Seeing the trees for the wood: random walks or bounded fluctuations of population size?*

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Summary. It is often claimed that the fluctuation of numbers in field populations is fundamentally different from random walks of densities, in that population size is kept between certain positive limits. To test this hypothesis patterns of fluctuation in field populations were compared with random walks of density of about the same duration. It was found that the boundaries (Log-Range) between which numbers fluctuate in field populations increase with time to about the same extent as in comparable random walks of density. Moreover, deviations of the trend of numbers over years (Average $\ln R$) from zero trend in populations of 62 (carabid) species were just those expected for simulated random walk runs, with the median value of $\mathrm{Var}(\ln R)$, and different values for mean population size that cover the possible range of "survival times" for these species. This means that the null hypothesis that in the field numbers would fluctuate as random walks of densities could not be rejected. Although it is not very probable that field populations fluctuate exactly like random walks of densities, random walk models appear to mimic the fluctuation patterns of field populations sufficiently closely to explain what happens in nature, and to deny the need for regulation. The same conclusion was drawn in earlier studies where statistical tests were applied to fluctuation patterns of field populations (Den Boer and Reddingius 1989; Den Boer 1990a). Random walks of densities do not exclude the possibility that local populations can persist for some centuries.

Key words: Regulation – Random walk – Density dependence – Survival time – Fluctuation pattern – Log-Range

A recent paper by Hassell et al. (1989) starts with the remarkable statement: "Most studies in which populations have been monitored over several generations show fluctuations of population size around some characteris-

tic level of abundance, quite unlike unbounded population growth or any "random walk" inevitably meandering to extinction". I wonder what kind of random walk models they have applied to support this statement. As my experiences with random walk models of densities are quite different, it seems useful to compare fluctuations observed in the more substantial field studies on population numbers, i.e. those lasting 12–20 years, with those obtained from random walk models. To state, as Hassell et al. (1989) do, that each random walk of densities will eventually surpass all bounds is hardly interesting since it is also true that all field populations will eventually become extinct (see Reddingius 1971). We are interested here in how random fluctuation patterns of densities compare with fluctuation patterns of field populations of about the same length.

Material and methods

Before comparing fluctuations of population size we must agree about the concept of "population" we want to use. In general, I adhere to the definition given by Bakker (1971: 565): "A population is a biological unit of study, with a number of varying statistics (e.g. number, density, birth rate, death rate, sex ratio, age distribution) and which derives a *biological* meaning from the fact that some direct or indirect interactions among its members are more important than those between its members and members of other populations". Den Boer (1977: 1.3, 1982: 213) called such a population an *"interaction group"*, which is living either in a local and physiognomically recognizable habitat, or in a larger more or less continuous area where it merges into other interaction groups. In the first case we will speak of *local populations,* in the latter of *subpopulations* that together form a *multipartite population* (Andrewartha and Birch 1984: 183). This means that the fluctuations in numbers of, for instance, the spruce budworm (Morris 1963), the grey larch bud moth (Van den Bos and Rabbinge 1976), and the forest insects of Schwerdtfeger (see Den Boer 1990a) are considered less adequate for comparison with random walk simulations of interaction groups, because the samples were not taken from a single interaction group but from large areas in which the fluctuation patterns of several interaction groups were mixed. We assume that the definition of Bakker applies sufficiently closely to all of the field populations discussed in this paper.

The random walks of density that will be compared with fluctuation patterns of field populations were derived from simulation experiments described by Den Boer (1981, 1985). This means that values of net reproduction (R) were randomly taken, either directly from frequency distributions of R-values of sampled interaction groups (Den Boer 1981), or from log-normal distributions fitted to these frequency distributions (Den Boer 1985). In all cases, we used the first 18 "years" from unselected random walks out of a larger collection, with the only restriction that we preferred series that looked different, so that as wide a range as possible could be presented. In some of the simulation experiments autocorrelation between successive R values was incorporated (see Den Boer 1981: Appendix Al), as such autocorrelations may result from an appreciable fraction of the individuals surviving to the next year – which is the rule among vertebrates and also occurs among most species of carabid beetles. About half of the random walks presented in this paper appeared to show some – usually not significant – autocorrelation between succeeding R values.

