

On the Survival of Populations in a Heterogeneous and Variable Environment*

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Summary. The survival time of small and isolated populations will often be relatively low, by which the survival of species living in such a way will depend on powers of dispersal sufficiently high to result in a rate of population foundings that about compensates the rate of population extinctions. The survival time of composite populations uninterruptedly inhabiting large and heterogeneous areas, highly depends on the extent to which the numbers fluctuate unequally in the different subpopulations. The importance of this spreading of the risk of extinction over differently fluctuating subpopulations is demonstrated by comparing over 19 years the fluctuation patterns of the composite populations of two carabid species, *Pterostichus versicolor* with unequally fluctuating subpopulations, and *Calathus melanocephalus* with subpopulations fluctuating in parallel, both uninterruptedly occupying the same large heath area. The conclusions from the field data are checked by simulating the fluctuation patterns of these populations, and thus directly estimating survival times. It thus appeared that the former species can be expected to survive more than ten times better than the latter (other things staying the same). These simulations could also be used to study the possible influence of various density restricting processes in populations already fluctuating according to some pattern. As could be expected, the survival time of a population, which shows a tendency towards an upward trend in numbers, will be favoured by some kind of density restriction, but the degree to which these restrictions are density-dependent appeared to be immaterial. Density reductions that are about adequate on the average need even not occur at high densities only, if only the chance of occurrence at very low densities is low. The density-level at which a population is generally fluctuating appeared to be less important for survival than the fluctuation pattern itself, except for very low density levels, of course. The different ways in which deterministic and stochastic processes may interact and thus determine the fluctuations of population numbers are discussed. It is concluded that some stochastic processes will operate everywhere and will thus *necessarily* result in density fluctuations; such an omnipresence is much less imperative, however, for density-dependent processes, by which population models should *primarily* be stochastic models. However, if density-dependent processes are added to model populations, that are already fluctuating stochastically the effects are taken up into the general, stochastic fluctuation pattern, without altering it fundamentally.

1. Introduction

During the many years I studied natural populations of carabid beetles I was increasingly struck by the severe contradiction between the holistic and deterministic structure of most mathematical population models, and the heterogeneous structure and highly variable – not to say turbulent – environment of field populations. I soon learned that heterogeneity is not an exclusive feature of carabid populations and variability not a special property of the environments in the northern parts of the Netherlands. I long believed that we should have to go to the tropics to meet with conditions that would not completely upset the assumption of an about constant physical environment, as it lies at the root of most deterministic population models. However, since my friend Wolda went there (Barro Colorado Island) to study the dynamics of insects living in the tropical rain forest, also this illusion was roughly disturbed: population numbers are fluctuating there as heavily as they do in comparable insects in our temperate regions (Wolda 1978a), and these fluctuations are clearly associated with unpredictable variations of the environment (especially with variable amounts of precipitation: Wolda 1978b). Hence, apparently we have to retire into the deep-sea or far into some cave to meet with natural conditions that will tolerate the greater and most favoured part of our theoretical considerations on populations. But see also Turanchik and Kane (1979) and Juberthie (1979) concerning the environmental conditions in caves.

However, meanwhile many field ecologists returned empty-handed from excursions into mathematical ecology, and thus continued their studies of real animal populations in real, i.e. heterogeneous and variable environments without much reference to adequate general principles. For many years already I realized, that we cannot go on for ever in this way, in spite of the many valuable and highly interesting – but mutually only little related – field-studies that thus emerge (see also: Watt 1971). In a desperate trial just to start from the crux of the problem I resolved to answer the question: “How do populations survive in a heterogeneous and changeable world?”

Admittedly only after some years, it became evident to me, that the answer to this question highly depends on the definition of “population” one adheres to. To keep as close as possible to our population models – where individuals are supposed to be continually able to interfere (via the “density” reached) – we should define a “population” as an “interaction group”, i.e. a local group living in a locality of such dimensions that the individuals are at least potentially able to meet (Den Boer 1977, 1979a, 1981), by which possible effects of interactions

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can be expected to be about averaged throughout the group, and can thus indeed be considered density effects. A related definition of "population" was already proposed by Bakker (1964, 1971), but met with the difficulty that ecologists did not see an easy way to generally dilimit "interaction groups" in the field.

We were happy to discover that, by sampling carabid populations with the help of pitfalls, we are actually sampling "interaction groups": the number of individuals caught during a reproductive season appeared to be a relative measure not only of the numerical size of the pertinent interaction group, but also of the mean density of that species around these pitfalls (see: Baars 1979b).

Also e.g. Zwölfer (1979), who studies population processes running within single thistle-heads, is evidently working with "interaction groups", which in this case are distinctly separated in space and often composed of the larvae of different species.

2. How Long will "Interaction Groups" Survive?

When we thus take (simple) "populations" to be "interaction groups" a hypothetical answer to our question might be: "Populations (at least simple ones) do not survive very long, but are continually becoming extinct and being founded again". This evidently applies to species occupying temporary or unstable habitats like fruits, heaps of dung, dead bodies, mushrooms, banks of pools, lakes and rivers, agricultural fields, etc. The survival of such species will highly – if not completely – depend on sufficiently high powers of dispersal. See further: Southwood (1962), Johnson (1969), and e.g. Dingle (1978). Remarkably enough have a number of ecologists tried to demonstrate the importance of density governing processes for the "regulation of numbers" by sophisticatedly arranging laboratory experiments with species of just this kind (like blow-flies, grain-weevils, *Tribolium*, *Drosophila*, etc.), for which it may be expected that under natural conditions the survival time of single interaction groups will only exceptionally suffice for such processes to reach "equilibrium values".

But also the survival time of interaction groups of species living in more stable or permanent environments can often hardly be expected to exceed – at least in arthropods – some decades or a few centuries at best. By an indirect approach we could show this indeed to be the case among carabid beetles inhabiting remnants of old forest or old heathland in Drenthe (Den Boer 1977, 1979a). On a more geological timescale also the survival of such species will thus highly depend on sufficiently high powers of dispersal, especially when many of the habitats are small and isolated and thus occupied by separate interaction groups.

Therefore, a first answer to our question apparently should indeed be: "The survival time – measured as number of generations – of populations taken as interaction groups is restricted and often very short indeed". See also Andrewartha and Birch (1954). However, most ecologists are convinced that under natural conditions many populations do live very long. This conviction is favoured by two circumstances: First, for practical reasons many students observe large and/or very dense populations in rather stable habitats, and these are less likely to die out within the comparatively short span of active life of a field ecologist than most others. Secondly, most long-term population studies are carried out in extensive areas where populations are composed of a continuum of many interaction groups. As for many species the latter situation also is the more natural one we will

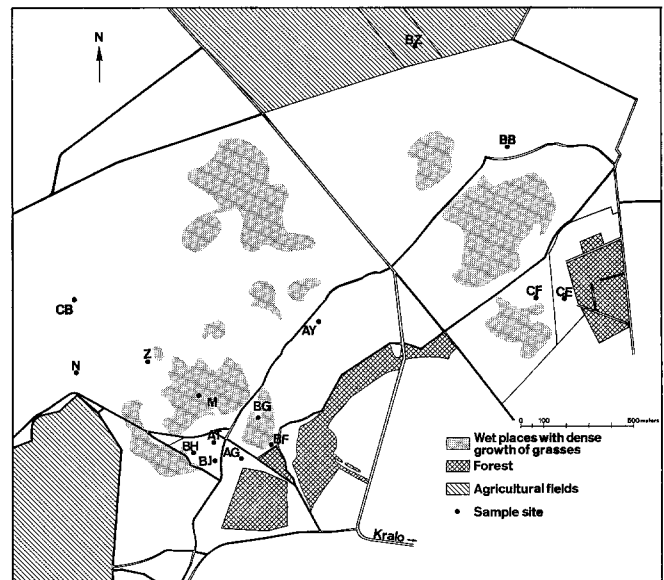


Fig. 1. Part of Kralo Heath with indications of the sample-sites the data of which are plotted in the Figs. 2 and 3

have to pay special attention to the survival time of such large and composite populations.

3. On the Risk of Extinction of Composite Carabid Populations

During twenty years already some carabid species living in such an extensive area, the Heath of Kralo and Dwingeloo (1,200 ha), in the northern part of the Netherlands, were studied by us with the help of a number of standardized sets of pitfalls (Fig. 1; descriptions and photographs of these sample sites can be found in: Den Boer 1977, Appendix A, Part II). An important question, that had to be answered to be able to get to grips with the structure of such a composite population, was: How far are the numbers of individuals of such a species, caught yearly in the different sets of pitfalls, samples from the same or from different interaction groups (subpopulations)? For two of our species, *Pterostichus versicolor* Sturm (= *coerulescens* L.) and *Calathus melanocephalus* L. this question was answered by Baars (1979a) by radioactively marking some individuals and localizing them each day. By repeating this kind of observations in different times of the year as well as in several years he was able to characterize and quantify the walking pattern of these species in day-units, at which scale it is composed of day-distances and day-directions. This pattern could be simulated in a computer model, by which he could not only adequately simulate our pitfall catches – which appeared to give a reliable estimate of mean density around these pitfalls (Baars 1979b) – but also verify this pattern with the results of several independent field experiments (Baars 1979a).

