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Stabilization of animal numbers and the heterogeneity of the environment: The problem of the persistence of sparse populations¹

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Abstract

To understand the persistence of sparse insect populations it must be supposed that the fluctuations in density are small and that the average in net reproduction is close to zero. By simulation experiments and by field observations it has been demonstrated that a relative restriction of density fluctuations may result both from heterogeneity of the environment (and from heterogeneity within the population) and from the number of 'factors' influencing net reproduction. It is argued that when an increase in the complexity of a biocoenosis is accompanied by an increase in the number of species, this will not only result in a decrease in the density fluctuations of many populations but also – because of a growing asymmetry in the distribution of the 'factors' according to their influence on net reproduction – in a lowering of the density level and in the keeping down of a potential upward trend in density.

Because my first experiences with natural populations were the experiences of an insect collector, I have always been impressed by the amazing number of insect species that may be found in a restricted natural locality. I was still more puzzled by the fact that, in most cases, the greater part of these insect species appeared to be relatively rare (cf. Williams, 1964). Although, in the course of years, I learned that some of these supposed rare species are mainly rare in insect collections, the apparent commonness of sparse insect populations remained a fascinating natural phenomenon in the background of my thoughts. Hence, it was almost inevitable that I should test the different population theories I came across on the degree to which they gave an explanation of the apparent persistence of sparse insect populations. However, most population theories – as far as they are based on concepts that can be tested by studying natural populations – appeared to be concerned with overcrowding or, at least, with phenomena connected with relatively high densities. Up till now remarkably little attention has been paid to phenomena connected with low densities, and it seems to me that it is not enough to state that low densities will be followed by higher densities or sometimes by extinction.

Restriction of density fluctuations

If we try to look at high and low densities with the same kind of interest, one thing will be evident: the less frequently the density approaches extremely high or low values the greater will be the population's chance to survive (see also Williams, 1966, p. 107). In other words,

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when we are equally interested in the persistence of dense and of sparse populations our problem is not only 'How are high densities limited?', but more generally 'How are the fluctuations of density restricted?' or 'How is density kept fluctuating between certain (safe) limits?' (See also Reddingius, 1970). When our problem is formulated in this way we also see a possible theoretical explanation for the persistence of sparse populations. If in a sparse population the density fluctuates between narrow limits, its chance to reach density zero need not be greater than in the case of a correspondingly dense population in which density tends to fluctuate much more violently.

Fluctuation characteristics

In order to be able to compare the patterns of density fluctuations of different populations, it will be necessary to calculate some adequate fluctuation characteristics (Reddingius and den Boer, 1970):

1. The difference between the logarithms of the greatest density and of the smallest density that was reached during a certain number of generations: 'logarithmic range' (LR). This measures the limits between which the density has been fluctuating. Of course, for different cases only the LR values of the same number of generations can be compared.
2. The variance of net reproduction (R : density in generation n divided by density in generation $n-1$) during a certain number of generations: $\text{var } R$. This measures the violence of density fluctuations and thus the chance of reaching values which differ greatly from the mean.
3. The average logarithm of net reproduction during a certain number of generations (= logarithm of the geometric mean of R): average $\ln R$. For m generations the average $\ln R$ is simply $1/m (\ln[n(m)] - \ln [n(o)])$. This measures the overall trend which density fluctuations have shown. It must be noted that, in any case, the longer a population is observed to persist the closer the average $\ln R$ will be to zero; this is a statistical truism which in itself has nothing to do with 'regulation'.

Our problem can now be formulated: Which circumstances in natural environments and/or in natural populations may generally favour such a restriction of density fluctuations that the persistence of sparse insect populations may be at least imagined? In other words, which circumstances will generally decrease the 'logarithmic range' and 'var R ' of natural populations and will keep 'average $\ln R$ ' close to zero?

Heterogeneity and the spreading of risk

Such general circumstances were found to be the heterogeneity in time and space of the natural population itself and of its effective environment (den Boer, 1968a). Because the habitats of natural populations generally are very heterogeneous, there will be local differences in microweather, food, natural enemies, etc. Therefore, the chances of surviving and of reproducing will be different for individuals living in different sites within a natural habitat, even when they are phenotypically identical. Hence, for each generation in turn, the change in numbers may be expected to be different in different parts of the habitat of a natural population; this means that, for the population as a whole, the effect of relatively extreme conditions in one place will be damped to some degree by the effect of less extreme conditions in others. In other words, from generation to generation the risk of wide fluctuation in animal numbers is spread unequally over a number of local

groups within the population; this will result in a levelling of the fluctuations in the size of the population as a whole. Moreover, the animals may move from one place to another within the habitat and such movements, even if they occur wholly at random, will contribute to this stabilizing tendency of spatial heterogeneity, since in this way very high or low numbers in some places will be levelled out more thoroughly. Although it is outside the scope of this paper, it must be noted here that heterogeneity within the population will also contribute to the relative stabilization of animal numbers; changes in numbers in one phenotypic or age group will be more or less counterbalanced by changes in other such groups. In this way, the effect of fluctuating environmental factors on the population as a whole is continuously damped to some degree by the phenotypic variation and/or by the variation in age composition (by this variation the range of tolerance of the population is increased as compared with that of the individual animals). (See den Boer, 1968a).

Subpopulations model

To check the correctness of these thoughts Reddingius did some simulation experiments (Reddingius and den Boer, 1970). A population is assumed to consist of 9 subpopulations, each of which occupies an area of unit size (total population with area of 9 units). Each subpopulation consists of animals in either one or three age classes. The time unit is 'a generation' (year). In each generation we have a reproduction period, and a migration period with separate emigration and immigration. It is assumed that during the reproductive period the animals stay in the subpopulations where they are, and that individuals do not reproduce during migration. Survival and reproduction are random variables, emigration and immigration are either both density-independent or both density-dependent. To get density-dependence of migration it was assumed in our model that the greater the density in a given subpopulation the greater the probability of an animal emigrating from, and the smaller the probability of an animal immigrating into, that subpopulation. Several cases were then compared:

1. NMSP (no migration, similar populations). All subpopulations consist of one age class only and have the same parameters; there is no migration. Simulation of this model serves as a kind of 'control experiment'; there is no spreading of risk.
2. DIMSP (density-independent migration, similar populations). Subpopulations as in 1, but now density-independent migration occurs.
3. DIMDP (density-independent migration, different populations). As in 1 and 2, but there are now 3 groups of subpopulations with different parameters.
4. DDMDP (density-dependent migration, different populations). As in 3, but now migration is density-dependent.
5. NMHP (no migration, heterogeneous populations). Each subpopulation consists of 3 age classes with different parameters; apart from this heterogeneity within subpopulations, the subpopulations are similar and there is no migration.
6. DIMHP (density-independent migration, heterogeneous populations). As in 3 (with 3 groups of subpopulations with different parameters) but now the subpopulations each consist of 3 age classes.
7. DDMHP (density-dependent migration, heterogeneous populations). As in 6, but now migration is density-dependent.

