

On the Stability of Animal Populations, or how to Survive in a Heterogeneous and Changeable World?

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1. Introduction

We are concerned here with "biological systems", and there immediately I am getting into trouble: must an animal population be considered a biological system, or only a group of biological systems (i. e., individual animals) that is found in a certain locality? That depends on the definition of "biological system", of course. Most things I could find about systems in general, somehow referred to a more or less organized entity, i. e., there are actual boundaries, there is an internal structure, and there are processes that - at least in principle - can be predicted (although they are not necessarily completely determined). Most animal populations do not fit this picture: boundaries are either arbitrarily set by the observer, or forced upon by abrupt environmental discontinuities (e. g., the boundaries of an island or a lake) and thus external; often boundaries are even not demonstrable and in fact only very broadly (or not at all) localizable; both population structure and population processes are usually as highly influenced by the environment that they can only be predicted with some precision at short notice and in terms of probabilities (compare weather-forecasts). Therefore, it would be wise to let pass the question whether or not an animal population is a "biological system", if it were not closely connected with the question after the stability of animal populations.

As far as I can see it, the stability of a "system" in the usual sense depends on the degree to which certain norms or equilibrium values (and/or stable limit cycles) can be maintained and/or reached by feedback processes, by which the stability of systems would thus highly depend on the transfer of some kind of "information": systems are "regulated". Individual organisms evidently come up to this notion: the normative information is even given beforehand in the genes (and reproduced). Most biomathematicians, however, take it for granted that also populations, communities

and ecosystems may be considered systems in this sense, i. e., the stability would be "neighbourhood stability": to what degree can the norm be reached or maintained? MAY (1973) discussed many kinds of models that can be constructed on this assumption. His general conclusion is that increased complexity of the biological system makes for diminished stability, unless long-term evolutionary processes have just sought out those tiny and mathematically unprobable parts of parameter space which endow the system with long-term stability. It must be noted, however, that this interesting conclusion depends on the assumption that not only the stability of individuals, but also that of populations, communities and ecosystems would indeed be neighbourhood stability, and I am afraid that this assumption is not so much forced upon the modellers by an overwhelming amount of field evidence about the occurrence of regulation, but much more by mathematical tractability.

For more than ten years already I tried to stimulate ecologists to investigate the possibilities of "spreading of risk" to get to grips with the tenacious problems around the stability of natural populations (DEN BOER, 1968).

The idea was that spreading of the risk to die without progeny over different individuals, different stages of development or age, different subpopulations, etc., might keep the overall density between certain positive bounds, i. e., might contribute to a "between-limits-stability" by decreasing the chance that the numerical changes of the population would either lead to extinction or to exceeding of the possibilities of environmental resources, by which the survival time of the population might be prolonged. This trial emerged from the conviction that ideas about the regulation of animal numbers force to accept a number of postulates that are difficult to test in natural populations, and such a situation must hamper progress. How to estimate the "equilibrium density" or "carrying capacity" independently of the actual population counts, especially if we realize that the values of such norms will depend on environmental conditions, and can thus be expected to change continually (see e. g., WILBERT, 1962; REDDINGIUS, 1971:13)? And thus: how to falsify the assumption that such a "norm" would actually exist and influence the fluctuations of numbers? This does not mean, however, that I should deny the possibility that in some (or even many) populations mean density will sometimes (or even frequently) be restricted by density effects, i. e., by interactions between the individuals. But such a restriction of mean density from above does not imply that mean density is regulated, i. e., that neighbourhood stability is necessarily improved by it. Other things being equal, such a restriction of density from above may even result in the chance of extinction of the population to be increased: regulation of numbers implies that there should also be a process that independent of environmental conditions will raise density the more the lower density has fallen. As most environmental influences (e. g., weather conditions) will generally change independently of mean density such a process can hardly be imagined to occur more than incidentally. This was already stressed by MILNE (1957,

1962), but at the time not accepted by population ecologists. In fact, at very low densities the chance of the sexes to meet, and thus to produce progeny, will often have decreased (underpopulation: KLOMP, VAN MONTFORT, and TAMMES, 1964), by which the chance of extinction of the population will have increased.

Hence, I decided, for the moment to forget the postulates from which the theory of the regulation of animal numbers was deduced, because - although mathematically tractable - for the time being they are untractable for the field-worker. It seemed better to start anew. By extensively analysing structure and assumptions of the current population theories REDDINGIUS (1971) reached a comparable conclusion. In the following I will try to show where we will get when we look at the extinction or persistence of animal populations without accepting postulates that are connected with considering a population a "system", an "entity", a "higher level of integration", or even "another kind of organism". Note, that I do not reject such concepts beforehand; they are only put aside for the moment to have an unbiased start.

2. The "unit of population"

To make the concept "population" operational for comparative studies we will have to standardize it, because in literature groups of animals ranging in size from small local groups up to all members of a species on earth can be considered populations, depending on the problems under study. To keep as close as possible to the interests of most population biologists we prefer to standardize "population" in such a way that each individual in such a unit of population is potentially able to interact directly or indirectly with all other individuals, by which possible effects of these interactions can be expected to be about averaged throughout the group, i. e., can be considered density effects. Hence, such an "interaction group" will be a group of individuals which live together on a site having spatial dimensions which do not substantially exceed the average distances covered by such individuals during one generation.

If such a site is sufficiently isolated, distinctly bounded and of the right - or less - dimensions the population living there will be a "simple population", i. e., coincide with a single interaction group (fig. 1 A), by which the fluctuation of numbers can be studied in a straightforward way.