To compare fluctuation patterns of densities, two statistics seem adequate: (1) *Log-Range* (LR), the difference between the (natural) logarithms of the highest and the lowest densities reached during a certain number of years, and (2) *Average* ln$R$, the average (natural) logarithm of net reproduction during a certain number of years ($=$ the logarithm of the geometric mean of R): Reddingius and Den Boer (1970). As LR will increase with time in a random walk of densities, whereas in a strictly regulated population this should not, or hardly, occur, I will compare the Log-Ranges for the first 5 years with both those for the first 10 years and those for a yet higher number of years, mostly 18–20. This should give us an idea as to what extent the distance between the boundaries of fluctuations increases with time, and whether or not this increase is smaller than in random walks of densities. For all patterns presented we give Average ln$R$ for the first 12 R values, as an estimate of the overall trend of density during that period.

Because we estimated the relative densities of the 64 more abundant carabid species in many habitats during a number of years, we could collect sufficient R values for each of these species (45 per species on average) to produce a reliable value of Average ln$R$ for that species (Den Boer 1985, 1990b). Populations of species which often show strong trends in numbers, i.e. with a rapidly growing Log-Range, are not expected to survive very long. In other words, the closer the Average ln$R$ is to zero the higher mean survival time, or, conversely, the chance of finding a particular field population is higher the closer its Average ln$R$ is to zero. Therefore, we will compare the frequency distribution of the values of Average ln$R$ for 62 of these species with the "mean survival times" of simulated random walks of densities based on 31 log-normal distributions of R values, with Average ln$R$ varying between -0.45 and $+0.45$, but with a common standard deviation of ln$R = 0.858$, which is the median value for the 62 carabid species. Each simulation was repeated 500 times with a different series of random numbers, and each set of 15500 simulations (31×500) was repeated for 5 different levels of initial population size, viz. 10^2, 10^3, 10^4, 10^5, 10^6. In these simulations we considered a population to have become extinct when population size surpassed either the lower limit of unity or the upper limit of the squared value of initial population size. For multiplicative processes (net reproduction) these limits are thus symmetrical around the initial value.

At the Heath of Kraloo, 32 interaction groups of 7 abundant carabid species were continuously sampled for 20 years with standard sets of pitfalls (Den Boer 1977: Ic). For each species the annual catches from each set can be considered reliable relative estimates of mean density of the interaction group living around this set of pitfalls (Baars 1979; Den Boer 1979; Baars and Van Dijk 1984a), so that these year-catches produced 32 fluctuation patterns of population sizes over 20 years. For each species the LR values over 5, 10, 15 and 20 years of these patterns could be compared with those produced by random walks of the population size of an average interaction group which were directly based on the frequency distribution of a minimum of 56 and a maximum of 94 R values available from the interaction groups of each species. Each

simulation was repeated 100 times with different series of random numbers.