The thus checked simulation model could again be used to registrate the distances that will have been covered on the heath by individuals of these species that were caught in our pitfalls. It then appeared, that 50% of the captured individuals of *P. versicolor* will have covered less than 100 m and 90% less than 200 m. In the case of *C. melanocephalus* these values are 40 m and 80 m respectively (Baars and Van Dijk, in prep.). Hence, with the exception – at least for *P. versicolor* – of the series AT, BH, BJ, most sets of pitfalls can be considered to sample

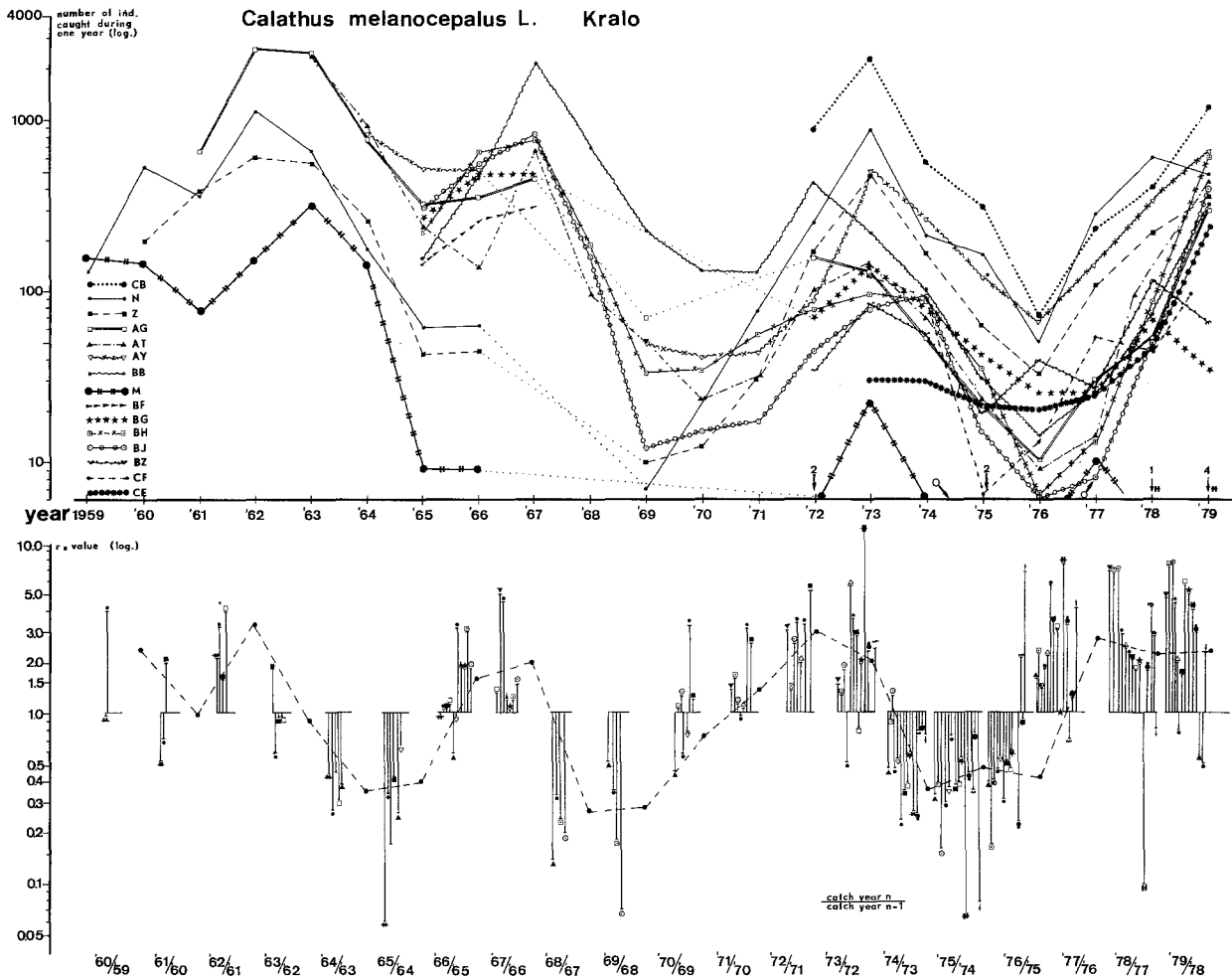


Fig. 2. Mean relative densities in different interaction groups (subpopulations) of *Calathus melanocephalus* (Col., Carabidae) at Kralo Heath during 21 years. In the lower part of the picture: values of net reproduction in the different subpopulations (vertical bars), and in the population composed of these subpopulations (points connected by broken line) respectively

different subpopulations for the greater part of the catches. Although the population processes, that are thus sampled by the different sets of pitfalls, can be considered to be sufficiently independent of each other (especially for the sets at greater mutual distances), the many interaction groups that can be supposed to exist on the heath are highly interconnected by the locomotory activities of the individuals. By this interconnection the quantitative effects of the events occurring in the different subpopulations together determine the chance of survival of the species in the whole area.

When we now turn to our observations on the fluctuations of the mean densities around different sets of pitfalls on Kralo Heath during 19 years, i.e. to the fluctuations of numbers within different interaction groups, we first establish that there are marked differences between the two species studied. In *C. melanocephalus* these fluctuations are heavy and in different subpopulations they run about in parallel (Fig. 2). In *P. versicolor* the fluctuations are less violent and are often running in opposite directions in different subpopulations (Fig. 3). Apparently, for *C. melanocephalus* the conditions that influence changes in numbers are about the same at different places of Kralo Heath, i.e. during an unfavourable season conditions will be more or less unfavourable at every site, and vice versa. For *P. versicolor*, however, in most seasons conditions may be favourable in some localities, whereas they are unfavourable in other ones, i.e. Kralo

Heath is much more heterogeneous for *P. versicolor* than it is for *C. melanocephalus*. This striking difference in the way these species react upon the actual spatial heterogeneity of Kralo Heath must have important consequences for the pattern of numerical fluctuations in the population as a whole: In *C. melanocephalus* these fluctuations will not differ very much from those in an average subpopulation, whereas in *P. versicolor* these fluctuations may be expected to be much smaller and much more levelled than those in an average subpopulation. This latter difference again will highly determine the risk of extinction of the pertinent species in this heathland area. In *C. melanocephalus* this risk will not differ very much from that of a collection of averaged – and thus identical – subpopulations, because its risk of extinction is hardly spread over differently fluctuating subpopulations. In *P. versicolor*, on the other hand, the risk of extinction is importantly spread over a number of differently fluctuating subpopulations (Den Boer 1968).

4. Comparing Patterns of Numerical Fluctuations

We now will have to quantify the above difference between the two species concerning the degree to which the risk of extinction of the composite population as a whole is spatially spread over subpopulations. This can be done by comparing for each of the species averages of a number of subpopulations, i.e. char-

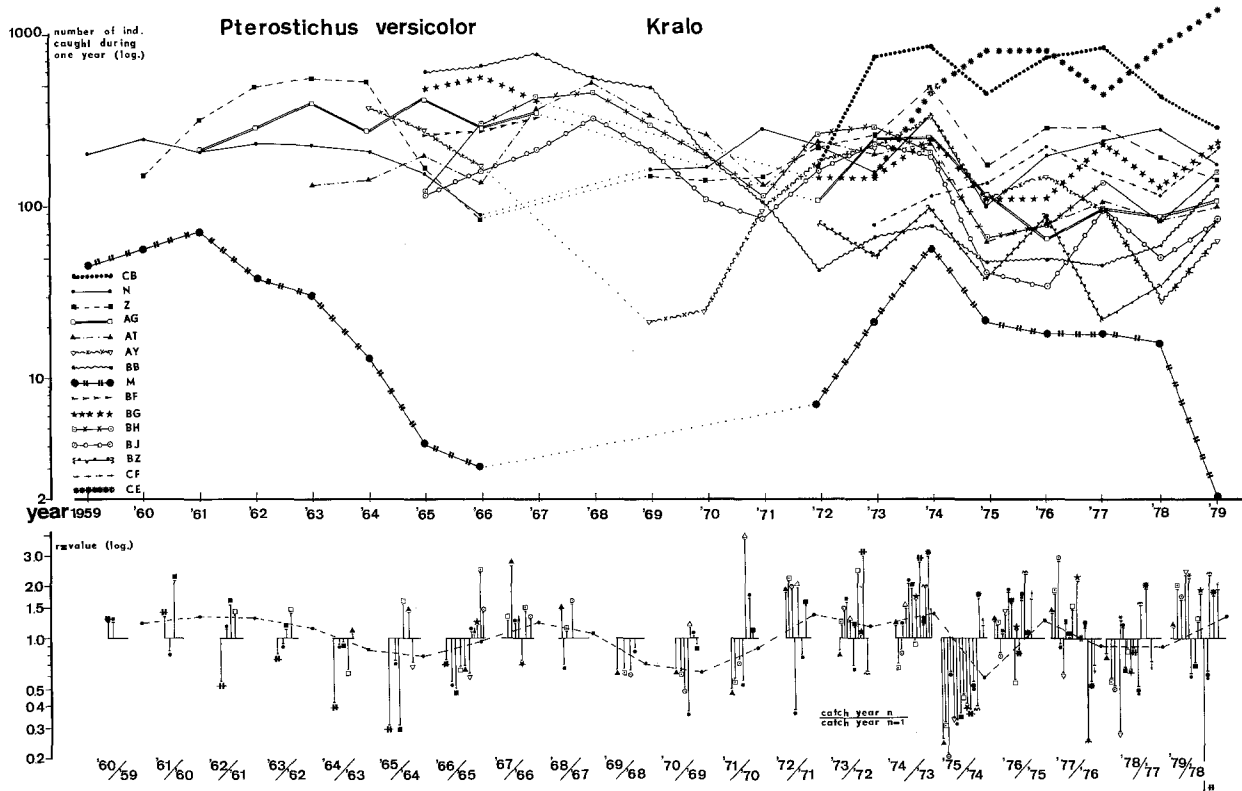


Fig. 3. Mean relative densities in different interaction groups (subpopulations) of *Pterostichus versicolor* (Col., Carabidae) at Kralo Heath during 21 years. See further Fig. 2

acteristics of the pattern of numerical fluctuations shown by a population that can be thought to be composed of identical (averaged) subpopulations (no spatial spreading of the risk), with the characteristics directly observed in a population composed of a representative set of natural (different) subpopulations. Though our sets of pitfalls were not consciously divided randomly over Kralo Heath they can be considered to sample a set of subpopulations that is representative for a composite population in which differences between subpopulations have a reasonable chance to manifest themselves. Moreover, as during the whole period both species were sampled with the same sets of pitfalls (i.e. also in the same places, and in the same years) the results are completely comparable.

To quantify patterns of numerical fluctuations we calculate some fluctuation characteristics (cf. Reddingius and Den Boer 1970; Den Boer 1971):

a) The difference between the logarithms of the highest number and of the lowest number that was reached during the period of observation: "logarithmic range" (LR). This measures the limits between which population size has been fluctuating.

b) The variance of net reproduction R (density (N) in generation n divided by density in generation $n-1$) during the period of observation: Var R . This measures the violence of numerical fluctuations.

c) Var R should be considered together with the average logarithm of R over the period of observation (the logarithm of the geometric mean of R): Average $\ln R$ (for m generations this is simply $1/m (\ln N_m - \ln N_0)$). It gives some idea of the overall trend in population fluctuations, but – except in very long series – it is highly influenced by the last population size estimated.