If the dimensions of the inhabited site greatly exceed the distances normally covered by the individuals, matters become more complicated, however: in such a situation "interaction groups" will gradually merge into one another and can only be separately defined around fixed points (fig. 1 B). This implies, however, that around different points that are sufficiently far apart (e. g., X and Y in fig. 1 B), population processes - also density-dependent ones - will act independently of each other (by definition). See also: DEN BOER (1977, 1979 a). As most natural environments are heterogeneous in space in many respects, and most animals - partly because of this -

are distributed unequally, this will often result in different numerical fluctuations in such different "subpopulations". To study the dynamics of such a composite population adequately it will be necessary, of course, to be able to estimate the magnitude of the differences between the fluctuation patterns of different subpopulations, i. e., it will be necessary to follow a number of interaction groups separately through time.

To be able to compare the fluctuation patterns of simple populations with those of composite populations (and also of composite populations mutually) we will have to consider the "interaction group", as defined above, to be a "unit of population". As around each point within the habitat of a composite population an interaction group can be defined, in principle there will be a continuous exchange of individuals between interaction groups, by which the composite population as a whole can be considered to be sufficiently characterized by a representative number of interaction groups defined around randomly distributed points in the habitat. Working along these lines will also deliver us from problems raised by the fact that the boundaries of most natural populations are difficult to indicate (often the occupied area only gradually merges into unhabited areas).

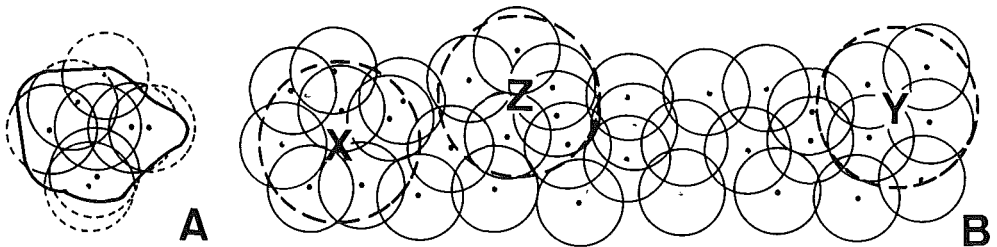


Fig. 1. Diagram of interaction groups. Each dot represents a place where an individual is supposed to have been born, and is the centre of a circle delimiting the maximum distances that can be covered by that individual in the normal patterns of activity, during its lifetime. Only a few of the individuals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

3. Fluctuation characteristics

The survival time of a population can be defined as the number of generations during which the size of the population has been fluctuating between save limits. As the lower save limit we will have to take that population size below which "under-population" (KLOMP, VAN MONTFORT, and TAMMES, 1964) is inevitable; for bisexual populations the most extreme lower limit will thus be 1. As the uppermost save limit we will consider some population size at which the vital resources (e. g., food) have become exhausted. The most straightforward measure of population stability will thus be: the chance that during a finite period of time population size will remain between these positive, save limits. Such a "between-limits-stability" does not necessitate any assumption about population processes, and thus is the most general measure possible. Unlike neighbourhood stability, which only refers to regulation models (e. g., MAY, 1973) and which even in relevant cases only indirectly - and thus incompletely - measures survival, this between-limits-stability applies to all kinds of models. See further: REDDINGIUS (1971).

The most straightforward estimate of the tendency of population size to remain between certain limits is "logarithmic range" (LR): the difference between the logarithms of the greatest mean density and of the smallest mean density that was reached during a certain number of generations. It measures the limits between which density has been fluctuating during the period of observation. A less direct measure is the variance of net reproduction (R : mean density in generation n divided by that in generation $n - 1$) over a number of generations: $\text{Var } R$. It measures the violence of density fluctuations and thus estimates the chance of reaching values which deviate greatly from the mean. Together with Average $\ln R$ (the logarithm of the geometric mean of R) it adequately characterizes the fluctuation pattern. Note, that for m generations Average $\ln R$ is simply $1/m (\ln n_m - \ln n_0)$; it measures the overall trend which density fluctuations have shown, and is only a reliable measure in very long series.

See further: REDDINGIUS and DEN BOER (1970); DEN BOER (1971). We are now ready to compare as unbiased as possible the stability levels of different natural populations. We only have to find suitable data over a sufficiently long series of years.

4. The estimation of mean density in interaction groups of carabid beetles

During many years already (started in 1959) carabid beetles are sampled continuously in different parts of Kralo Heath (in the northern part of the Netherlands: Drenthe, fig. 2) with standard sets of pitfalls. Most species are uninterruptedly inhabiting this heath-area of about 1200 ha as composite populations (cf. 2). BAARS

(1979 a) could show - at least for the two species of heath studied by him (*Pterostichus versicolor* and *Calathus melanocephalus*) - that the catches in such a standard set of pitfalls, summed over the whole reproductive season (year-sample), result in a reliable (relative) estimate of mean density around these pitfalls, fig. 3 (see also: DEN BOER, 1979 a, fig. 2). Via capture-recapture experiments DEN BOER (1979 b) could support this conclusion for four carabid species of forest. In spite of critical notes in literature about the use of pitfall traps for estimating mean densities of carabid populations (reviewed by SOUTHWOOD, 1966), BAARS (1979 a) demonstrated that even the data of these critics - on six more carabid species - are in reasonable agreement with the postulated relationship, if only year-samples and not the catches during a few weeks are taken as an estimate of mean density. Hence, the satisfactorily linear relationship between mean densities and year-samples from pitfalls, that could be established in all these cases, probably is a general feature of carabid populations.