Results

Values of Log-Range for 5, 10 and 20 (at one site 19) years, as well as those of Average ln$R$ for the first 13 years for each of 32 interaction groups of 7 carabid species at the Heath of Kraloo, are given in Table 1; some of the fluctuation patterns concerned are also pictured in Fig. 1. Table 1 shows that, in general, the distance between the upper and lower limit of the fluctuations in population size (Log-Range) increases with the number of years. The most remarkable exceptions are *Calathus melanocephalus* at site N and *Amara lunicollis* at site BB, because during the first 5 years extreme values (7, 873, and 26, 944 respectively) were reached which were not surpassed in the next 15 years. This is similar to *Panolis* in Neubrück (see Den Boer 1990a: Table 3), though at a less dramatic scale. To some extent we find comparable phenomena in a few other interaction groups: because in an extreme year an exceptionally high and/or low density is reached the resulting value for Log-Range was not surpassed in the next 5 or 10 years. In these cases the LR values for 20 (or 19) years do not differ significantly from those of interaction groups of the same species where the LR values were continuously increasing (Mann-Whitney tests combined for 6 species – see Siegel 1956 – $Z = 0.51$, $P = 0.61$). A different set of data collected from the literature is presented in Table 2 and in Fig. 2. In Table 2 a phenomenon similar to that in Table 1 is shown: in general Log-Range increases continuously with time, with the most obvious exception being the pine looper (but see Den Boer 1990a). The fluctuation patterns shown in Fig. 2 do not differ fundamentally from those in Fig. 1. Compare, for instance, Fig. 1E with the first part of Fig. 2B, or Fig. 2E with the last part of Fig. 1B.
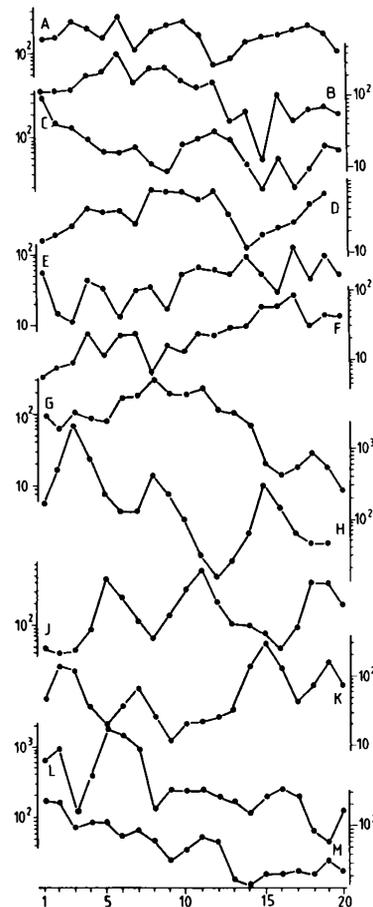
To test whether or not the data shown in Tables 1 and 2 and in Figs. 1 and 2 conform with current ideas on bounded fluctuations of population size we will consider a comparable set of random walks of densities presented in Table 3 and in Fig. 3. The Log-Range values in Table 3 grow to about the same extent with time as the majority of those in Tables 1 and 2, again with a few exceptions (e.g. B, F and N). Also, the fluctuation patterns of Fig. 3 do not differ fundamentally from those in Figs. 1 and 2. Compare, for instance, Fig. 2H with Fig. 3H, or Fig. 1J with Fig. 3J, or Fig. 2D with the first part of Fig. 3B, or Fig. 2F with Fig. 3G, and so on. Such similarities illustrate that it is difficult to find fundamental differences between random fluctuations of density and actual fluctuations of population size, as claimed to exist by Hassell et al. (1989). An unambiguous method of quantifying the growth of the LR values in the three tables and testing for the significance of the differences between those of Tables 1 and 2 and those of Table 3 is not obvious to me. Therefore another line of enquiry is preferred.

Simulations of random walks of densities, based on log-normal distributions of R values with 31 different values for Average ln$R$ and with the median standard

Table 1. Log-Range (LR) for periods of 5, 10, 20 years, and Average ln R for the first 13 years, of all interaction groups (subpopulations) of 7 carabid species that were continuously sampled over at least 20 (in BB 19) years with standard sets of pitfalls (Den Boer 1977: Ic) at the Heath of Kraloo (Drenthe, The Netherlands). The sites sampled (Den Boer 1981: Fig. 1) are: N, Z, AY (1969 up to 1988 inclusive), BB (1965–1983 inclusive) and AT (+BH+BJ) (1963–1982 inclusive)

LR: Site	5 years	10 years	20 years	Average ln R	in Fig. 1
Pterostichus versicolor Sturm					
N	0.5978	1.1017	1.6317	− 0.0620	A
Z	0.6029	1.2497	3.6192	− 0.0956	B
AY	2.3215	2.7175	2.7175	0.0756	
BB	0.4426	2.9132	2.9132	− 0.2152	
AT	0.8908	1.3632	2.0281	− 0.0719	
Pterostichus lepidus Leske					
N	0.6130	1.3863	3.2581	− 0.0800	
Z	1.2321	2.3026	4.9416	− 0.1493	
AY	0.5431	1.6606	3.5742	0.0191	G
BB	1.0366	2.0565	4.0489	− 0.1017	
AT	1.4929	1.4929	2.6822	0.1322	F
Pterostichus diligens Sturm					
N	1.6946	1.6946	3.3759	0.0603	
Z	1.6452	1.6452	2.4541	− 0.0093	E
AY	hardly any catches				
BB	1.0341	1.5841	1.8718	0.0652	D
AT	1.7479	2.4296	2.9901	− 0.1165	C
Calathus melanocephalus L.					
N	4.8260	4.8260	4.8260	0.1844	
Z	3.8437	3.8437	6.1463	0.1020	
AY	2.4434	2.4434	2.7401	0.0701	J
BB	2.6181	3.0664	5.0225	− 0.1520	H
AT	2.2386	4.6085	5.8406	− 0.3830	
Calathus erratus Sahlb.					
N	3.0910	3.0910	4.7005	0.1272	
Z	4.5850	4.7230	5.4161	0.0000	
AY	1.0896	1.6094	6.0868	− 0.1585	
BB	1.5709	5.1818	5.1818	− 0.0147	
AT	2.4596	3.1905	3.6964	0.2071	
Amara lunicollis Schiødte					
N	2.7006	4.2047	4.7958	− 0.0684	
Z	2.7081	2.7081	4.6269	0.0874	
AY	1.9042	2.4639	3.2517	− 0.0305	K
BB	3.5920	3.5920	3.5920	0.1025	
AT	2.7751	2.7751	3.7759	− 0.1082	L
Harpalus latus L. in N and Z hardly any catches					
AY	1.2040	1.4271	3.3673	− 0.0578	
BB	2.2687	2.6742	3.3673	− 0.1253	
AT	0.8677	1.9161	2.6888	− 0.2082	M