5. Spreading of Risk in Two Composite Carabid Populations

Table 1 distinctly shows that the limits between which population numbers have been fluctuating during 11 as well as during 19 years in the composite population of *C. melanocephalus* are hardly different from those of an average subpopulation, 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 contrary, this fluctuation range is reduced to the half as compared with the average range of 9 subpopulations, and this undoubtedly will favourably influence the chance of survival of this composite population. Also Var R is much more reduced in the composite population of *P. versicolor* (about 5 times) than in that of *C. melanocephalus* (about 2 times), as compared with the weighted average of Var R for 9 subpopulations (compare also S_R^2 with S_p^2 in the Tables 3 and 4 of Den Boer 1971). Note, that in all cases Average $\ln R$ has increased by integrating the subpopulations into a composite population. Though the movements of individuals can only level part of the differences in the fluctuation patterns between subpopulations (especially in *P. versicolor* where these differences are very great), the effect of such an exchange is apparently sufficient to already let increase somewhat net reproduction in the population as a whole, according to the phenomenon mentioned by Kuno (1981).

When looking at the Figs. 2 and 3, especially at the course of R for the population as a whole through time (broken line in lower part), one will be struck by the seemingly cyclic fluctuation of numbers: if numbers start to increase (or decrease) these

Table 1. Characteristics of the fluctuations of mean density over 11 and 19 years respectively for two carabid species at Kralo Heath, The Netherlands.

A=average of the separate values for the 9 subpopulations (M, N, Z, AG, AT, AY, BB, BH, BJ: Figs. 2 and 3) that have been sampled longest (during at least 4 years in 1970, and at least 12 years in 1978).

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

C=value for a population that is composed of all subpopulations sampled (Figs. 2 and 3)

I. Over 11 years (1959–1970). All data from which these characteristics were computed were already published by Den Boer (1971: Tables 3 and 4)

	A	B	C
<i>Calathus melanocephalus</i>			
LR	3.6769	3.5248	3.6259
Var R	1.7925	1.1059	1.0547
Average ln R	-0.4141	-0.1537	-0.1637
<i>Pterostichus versicolor</i>			
LR	1.5328	0.8786	0.8786
Var R	0.2482	0.0578	0.0462
Average ln R	-0.0460	0.0457	0.0384

II. Over 19 years (1959–1978). See also, Den Boer (1981)

	A	B	C
<i>Calathus melanocephalus</i>			
LR	4.8777	4.3499	4.4379
Var R	3.2712	1.1609	1.0507
Average ln R	-0.1291	-0.0660	-0.0807
<i>Pterostichus versicolor</i>			
LR	2.2559	1.2912	1.0417
Var R	0.4252	0.0846	0.0656
Average ln R	-0.0320	-0.0005	0.0142

continue to do so for some years. Baars and Van Dijk (in prep.) will show that this curious pattern results from the combined effects of some meteorological factors on the magnitude of recruitment and of survival of individuals respectively. Such a pattern will account for some serial correlation between succeeding values of R: especially the rather high autocorrelation between R_t and R_{t-3} (about -0.6 for 19 years) significantly keeps up such a long term pattern. It is highly interesting that this pattern is about similar in the composite populations of both species (though *C. melanocephalus* generally is one year ahead of *P. versicolor*; see also Fig. 1 in Den Boer 1979b), in spite of the fact that *P. versicolor* (a spring breeder) is influenced in other stages of the life-cycle by other meteorological factors than *C. melanocephalus* (an autumn breeder); see further Baars and Van Dijk (in prep.). Still more interesting is, that the great difference between the species concerning the spatial spreading of the risk of extinction – low in *C. melanocephalus* with subpopulations that fluctuate about in parallel (Fig. 2), and high in *P. versicolor* because of quite differently fluctuating subpopulations (Fig. 3) – is apparently not abolished (including the Kuno (1981) – effect) by these meteorological patterns: Table 1.

6. Estimating the Survival Time of Carabid Populations by Simulation

It is nice, of course, that we could obtain some numbers that apparently indicate the magnitude of the difference between these two species in the degree to which the risk of extinction is spatially spread over a number of subpopulations, but how do we show that this difference is more important for the survival time of these species on Kralo Heath than e.g. the fact, that in many years and in the greater part of the localities the mean density of *C. melanocephalus* is about 50 times (or even more) higher than that of *P. versicolor*? (not only the catches of *C. melanocephalus* are much higher than those of *P. versicolor* (Figs. 2 and 3), but also the catch efficiency (Luff 1975) of our pitfalls is more than 5 times lower for the former than for the latter species: Den Boer, 1977: 4.4.2). Because we cannot observe the survival time of such large populations, we can only try to simulate our populations as well as possible in computer models, and then run these programs until the simulated populations have become “extinct”, under the assumption, of course, that the future (especially concerning the conditions that influence numbers) will not differ fundamentally from the past 19 years we studied, i.e. under the assumption of a stationary environment. If we simulate these two species in two versions, one as “composite population” (i.e. differences between subpopulations included), and the other as a collection of averaged subpopulations with the same start value (i.e. differences between subpopulations excluded), we will learn what may be the significance of differences between subpopulations and thus of the spatial spreading of the risk over subpopulations, for the survival time of the composite population. At the same time we will learn what is the predictive value of our fluctuation characteristics, especially of LR (Table 1).

The manner we simulated (in Fortran IV) the autocorrelation between R_t and R_{t-3} is given in the Appendix (A1). As we had to use rather long sequences of random numbers (two in each “year”), and we did not like to let determine our results by some peculiar series of random numbers, each version of each program in this paper was run thirty times, each time with a quite different sequence of random numbers; the results of these thirty runs are averaged. By doing thirty extra runs with still other sequences of random numbers in some cases we could check that such an average is thus very stable indeed. We could only change it 5–15% by using a new set of thirty runs, whereas the standard deviation of survival time within such a set of thirty runs amounts to 60–90% of the mean in all stimulations in this paper. In terms of a t-statistic we can keep the rule of thumb that only mean survival times that are more than 30–50% apart from each other can be considered actually to be different. After having read a start value (PP) following population sizes (PI) are computed according to A1, and each run is thus continued until the “population” contains less than a single “individual”; the survival time in “years” is then printed, and the program turns to a new run. In these open programs there is also a chance that some (or even many) “populations” will exceed all bounds; such “populations” were considered also to have become “extinct” if numbers (PI) passed an “upper limit” which is equally distant as the “lower limit” (1) from PP (start value), i.e. this value was fixed at PP^2 .

The results of these simulations are given in Table 2. It must be noted that nearly all “populations” surpassed the lower limit (1), i.e. we did not need some “density-restricting mechanism” to run these simulations. The simulations of *P. versicolor* are satisfactory in many respects: in different as well as in similar

Table 2. Survival times of simulated populations of two carabid species in which R_t shows a negative autocorrelation with R_{t-3} of a value as found in the field during 19 years. The 3 first values of R are given (from the field population); following values are found according to $R_t = \exp(a + b \cdot \ln R_{t-3} + z.c.)$, in which a , b and c are computed by regressing $\ln R_t$ on $\ln R_{t-3}$ for the 19 years available, and in which z is a random variable normally distributed on (0,1). Populations composed of the subpopulations as sampled in the field (different subpop.) are compared with populations composed of (similar) subpopulations obtained from averaging over the sampled subpopulations (similar subpop.). Each value is the average of 30 runs with different random numbers

Pterostichus versicolor

	Start value (PP)				
	10^2	10^3	10^4	10^5	10^6
Different subpopulations	613	1,109	1,483	2,457	2,897
Similar subpopulations	65	98	131	158	195
	a	b	c	autocorrelation ln R_t , ln R_{t-3}	mean LR over 19 year-periods ^a
Different subpopulations	-0.0068	-0.6533	0.27525	-0.5889	1.6611 ($n=24$)
Similar subpopulations	0.1175	-0.5487	0.32469	-0.4538	2.2582 ($n=51$)

Calathus melanocephalus

	Start value (PP)				
	10^2	10^3	10^4	10^5	10^6
Different subpopulations	45	61	75	83	96
Similar subpopulations	66	86	141	209	259
	a	b	c	autocorrelation ln R_t , ln R_{t-3}	mean LR over 19 year-periods ^a
Different subpopulations	-0.2609	-0.5806	0.89177	-0.5954	4.7947 ($n=27$)
Similar subpopulations	-0.0480	-0.3667	0.95178	-0.3637	4.7647 ($n=25$)

^a Periods of 19 years were taken randomly from the first 180 years of the first 6–15 runs of the simulation with $PP=10^5$. Compare Table 1

subpop. the intended autocorrelation was touched very closely in all runs, and the frequency distributions of R -values (first 180 years, $PP=10^5$) fitted that of the 18 R -values from the field (cf. Appendix: A2), very closely in the composite population ($P>0.70$), and not too bad in similar subpopulations (no run with $P\leq 0.05$); also LR was touched sufficiently (even very well in similar subpop.): Table 2. We are therefore convinced that the survival times of *P. versicolor* in Table 2 indeed illustrate the highly favourable effect of spreading the risk of extinction over a number of differently fluctuating subpopulations. The simulations of *C. melanocephalus* are less satisfactory: the simulated autocorrelations are too low (especially in similar subpop.), and the frequency distributions of R -values often deviate significantly from that of the 18 R -values in the field; it is apparently impossible to simulate this bimodal distribution (A2) adequately by a single autocorrelation. The simulated populations nevertheless show the right range of fluctuations (LR). In spite of these shortcomings we have reasons (which will become obvious in the continuation of this paper) that not only the LR-values of Table 1 but also the survival times of Table 2 rightly show that the composite population of *C. melanocephalus* at Kralo Heath is greatly deprived of the favourable effects of spreading the risk of extinction over subpopulations. Hence, the fluctuation characteristics of Table 1 (especially LR) adequately predict the expected differences between survival times.

7. Random Fluctuations of Population Size, and Survival Time

Now we have constructed these first-generation survival models (second-generation models will not use R -values, but directly simulate processes that influence recruitment and survival of individuals: Baars and Van Dijk in prep.), we are in a favourable position to also try answering some more theoretical questions, such as:

a) Does the pseudo-cyclic fluctuation pattern (Figs. 2 and 3) influence the effects of spreading the risk of extinction over subpopulations?

b) Do density-restricting processes interfere with spreading of risk, and is the influence of the former processes on survival time more important than the latter phenomenon?