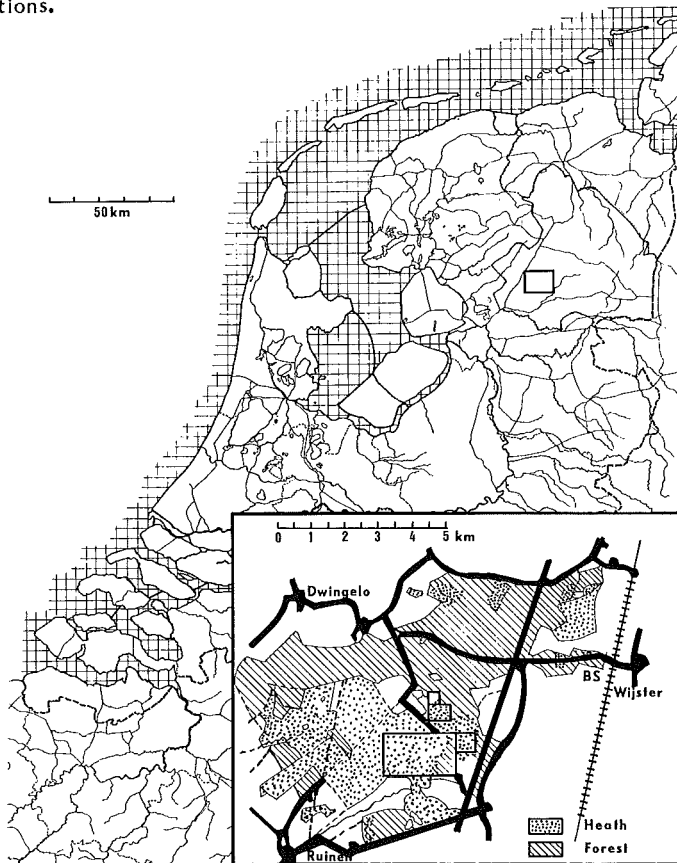


Fig. 2. Situation of the area of investigation in the northern part of the Netherlands (rectangle), enlarged in the lower right; in the outlined areas several sets of pitfalls are placed.

This distinct relationship leads us to the conclusion that within the same species the mean level of locomotory activity in the horizontal plan of an average individual during one season neither differs very much between different sites (within the same area), nor between different years. This conclusion is a very remarkable one, because we experienced already that there may exist great differences in activity both between coexisting individuals (see e. g., DEN BOER, 1979 b), and in the same individual at different times (e. g., dependent on weather conditions). Apparently, individually determined differences in activity as well as changes of individual behaviour in time, when taken together both over the whole season and for all individuals living around a set of pitfalls, work out statistically in such a way that the chance of an average individual being captured does not vary very much.

Calathus melanocephalus

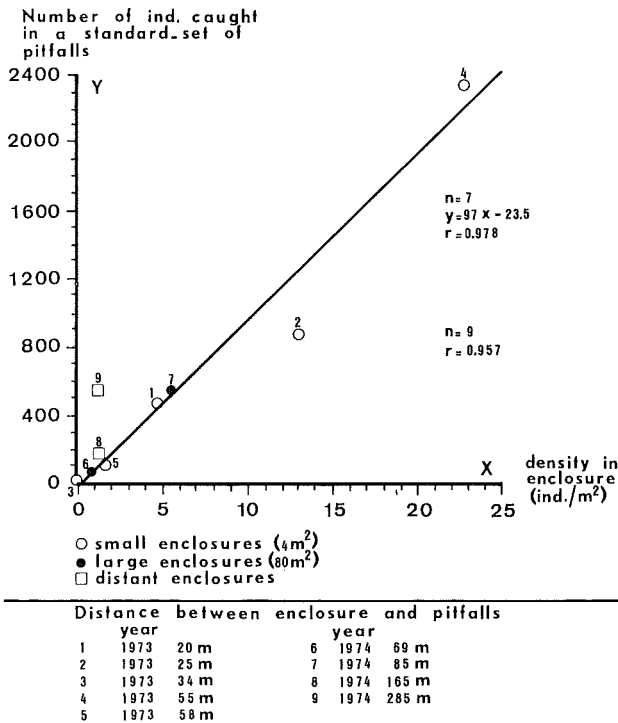


Fig. 3. Relationship between the mean density within an enclosure (from which all individuals could be caught away) and the value of the nearby year-sample - i. e., number of individuals caught in a standard set of pitfalls during a whole season (from data of BAARS, 1979 a).

This conclusion could be supported again from a different side by BAARS (1979 b), who daily tracked radioactively marked individuals of two carabid species of heath (see above) to study the walking pattern. He found that in all individuals of both species studied periods of small distances covered per day in random directions alternated with periods of directed movement with large distances covered per day. Individuals walked independently of each other and covered highly different distances on the same day, whereas the day-distances additionally varied greatly - also within the same individuals - between days with different weather conditions (especially temperature). In spite of this great variability of walking behaviour BAARS (1979 b) could simulate this walking pattern in a computer program, and thus satisfactorily simulate the results of an independent field experiment in which high numbers of brandmarked beetles were released at a central point and recaptured in pitfalls along fences at different distances from that point, not only during that season but even during a second and a third season. In this way he not only demonstrated the reliability of his walking-program, but also showed - supplemented with still other simulation experiments (see BAARS, 1979 a) - that in spite of the great variation in activity both between individuals and in time the mean density of carabid populations can indeed be estimated adequately with the help of standardized and continuous pitfall sampling. Note, that this latter conclusion is independent of the data plotted in the Figure 3.