Fig. 1. Fluctuation patterns of year-catches from interaction groups of some carabid species at the Heath of Kraloo. The course of these annual catches over years mimics that of population size closely (Baars 1979; Den Boer 1979). For more information see Table 1

deviation of the 62 more abundant carabid species in common, show that the highest expected "survival times" occur around Average ln $R = 0$ and decrease progressively the greater the deviation of Average ln R from zero (Fig. 4). From estimates of absolute population sizes of interaction groups in a number of carabid species, we estimate that, for the 62 more abundant species in the better habitats, mean population size is between 10^3 and

10^5. As the chances of a certain species maintaining itself in a certain area are better the smaller the chance that Average ln R deviates appreciably from zero, I expect that the probability of observing more abundant populations of (carabid) species will be higher the closer the Average ln R is to zero. In other words: if the fluctuations of population size of these 62 species do not deviate appreciably from random walks, we expect the frequency distribution of their Average ln R values to be about similar to that of the "survival times" of the random walk simulations (Fig. 4). Comparison results in (χ^2 with df = 6): 10^3: 5.29, $0.70 > P > 0.50$; 10^4: 3.25, $0.80 > P > 0.70$; 10^5: 2.76, $0.90 > P > 0.80$; and to complete the series, 10^2: 7.66, $0.30 > P > 0.20$; 10^6: 3.92, $P \approx 0.70$.

These results do not support the assumption that fluctuations of population size (at least in these species) are generally bounded in some way, because under that hypothesis one would expect to find a much stronger concentration of Average ln R values around zero than was observed. It does not prove, but is consistent with, the hypothesis that these populations fluctuate like random walks. In Den Boer (1985, 1986c, 1990b) independent arguments are given that point in the same direc-

Table 2. Log-Ranges (LR) for periods of 5, 8–10, 13–20 years (. .,. .), and Average ln$R$ for the first 13 years of local populations of some animal species the data of which are taken from literature

Species, locality, etc.	LR: 5 years	8–10 years	13–20 years	Average ln$R$	in Fig. 2
Garden chafer larvae, Rydal Farm, Ambleside 1947–75 (5, 10, 20); Milne (1984)	1.3200	3.6470	4.3406	−0.1557	A
Great tit O.N.O. Netherlands 1912–50 (5, 10, 20); Kluyver (1951)	1.0590	1.2432	1.5555	0.0215	B
Pine looper larvae, Hoge Veluwe 1950–64 (5, 10, 15); Klomp (1966)	2.7246	2.7246	2.7996	0.0800	C
Cockles, Burley Inlet 1958–69(70) (5, 8, 12(13));					
Hancock (1971), in November	0.6764	1.2523	1.8076	−0.0286	D
these cockles, in May	1.0002	2.6140	2.6140	0.0902	E
White stork, Baden-Würtemberg 1948–63					
(5, 10, 17); Lack (1966), Favourable habitat	0.4539	0.6028	0.7919	−0.0270	F
Less favourable habitat	0.7885	1.3481	2.2644	−0.1363	G
Muskrats, Wall Lake (1000 acres) North Carolina 1939–56 (5, 10, 18); Errington (1957)	2.3026	5.4272	5.4272	0.2105	H
Bobwhite quail, Prairie du Sac (4500 acres) Wisconsin 1930–48 (5, 10, 18); Errington (1957)	1.1075	2.1624	2.1624	0.0071	J
Winter moth larvae, Wytham Wood, Oxford 1950–68 (5, 10, 19); Varley et al. (1973)	2.1643	2.7168	3.5901	−0.1765	K
Pyrrhosoma (Odonata) nymphs, English pond 1955–71 (5, 10, 17); Macan (1974)	0.6825	0.7714	3.8395	−0.1867	L

