values must be available, I suppose.

As it will not often occur that conservationists can collect many adequate data from many different sites, over many years for a reasonable number of species, as thus can make use of some variant of the zero year-catches model to estimate survival times, I looked for an estimator that can give at least a reasonable indication from a more generally available amount of data. As the fluctuation pattern of densities, whether a random walk or not, is roughly indicated by the Logarithmic Range (LR) I correlated mean LR-values over 8 years (from 3-6 series) for 55 of the 64 more abundant carabid species with the mean survival times for interaction groups of these species derived from the zero year-catches model. There appeared to exist a highly significant, negative correlation: $r_s = -0.593$ ($P < 0.0435$), which can be adequately represented by the first principal axis Y (mean survival time) = $6.5491 - 1.2337LR$. The survival times read from the first principal axis are not biased concerning the survival times plotted: Wilcoxon's signed ranks test (Sokal & Rohlf, 1969) for all 55 species results in $T_{pos.} = 721.5$ and $T_{neg.} = 763.5$ ($P = 0.86$). Moreover the survival values read for 22 of the 25 most abundant species are within the 90% confidence interval of the estimates from the zero year-catches model.

Such a relatively favourable result cannot be reached for mean LR-values

for 5 year periods. Wilcoxon's signed rank test for the 65 more abundant species gives $T_{\text{pos.}} = 756$ and $T_{\text{neg.}} = 1389$ ($P = 0.017$), whereas only 7 of the 25 most abundant species are within the 90% confidence interval of the estimates from the zero year-catches model. LR-values for periods of 5 years highly overestimate survival times for many species when these are read from the first principal axis, as compared with the values from the zero year-catches model.

Of course, the methods for estimating survival times and turnover frequencies presented here have some weaknesses. The most important might seem that for extrapolation models I had to introduce an upper limit of extinction, which was fixed at the square of the density level. For carabid beetles this upper limit means impossible densities between 100 and 20,000 beetles per square meter, whereas we never observed densities above 2-20 beetles per m^2 . Therefore, we are sure that these upper limits were well-considered, because survival at such densities would have been impossible. An advantage of the zero year-catches model is that in the short random walk for pseudo-turnover simulations we had no problems with upper limits which were never reached, because I only considered catches at the right catch-level.

Another weakness might be that all data and simulations concern the numbers of individuals in interaction groups (den Boer, 1977), i.e. 'populations' in the sense of Bakker (1971), which in most cases will be identical with the 'local populations' of Andrewartha & Birch (1954, 1984). Individuals in an interaction group around some point, e.g. a standard set of pitfalls, significantly interact directly or indirectly. In the case of carabid beetles these interactions, e.g. copulations, occur via the walking pattern, so that the area covered by an interaction group is determined by the walking pattern of beetles of that species. The size of the area occupied by an interaction group of carabid beetles largely depends on the size of the individuals: for beetles of 2-4 mm this probably is about 0.02-0.2 ha, for beetles of 6-8 mm about 1-3 ha, for beetles of 10-12 mm about 8-14 ha, and for beetles of 20-30 mm about 100-650 ha or even more.

However, many continuous habitats are larger than the area covered by a single interaction group. In such cases there will be exchange of individuals between interaction groups, which are defined around some sets of pitfalls or some other points of observation. The survival time of such

a **multipartite population** will be much higher than that of a single interaction group, because **spreading the risk** of great fluctuations in numbers will result in levelling of density fluctuations in the population as a whole. For instance, the multipartite population of *Pterostichus diligens* consisting of the 9 interaction groups studied by us, would show a much more favourable fluctuation pattern of numbers than the individual interaction groups and is supposed to survive more than 100 years instead of the 30 years estimated for a single interaction group. In other carabid species the expected survival time of multipartite populations of that size can be more than 1000 years.

But let us not be too optimistic: many nature reserves are too small to accommodate many interaction groups of endangered species, especially of bigger animals than carabid beetles. Metapopulations consisting of a number of isolated groups with dispersal between have lower chances to survive than multipartite populations in an area of the same total surface. Hence, nature reserves should be as large as possible, and fragmentation should be avoided.

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