These satisfactory results cleared the way for simulating the distances covered by thousand individuals of both species during one season, two seasons, etc. (fig. 4), by which we could get a first impression of the size of the area occupied by an interaction group (cf. 2). In the case of *P. versicolor* (= *coeruleescens*) we could also calculate the area of an interaction group from a simulated capture-recapture experiment with pitfalls on Kralo Heath and found an area of nearly 40,000 m² (a circular surface with a radius of about 100 m). If we take into account that the chance of an individual to actually reach the fixed site of a set of pitfalls - and thus to be captured - will be the smaller the greater the distance from the pitfalls at which it starts activities, this value is in reasonable agreement with the 160 m covered by an average individual of *P. coeruleescens* after one season (90 days) as it is shown in fig. 4. It will also be clear from fig. 4 that in *Calathus melanocephalus* the area of an interaction group must be much smaller than in *P. versicolor*, viz. not larger than 10,000 m² (radius 50 m). Note, that for the points that do not fit the linear relationship in fig. 3 very well the distance between pitfalls and enclosure was indeed greater than the estimated radius of an interaction group. Hence, continuous sampling with standardized sets of pitfalls appears to be a simple and reliable method to comparatively estimate the mean densities in interaction groups of carabid beetles that live around these fixed sets.

5. Fluctuations of mean densities in different interaction groups of two composite populations of carabid species at Kralo Heath

The standard sets of pitfalls, used to study the fluctuations of mean density in interaction groups of carabid species during a number of succeeding years, are not distributed at random over Kralo Heath. Circumstantial evidence of various origin suggests that the chance to survive and reproduce is in many carabid species influenced (directly and/or indirectly) by the moisture content of the soil and by the spatial structure of vegetation, or more generally spoken, by abiotic factors (see e. g., THIELE, 1977).

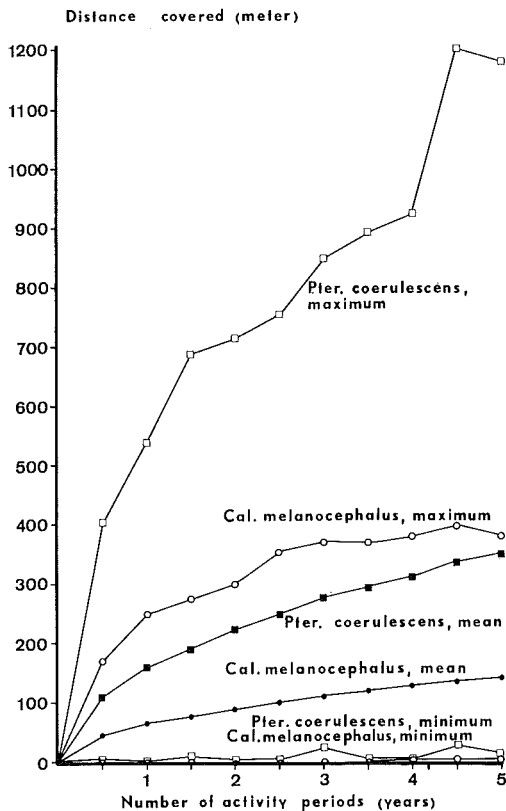


Fig. 4. Distances covered at the Heath of Kralo by individuals of *Pterostichus coeruleus* and *Calathus melanocephalus* respectively during a number of seasons. The data were obtained from simulations of the walking pattern by BAARS (1979 b). One activity period was estimated at 90 days in *P. coeruleus*, and at 60 days in *C. melanocephalus*.

Hence, to get in spite of restricted assistance (in 1959 I started all by myself) an adequate idea of the magnitude of the possible differences between the fluctuation patterns of different subpopulations it seemed best to sample some differently structured and/or watered sites within this heath area; in the course of years the number of these sites could be extended from a few in the first years until 14. At present we sample: one moist *Erica-Calluna* site (N), one moist *Calluna* site (Z), one wet *Molinia*-stand (M), two wet sites with a mosaically structured vegetation (AG, BG), two dry sites with another kind of mosaic vegetation (AY, BB), one moist area with a more large-scale mosaically composed vegetation (CB), an elevated area with a short, grassy vegetation (3 sets: AT, BH, BJ), one wet *Erica* vegetation (CF), an abandoned agricultural field (CE) and an abandoned pasture (BZ) which are both bordering the heath area and gradually changing into a heathery vegetation again. More detailed descriptions of many of these sites (some with photographs) can be found in DEN BOER (1977: Appendix A, part II). Although we mainly cover the southeastern part of the heath area with our pitfall sets we rely on sampling the respective composite populations (cf. 2) of different carabid species representatively in this way. In any case can we satisfactorily compare the fluctuation patterns of those species that were captured in all sets and in all years, i. e., which are sampled exactly similar. This condition is especially satisfied in the two most abundant species of the area: *Calathus melanocephalus* and *Pterostichus versicolor* (= *coeruleus*).

In the Figures 5 and 6 the available data on the fluctuations of mean density in the interaction groups (subpopulations) sampled, are plotted, together with the values of net reproduction (lower part).