To answer the first question (a) we had only to adapt our models (section 6) in that – after having read the start value (PP) – new population sizes (PI) had to be generated by drawing subsequent R -values at random from a frequency distribution that equals the distribution of the relevant field data. The frequency distributions of R -values from our field data, both for composite populations and for similar subpopulations, can be found in Appendix A2, while the simulations of these distributions are given in A3. The survival times from these simulations are shown in the columns OPEN of Table 3.

Table 3. Comparison of the survival times of different simulated populations in which R-values succeed each other randomly (short runs). Frequency distributions of R as found in the field (Appendix A2) during 19 years. For each start value the survival times of the composite populations are compared with those of similar subpopulations (compare section 6 and Table 2). Each value is the average of 30 runs with different sequences of random numbers.

OPEN: no density restrictions; lower limit of extinction = 1, upper limit = PP^2 .

INDR: independent (constant) density restrictions at independent moments (mean frequency of restrictions as in INCC).

INCC: independent (constant) restrictions if “carrying capacity” (at $99 \cdot PP$) is exceeded.

DDCC: density-dependent restrictions if “carrying capacity” is exceeded (mean frequency of restrictions as in INCC).

DDSC: density-dependent restrictions occur in the greater part of the range between the start value and carrying capacity.

DDS: density-dependent restrictions for all population numbers above the start value

Start value (PP)	<i>Pterostichus versicolor</i>						<i>Calathus melanocephalus</i>					
	OPEN	INDR	INCC	DDCC	DDSC	DDS	OPEN	INDR	INCC	DDCC	DDSC	DDS
10^2												
Different subpop.	241	1,404	1,735	1,631	1,065	428	38	91	115	63	68	54
Similar subpop.	103	207	233	169	185	99	34	97	99	85	83	56
10^3												
Different subpop.	607	1,787	2,600	2,696	2,319	959	74	118	151	91	115	79
Similar subpop.	216	380	440	317	372	194	76	126	142	99	102	84
10^4												
Different subpop.	1,117	2,275	4,150	4,144	3,339	1,916	144	161	206	117	146	122
Similar subpop.	342	507	612	445	536	368	115	165	178	129	144	106
10^5												
Different subpop.	2,009	3,710	6,118	6,116	4,837	3,017	182	195	249	133	203	163
Similar subpop.	548	760	802	615	724	494	161	185	256	153	205	161
10^6												
Different subpop.	2,980	4,784	7,711	7,701	6,561	4,174	290	271	309	155	241	217
Similar subpop.	744	1,052	943	689	875	705	259	227	370	200	295	229

Apart from a greater influence of the start value, the results of these “short run” simulations of our “open” model (columns OPEN in Table 3) apparently are not very different from those of the autoregressive version (Table 2): again, the composite population of *P. versicolor* distinctly shows the favourable effect of spreading the risk of extinction over differently fluctuating subpopulations, which effect is absent from the composite population of *C. melanocephalus*. There is one important difference, however, between the “short run” version and the autoregressive version of our open models: in the “short run” simulations most populations passed the upper limit of extinction (in the composite population of *P. versicolor* even accompanied by a higher value of LR over 19 year-periods than in Table 2). The autocorrelation between R_t and R_{t-3} as it was simulated in the autoregressive model – and which can be traced back to the influence of weather factors: Baars and Van Dijk (in prep.) – apparently favours a downward trend of population numbers. At the same time, the opposite feature of the “short run” simulations gives an excellent starting point to study the possible effects of density restricting processes on the time of survival, i.e. to try to answer the second question (b).

8. The Effects of Density Restricting Processes on the Time of Survival

The most obvious way to prevent population size from reaching the upper limit (PP^2) is diminishing numbers with a certain value as soon as some less high limit, called “carrying capacity” (fixed at 99 times PP) is passed. Such a diminishing of numbers can be independent of the amount of exceeding, either a constant

or a variable reduction of R: INCC, or proportional to the extent to which “carrying capacity” is exceeded: DDCC (see further Appendix: A4). From Table 3 can be learned that in *C. melanocephalus* the survival times from INCC are possibly somewhat better than those from DDCC, whereas in *P. versicolor* the two processes gave similar results (the mean frequency of restrictions is kept the same in both versions). In Table 4 is shown, that the level at which “carrying capacity” is fixed in itself is not very important: putting this level at 20 times PP in most cases reduces the averaged survival times only for 10–20%, which is less than required to consider such a reduction probably significant (see also section 6). Taking either “carrying capacity” itself, or the reduction of density after exceeding, variable instead of constant does not influence survival times at all (Table 4). Such a kind of stochasticity completely depends on the laws of large numbers and needs not be incorporated as such in our simulations to increase our understanding of processes affecting survival times. Therefore, in all simulations with density restrictions we kept both “carrying capacity” and the degree of restriction deterministic: we replaced the (more realistic) variations by their expectation values, so to say. Note, that spreading of risk is fundamentally different from the above kind of stochasticity within a single process: spreading of risk comes into play if there is some kind of exchange between differing stochastic processes (e.g. between differently fluctuating subpopulations as a result of the movements of individuals, but also e.g. between differently sized patches of prey as a result of the exploitation by foraging predators).

It could be expected, of course, that in INCC and DDCC survival times would be generally better than in OPEN: the

Table 4. Comparison of the influence on survival times of the level of “carrying capacity” (1 and 3), and of a constant versus a variable density reduction after exceeding (1 and 2). Given are the data on *P. versicolor*, frequency distribution of R as found in the field, program INCC, “short runs” (other cases show about similar features)

Start value (PP)	“carrying capacity” at 99.* PP		“carrying capacity” at 20.* PP. Reduction as in 1
	density reduction constant ^a	density reduction variable ^b	
	1.	2.	3.
10^2			
Different subpop.	1,735	1,625	1,064
Similar subpop.	233	256	184
10^3			
Different subpop.	2,600	2,578	2,250
Similar subpop.	440	416	396
10^4			
Different subpop.	4,150	4,143	3,321
Similar subpop.	612	608	521
10^5			
Different subpop.	6,118	5,863	4,820
Similar subpop.	802	803	724
10^6			
Different subpop.	7,711	7,586	6,545
Similar subpop.	943	929	876

^a In 1 and 3 the constant reduction of density after exceeding of “carrying capacity” exists of subtracting 0.4054651 from $\ln R$ (i.e. $R = R/1.5$)

^b In 2 the reduction of density is made variable by multiplying with a random number (homogeneous distribution) between 0.5 and 1.5

populations that passed the upper limit in OPEN (most of them did so), and were thus considered “extinct”, were prevented from doing so in INCC and DDCC by the restricting processes, by which they were allowed to continue fluctuating at or below “carrying capacity” until they would eventually pass the lower limit. The more surprising, that in *C. melanocephalus* this potential delay of extinctions does hardly work in INCC and not at all in DDCC (Table 3): especially at higher start values the lower level of “carrying capacity” (99.*PP) in INCC and DDCC, as compared with the upper limit (PP²) in OPEN, together with the unfavourable distribution of R-values, is apparently more influential in many cases (at least in DDCC). The composite population (different subpop.) of *P. versicolor*, on the other hand, highly benefits under this potential delay of extinctions by restricting processes (similar subpop. much less, however, probably because of the more vigorous density fluctuations): Table 3.

One will wonder now whether or not it is essential that density restrictions exclusively occur at very high densities as in INCC and DDCC. We therefore also tried constant density restrictions of the same value as in INCC, that were applied randomly with respect to density, but with the same mean frequency as in INCC to save comparability: INDR (cf. Appendix: A4). Neither in *C. melanocephalus*, nor in similar subpop. of *P. versicolor* the survival times of INDR are different from those of INCC (cf. section 6): Table 3. Only in the composite population of *P. versicolor* the survival times of INDR seem to be

lower than those of INCC (Table 3), but at most start values it is somewhat doubtful whether this difference is real because the survival times are only 30–50% apart from each other (cf. section 6). As soon as an only small deviation from a random application of the constant density restrictions – in the direction of some preference for high densities – would be built in INDR, survival times will already sufficiently increase to be sure that no actual differences between the survival times of INDR and INCC are left. Hence, as could be expected, density restrictions of about the right size and occurring in about the right mean frequency will appreciably prolong the survival times of populations that otherwise would have shown an upward trend of numbers, but it will be less expected, that it does not make much difference whether such restrictions occur about randomly or only at very high densities, though a rather low probability of occurrence at very low densities must generally be favourable, of course. The same conclusion was already reached by Reddingius and Den Boer (1970) with some single simulation experiments of a different kind.

Many population ecologists will have a notion of the generally supposed stability-favouring influence of density-dependent mortality that is different from the manner we simulated it in DDCC (or even in INCC); see e.g. Murdoch (1979). They will think of a density-dependent mortality (e.g. by predation) that potentially is operating continuously over a broad range of densities (and not only at “carrying capacity”) in such a way that the “built-in tendency” towards an upward trend in numbers is just counteracted sufficiently to prevent exceeding of “carrying capacity”. In DDSC we constructed such a mild kind of density dependence that operated continuously over the greater part of the density-range between the start value and “carrying capacity” in such a way that numbers were fluctuating around the start value as in INCC (the mean frequency of passing the start value was kept about similar to that in INCC), whereas at the same time “carrying capacity” was just never exceeded (see: Appendix A4). In DDS the same mild form of density dependence was kept operating continuously over the whole range between PP and 99 times PP. In the latter case the mean frequency of passing the start value was different, of course, from that in INCC, because numbers were fluctuating now below the start value for a greater part of time than in DDSC and INCC.

Table 3 shows that in DDSC in none of the cases survival times are actually different (cf. section 6) from those in DDCC (or INCC), and if such a difference seems to be indicated (as in *P. versicolor*, different subpop., PP=100) DDSC is inferior to DDCC or INCC. DDS is generally worse than either DDSC, DDCC or INCC and not better than INDR. The values of mean LR over 19-year periods in the simulations discussed in this section do not deviate importantly from those of the autoregressive simulation (section 6, Table 2), e.g. in different subpop. *P. versicolor* INCC: 1.3912 ($n=27$), DDSC: 1.4096 ($n=23$); *C. melanocephalus* INCC: 4.1775 ($n=29$), DDSC: 4.1674 ($n=29$), and in similar subpop., *P. versicolor* INCC: 3.0905 ($n=27$), DDSC: 2.0227 ($n=16$); *C. melanocephalus* INCC: 5.1121 ($n=28$), DDSC: 3.1715 ($n=18$).