For a detailed discussion see: Reddingius and den Boer (1970).

It was evident from these simulations that NMSP (1) is much less stable than all other

Table 1. Fluctuation characteristics of simulation experiments (explanation see text). (From Reddingius and den Boer, 1970.)

	LR	var R	Average ln R
1. NMSP	5.318	0.417	-0.067
2. DIMSP	2.366	0.062	-0.014
3. DIMDP	3.608	0.068	-0.024
4. DDMDP	1.761	0.078	-0.005
5. NMHP	2.112	0.113	+0.004
6. DIMHP	1.521	0.054	-0.006
7. DDMHP	1.767	0.040	+0.019

cases. When we consider LR and var R (Table 1) most cases with 3 age classes appear to do better than the corresponding ones with only one age class; this is most apparent when comparing NMSP (1) and NMHP (5). All cases with migration are more stable than those without, whereas density-dependent exchange is not distinctly more favourable than density-independent exchange. From this simulation experiment it appears that the spreading of risk brought about by exchange between subpopulations and by heterogeneity according to age within subpopulations, may importantly contribute to a restriction of density fluctuations in the population as a whole and, therefore, to a stabilization of animal numbers. Moreover, the occurrence of exchange appears to be more important than whether or not such an exchange is density-dependent.

Stabilization of numbers in carabid populations

Now that we have shown that a stabilization of numbers by spreading of risk may occur in some imaginary populations, one may ask whether it may also occur in natural populations. Although there are suggestive indications that in some carabid populations phenotypic variation and variation in age composition may contribute to a stabilization of numbers (some preliminary notes in den Boer, 1968b), I will restrict myself here to the possible effect of spatial heterogeneity.

In the northern part of the Netherlands (Drenthe, Fig. 1) on the Heath of Kralo (Fig. 2), during a number of years carabid beetles were sampled in a number of different sites with standard sets of pitfalls. From capture-recapture experiments (Table 2) it was concluded that, in general, the pitfall-catches of a carabid species summed over the period of activity is itself a useful measure of relative density. From such measurements it is possible to estimate the net rate of reproduction (r) from year to year for a number of subpopulations occurring in those sites in which the catches were continued during a succession of years. For a number of species such data are available; the two most reliable cases will be discussed here (Tables 3 and 4). In these cases we may be sure that direct exchange of individuals between sample sites will be quantitatively unimportant (with the possible exception of sites AT, BH and BJ); dispersal occurs by running, and within one year only very few individuals are able to cover distances of 100 m or more as was shown by capture-recapture experiments with different species. However, because the Heath of Kralo will be more or less uninterruptedly populated by these two species, indirect exchange in the course of a number of generations over far greater distances may be important. Hence a comparison

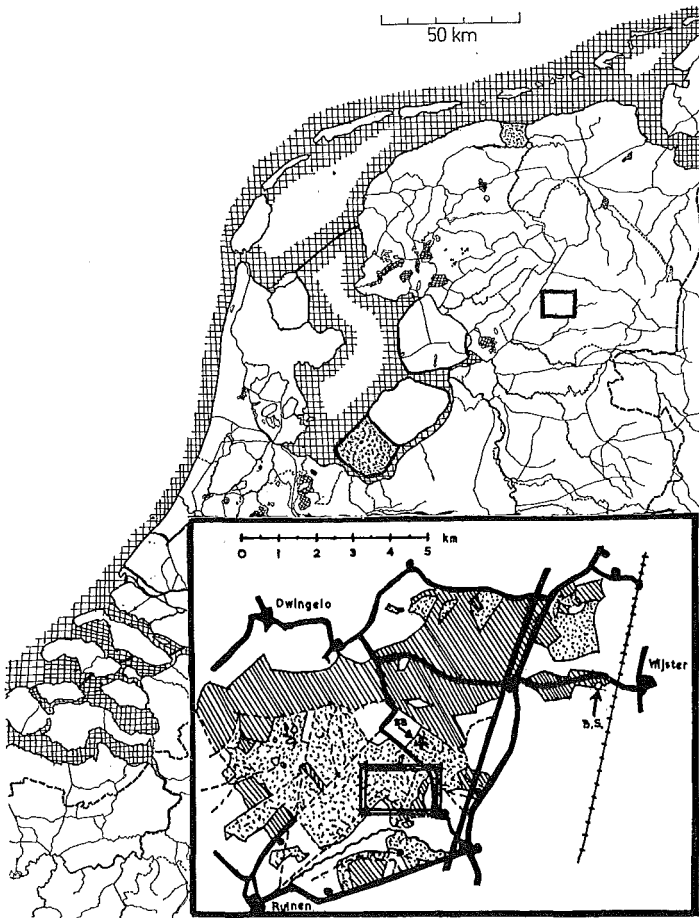


Fig. 1. Situation of the area of investigation in the northern part of the Netherlands (rectangle), enlarged in the lower right; the outlined area is enlarged again in Fig. 2.

of the density changes in different sites – in which the possible results of indirect exchange between sites are included – may give some impression of the relative contribution of these sites to the overall density changes in that area. ‘Var R’ seems to be the most adequate measure for such a comparison (see Fig. 7 and Reddingius and den Boer, 1970). For each row (site) ‘ s_j^2 ’ gives an estimate of the violence of density fluctuations. The weighted average of these row variances (S_p^2) gives some impression of how violent density fluctuations were in an average site on the Heath of Kralo. Not in all sites, however, did density fluctuate in parallel and to the same degree; for each column (pair of years) ‘ v_i^2 ’ gives an estimate of the degree of dissimilarity of density changes in the sites concerned. The weighted average of these column-variances (S_t^2) gives some impression of how different the density changes were in different sites during an average pair of years. In the case of *Pterostichus coeruleus* (Table 3) S_p^2 and S_t^2 are of the same magnitude, which may indicate that the differences between sites might be great enough to counterbalance the density changes in