When comparing these pictures one is struck by the quite different patterns in these two species: in *C. melanocephalus* the fluctuations of mean density are violent and they run about in parallel in different subpopulations; in *P. versicolor* (= *coeruleus*) these fluctuations are less and they often run in opposite direction in different subpopulations. Apparently, for *C. melanocephalus* in most years the effective environment does not change very differently between sites, i. e., during an unfavourable season conditions will be more or less unfavourable everywhere at Kralo Heath, and vice versa. For *P. versicolor*, however, in most years conditions are unfavourable in some localities but favourable in others. Hence, Kralo Heath is much more heterogeneous for *P. versicolor* than it is for *C. melanocephalus*. This difference must have important consequences for the stability of the composite populations concerned: Table 1.

Table 1 indeed shows that the range over which density fluctuations occurred during 19 years in the composite population of *C. melanocephalus* is hardly reduced as compared with the average range of 9 subpopulations, i. e., the chance of survival of this population of *C. melanocephalus* will not be favoured by its being composed of a number of subpopulations with continuous exchange between. In the composite

population of *P. versicolor*, on the other hand, this fluctuation range is reduced about 50 % as compared with the average range of 9 subpopulations, and this must favourably influence the chance to survive of this composite population. With the help of simulation experiments we tried to test the above hypothesis that a population, which is composed of subpopulations as in *C. melanocephalus* at Kralo Heath, is not expected to survive longer than a comparable population composed of identical (average) subpopulations, whereas in the case of *P. versicolor* a composite population as at Kralo Heath is expected to survive much longer than a comparable population composed of identical (average) subpopulations. .

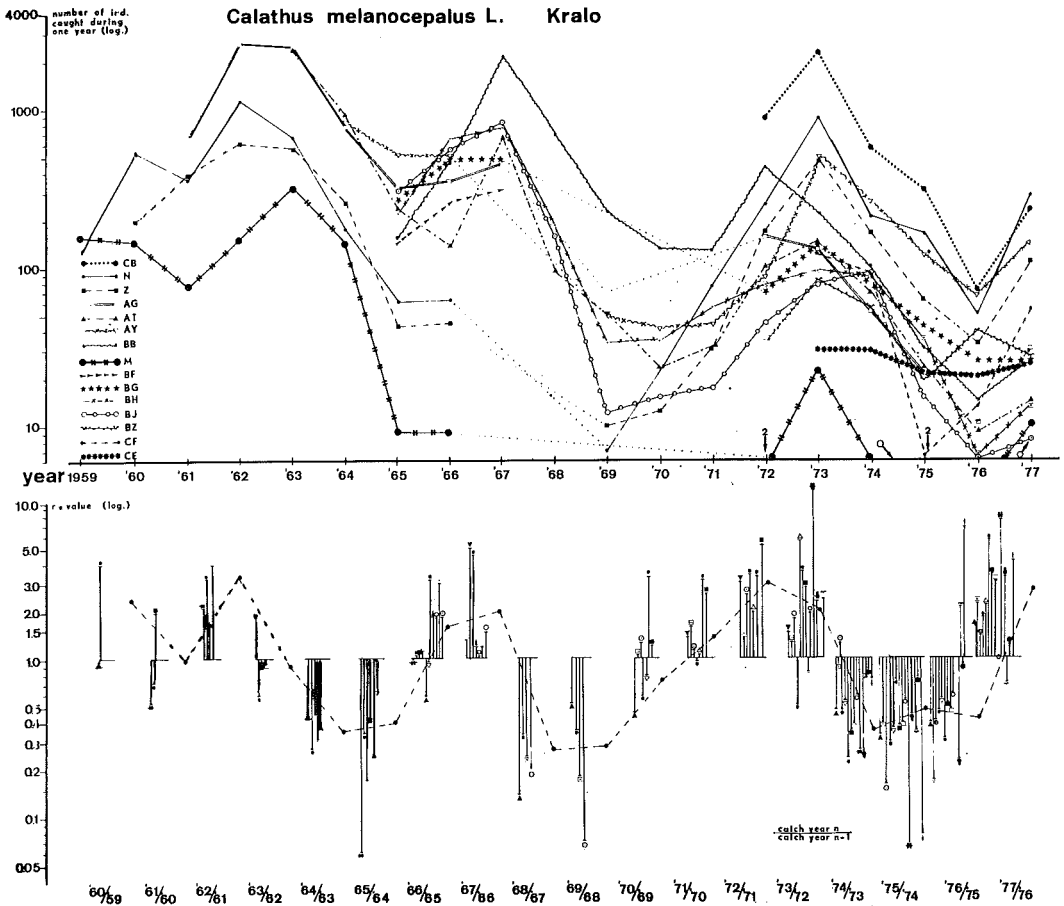


Fig. 5. Mean densities in different interaction groups (subpopulations) of *Calathus melanocephalus* at Kralo Heath during 19 years. In the lower part of the picture: values of net reproduction in the different subpopulations (vertical bars), and of net reproduction in the whole composite population (points connected by broken lines).

Each run started with 20,000 individuals of *P. versicolor*, or 200,000 individuals of *C. melanocephalus*, and was continued until less than a single individual was left (or - in some versions - a symmetrically fixed "upper limit" was passed). Each version of each program was run thirty times, each time with a different sequence of random numbers; the survival times from these thirty runs were averaged. The results of these simulations are discussed in a paper that shortly will be presented to *Oecologia*. Here we will only mention the general trends. In these simulations net reproduction values are taken from frequency distributions that were directly derived from our field data (lower parts of the Figures 5 and 6), viz. for the composite population the distribution of the 18 points connected by broken lines, for the population composed of identical (average) subpopulations the distribution of the 138 values represented by bars.