tion. The frequency distribution of the 32 values for Average ln$R$, mentioned in Table 1 neither deviates significantly from that for 62 carabid species from all sites ($\chi^2 = 1.44$), nor from that of the survival times of the above random walk models ($\chi^2 = 1.41$): 3 classes, df = 2,
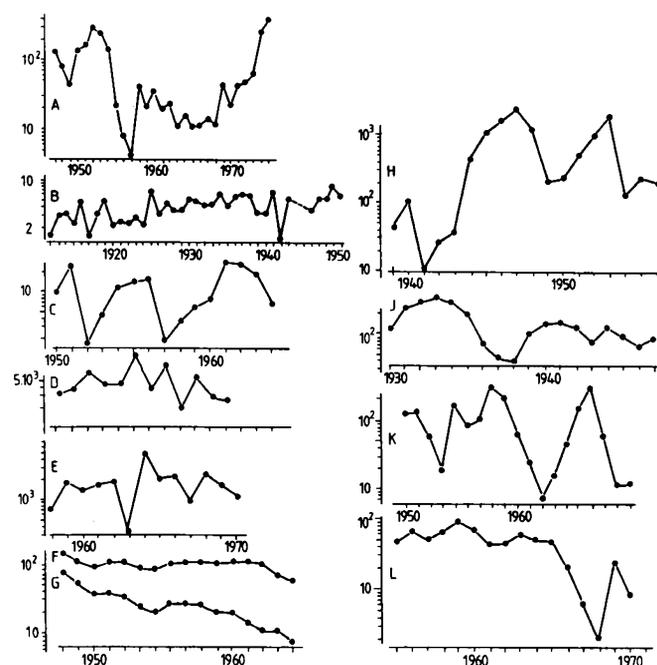
Fig. 2. Fluctuation patterns of (samples from) the population size of different kinds of animals. The data is taken from long-term (12–39 years) studies in the literature. More information in Table 2

$P \approx 0.50$. In this case too, population sizes apparently fluctuated as expected for random walks.

For 2 of the 7 abundant carabid species sampled continuously at the Heath of Kraloo over 20 years, *Calathus melanocephalus* and *C. erratus*, the simulated random walks of the population size of an averaged interaction group gave similar mean LR values or even lower ones (*C. melanocephalus*, 5 yr: 2.4112; 10 yr: 4.0116; 20 yr: 5.728; *C. erratus*, 5 yr: 2.4191; 10 yr: 3.9026; 20 yr: 5.5695) than the 5 field populations of that species (Table 1). In *Amara lunicollis*, after 5 years, the mean LR value of the simulated random walks is lower (2.3927) than the field values in Table 1, but after 20 years the opposite situation is reached (5.6561). *Harpalus latus* and *Pterostichus diligens* do not give consistent results in this respect.

In *Pterostichus versicolor* 12, and in *P. lepidus* 14, out of the 15 LR values given in Table 1, are lower than those simulated with the random walk models for an averaged interaction group of the species. These species are especially interesting because population sizes do not change synchronously at all sites (for *P. versicolor* see Den Boer 1981: Fig. 3, and Den Boer 1986d: Fig. 7). This means that the fluctuation patterns – and LR values – of these interaction groups may be affected by exchange of individuals between the groups. Such an influence is not incorporated in the random walk models, however. Therefore, we provided the models with some emigration and immigration: a random (homogeneously distributed) emigration between 0.2% and 2% of population size per year, and a random immigration of 0.2–2% of initial population size per year. Figures 5 and 6 show that