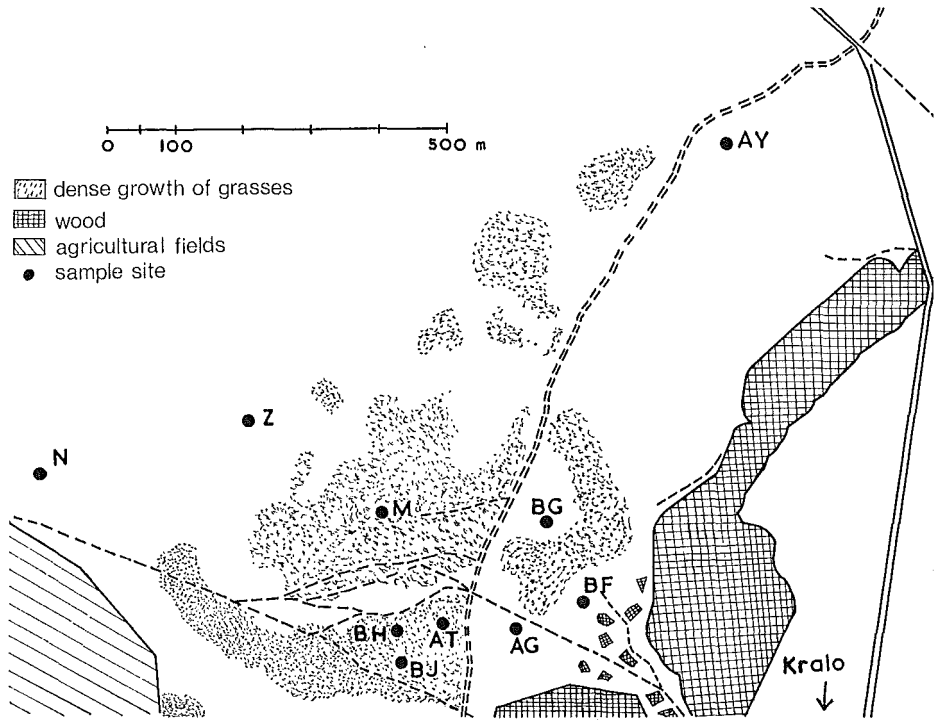


Fig. 2. Sample sites in the S.E.-part of the Heath of Kralo. Note: sample-site BB is not in the picture; it is indicated in the outlined part in the lower right of Fig. 1.

time within a group of subpopulations. To what degree this compensation really occurs is roughly estimated by the variance of the average column-r's (S_r^2). We may also use $\text{var } R_1 (S_R^2)$ but this will not influence our conclusions.

In *P. coerulescens* (Table 3) S_r^2 is much smaller than S_p^2 , which may indicate that, in this group of subpopulations on the Heath of Kralo, there is a considerable levelling down of density fluctuations as a result of effective differences between the sites. This, indeed, corroborates my statement that in many natural populations the risk of wide fluctuation is spread from generation to generation over a number of local groups within the population, and that this will result in a relative stabilization of numbers in the population as a whole (see also Fig. 3).

In *Calathus melanocephalus* (Table 4), however, S_r^2 is much smaller than S_p^2 , which indicates that the differences between sites have not been great enough to counterbalance the density changes in time within this group of subpopulations. This seems to be confirmed by the fact that the difference between S_r^2 and S_p^2 is relatively much smaller in this species than in the case of *P. coerulescens* (see also Fig. 4). Hence, on the Heath of Kralo the population of *P. coerulescens* seems to be more favoured by spatial spreading of the risk of extinction than is that of *C. melanocephalus*. We do not yet know what are the causes of this difference between the two species.

Table 2. Pitfall-catches as a relative measure of mean density (carabid beetles).

For most weeks during the reproductive period of some populations, reliable estimates of density could be derived from capture-recapture experiments (Jolly's stochastic method: 1965). The mean density (per week) during the same (main) part of the reproductive period in two successive years (or in two sites in the same year) was compared with the total number of unmarked individuals caught during that period. (All available data are presented.)

	Total number of unmarked individuals (not caught before)			Mean density (from capture-recapture exp.) per week			Difference between the quotient of pitfall-catches and that of densities
	year n-1	year n	$\frac{\text{year n}}{\text{year n-1}}$	year n-1	year n	$\frac{\text{year n}}{\text{year n-1}}$	
The same site in two successive years							
<i>Agonum assimile</i> PAYK. 1966-'67: 8 weeks	459	670	1.46	474.2	785.8	1.66	$\chi^2 = 2.287$ $P \approx 0.15$
<i>Agonum assimile</i> PAYK. 1968-'69: 17 weeks	1048	1011	0.96	560.1	462.8	0.83	$\chi^2 = 3.963$ $P \approx 0.05$
<i>Calathus erratus</i> SAHLB. 1968-'69: 15 weeks	1649	1207	0.73	1956.0	1552.1	0.79	$\chi^2 = 2.484$ $P \approx 0.13$
<i>Nebria brevicollis</i> F. 1968-'69: 10 weeks	231	264	1.14	158.0	205.8	1.30	$\chi^2 = 0.943$ $P \approx 0.35$
<i>Pterostichus oblongopunctatus</i> F 1968-'69: 14 weeks	644	1151	1.79	371.8	690.6	1.86	$\chi^2 = 0.235$ $P \approx 0.60$
Two sites during the same year	site I	site II	$\frac{\text{site I}}{\text{site II}}$	site I	site II	$\frac{\text{site I}}{\text{site II}}$	
<i>Calathus erratus</i> SAHLB. 1969: 6 weeks	458	383	1.20	999.5	788.0	1.27	$\chi^2 = 0.07$ $P \approx 0.80$

Note that: *Agonum assimile* and *Pterostichus oblongopunctatus* (both studied in a small deciduous wood) reproduce in spring, whereas *Nebria brevicollis* (studied in a small deciduous wood) and *Calathus erratus* (studied in an area of blown sand) reproduce in late summer and autumn.

Table 3. *Pterostichus coerulescens* L. (Col., Carabidae) in different sites on the Heath of Kralo (the Netherlands, Drenthe; Fig. 2).

n_{ji} : number of individuals caught during year i in site j ; $r_{ji} = \frac{n_{j,i}}{n_{j,i-1}}$.

Sub-population (j)	n_{ji} r_{ji}	Year (i)										s_j^2	k_j	
		1959	1960	1961	1962	1963	1964	1965	1966	1967	1968			1969
N	n_{11} r_{11}	202	246	206	230	223	206	154	86			162		
Z	n_{21} r_{21}		150	317	493	550	525	163	83			148		
AG	n_{31} r_{31}			209	282	393	265	412	283	354				
AT	n_{41} r_{41}				132	139	196	133	353	506	336			
AY	n_{51} r_{51}					367	264	163			21			
BB	n_{61} r_{61}						595	625	755	543	485			
M	n_{71} r_{71}	45	55	72	37	30	13	4	3					
BF	n_{81} r_{81}							256	260	315				
BG	n_{91} r_{91}							463	548	405				
BH	n_{101} r_{101}							119	287	410	444	292		
BJ	n_{111} r_{111}							114	157	202	320	209		
	v_1^2		0.000	0.438	0.183	0.064	0.063	0.283	0.300	0.351	0.148	0.014		$i = 1, 2, \dots, t$
	\bar{r}_1		1.22	1.44	1.14	1.06	0.80	0.84	0.99	1.40	1.20	0.72		$j = 1, 2, \dots, p$
	R_1		1.22	1.32	1.30	1.15	0.86	0.79	0.96	1.22	1.05	0.73		
	$(R_1 - \bar{r}_1)^2$		0.000	0.014	0.026	0.008	0.004	0.003	0.001	0.032	0.023	0.0001		$s_j^2 = \frac{\sum (r_{j,i} - \bar{r}_j)^2}{k_j - 1}$
	m_1		2	3	4	4	5	6	11	7	4	4		$v_1^2 = \frac{\sum (r_{1,i} - \bar{r}_1)^2}{m_1 - 1}$

$$S_p^2 = \frac{\sum (k_j - 1) s_j^2}{\sum (k_j - 1)} = 0.2384; S_t^2 = \frac{\sum (m_i - 1) v_i^2}{\sum (m_i - 1)} = 0.2218; S_p^2 / S_t^2 = 1.07; S_r^2 = \text{var } \bar{r}_1 = 0.0604; S_R^2 = \text{var } R_1 = 0.0462; S_{(R-\bar{r})^2} = \frac{\sum (R_1 - \bar{r}_1)^2}{9} = 0.0122$$