The general conclusion from this section thus can be: as far as population size is bounded from above (and this will often occur when numbers show an upward trend) it is not so much the degree to which the limitation or decrease of numbers is density-dependent that is important for survival, but the limitation or decrease itself. This conclusion was already expected by Den Boer (1968: III.4). Even random restrictions (INDR) do rather well. It will also be apparent that density-restricting processes do not interfere with spreading of risk (com-

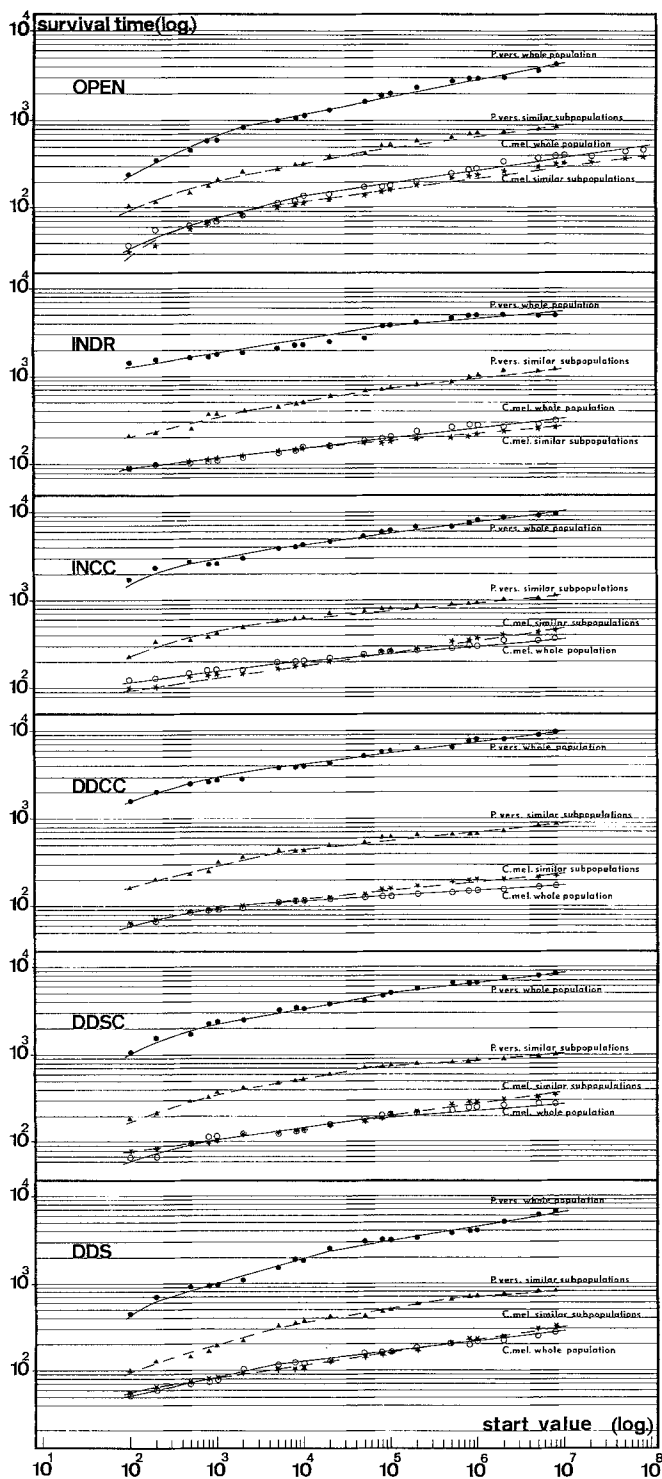


Fig. 4. Relationship between the survival times of simulated populations of *Pterostichus versicolor* and *Calathus melanocephalus* respectively and the start value (estimate of the overall density level) of simulations in which R-values are taken randomly from frequency distributions as found in the field during 19 years (short runs). In both species "different subpop." (solid lines) is compared with "similar subpop." (broken lines) in simulations without density restrictions (OPEN) and in simulations with different kinds of density restricting processes (for further explanations, see Table 3). Each point is the mean survival time from 30 runs with different sequences of random numbers but with the same start value. See further text

pare OPEN with the other versions in Table 3). Probably this is still more evident from Fig. 4, where it is clearly shown that in each version of our simulations the same pattern is repeated: a great difference in survival times between different and similar subpop. in *P. versicolor* and no actual difference in *C. melanocephalus*. Figure 4 also indicates that at higher start values an almost linear relationship exists between log start value and log survival time. Only with very low start values survival time decreases more rapidly, as could be expected. Apparently, survival time depends less on the level of population numbers (estimated here by the start value) than is often supposed: to increase survival time twice we will have to increase the level of numbers 80–500 times in the composite population of *P. versicolor* (only in OPEN 33 times) and 200–1,000 times in similar subpopulations, 100–2,000 times in the composite population of *C. melanocephalus* and 100–1,000 times in similar subpopulations, as can easily be read from Fig. 4. We can also answer now the question posed at the start of section 6: the much higher densities of *C. melanocephalus* as compared with *P. versicolor* apparently are of only little value for survival; compare e.g. in Table 3 start value 10^4 in different subpop. of *P. versicolor* with 10^6 in *C. melanocephalus*, which population sizes will be about those of the composite populations at Krato Heath that were studied by us (i.e. composed of 5 (8)–14 subpopulations).

9. On the Importance of the Amplitude of Fluctuations

We have still to take away the last possible doubt that the great difference in survival time between different and similar subpop. in *P. versicolor* only results from the high degree to which the risk of extinction is spread over differently fluctuating subpopulations, i.e. from a much more favourable pattern of numerical fluctuations in different subpop. than in similar subpop. It could still be argued that part of the effect as it is given in Table 3 might result from the fact that in different subpop. we directly used the frequency distributions of R-values as found in the field, and in similar subpop. the best fitting ln-normal distributions of the subpop. R-values (Appendix A2). Therefore, we also estimated the ln-normal distributions best fitting the 18 R-values from the field for the composite populations of *P. versicolor* and *C. melanocephalus* respectively: Appendix A5. We will still go one step further: though the values of $E(\ln R)$ of the respective ln-normal distributions now available do not differ very much from zero, even these rather small differences between different and similar subpop. might be sufficient to give different trends of numbers through time, which may result again in markedly different survival times (as can easily be checked by simple simulation models). To avoid also this influence, in all simulations treated in this section we put $E(\ln R) = 0$. Hence, the different ln-normal distributions only differ in the value of the standard deviation, i.e. we can study now the pure influence of the amplitude of fluctuations on the time of survival.

After having adapted DDCC, DDSC and INDR to INCC anew (Appendix A4) we could again simulate the cases that were treated in section 8: Table 5. Though we now avoided each kind of trend in numbers the survival times in OPEN, especially in *P. versicolor*, cannot be considered different from those in Table 3 (contrary to expectations in the present simulations of OPEN still somewhat more than half of the populations passed the upper limit). Also the survival times of INDR are hardly influenced (possibly only $PP = 10^2$ in *P. versicolor*, different subpop. is actually lower, and $PP = 10^5$ and $PP = 10^6$ in

Table 5. Comparison of the survival times of different simulated populations in which R-values succeed each other randomly (short runs). In all cases are used the ln-normal frequency distributions of R-values best fitting the field data during 19 years, but with $E(\ln R) = 0$ to maximize the mutual comparability of the fluctuation patterns. For further explanations, see Table 3

Start value	<i>Pterostichus versicolor</i>						<i>Calathus melanocephalus</i>					
	OPEN	INDR	INCC	DDCC	DDSC	DDS	OPEN	INDR	INCC	DDCC	DDSC	DDS
10^2												
Different subpop.	374	790	1,083	1,054	853	405	41	93	150	84	129	82
Similar subpop.	94	226	273	195	187	99	35	78	100	72	86	59
10^3												
Different subpop.	734	1,357	1,442	1,432	1,200	808	118	165	260	118	197	116
Similar subpop.	214	399	448	332	375	220	75	117	143	85	114	88
10^4												
Different subpop.	1,244	2,313	2,707	2,687	2,160	1,186	226	231	403	150	358	221
Similar subpop.	344	663	693	487	600	372	129	157	206	96	151	117
10^5												
Different subpop.	1,754	2,951	3,531	3,230	3,027	1,814	322	383	571	173	423	365
Similar subpop.	483	825	898	653	773	547	196	188	361	161	237	188
10^6												
Different subpop.	3,188	4,282	4,554	4,242	3,796	2,907	386	549	695	213	638	422
Similar subpop.	697	1,164	1,033	729	916	727	274	246	413	177	362	273

Table 6. Comparison of the survival times of different simulated populations in which R_t shows a negative autocorrelation with R_{t-3} (Appendix A5) of a value that is generally lower than found in the field during 19 years (long runs), but which could be combined with the best fitting ln-normal frequency distributions of R-values. To maximize the mutual comparability of the fluctuation patterns $E(\ln R)$ was put at zero in all cases. For further explanations, see Table 3

Start value	<i>Pterostichus versicolor</i>						<i>Calathus melanocephalus</i>					
	OPEN	INDR	INCC	DDCC	DDSC	DDS	OPEN	INDR	INCC	DDCC	DDSC	DDS
10^2												
Different subpop.	686	1,588	1,506	1,482	1,375	567	106	202	261	178	195	78
Similar subpop.	184	306	392	308	322	166	70	66	172	112	87	66
10^3												
Different subpop.	1,579	2,234	2,679	2,620	2,387	1,317	217	260	402	256	286	229
Similar subpop.	362	506	650	472	540	298	156	184	261	175	194	103
10^4												
Different subpop.	3,263	3,431	4,411	4,354	3,648	2,234	400	347	560	364	503	303
Similar subpop.	614	765	843	701	767	554	231	219	367	216	269	229
10^5												
Different subpop.	4,975	5,042	6,130	6,146	5,485	3,129	567	470	797	395	653	512
Similar subpop.	813	979	1,356	856	1,176	790	334	299	469	283	371	286
10^6												
Different subpop.	5,965	6,498	8,436	8,390	6,597	4,691	641	653	972	428	797	657
Similar subpop.	1,314	1,274	1,759	1,113	1,647	1,015	471	413	611	382	514	401

C. melanocephalus, different subpop.¹ are actually higher than in Table 3; compare section 6). More interesting is that in *P.*

¹ As in *C. melanocephalus*, different subpop. the frequency distribution of R-values from the ln-normal distribution is quite different from that used in section 8 (A5), comparing survival times from the Tables 3 and 5 respectively is not very useful in the case of *C. melanocephalus*, different subpop. On the other hand, the survival times of *C. melanocephalus*, different and similar subpop. as given in Table 5 are better comparable mutually than in Table 3, but they are more deviating from the natural situation, of course

versicolor, different subpop. survival times are distinctly lower now in INCC, DDCC, DDSC and possibly also in DDS, especially with higher start values. As the field distribution of R-values is somewhat asymmetrical (Appendix A2, Table A.2.1) in the simulations treated in section 8 reductions of numbers occurred about 40% more frequently than in the present ones, i.e. below the level of numbers where restrictions occurred the chance that in any year numbers would increase was also about 40% higher in the former than in the present simulations.