Table 3. Log-Ranges (LR) for periods of 5, 10, 18 years, and Average $\ln R$ for the first 13 years of random walks of density, which are constructed from field data of separate species by taking net reproduction (R) values at random either from log-normal distributions that fit the 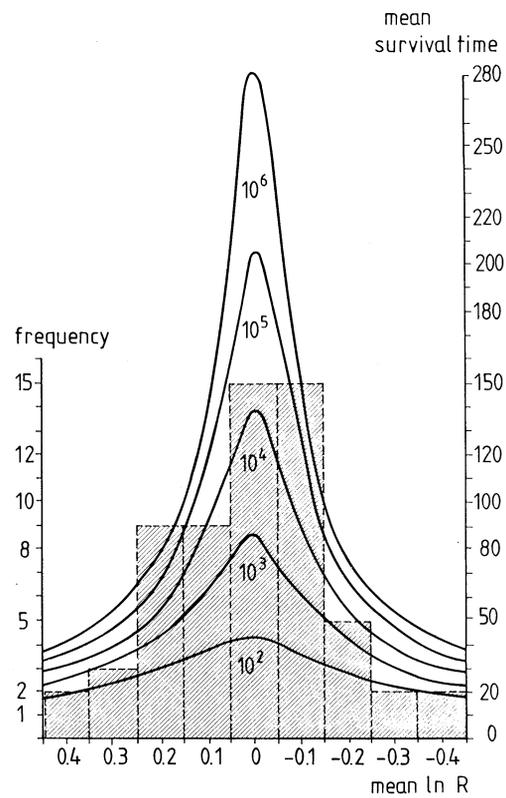field data (Den Boer 1985: Fig. 1) or from the actual frequency distribution of R values (Den Boer 1981: Appendix). In some of the cases succeeding R values are allowed to show some autocorrelation (see De Boer 1981) to mimic animals that stay (and usually reproduce) in the population for more than 1 year (C, D, E, H, J, K, N)

| In Fig. 3	LR: 5 years	10 years	18 years	Average $\ln R$
A	1.627	2.477	3.389	0.0890
B	1.680	1.680	2.918	0.0830
C	1.771	2.079	2.521	−0.0152
D	0.560	1.674	1.930	0.0000
E	1.099	1.452	2.124	0.1009
F	1.878	1.878	2.516	0.0126
G	0.305	0.547	0.747	−0.0143
H	2.485	3.054	3.565	−0.0102
J	1.609	2.225	3.409	−0.0240
K	0.847	1.276	1.447	0.0916
L	0.511	0.981	1.204	−0.0392
M	1.181	3.535	3.807	−0.2195
N	0.194	0.580	0.580	0.0265
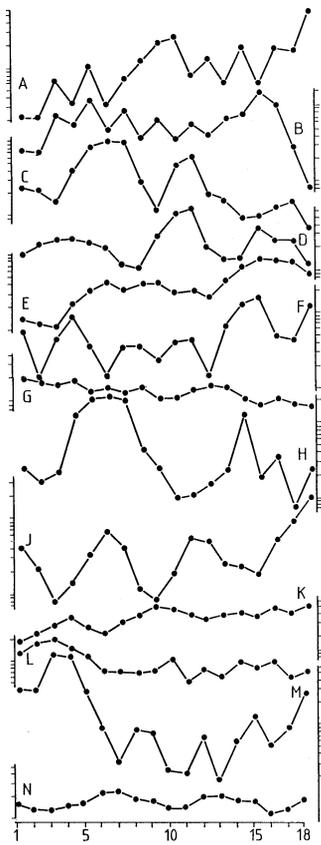
Fig. 3. Random walks of densities of about the same length as the majority of the patterns shown in Figs. 1 and 2. See also Table 3

Fig. 4. *Hatched histogram:* frequency distribution of Average $\ln R$ values for 62 carabid species (scale on the *left*). *Smooth curves:* mean survival times for 500 independent simulation runs of random walks of densities (see text) for initial values 10^2, 10^3, ...10^6 (scale on the *right*)

even such a small exchange of individuals with other groups may distinctly influence the LR values. A more realistic, i.e. 10 times greater (2–20%), exchange of individuals with adjacent groups gives LR values that fit the field values reasonably well. Although these models with exchange are no longer simple random walk models, they still simulate unbounded fluctuations of population size, which are accompanied by LR values that grow with time. Accordingly, this growth can be adequately de-