TABLE 1. Characteristics of the fluctuations of mean density over 19 years for two carabid species at Kralo Heath.

A = values averaged from the values for the 9 subpopulations (M, N, Z, AG, AT, AY, BB, BH, BJ) that were sampled during at least 12 years.

B = values for a population that is composed of the above 9 subpopulations.

C = values for a population that is composed of all the subpopulations sampled.

	<i>Calathus melanocephalus</i>		
	A	B	C
LR	4.8777	4.3499	4.4379
Var R	3.2712	1.1609	1.0507
Average ln R	- 0.12914	- 0.06604	- 0.08069

	<i>Pterostichus versicolor</i>		
	A	B	C
LR	2.2559	1.2912	1.0417
Var R	0.4252	0.0846	0.0656
Average ln R	- 0.03201	- 0.00045	0.01420

In none of the versions of our program did we find a substantial difference in survival time between the naturally composed population of *C. melanocephalus* and the population composed of identical subpopulations. A reasonable guess of the survival time of this species at Kralo Heath (under stationary environmental conditions) from these simulations seems to be 200 years. In the case of *P. versicolor* the population composed of identical subpopulations was computed to survive between 300 and 600 years, depending on the version of the program used (e. g., whether or not the actual autocorrelations between succeeding values of net reproduction are taken into account to some extent), whereas the naturally composed population can be expected to survive for some thousands of years under stationary conditions (which is an inevitable assumption in these simulations, of course).

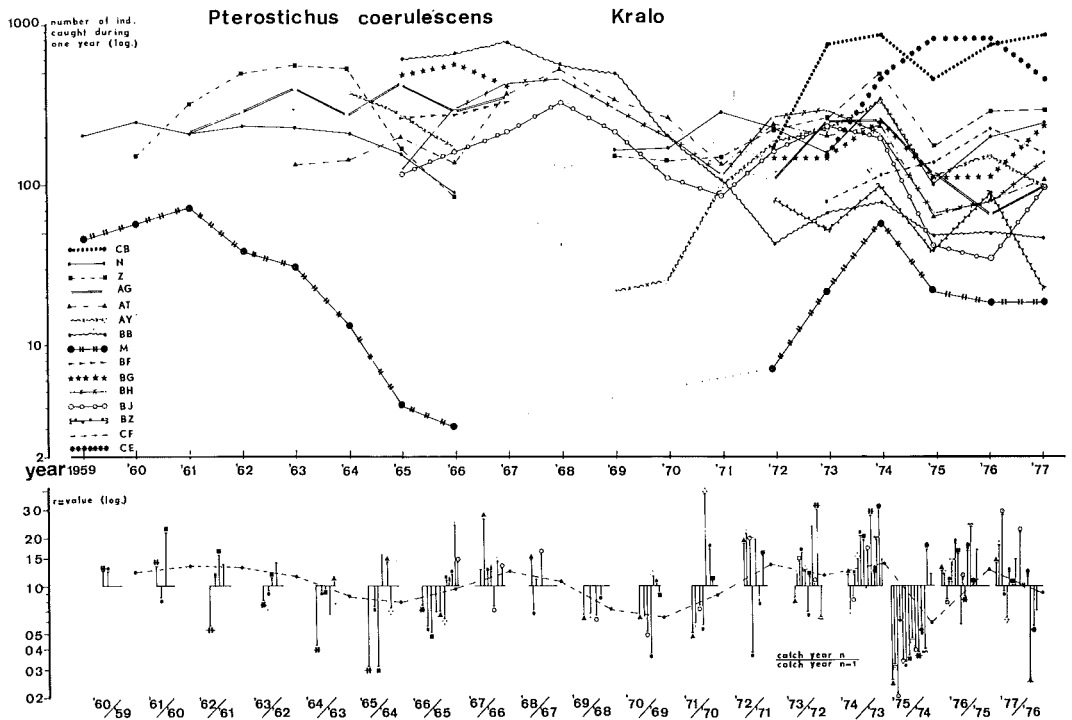


Fig. 6. Mean densities in different interaction groups (subpopulations) of *Pterostichus coeruleus* (= *versicolor*) at Kralo Heath during 19 years. see further Figure 5.

Hence, the chance of survival of a composite population is highly favoured by the density fluctuations in different subpopulations not running in parallel in general. This phenomenon, that is based upon losses in one case being compensated more or less by gains in another, is called by me "spreading of risk". In the present case the risk of extinction of the composite population of *P. coeruleescens* is spread significantly over a number of subpopulations, which because of highly different fluctuation patterns will not die out simultaneously.

By a continuous movement of individuals between subpopulations - which will generally occur to some extent - both the chance of a subpopulation to become extinct will be lowered substantially and the chance of refoundation will be increased.

It must be emphasized here that spreading of risk is neither identical to a reduction of the "effective environmental variance" by a complete mixing of individuals within the population, as it is thought to be by MAY (1973:137), nor similar to a related reduction of the variance of density itself by a complete mingling of individuals (cf. Appendix). This reduction of variance by a complete mingling of individuals is maximal between patches and/or clutches within the same interaction group, i. e., it is the main argument to consider the interaction group the basal unit of population (cf. 2 and 4). Although such a reduction of the variance of density (or of the effective environment) will usually also contribute to the stability of a composite population, of course, spreading of risk is much stronger than these general averaging effects. This can be illustrated best by returning to Table 1: in both species the average value of Var R for the 9 subpopulations (i. e., if these subpopulations are considered separate units) is much higher than the value of Var R for the population composed of these 9 subpopulations (i. e., if these subpopulations are considered to merge into each other by a continuous movement of individuals), which seems not to be in concordance with the "behaviour" of the range of density fluctuations (LR). As the different Var R's are not influenced by the degree of parallelism between density fluctuations, the phenomenon, that also in *C. melanocephalus* the subpopulations are still sufficiently different to allow a considerable effect from yearly summing or averaging their densities, does hardly affect LR. Hence, though the phenomenon described in the Appendix can be shown also to have some effect in the composite populations of both species, only the stability of the population of *P. versicolor* is significantly favoured by spreading of the risk of extinction over a number of differently fluctuating subpopulations.