Note that $R_1 = \frac{\sum n_{j,1}}{\sum n_{j,1-1}}$ for those subpopulations that were sampled during both successive years. Compare: Fig. 3

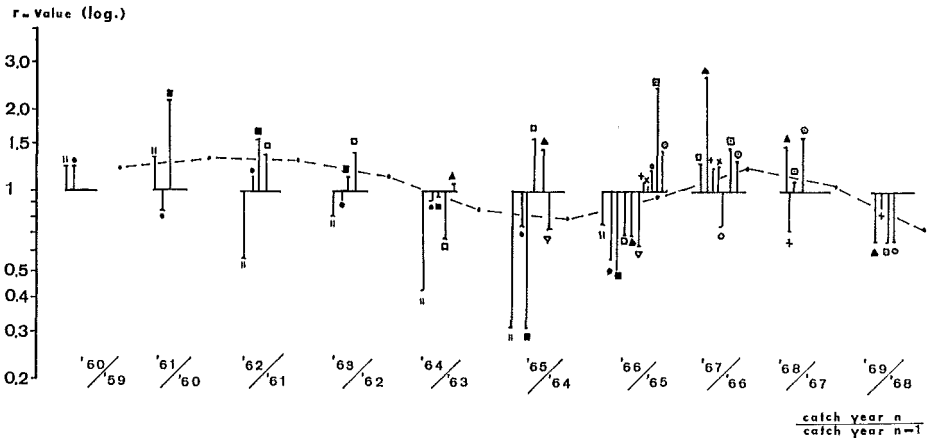
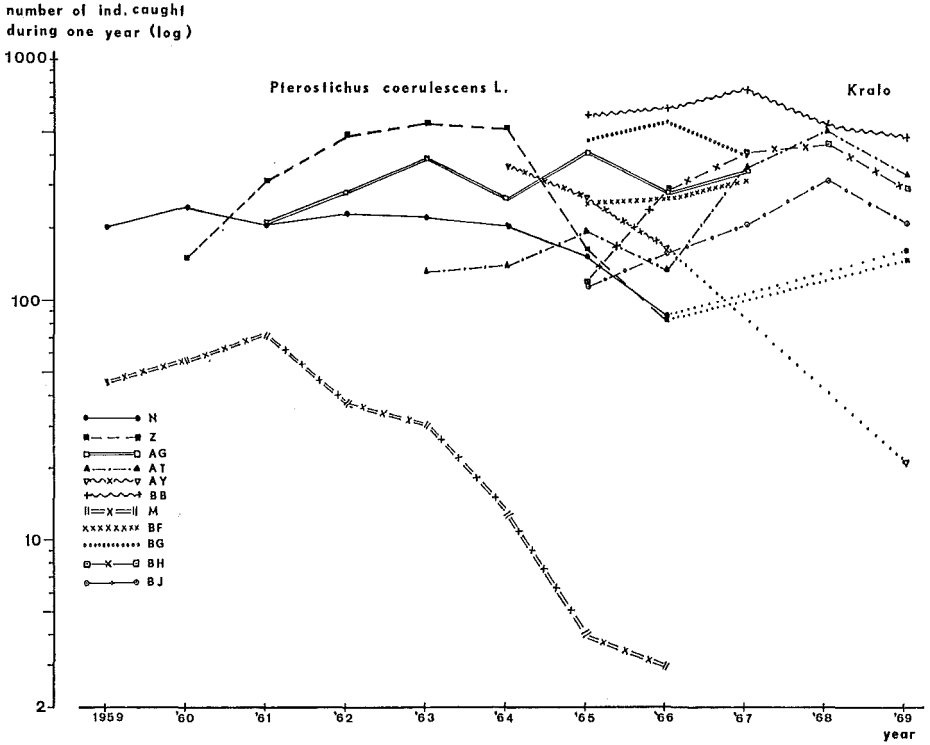
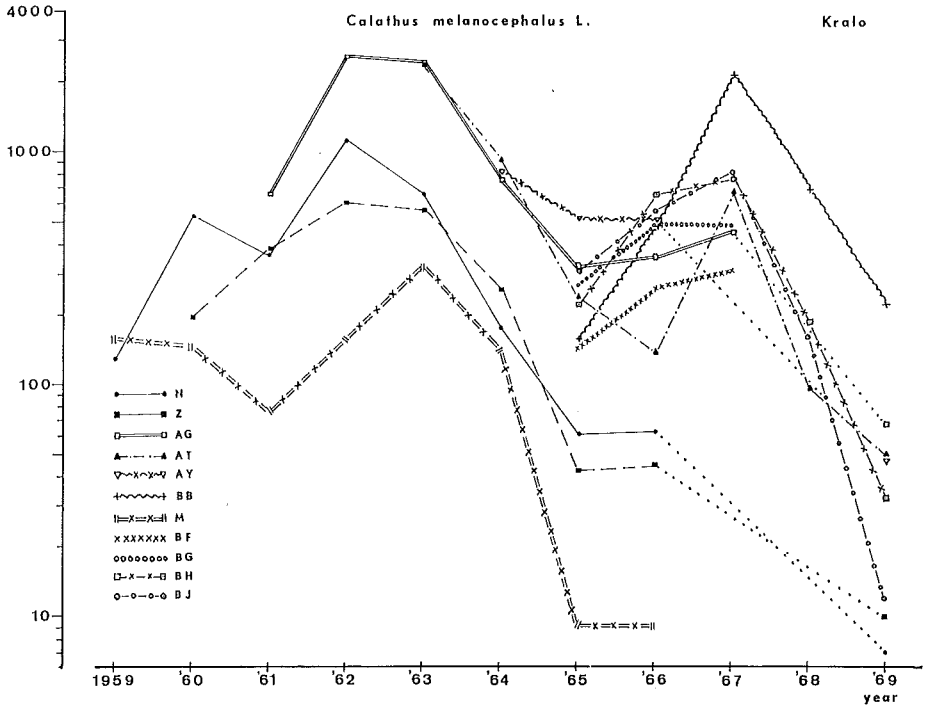