scribed by exponential functions in all cases (Table 4), and also for the multipartite population consisting of these interaction groups (Den Boer 1986d). Figures 5 and 6 show that the LR values of the interaction groups grow to about the same extent with time as the exponential functions that describe the random walk models, regard-
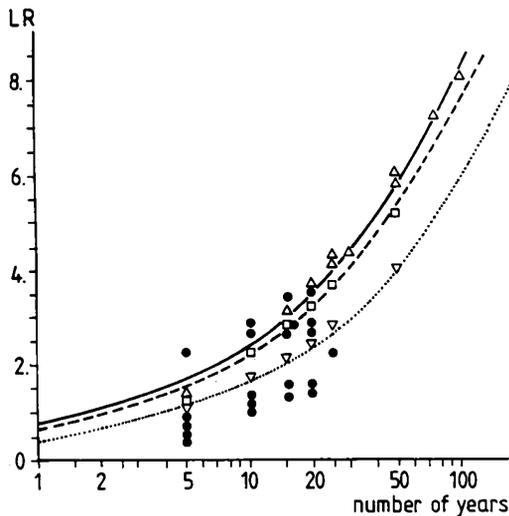
Fig. 5. Mean Log-Range values of 100 simulations of random walks of densities for an averaged interaction group of *Pterostichus versicolor* based on the frequency distribution of the 96 *R* values from 5 interaction groups (see Table 1), plotted as a function of time. *Filled circles:* LR values of field populations; *open triangles:* mean LR values of simulations without exchange of individuals *(solid line)*; *open squares:* mean LR values of simulations with 0.2–2% exchange of individuals *(broken line)*; *reversed triangles:* **mean LR** values of simulations with 2–20% exchange of individuals *(stippled line)*. The equations of the exponential functions fitted to the simulated mean LR values are given in Table 4
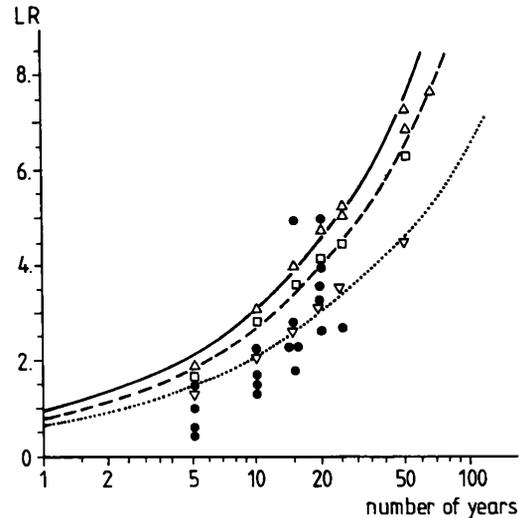
Fig. 6. Mean Log-Range values of 100 simulations of random walks of densities for an averaged interaction group of *Pterostichus lepidus* based on the frequency distribution of the 96 *R* values from 5 interaction groups (see Table 1), plotted as a function of time. *Filled circles:* LR values of field populations; *open triangles:* mean LR values of simulations without exchange of individuals *(solid line)*; *open squares:* mean LR values of simulations with 0.2–2% exchange of individuals *(broken line)*; *reversed triangles:* **mean LR** values of simulations with 2–20% exchange of individuals *(stippled line)*. The equations of the exponential functions fitted to the simulated mean LR values are given in Table 4

Table 4. Exponential functions that describe the increase of Log-Range with time for random walk models of an averaged interaction group of two carabid species. The models are based on the actual distributions of 94 *R* values available from 5 interaction groups continuously sampled at the Heath of Kraloo during 20(19) years; a = number of years over which LR was estimated

Species	With no exchange of individuals	With 0.2–2% exchange of individuals	With 2–20% exchange of individuals	Multipartite population
Pterostichus versicolor	$0.72 \times a^{0.53}$	$0.67 \times a^{0.53}$	$0.49 \times a^{0.53}$	$0.36 \times a^{0.53}$
P. lepidus	$0.93 \times a^{0.53}$	$0.80 \times a^{0.53}$	$0.60 \times a^{0.53}$	$0.55 \times a^{0.53}$

less of whether models with or without exchange of individuals between groups are considered. It will be clear that the frequency distributions of *R* values, which may be changed somewhat by introducing exchange of individuals, are not principally responsible for these results. What matters much more is the way *R* values succeed each other in time, and the present results do not support the hypothesis that the succession of *R* values is such that the fluctuation of population size is bounded.