Hence, if population numbers show an upward trend survival

times are favourably affected if population size is somehow bounded from above. However, Table 5 again clearly illustrates that the degree to which this necessary limitation or decrease is density-dependent in fact is immaterial. The only significant point is, that the necessary restrictions of numbers occur in about the right mean frequency and are of about the right mean size; even nearly random restrictions (a little better only than INDR), if answering the above conditions of mean frequency and mean size, will do sufficiently well in many cases. On the other hand, it will be evident from this section, that the favourable effect of spreading the risk of extinction over differently fluctuating subpopulations as it is shown in *P. versicolor*, primarily results from a decrease of the amplitude of fluctuations in the population as a whole (different subpop.) as compared with that in separate subpopulations (similar subpop.).

We are also in a position now to better compare the possible influence of some autocorrelation between R_t and R_{t-3} than we could in section 7, because we have eliminated now all other differences that might obscure this effect. In Appendix A5 is shown how we could introduce some autocorrelation between R_t and R_{t-3} without altering anything else in our simulations (the ln-normal frequency distributions of R-values actually used in these “long run” simulations appeared to be similar to those in the “short run” simulations already discussed in this section; only the sequence in which R-values are taken from the ln-normal distributions has changed).

In Table 6 the results of these “long run” simulations are shown. When comparing the Tables 5 and 6 it appears that nearly all survival times have improved in the “long run” simulations, and probably also has the effect of the spreading of risk in *P. versicolor* become somewhat more pronounced. All other conclusions – e.g. about the importance of density restrictions – are the same as for the “short run” simulations. Apparently, the effect of an autocorrelation between R_t and R_{t-3} on survival times is somewhat unpredictable: the strong autocorrelation as found in the field, the simulation of which was discussed in section 6, seems to be unfavourable, whereas the lower autocorrelation as used in the present “long run” simulations appears to be favourable. This aspect will have to be studied more closely. For the moment we have the impression, that such an autocorrelation may promote the effect of spreading of risk: the differences in survival times between different and similar subpop. in *P. versicolor* are greater in Table 2 than in Table 6, and in the latter they are greater again than in Table 5. As could be expected, the values of mean LR over 19-year periods in the simulations treated in this section are somewhat smaller than those in the simulations of section 8, and thus more similar to the values from our field populations (Table 1), e.g. in the “long run” simulations in the case of composite populations we found mean LR = 1.048132 ($n=33$) for *P. versicolor* and mean LR = 3.25398 ($n=30$) for *C. melanocephalus*.

10. Discussion

Are we able now to answer the question: “How do populations survive in a heterogeneous and changeable world?” I hope to have shown in this paper (sections 5 through 9), that apparently there can only be one answer to this question: Although “populations” taken as “interaction groups” cannot be expected to survive very long (similar subpop. in Tables 2 and 3), populations that are composed of large numbers of highly interconnected “interaction groups” (subpopulations) may show an impressive survival time, if the risk of extinction is *sufficiently spread over a great part of these subpopulations* (different subpop.

in *P. versicolor*). This does not mean, that interaction groups within composite populations necessarily survive much longer than isolated interaction groups: In our long-term samplings on Kralo Heath we repeatedly recorded species that, after a decrease of numbers during some years, disappeared from the catches of a certain set of pitfalls; Figure 2 shows that even in *C. melanocephalus*, by far the most abundant species of this area, some subpopulations have been very close to this (e.g. in 1969 and 1976). We also observed the reversed case: after a number of years of sampling in a certain site a locally new carabid species appears in the catches and will sometimes increase in numbers during some years (cf. Den Boer 1977: Table 9). This means, that within such a composite population even a species with rather poor powers of dispersal will easily repopulate (mainly by immigration) a depopulated site when conditions become favourable again. It will be clear that the difference between such a composite population and a species, that inhabits a less continuous area with a number of more or less isolated populations, the sites of which are all within reach of dispersing individuals, will only be a gradual one: in the latter case the survival time of the species in that area will depend on the degree to which the risk of extinction is spread over these more or less isolated populations. The most important difference between these two cases will be found in the powers of dispersal, which will have to be much better in the latter case. In general, the more isolated the natural units of (local) population and/or the more unstable the habitats occupied, the higher should be both the powers of dispersal and the numbers of individuals that take part in dispersal to sufficiently spread the risk of extinction over these units of population. In the extreme case the survival of a species will thus be reduced to a lottery with on the average about equal chances of extinction and of founding of local units of population, with sufficient powers and amount of dispersal as a *necessary condition* to keep playing in this lottery. I always understood that Andrewartha and Birch (1954) tried to tell us this, whereas Southwood (1962) recognized only one aspect of it: the relationship between powers of dispersal and degree of instability of the habitat. It will be evident, however – especially in the case of composite populations occupying rather stable habitats (e.g. *P. versicolor* and *C. melanocephalus* at Kralo Heath) – that the degree of instability of the habitat is not the only factor that determines the degree of “turnover” of the units of population. Instead of redefining “habitat” in such a way that it contains everything (and becomes useless), we can better state, that the degree of turnover of the units of populations will depend on the degree of instability (pattern of density fluctuations – exchange between units included) of these population-units themselves. See further Den Boer (1970, 1977, 1979 a).

Returning to the composite populations of carabid species at Kralo Heath, our simulations of these populations not only showed the magnitude of the influence of spreading of risk in the case of *P. versicolor* (which thus appeared to be correctly indicated by the value of LR from our field data: Table 1), but also illustrated that the effect of spreading of risk is not disturbed by density restricting processes. On the other hand was also shown that during prolonged periods with an upward trend in numbers at least some, but possibly many populations can be expected to need some ceiling to growth to survive. The most interesting point in this is not, however, that at least in principle populations need to be bounded from above, but that density-dependence – that achieved the status of a paradigm (Kuhn 1970) in population dynamics concerning the survival of populations (see e.g. Murdoch 1979) – appeared to play an

only minor part in it. In general, survival will be promoted if the necessary restrictions of numbers have a higher chance of occurrence at high densities than at low ones, i.e. it is a sufficient condition that restrictions do not occur completely at random but with a lower chance at low densities (cf. section 8, and compare INDR with INCC and DDCC in the Tables 3, 5 and 6). The degree to which these necessary reductions of numbers are density-dependent, irrespective as to whether they occur only at “carrying capacity” (DDCC) or over a wide range of densities (DDSC), is immaterial to survival, however.

How could we attain such results (which were already foreshadowed, however, by Reddingius and Den Boer 1970), that seem to contradict everything that could be expected from the current (deterministic) population modelling? Can it be that our simulations – that cannot give truly “universal” results, of course – just picked out some exceptional situations? I don’t think so, but on the other hand: what is the use of truly “universal” deterministic models that do not fit any situation in nature (see: Introduction)? Should we not prefer less general but more realistic models, in spite of the small chance that there can be found – either in the field or in the head of some ecologist – a few cases that are not covered by the models? The more so, because I think, that our results have to do something with the interactions between deterministic and stochastic processes. If we start from deterministic population processes and add stochasticity, the deterministic processes will often not be altered fundamentally. In many cases the effect will even be restricted to introducing more uncertainty into the deterministic relationships, e.g. the neighbourhood (equilibrium-defined) stability of the “system” will be lowered, as in the models of May (1973); see also: Den Boer (1981). Such kinds of stochasticity generally depend on the laws of large numbers (see e.g. section 8), and in fact do not change the deterministic character of our population models (see further: Reddingius 1971, Ch. 4). If we start, however, from stochastic population processes and add some deterministic relationships (such as density-dependence) matters may stand quite differently. In most cases the special effects of the deterministic relationships (e.g. the degree of density-dependence) will be taken up into and thus be levelled out by the more general stochastic relationships, and it will thus not – or only slightly – alter the “between-limits stability” (Den Boer 1981), estimated by LR (section 4), of the population. This effect was already expected by Den Boer (1968: III.3); see also: Reddingius (1971).

Spreading of risk comes into play if a number of more or less independent stochastic processes interact to end up in a single quantity (e.g. population size). To conclude, we are left with the question whether stochastic or deterministic processes *necessarily* result in the kind of changes in population numbers that is observed in the field. As probably no organism can completely withdraw itself from the vagaries of its physical environment (cf. Introduction) unpredictable changes of the physical environment will *necessarily* result in fluctuations of population numbers. Though relevant to both, this will be more self-evident for poikilothermic than for homoiothermic organisms. On the other hand, it is quite possible that a population survives for some (or even a long) time without density-dependent relationships (such as intraspecific competition, a high mortality by monophagous predators and/or parasites). Note, that I don’t deny the possibility that density-dependent relationships exist in nature, (apart from difficulties in unequivocally demonstrating their existence, see e.g. Reddingius 1971; Kuno 1971). I only question the *necessity* of occurrence to understand fluctuations of numbers. Neither do I suggest that density effects would

be uninteresting, but only that this interest will be found in other phenomena than the survival time of populations, e.g. in stimulation of a better exploitation of resources, or giving structure to predator/prey or parasitoid/host relationships. In my opinion, we must thus conclude, that population-models should *primarily* be stochastic (see also: Andrewartha 1957), and that more deterministic relationships can be incorporated as far as needed (as we did in our stimulations), and *not* the other way round (see also: Reddingius 1971).