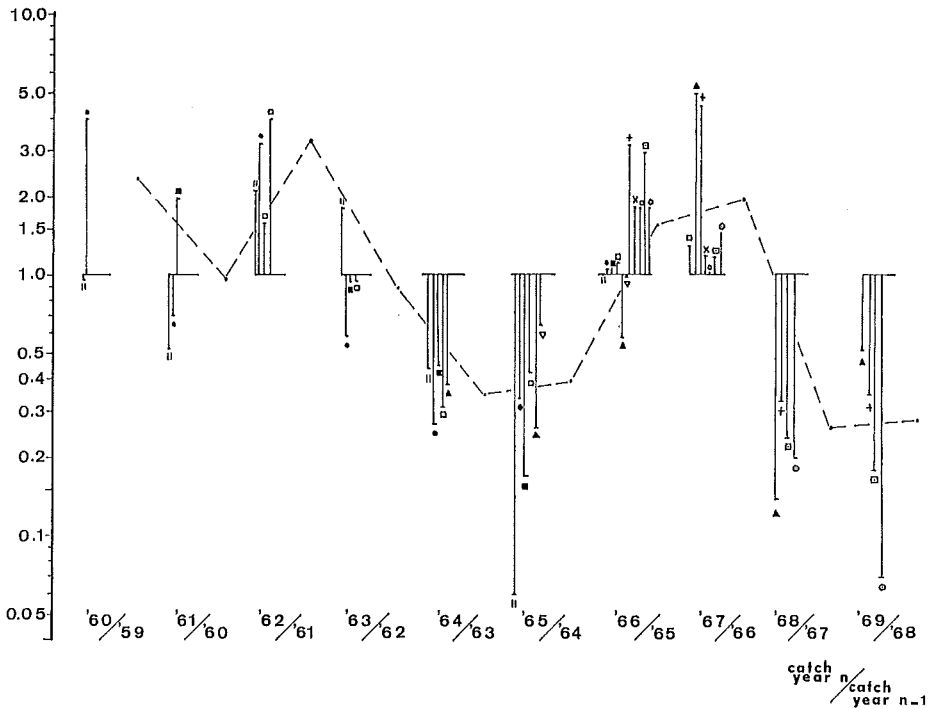
Fig. 3. Catches of *Pterostichus coeruleus* L. in sample-sites on the Heath of Kralo (Fig. 2). In the lower part of the figure are values of r_{11} (vertical lines) and values of R_1 (broken line) (See Table 3).

Fig. 4. Catches of *Calathus melanocephalus* L. in sample-sites on the Heath of Kralo (Fig. 2). In the lower part of the figure are values of r_{11} (vertical lines) and values of R_1 (broken line) (See Table 4).

number of ind. caught during one year (log)



r. value (log)



Stabilization of numbers in the Oak tortrix

Another example of stabilization of numbers by spatial spreading of risk is given by Schütte (1957) for the Oak tortrix, *Tortrix viridana* L. in the vicinity of Münster. The chief mortality factor appeared to be: lack of coincidence between the hatching of larvae and the opening of oak buds, which are both influenced by weather conditions. The larvae of *Tortrix* hatch within a period of 7 days, whereas there is considerable variation in the time of bud-opening between individual oaks; 19 days in 1952 and 26 days in 1953.

However, the sequence in which a number of trees open their buds remains the same in different years, this allows one to distinguish between 'early-opening' and 'late-opening' trees (4 groups were distinguished). In some years the hatching of larvae coincided with early opening oaks, in other years with late opening oaks. The dynamics of *Tortrix viridana* were studied by Schütte in 4 plots of oaks (Fig. 5). He discovered that the density was most stable in plot A in which the mortality due to a lack of coincidence between the hatching of larvae and the bud-opening of oaks was nearly constant (60%). This constant mortality apparently results from the oaks being distributed almost equally within the four groups. In other words, in plot A the risk of lack of coincidence between hatching of larvae and opening of oaks is spread almost equally over the different trees, which results in an important stabilization of numbers.

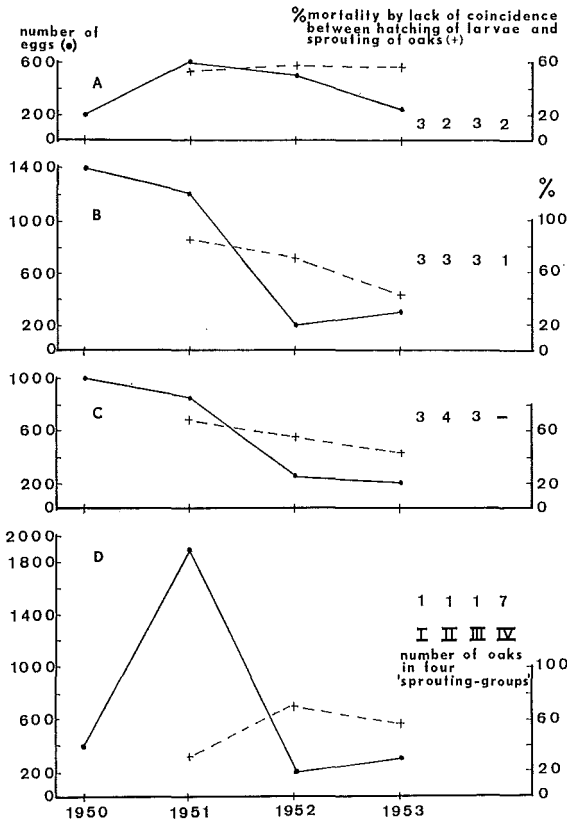


Fig. 5. Density of eggs, and % mortality of *Tortrix viridana* L. due to a lack of coincidence between hatching of larvae and bud-opening of oaks in 4 plots with different distribution of oaks over 4 'opening groups'. (Modified from: Schütte, 1957).

Number-of-factors model

The stabilization of animal numbers does not only result from spatial heterogeneity in the effective environment (and from heterogeneity within the population), but also from the number of 'factors' that influence density. Animal numbers will be influenced by a smaller or greater number of meteorological 'factors', of species of natural enemies, of kinds of food, of kinds of hiding places, etc, and sometimes some of these 'factors' may tend to counterbalance the effects of some others. In fact this is only another way of looking at the influence of the complexity of natural situations, a view, however, that has been put forward already by different authors in various forms, e.g. by Thompson (1929, 1939, 1956), Andrewartha and Birch (1954), Glen (1954), Milne (1957, 1962), Schwerdtfeger (1958), Richards (1961).