6. Spreading of risk

In section 5 we saw that spreading of risk results from different subpopulations fluctuating differently in density over years. Nevertheless, the subpopulations of *P. versicolor* do not fluctuate completely independently; there is still left some positive

correlation between the net reproduction values in succeeding years: for 10 subpopulations during 5 years the coefficient of concordance W (KENDALL, 1962) amounts to 0.52, and for 4 subpopulations during 10 years to 0.54, which both are significant at $p = 0.01$. This means that even in this favourable case, in which the survival time of the population has already been prolonged until a multiple of that in the null-case (cf. 5: simulation), the spreading of risk, i. e., the reduction of the range of density fluctuations, would still be capable of an impressive improvement, e. g., by a further increase of the degree of heterogeneity of the effective environment.

In different papers (DEN BOER, 1968, 1971, 1973), also illustrated by simulation experiments (REDDINGIUS and DEN BOER, 1970), we explained already that the possibilities of a reduction of the range of density fluctuations by spreading of a risk are not restricted to the composition of a population of differently fluctuating subpopulations. VAN DIJK (this volume, see also VAN DIJK, 1979) will show that also the composition of an interaction group of different age classes can result in a significant reduction of the fluctuation range, and the same will apply to pheno(gen)otypes that differ in dynamically important features such as egg production and rate of development. He will show that the individual variation in some of these features is indeed astonishingly high, even within the same population. Such a situation must contain many possibilities to spread the risk of dying without progeny over different individuals (some examples of this are already given in DEN BOER, 1968).

TABLE 2. Characteristics of the density fluctuations in two experimental populations of the azuki bean weevil (*Callosobruchus chinensis* L.) during 68 generations. Modified from UTIDA (1957).

A = Culture with one parasite species

B = Culture with two parasite species (other conditions similar as in A)

	A	B
LR	4.0073	2.8744
Var R	4.6437	2.1855
Average $\ln R$	0.0281	0.0176

It may even be expected that a high degree of variation in some vital properties will be directly favoured by natural selection by the way of frequent and unpredictable changes in the effective environment (e. g., weather conditions).

Another kind of spreading of risk, the effect of the number of "factors" influencing density, seems to be little understood in general, though it was illustrated by a simulation experiment (REDDINGIUS and DEN BOER, 1970). Therefore, we once again present here the fluctuation characteristics of two experimental populations of the azuki bean weevil, that were bred by UTIDA (1957) during 68 generations under identical conditions except for the number of parasite species added: Table 2 (see also: DEN BOER, 1971). In spite of the much lower density level in the culture with two parasite species the range of density fluctuations is reduced significantly by the increase of the number of "factors" from one to two. In a similar way as indicated in section 5 we simulated these two populations (start density: in case A 2000 individuals, in case B 1000 individuals), and indeed found that the population with two parasite species can be expected to survive at least twice as long than the population with only one parasite species. This result directly contradicts the conclusion of MAY (1973) from his models of the predator-prey type, that models with more species are generally less stable than models with only one prey (host) and one predator (parasite) species. Even to these very simple experimental populations of UTIDA (closed populations under constant environmental conditions) regulation models with neighbourhood stability seem not to apply very well. The much less restrictive concept of spreading of risk apparently gives better possibilities to understand what actually may happen in these simple communities.

7. Concluding remarks

We started this paper with the question whether an animal population must be considered a biological system or only a group of biological systems (individuals). I hope to have shown with my survey that density fluctuations can best be studied and understood as statistical processes, i. e., as resulting from group features. This does not mean that feedback processes would not occur at all, it only says that such processes are apparently dominated by, and thus taken up into, statistical processes (see also REDDINGIUS, 1971). Through that also the stability of most animal populations essentially will be a statistical property (between-limits-stability) and not a systems property (neighbourhood stability). The statistical properties of a group are studied by taking samples, and this implies that asking how and exactly where a population is bounded spatially, in fact is not very important. It suffices to know where individuals of that population can be found, and where they will certainly not be found (except as migrants). Possibly we can get out of these questions of concept by discriminating between "biological systems" s. s. or "biological entities" (individuals

and some lower "levels of integration"), "biological groups" (populations, communities and still more complicated situations), and "biological species".

It is highly interesting to note that considering a population (or a simple community, such as the azuki bean weevil with one or two parasite species) a system leads to conclusions about its stability which are quite opposite to that from considering a population a group of individuals. The latter point of view is not only in concordance with observations in natural populations (cf. 5), it also makes comprehensible why most natural populations show such a surprisingly high level of individual variability: because in general it will promote stability. The best "strategy" to survive in a heterogeneous environment seems thus to be: becoming as heterogeneous as that environment, i. e., there must be a sufficiently high level of individual variability. And the best "strategy" to survive in a changeable world is: trying to keep up with these changes, i. e., there must be a sufficiently broad base for natural selection to realize the chance that after each change individuals with combinations of properties will become available, that are more or less "adaptive" under the new conditions.