It may possibly be objected, that populations that by chance are reduced to very low numbers will show logistic growth and will thus rapidly reach again the “normal” density level (or even “carrying capacity”). As far as may field experiences are concerned this argument is not confirmed by observations on populations living in more stable habitats. At low densities such populations are at the mercy of chance to recover again or to die out, which was already pointed out by Milne (1957, 1962) and in connection with “underpopulation” by Klomp et al. (1964). See also our Fig’s 2 and 3. I suppose, that the above argument was derived from laboratory experiments with animals occupying highly unstable habitats, a kind of animals that under natural conditions show a high turnover of populations: founding in a (temporarily) favourable place, rapid growth, disappearance after one (or a few) generations by a high level of dispersal, founding in some other temporarily favourable places, etc. (see also: section 2). Such species are playing the lottery mentioned above, and are thus irrelevant in discussions on “the regulation of population numbers”.

It will have become apparent already from the above discussions that spreading of risk will not only influence the quantitative relationships *between* interaction groups and *between* other units of population, it will also be “at work” *within* interaction groups. Just as the risk of extinction of a composite population can be spread over a number of differently fluctuating subpopulations, so too the risk of extinction of an interaction group may be spread over a number of different individuals, viz. different genotypes, different developmental stages, different age classes. Examples of this are discussed by Van Dijk (1981); see further: Den Boer (1968, 1971, 1981)). If the interaction group occupies a site with a high level of effective, spatial heterogeneity, the movements of individuals between environmental patches will lower the variance of numbers in the interaction group as a whole (Den Boer 1981: Appendix), as well as increase the general level of net reproduction (Kuno 1981). Spreading of risk will also come into the picture when studying the interactions between species. If a population of predators exploits a kind of prey the stability of both the predator and the prey population will generally be enhanced by a high degree of clumping of the preys and thus by the occurrence of significant distances between prey patches. These effects are as robust as to appear already if this heterogeneity is modelled deterministically and the stability is estimated as neighbourhood stability (Hassell 1978).

To come to a conclusion, I hope to have made clear that heterogeneity and variability should not be considered as just drawbacks of field situations, that can best be circumvented by retreating into the laboratory or even into deterministical mathematics. On the contrary, heterogeneity and changeability must be recognized as fundamental features, not only of the natural environment of a population but even of life itself. The enormous genetical and phenotypical variation of a natural population is in some way a reflection of the heterogeneous and variable conditions in spite of which, but – as I tried to show – also with the help of which, it is able to survive for a shorter

or longer time. And on a larger scale, the incredible diversity of life reflects the nearly infinite heterogeneity of natural habitats, which is again importantly increased by the presence and the actions of living creatures themselves (see e.g. Zwölfer 1978). As long as heterogeneity and variability are considered to be mere deviations from "typical" cases, that are the only ones that are grasped by our intellect and caught in preconceived and often static (equilibria) theoretical structures, I fear we will deny some of the most fundamental features of organic life.

11. Acknowledgements. In the course of many years (and still at present) many people went into the field each week to collect or note our pitfallcatches. I like to thank all of them, because without their help it would not have been possible to continue studying carabid populations at Kralo Heath during so many years and at so many sites. I also thank my Dutch colleagues, who – especially within the "Discussion-club on population dynamics" – are always willing to reopen discussions without agreeing at all points, of course. Special thanks are due to Theo von Dijk and Martien Baars for their reliable but critical cooperation, and to Hans Reddingius for his interest in the development of our ideas and for mathematical help whenever needed. I am greatly indebted to the Computing Centre of the Agricultural University Wageningen. With a terminal from Wijster I had nearly unrestricted access to the time-sharing DEC-10 system of the Computing Centre, which enabled me to extend my simulations as far as needed. I am grateful to Gerda Weijenberg-Boer for typing the manuscript and to Arnold Spee for preparing the figures.

Appendix

A1. To simulate an autocorrelation of the desired value between R_t and R_{t-3} we make use (after having fixed the first three R-values: RY_1 , etc., from the field data) of a simple linear regression of the form $R_t = \exp(a + b \cdot \ln R_{t-3} + z \cdot c)$, which is simulated (Fortran IV), e.g. in the case of the composite population of *P. versicolor* (compare Table 2), as:

A3 = -0.0068
 B3 = -0.6533
 SDY = 0.275249

```

-----
-----
CALL RANDU(IX, IY, RNDGEN)
X=RNDGEN
CALL RANDU(IX, IY, RNDGEN)
Y1=COS(6.2831185307*X)
Y2=SQRT(-2.*ALOG(RNDGEN))      (compare A3)
Y3=A3+B3*ALOG(RY1)
T=EXP(Y1*Y2*SDY+Y3)
PI=PI*T
-----
-----
RY1=RY2
RY2=RY3
RY3=T
    
```

Table A.2.1. R-values in *P. versicolor*

	-0.72	-0.545	-0.37	-0.195	-0.02	0.155	0.33
ln R	t. -0.545	t. -0.37	t. -0.195	t. -0.02	t. 0.155	t. 0.33	t. 0.505
	0.49	0.58	0.69	0.82	0.98	1.17	1.39
R(\times 1.19)	t. 0.58	t. 0.69	t. 0.82	t. 0.98	t. 1.17	t. 1.39	t. 1.66
Freq. R_i	—	2	2	4	3	7	—
ib. \bar{r}_i	1	—	3	1	3	6	4

A2. The 18 R-values of the composite population of *P. versicolor* are (for the first 10 values, see also: Den Boer 1971: Table 3, R_i): 1.22; 1.32; 1.30; 1.15; 0.86; 0.79; 0.96; 1.22; 1.05; 0.73; 0.65; 0.89; 1.37; 1.14; 1.38; 0.58; 1.29; 0.93, which can be brought into 5 classes of a frequency distribution with a class-width (ln) of 0.175: Table A.2.1; in the same table the distribution of the 18 averaged subpop. – R-values (\bar{r}_i in Table 3 of Den Boer 1971) is shown.

The 18 R-values of the composite population of *C. melanocephalus* are (see also: Den Boer, 1971: Table 4, R_i): 2.32; 2.06; 3.28; 0.89; 0.35; 0.39; 1.56; 1.93; 0.26; 0.28; 0.73; 1.36; 3.04; 2.08; 0.36; 0.47; 0.42; 2.71, which can be brought into 5 (ln)-classes with a class-width of 0.5: Table A.2.2.

Table A.2.2. R-values in *C. melanocephalus*

	-1.81	-1.31	-0.81	-0.31	0.19	0.69
ln R	t. -1.31	t. -0.81	t. -0.31	t. 0.19	t. 0.69	t. 1.19
	0.16	0.27	0.44	0.73	1.21	1.99
R(\times 1.65)	t. 0.27	t. 0.44	t. 0.73	t. 1.21	t. 1.99	t. 3.29
Freq. R_i	—	6	1	3	3	5
ib. \bar{r}_i	1	4	1	3	3	6

Instead of using the frequency distribution of the 18 averaged subpop.-R-values to simulate "similar subpop." it seems better directly to use the frequency distribution of the subpop.-R-values themselves (except in the simulations treated in section 6). Both in *P. versicolor* and in *C. melanocephalus* the distributions of the 138 subpop.-R-values available can reasonable be fitted by ln-normal ones: Table A.2.3.

To convert a known distribution (of \bar{R}) to the best fitting ln-normal one (of \bar{Y} , say) we can make use of: $E(\bar{Y}) = 2 \ln M - \frac{1}{2} \ln(V^2 + M^2)$ and $Var(\bar{Y}) = \ln(V^2 + M^2) - 2 \ln M$, if $E(\bar{R}) = M$ and $Var(\bar{R}) = V^2$ (Reddingius pers. comm.). The best fitting ln-normal distribution of subpop.-R-values thus has $E(\ln R) = -0.0130142774$ and $s(\ln R) = 0.91689$ in the case of *C. melanocephalus*, but $E(\ln R) = -0.0027150241$ and $s(\ln R) = 0.520982771$ in *P. versicolor*.

Whether we used the above ln-normal distributions of subpop.-R-values or the distributions of averaged subpop.-R-values (given in Tables A.2.1 and A.2.2) to simulate cases of "similar subpop." did not influence our results. Therefore, we preferred to simulate with the best fitting ln-normal distributions.

A3. Drawing R-values at random from an explicitly defined distribution, e.g. in the case of the composite population of *C. melanocephalus* (Table A.2.2), is simulated as:

S=0.27
 A1=0.17
 A2=0.29
 A3=0.48
 A4=0.78
 A5=1.30

Table A.2.3. R-values of subpopulations

R(×2)	<0.093	0.09375 t. 0.1875	0.1875 t. 0.375	0.375 t. 0.75	0.75 t. 1.50	1.50 t. 3.00	3.00 t. 6.00	6.00 t. 12.00
<i>P. versicolor</i>	–	–	10	34	63	29	2	–
<i>C. melanocephalus</i>	3	6	17	32	36	23	18	3

```
CALL RANDU(IX, IY, RNDGEN)
RA=RNDGEN*18.
CALL RANDU(IX, IY, RNDGEN)
V=RNDGEN
IF(RA.LE.6.)T=S+V*A1
IF(RA.GT.6..AND.RA.LE.7.)T=S+A1+V*A2
IF(RA.GT.7..AND.RA.LE.10.)T=S+A1+A2+V*A3
IF(RA.GT.10..AND.RA.LE.13.)T=S+A1+A2+A3+V*A4
IF(RA.GT.13..AND.RA.LE.18.)T=S+A1+A2+A3+A4+V*A5
PI=PI*T
```

Taking R-values at random from a ln-normal distribution, e.g. in the case of “similar subpop.” in *P. versicolor*, is simulated as:

```
CALL RANDU(IX, IY, RNDGEN)
X=RNDGEN
CALL RANDU(IX, IY, RNDGEN)
Y1=COS(6.283185307*X)
Y2=SQRT(-2*ALOG(RNDGEN))
T=EXP(Y1*Y2*0.520982771-0.002715024)
PI=PI*T
```

Note: like in the models of section 6, also in these models (and in all following ones) the 3 first R-values are given from the relevant field data.