We attempted to demonstrate the supposed stabilizing influence of an increasing number of factors affecting net reproduction by a model (Reddingius and den Boer, 1970). In this model net reproduction was allowed to vary between a very low value $r_{\min} = 0.02$ and a very high value $r_{\max} = 50$ under the influence of 1, 2, etc. up to 10 meteorological 'factors' such as average temperature, total rainfall, etc. over a given month. These 'factors' were taken, irrespective of whether they would be serially correlated in time or not and/or whether their frequency distributions would be about normal or not; in fact one or more of these features appeared to occur in some of the factors (Reddingius and den Boer, 1970). The values of the meteorological 'factors', the only kind of environmental 'factors' of which real values over long series of consecutive years are available, were taken from published tables of the Meteorological Institute, De Bilt, the Netherlands. Each factor f_i was allowed to influence net reproduction between certain limits u_i and b_i corresponding with r_{\min} and r_{\max} ; u_i and b_i were fixed arbitrary somewhere outside the values of the tables, which resulted in quantitatively different influences in different factors. The meteorological data were used in the same annual sequence in which they appear in the original tables and in the same sequence values of r were given by

$$y(t) = \ln[r(t)] = y_{\min} + \frac{y_{\max} - y_{\min}}{k} \cdot \frac{\sum_{j=1}^k |f_j(t) - u_j|}{\sum_{j=1}^k |b_j - u_j|}$$

In this way a number of populations were simulated which were influenced by a different number of factors; all possible combinations of up to 10 factors were simulated and the calculated values of the fluctuation characteristics for the total number of combinations were averaged. It must be noted that by increasing the number of factors one certainly does not decrease 'LR' and 'var R' in all individual cases (individual results are highly variable). Therefore, averages were calculated to show the general trend with which we are concerned in these theoretical considerations. Two versions of this additive linear model were used:

- A. Very different 'factors' (air temperature, rainfall, evaporation, 'sunshine, soil temperature) during 30 years.
- B. Only values on temperature and rainfall during a period of 210 years (the longest series available).

To be sure that our modeled populations would 'persist' for some time it was assumed that, in the case with 10 factors after a given sequence of years (30 in version A and 100 in

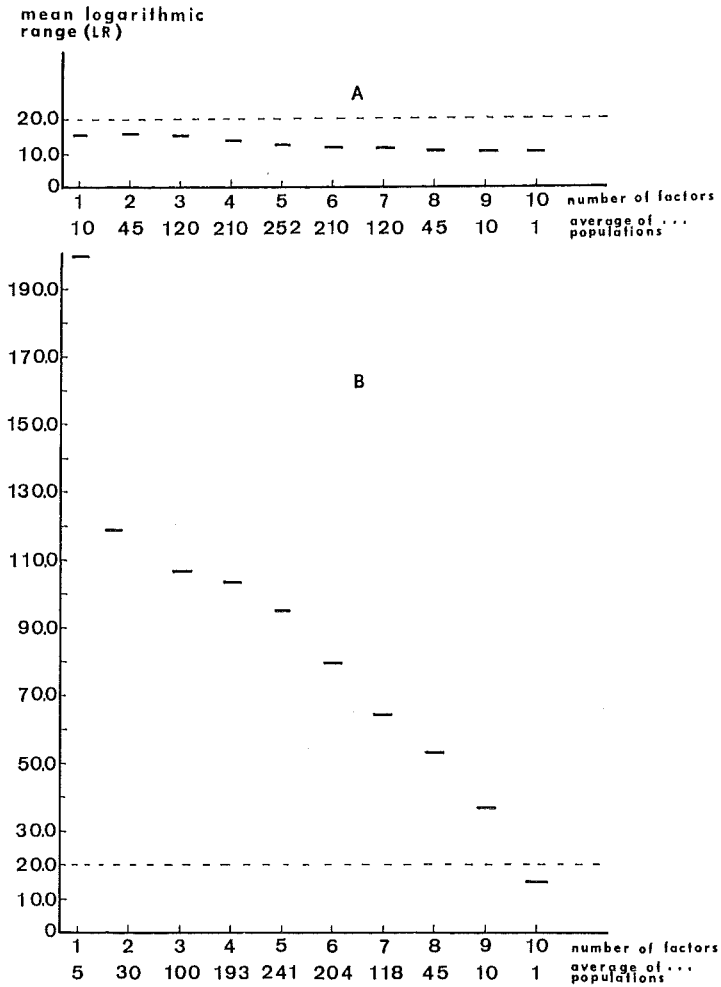


Fig. 6. Mean logarithmic range (LR) of density fluctuations in simulation experiments on the stabilizing influence of the number of (meteorological) factors determining the net rate of reproduction. The experiment was repeated for each possible combination of 2, 3, etc. factors out of 10, except cases in which population density became too high (higher than 10^{130} ; Experiment B). LR was averaged over all calculated combinations (populations) with the same number of factors. A. Models for 30 generations (years) with very different meteorological factors. B. Models for 210 generations (years) with only mean air temperature and/or total rainfall over a given month (the only data available).

version B), density attains about the initial value once more (see Reddingius and den Boer, 1970). Hence, the case with 10 factors did not show a strong trend in density.

In both versions, LR steadily decreases with an increase in the number of factors (Fig. 6); in the case with 210 years, LR starts, of course, with much higher values and the decrease is much steeper than in the case with 30 years. The decrease of var R with increase of the number of factors is very convincing in both versions (Fig. 7). From this figure (compare A and B) one even gets the impression that the number of factors may have a

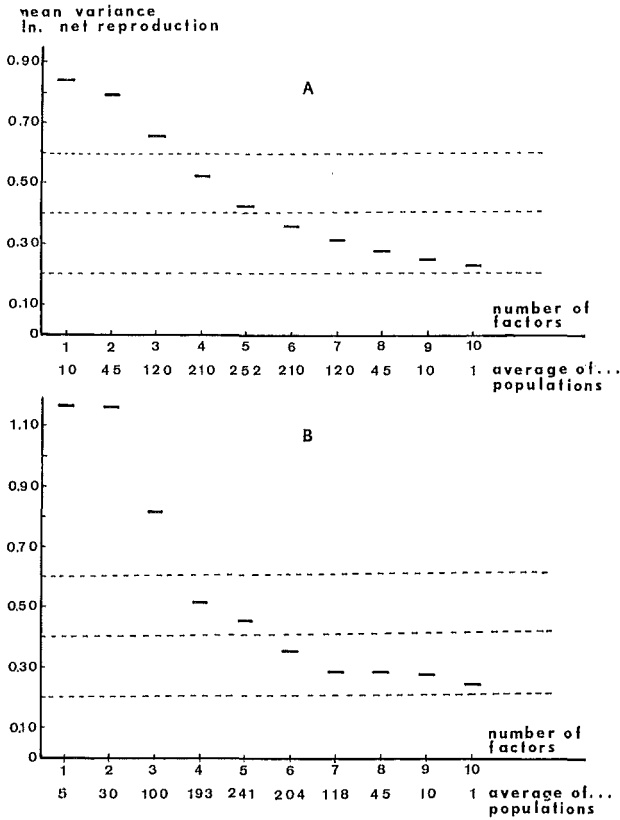


Fig. 7. Mean variance of \ln net reproduction ($\text{var } R$) in the same simulation experiments as those in Fig. 6.

more important influence on $\text{var } R$ than the 'kind of factor' and/or than the number of years over which $\text{var } R$ was calculated (this latter feature of $\text{var } R$ is used in the interpretation of Tables 3 and 4). The correctness of this interpretation was made probably by Reddingius (Reddingius and den Boer, 1970); he was able to prove that within the premises of our model, even when this was weakened regarding the limits b_1 and u_1 , $\text{var } R$ approaches zero when the number of factors becomes infinite. The factors need not be uncorrelated among themselves and in all probability they may even depend on density.