Hence, there must be a very high level of individual (especially effective genetic) variation. Individual variation seems thus to be an indispensable property of groups of individuals (populations) to survive in a heterogeneous and changeable world.

8. Abstract

The question is discussed whether or not an animal population can be considered a "biological system" or only a group of "systems" (individuals). This implies the question whether the stability of an animal population should be "neighbourhood stability" (see e. g., MAY, 1973) or some kind of "between-limits-stability" (see e. g., REDDINGIUS, 1971). As a "between-limits-stability" is the most general possible it includes other stability concepts, by which it can be used to study what promotes the stability of an animal population.

From the work of BAARS (1979 a, b) it could be derived that the catches of carabid beetles in a standard set of pitfalls, if summed over the whole season, can be considered a reliable estimate of the mean density in the subpopulation (interaction group) concerned. After having defined some adequate fluctuation characteristics (REDDINGIUS and DEN BOER, 1970) data on the fluctuations of mean density in a number of subpopulations of composite populations (DEN BOER, 1977, 1979) of the carabid species *Calathus melanocephalus* and *Pterostichus versicolor* (= *coerulescens*) at Kralo Heath during 19 years could be used to show that a high level of heterogeneity of the effective environment - as in *P. versicolor* as compared with *C. melanocephalus* - promotes (between-limits) stability. By comparing the (between-limits) stability of two experimental populations of *Callosobruchus chinensis*, one with one parasite species and the other with two parasite species, during 68 generations

(from data of UTIDA, 1957), it could be concluded that the stability of a simple community is promoted by a greater "complexity". These results, which are supported by simulation experiments, contradict the general conclusions of MAY (1973) concerning neighbourhood stability.

It is generally concluded that an animal population should be considered a group of "biological systems" (individuals), the stability of which will usually be favoured by different kinds of "spreading of the risk of extinction" (DEN BOER, 1968), which concept is stronger than mere averaging effects concerning the effective environment and/or density itself. The same will apply to the stability of simple communities.

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11. Appendix

At p. 137 MAY (1973) states that, if in each of p patches of population (each with logistic growth) the stochastic environment (symbolized by the "carrying capacity" k) has variance σ^2 , and if there is continuous movement and mingling among all p patches, then for each patch the effective environmental variance will tend to σ^2/p rather than to σ^2 .

To keep close to the tenor of his book we may suppose that MAY would possibly postulate a "neighbourhood stability" for his population, which is diminished then by each kind of "complexity" or "noise" (the general conclusion of the whole book), so that a decrease of environmental variance may be favourable for the survival of the whole population.

But why not applying this argument directly to the population numbers?

If n_{ij} = density in year i in patch j ;

$$\bar{n}_{i.} = \text{average density in } i\text{th year: } (\sum_{j=1}^p n_{ij})/p, \quad j=1,2,\dots,p$$

$$\bar{n}_{.j} = \text{average density in } j\text{th patch: } (\sum_{i=1}^m n_{ij})/m, \quad i=1,2,\dots,m \text{ and}$$

$$\bar{n} = \text{overall average of density: } (\sum_{i=1}^m \sum_{j=1}^p n_{ij})/m p,$$

then the variance of density in the j^{th} patch will be:

$$s_j^2 = (\sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/(m-1),$$

the total variance will be: $s^2 = (\sum_{i=1}^m \sum_{j=1}^p (n_{ij} - \bar{n})^2)/(m p - 1),$

the variance within patches will be: $s^2_{\text{within}} = (\sum_{j=1}^p \sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/p(m-1),$

and the variance between patches will be: $s^2_{\text{between}} = (\sum_{j=1}^p (\bar{n}_{.j} - \bar{n})^2)/(p-1).$

If there is continuous movement of individuals between patches (or clusters) the different values of $\bar{n}_{.j}$ will approach each other and all tend to \bar{n} , because in each year the values of n_{ij} will come closer to their respective $\bar{n}_{i.}$ -values. Hence, $\bar{n}_{.j} - \bar{n} \rightarrow 0$, by which also $s^2_{\text{between}} \rightarrow 0$. But then s^2_{within} will approach s^2 , or

$$(\sum_{j=1}^p \sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/p(m-1) \rightarrow \sum_{i=1}^m \sum_{j=1}^p (n_{ij} - \bar{n})^2)/(m p - 1).$$

If the mingling is complete

$$(\sum_{j=1}^p \sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/p(m-1) \rightarrow p (\sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/p(m-1) = (\sum_{i=1}^m (n_{ij} - \bar{n}_{.j})^2)/(m-1),$$

or the variance of n_{ij} for the population approaches the variance of n_{ij} for an average patch, which essentially is the same argument as that used by MAY (1973:137) for the effective environmental variance. But now it is used *directly* - and without any assumption, e. g., about neighbourhood stability - to show that the (between-limits) stability of a population will be promoted by the complexity itself (a population, even if there is continuous movement and mingling of individuals, must be considered more complex than a single patch, which is rather contrary to the general conclusion of MAY.

This reasoning needs not be restricted, of course, to populations consisting of different genotypes or age-classes (with the difference that between age-classes the "mingling of individuals" is in only one direction). Hence, within each "interaction group" the variance of n_{ij} will be lowered substantially by its complex composition of different clusters, genotypes, age-classes, etc., and the variance of n_{ij} in the population as a whole will be lowered again to some degree by its composition of different "interaction groups".