A4. Reductions of population numbers in INCC occurred as (PM = carrying capacity = 99.*PP):

```
after PI=PI*T,
  IF(PI.LE.PM)GO TO 15
  PI=PM*T/1.5 (or: PI=PI/1.5),
```

in the case of *P. versicolor*, and as:

```
-----
PI=PM*T/4. (or: PI=PI/4.),
in the case of C. melanocephalus.
```

In this way the reductions were about in relation to the violence of fluctuations in the species concerned (fluctuations are nearly 3 times heavier in *C. melanocephalus* than in *P. versicolor*).

Density-dependent reductions of population numbers in DDCC occurred as:

```
after PI=PI*T,
  IF(PI.LE.PM) GO TO 15
  PI=2.0*PM-PI,
```

in the case of *P. versicolor*, composite population, and as:

```
-----
PI=2.0*PM-0.4*PI
```

in the case of *P. versicolor*, similar subpop.

In *C. melanocephalus*, composite population, was used:

```
-----
PI=2.0*PM-0.75*PI
```

and:

```
PI=2.0*PM-0.38*PI
in similar subpop.
```

The fraction of PI that was subtracted from 2.0*PM could be adapted in such a way that the mean frequency of exceeding carrying capacity was kept the same as in the pertinent versions of INCC.

To keep the mean frequency of reductions of population numbers in INDR about the same as in INCC we had to build a counter into the program. As an example we mention *P. versicolor*, different subpopulations:

```
AP=KP (KP is a small integer that differs with different start values)
M=1
VX=0.9
WRS=VX*AP+54.3
-----
-----
```

```
PI=PI*T
WV=20.*RNDGEN
MRES=WRS+WV
IF(M.LE.MRES)GO TO 15
PI=PI/1.5
M=1
15 -----
-----
M=M+1 (counter of “years”)
```

WV results in a random variation between -10 and +10 “years” in the computed “distance” between two reductions of numbers. WRS could be adapted in such a way that the mean frequency of reductions was kept the same as in INCC.

In the case of *P. versicolor*, similar subpop. we had to use for that: VX=1.14 and WRS=VX*AP+22.4, in *C. melanocephalus*, different subpop. VX=1.075 and WRS=VX*AP+22.3 and in similar subpop. VX=0.625 and WRS=VX*AP+17.7.

To get continuous and mild density dependent reductions over a wide range of population numbers in DDSC we simulated, e.g. in the case of *P. versicolor*, different subpop.:

```
PI=PI*T
SDD=2.6
APP=ALOG(PP)
API=ALOG(PI)
DD=API-APP
IF(DD.LE.O.)GO TO 15
SDL=SDD-1.
DD=SQRT(DD)
IF(DD.LE.SDL)GO TO 15
PI=PI*SDD/(1.+DD)
IF(PI.LE.PM)GO TO 15
LC=LC+1 (to check if indeed PM is never exceeded)
```

In this way density dependent reductions of numbers occurred between 13 and 99 times PP. We could adapt SDD in such a way that the mean frequency of passing the start value was kept about the same as in INCC.

In *P. versicolor*, similar subpop. we had to put SDD=3.3 (without SQRT(DD)), and got reductions between 10 and 99 times PP.

In *C. melanocephalus*, different subpop. SDD=1.7 (reductions between 2 and 99 times PP), and in similar subpop. SDD=1.8 (reductions between 4¹/₂ and 99 times PP).

With the same procedure and setting SDD=1.0 in DDS we got density dependent reductions over the whole range between PP and 99.*PP.

Note: In all simulations with some reduction of numbers the value of R was recalculated after the reduction had occurred, in order to be able to compose the frequency distribution of the R -values actually used.

A5. In A2 are given the R -values of the composite populations of *P. versicolor* and *C. melanocephalus* during 19 years, as well as the method to convert these distributions into the best fitting ln-normal ones. In the case of the composite populations of *P. versicolor* we thus got a best fitting ln-normal distribution with $E(\ln R)=0.01596$ and $s(\ln R)=0.2412832$, and in the case of *C. melanocephalus* a ln-normal distribution with $E(\ln R)=0.0200326$ and $s(\ln R)=0.6955634$. In *P. versicolor* this ln-normal distribution fitted the frequency distribution of the field data as given in Table A.2.1 rather well, even if $E(\ln R)$ is put at zero ($P>0.30$), both in the "short run" (Table 5) and in the "long run" version (Table 6). In *C. melanocephalus* the frequency distribution of R -values from the field as given in Table A.2.2 is very different from a ln-normal one, by which "the best fitting ln-normal distribution" is a quite different distribution indeed.

An autocorrelation between R_t and R_{t-3} within an already defined ln-normal distribution of R -values could be attained by the following trick, e.g. in the case of *P. versicolor*, composite population (compare A1 and A3):

```
CALL RANDU(IX, IY, RNDGEN)
X=RNDGEN
CALL RANDU(IX, IY, RNDGEN)
Y1=COS(6.283185307*X)
Y2=SQRT(-2.*ALOG(RNDGEN))
T=EXP(Y1*Y2*0.2412832)
IF(T.GT.1..AND.R(K-3).GT.1..OR.T.LT.1..AND.R(K-3).
LT.1.) T=EXP(SIN(6.283185307*X)*Y2*0.2412832)
PI=PI*T
```

The autocorrelation between $\ln R_t$ and $\ln R_{t-3}$ attained in this way had a value around -0.35 in most simulations. This value is lower than those from the field data of the composite populations during 19 years (-0.6), but of the same value as that in the composite population of *P. versicolor* after 21 years (-0.357). Apparently, the pattern of weather conditions that resulted in these high autocorrelations during the first 19 years changed during the last two years, at least as far as *P. versicolor* is concerned.

References

- Andrewartha HG (1957) The use of conceptual models in population ecology. Cold Spring Harb Symp quant Biol 22:219-236
- Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. Chicago Univ Press, Chicago, p 782
- Baars MA (1979a) Patterns of movement of radioactive carabid beetles. Oecologia (Berl) 44:125-140
- Baars MA (1979b) Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia (Berl) 41:25-46
- Bakker K (1964) Backgrounds of controversies about population theories and their terminologies. Z angew Entom 53:187-208
- Bakker K (1971): Some general remarks on the concepts "population" and "regulation". Proc Adv Study Inst Dynamics numbers Pop (Oosterbeek 1970):565-567
- Den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheor 18:165-194
- Den Boer PJ (1970) On the significance of dispersal power for populations of Carabid-beetles (Coleoptera, Carabidae). Oecologia (Berl) 4:1-28
- Den Boer PJ (1971) Stabilization of animal numbers and the heterogeneity of the environment: The problem of the persistence of sparse populations. Proc Adv Study Inst Dynamics numbers Pop (Oosterbeek 1970):77-97
- Den Boer PJ (1977) Dispersal power and survival. Carabids in a cultivated countryside. Miscell papers LH Wageningen 14, p 190
- Den Boer PJ (1979a) The significance of dispersal power for the survival of species, with special reference to the carabid beetles in a cultivated countryside. Fortschr Zool 25 2/3:79-94
- Den Boer PJ (1979b) Populations of Carabid beetles and individual behaviour. General aspects. Miscell Papers LH Wageningen 18:145-149
- Den Boer PJ (1981) On the stability of animal populations, or how to survive in a heterogeneous and changeable world? Paper read at Bremen Univ, will be published in Fortschr Zool
- Dingle H (1978) Evolution of insect migration and diapause. Springer Verlag, Berlin Heidelberg New York, p 350
- Hassell MP (1978) The dynamics of arthropod predator-prey systems. Monogr Pop Biol 13, p 237
- Johnson CG (1969) Migration and dispersal of insects by flight. Methuen London, p 763
- Juberthie C (1979) L'évolution des coléoptères Trechinae souterrains (Coleoptera, Carabidae). Miscell Papers LH Wageningen 18:83-99
- Klomp H, van Montfort MAJ, Tammes PML (1964) Sexual reproduction and underpopulation. Arch Néerl Zool 16:105-110
- Kuhn TS (1970) The structure of scientific revolutions. 2nd enlarged edn Univ of Chicago Press, Chicago, p 210
- Kuno E (1971) Sampling error as a misleading artefact in "key factor analysis" Res Popul Ecol 13:28-45
- Kuno E (1981) Dispersal and the persistence of populations in unstable habitats: A theoretical note. Oecologia (Berlin) 49:123-126
- Luff ML (1975) Some features influencing the efficiency of pitfall traps. Oecologia (Berl) 19:345-357
- May RM (1973) Stability and complexity in model ecosystems. Monogr Pop Biol 6, p 235
- Milne A (1957) Theories on natural control of insect populations. Cold Spring Harb Symp quant Biol 25:253-271
- Milne A (1962) A theory of natural control of insect populations. J theor Biol 3:19-50
- Murdoch WW (1979) Predation and the dynamics of prey populations. Fortschr Zool 25 2/3:296-310
- Reddingius J (1971) Gambling for existence. A discussion of some theoretical problems in animal population ecology. Acta Biotheor 20 (suppl) 1-208
- Reddingius J, den Boer PJ (1970) Simulation experiments illustrating stabilization of animal numbers by spreading of risk. Oecologia (Berl) 5:240-284
- Southwood TRE (1962) Migration of terrestrial arthropods in relation to habitat. Biol Rev 37:171-214
- Turanchik EJ, Kane TC (1979) Ecological genetics of the cave beetle Neaphaenops tellkampffii (Coleoptera, Carabidae). Oecologia (Berl) 44:63-67
- Van Dijk Th S (1981) Individual variability and its significance for the survival of animal populations. Paper read at Bremen Univ, will be published in Fortschr Zool
- Watt KEF (1971) Dynamics of populations: A synthesis Proc Adv Study Inst Dynamics numbers Pop (Oosterbeek 1970) 568-580
- Wolda H (1978a) Fluctuations in abundance of tropical insects. The Amer Naturalist 112:1017-1045
- Wolda H (1978b) Seasonal fluctuations in rainfall, food and abundance of tropical insects. J anim Ecol 47:369-381
- Zwölfer H (1978) Mechanismen und Ergebnisse der Co-Evolution von phytophagen und entomophagen Insekten und höheren Pflanzen. Sonderbd. naturw Ver Hamburg 2:7-50
- Zwölfer H (1979) Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. Fortschr Zool 25 2/3:331-353

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