Trends in density

Hence, under the conditions of our model we may get density fluctuations as small as we want by assuming the influence of an appropriately large number of 'factors' on density, and this may serve as a conceptual model for the persistence of sparse insect populations; but in that case it must also be assumed that 'average $\ln R$ ' is close to zero. In an overall highly unfavourable environment most 'factors' during most of the time will have an unfavourable influence, and density will show an overall downward trend albeit with small fluctuations. In an overall highly favourable environment density will show an upward

trend and, in the long run, the sparse population will become a dense one unless the environment shows some limiting tendency. Although some kind of density-dependent limitation may, of course, keep 'lnR' close to zero, such limitation is not a 'conditio sine qua non'. Even some very incidental random crashes in random years (once in 30–100 years in the population with 10 factors in our model with 210 years) may keep in persistence a population which otherwise would have shown an overall upward trend. For a more detailed discussion see: Reddingius and den Boer (1970).

Environmental resistance

But another line of thought is possible to introduce some limiting tendency of the environment; in many cases, such a limiting tendency appears to be theoretically necessary to keep down a strong upward trend and thus to supplement the restriction of density fluctuations resulting from a great number of 'factors'. Let us imagine some animal population influenced only by a small number of 'factors', e.g.: a homogeneous population of some not very polyphagous phytophagous insect in a homogeneous environment poor in animal species.

If we now visualise that for some reason the number of 'factors' gradually increases, we may wonder what 'kind of factors' most probably will be added. The population will become more heterogeneous; more phenotypes, a more heterogeneous age composition, more variation in development, etc. The environment will become more heterogeneously structured, which will result in a breaking up of the population into a number of local groups, each with an effective environment (e.g. microweather; see den Boer and Sanders, 1970) somewhat different from that of the other groups. Perhaps there will also be more variation in the distribution, the composition and the quality of the food, etc. This increase in the number of 'factors' will result, of course, in a decrease of density fluctuations; but there is no reason to suppose that – averaged over a great number of such cases – the overall favourability of the circumstances always will be altered in one and the same direction i.e. that 'average ln R' always will shift significantly in the same direction. However, we have left out another 'kind of factors' that must also take action in our 'concept adding procedure'. The number of other species will also increase, and among them the number of species of parasites, predators, competitors and other enemies generally will greatly outnumber the number of beneficial species (indifferent species need not be considered). Hence, adding this kind of factors will result in a relative increase in the limiting tendency of the environment, increase of 'environmental resistance' (Chapman, 1928); contrary to Chapman this term does not imply here any 'mechanism(s)', whether density-dependent or not, but only points to the existence of some general limitation or resistance.

In my opinion there are good reasons to suppose that an increase in the number of species of a biocoenosis will not only contribute – via an increase in the number of 'factors' – to a relative reduction of density fluctuations in many populations, but will also result in an increase of some general kind of 'environmental resistance'. The latter – mainly resulting from an asymmetrical increase of different kinds of factors (beneficial, indifferent, limiting) – will lower the density level of many populations and may keep down possible upward trends in density which might have become manifest under less complex circumstances.

In a very simple – but appropriate – situation, an experiment by Utida (1957) nicely demonstrates that in a population of the azuki bean weevil (*Callosobruchus chinensis* L.)

an increase in the number of parasite species from one to two (other things being equal) not only results in a decrease of density fluctuations (Fig. 8 compare In-range and var R in A and B), but also in a lowering of the density level of the host population. Moreover 'average $\ln R$ ' is indeed closer to zero in the case with two parasite species (0.0176) than in the case with one (0.0281). The experiment also illustrates that hypotheses on stabilization of numbers by spreading of risk may be tested experimentally.

Density-related limitation

It may be expected that the total action of all kinds of predators, parasites and competitors ('environmental resistance') will often be related to density in a very broad sense. In general, dense populations will be affected more than sparse ones, especially when polyphagous predators (and parasites?) are able to develop 'specific searching images' (Tinbergen, 1960) for numerous prey species; sparse prey species will then experience some 'protection' from severe predation. But a relative 'protection' of sparse prey species may also result from other circumstances, e.g. a more 'clustered' distribution of individuals in some numerous species than in sparse ones, the occurrence of Batesian mimicry, adequate differences in hiding abilities, patterns of activity, palatability, etc. between some numerous species and sparse ones. However, this kind of limiting tendency of the environment also

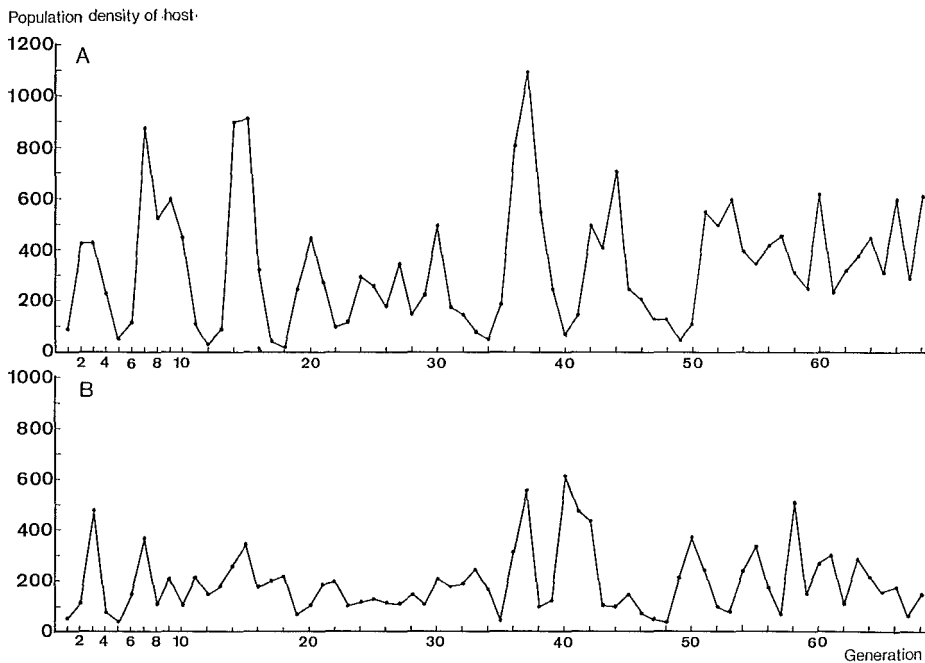


Fig. 8. Density fluctuations in experimental populations of the azuki bean weevil (*Callosobruchus chinensis* L.) during 68 generations.

A. Culture with one parasite species; \ln range 4.00733; variance R 4.6437; average $\ln R$ 0.0281.

B. Culture with two parasite species; \ln range 2.87437; variance R 2.1855; average $\ln R$ 0.0176. (Modified from; Utida, 1957).

must be seen as part of a very complex pattern of environmental (and 'populational') influences on net reproduction (number of factors) from which separate density-dependent 'factors' generally cannot easily be singled out. Moreover, it may be expected that, in general, the greater the complexity the smaller will be the specific effect of individual 'factors' – e.g. the density-dependent effect of some of these 'factors' – and the smaller will be the significance of these special influences for the overall stabilization of numbers. This does not imply that I would deny that density-dependent limitation of density can make an important contribution to the stabilization of animal numbers in some or in many cases. However, it may generally be expected that, in these cases, the limitation or decrease of density will be more important than the degree to which it is density-dependent (see also den Boer, 1968a).

Sparse insect populations

Returning to our problem 'the apparent persistence of sparse insect populations', I should like to pose the following hypothesis:

In a complex biocoenosis many species will show restricted density fluctuations as a result of the great number of 'factors' affecting net reproduction; such a situation – by a relative preponderance of mainly non-specific density-limiting factors – results in a kind of 'environmental resistance' keeping down both the density level of many populations and any possible tendencies for an upward trend in density.

Extinction is incorporated in this concept as the realization of chance in the course of time. Hence, the persistence of a species will depend on the relationship between the chance of extinction of existing populations and the chance to found new populations. On this point, the fundamental significance of dispersal phenomena, and its relations with the heterogeneity and degree of stability of the environment, is brought into the picture. But this is outside the scope of this paper (see Andrewartha and Birch, 1954; Birch, 1957; Southwood, 1962; den Boer, 1970).

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Discussion

Participants: den Boer (Author), Beukema, Frank, Gradwell, Jacobs, Jain, Lawton, Murdoch, Ohnesorge, Platt, Royama, Solomon, Southwood and Walker

The initial discussion concerned the features of the number-of-factors model. Many of these points can be clarified by referring to Reddingius and den Boer (1970), but some need to be mentioned here too –

Simple models of population fluctuation often have a built-in balance inasmuch as the chances of increase and decrease are made quantitatively equal. It seems unlikely that many populations would be matched to their habitats in this way, for habitats vary, and such a balance could exist for only one or a few among the many in which the species is found. It seems that in nature populations would mostly have an overall net reproductive rate above the value needed just to replace regular losses, and that the consequent tendency to net increase would be offset by density-dependent processes (SOLOMON). Hence, models for which density dependent factors are not essential to prevent eventual overpopulation or extinction are concerned with fluctuations rather than with trends and will have a built-in balance (SOUTHWOOD). A distinction between long-term trends in the numbers and fluctuations around that trend is fine in a model. In nature, however, we have time to observe rather few fluctuations in annual species, and, thus, purely by observing changes in numbers it is very difficult to distinguish between fluctuations around a trend-line (or 'equilibrium' level) and changes in the trend itself (MURDOCH).

I admit that the distinction between amplitude of fluctuations and long-term trend is essential in the models. Fluctuations could be made as small as one wanted by increasing the number of 'factors' but to be sure that the model 'populations' would 'persist' for some time (no pronounced trend) a very crude 'safety-valve' had to be built in, as is mentioned in the paper. The models are only intended to give a possible understanding of the often

observed restriction of density fluctuations in supposedly persisting populations, which is illustrated by some examples. It is hardly possible at this moment to give sensible thoughts about the problem of the supposed persistence (absence of trend) of populations itself. To make an attempt:

1. One can deny the problem by stating that there is a more or less continuous 'turnover' of populations (extinction and refounding) ending ultimately in extinction of the species (in different species the time-scale of this 'turnover' may be very different).
2. As is discussed in this paper, one can accept eventual extinction (the end of a downward trend) of populations as a realization of chance, and state that the eventual keeping down of upward trends may be a function of the complexity of the effective biotic environment as a whole ('environmental resistance').
3. One can state that 'self-regulatory mechanisms' are necessary to prevent overpopulation and/or extinction in the long run (no pronounced trend). Although at this moment I guess that the possibilities (1) and (2) will turn out to present the more general cases, I am sure that at least in a number of cases possibility (3) will be involved to some degree (if 'regulation' is not defined too strictly in a Nicholsonian sense) (AUTHOR).

Some kind of environmental predictability was not incorporated into the models, because the environment is hardly supposed to show it (except for the existence of seasons); real meteorological data are used (AUTHOR to LAWTON).

In many cases adding a factor actually decreases stability, because the factors are not selected to have special features and are taken together in all possible combinations; the stabilizing trend becomes especially apparent when considering the averages (AUTHOR to JACOBS).

It is difficult to see how the number of factors is important to stability unless their effects are very similar, and there is no single dominating factor (FRANK, GRADWELL, OHNESORGE). The very different (arbitrary) values of the limits b_i and u_i prevent the factors from having very similar quantitative effects, although it is not expected that one factor will dominate the quantitative effects of all the others. Because population numbers are undoubtedly influenced by many factors, to obtain a generalization it seemed more relevant at the moment to test the influence of the number of factors rather than to study what kinds of effects of some single factor may still be measured against the background of the effects of many others. Of course, very different relationships between factors can be imagined, which can hardly ever all be covered by simulation models. On the other hand, we expect that the conclusions drawn are valid for a more general class of models as well. But it will always be possible to construct exceptional situations or even to trace them in nature (AUTHOR).

'LR' and 'var R' cannot be mathematically independent because a small 'LR' can hardly coincide with a great 'var R', but they measure different features of a set of fluctuations, 'LR' being more susceptible to trend than 'var R' (AUTHOR to BEUKEMA).

No special features of 'model animals' are taken into account besides perhaps the values of r_{\min} and r_{\max} and the - arbitrary taken - parameters in the subpopulations model (AUTHOR to ROYAMA).

What kind of differences in the environment are important for carabid beetles? (FRANK), how are they quantified? (WALKER), and which quantitative operational measure of the spatial heterogeneity of a natural environment may be used or suggested? (PLATT) In order to effectively measure heterogeneity, it would be necessary to know the variation in space

and time of all factors significantly influencing density. As a start, we tried to develop techniques for measuring spatial and temporal variation in the temperature and humidity of the surface layer, and we hope to develop techniques for measuring the spatial structure of vegetation, because these factors are found to correlate highly – in an estimated ordinal scale – with habitat-selection. But apart from this we may simply observe that changes of density are different in different places within the habitat of a population, and try to estimate how this affects a group of such subpopulations in order to learn whether stability is favoured by such a situation or not (AUTHOR).

Several ideas (Mayr, Wright) invoke 'regular' or occasional bottlenecks of numbers to allow 'genetic revolution' – a new breakthrough in the genetic system. The role of drift or founder effect is directly relevant to fluctuations in numbers, either locally or to the species as a whole. If sparser species would indeed show relatively greater stability, one may wonder whether their being sparse may imply a lack of such 'genetic revolution events' (JAIN).