Discussion

The hypothesis that populations "exist in a state of balance because densities fluctuate about a relatively stable norm" (e.g. Nicholson 1933: 133; Smith 1935: 877) is not supported by the present data. Neither is it supported by appropriate statistical tests (Pollard et al. 1987; Reddingius and Den Boer 1989; Den Boer and Reddingius 1989; Den Boer 1990a). Does this mean that we must accept the null hypothesis that population size is fluctuating as a random walk? I do not think so, for I believe that there are always some processes that show a weaker or stronger correlation with density; fluctuations absolutely independent of density are highly improbable in nature. However, in many, or even most cases, a random walk model with the right parameters could give a close imitation of the fluctuation pattern of population size. Moreover, random walks of densities need not lead to short survival times; depending on the frequency distribution of *R* values both "survival times" of local populations of a few years and of a few hundred years can be simulated. In my opinion, nothing more is needed to understand what happens in nature. Longer survival times, e.g. geological periods, will always concern complexes of local populations, either multipartite populations (Andrewartha and Birch 1984; Den Boer 1986d) or metapopulations (Levins 1968), the natural populations of Andrewartha and Birch (1954). These, moreover, might have been confronted with major changes in the environment (e.g. climate), and/or with crucial changes of genetic composition, which take such cases outside the present

discussion. If a sufficiently reliable frequency distribution of R values can be obtained, simulated random walks of densities can enable us to predict LR values and even survival times of local populations. Predicting LR values for 64 carabid species in that way, we found a close fit with values estimated in field populations in 38 of these species, whereas in 22 others the models predicted even lower LR values than those found in field populations, i.e. just the opposite of what one would find in bounded populations (Den Boer 1985, 1990b: Table 3). In the only case so far where we could check the predicted mean survival time of isolated local populations, *Agonum ericeti*, the fit could not have been better (De Vries and Den Boer 1990).

In general I expect random walk models – with the right parameters – to give better estimates of crucial properties of the population, such as Log-Range, Variance ln$R$, Average ln$R$ and expected mean survival time, than "regulation" models, such as those of Varley and Gradwell (1968), Varley et al. (1973), Begon and Mortimer (1981), Baars and Van Dijk (1984b). This does not mean, however, that population size will always be completely unbounded. In some, or even many, cases, there may be an upper limit to density. For instance, in the great tit in Oranje Nassau Oord (O.N.O.) (Kluyver 1951; Table 2, Fig. 2B), there cannot be many more breeding pairs than there are nest boxes; in a number of pest insects of forests there is no more food available to those insects than is produced by the trees (see Den Boer 1990a). However, in such cases the crucial point is not that there is such an upper limit, but how often it will be approached and still more what will happen *after* that. The occurrence of a non-random reduction of density does not rule out the possibility that, in a subsequent generation, the weather may be so bad as to remove most of the animals, so that the chance of the population becoming extinct is increased (Den Boer 1968: 183–184). Non-random, or density-dependent, reductions of density need not increase the chance of survival of the population: see further Den Boer (1981), where the effects of different kinds of density reduction are compared. As soon as a population is bounded by an upper limit and this is not effectively compensated by density-dependent reproduction, the chance that it will cross the lower limit of "underpopulation" (Andrewartha and Birch 1954: 9.1) will be increased. Therefore, a significant correlation between some mortality factor and the density which is affected by it need not contribute to the stability of the population (Den Boer 1986a, 1987, 1988), because in many cases reproduction, which is a restricted power, will not be able to compensate for the losses, especially in arthropods where egg production and larval development are highly temperature-dependent (e.g. Uvarov 1931).

In spite of the fact that population size need not be completely unbounded, we may wonder whether it would be possible to distinguish between a piece of fluctuation pattern as observed over 12–25 years (say) in some field population and a piece of random walk of densities of the same length and based on the same parameters. This question can be answered by applying statistical tests (see Reddingius 1971; Bulmer 1975; Gaston and Lawton 1987; Pollard et al. 1987; Den Boer 1986a, b, 1987, 1988, 1990a; Reddingius and Den Boer 1989; Den Boer and Reddingius 1989), especially the permutation test, which can tell us whether or not the sequence of R values observed in the field keeps the density between narrower limits than may be expected from a comparable random walk of densities. For instance, what might be the fundamental difference, in terms of "regulation" around some norm, between the pattern of Fig. 2K, for which it is known that a powerful density-dependent mortality factor (pupal predation) accounts for 35% of the generation mortality on average, and the random walk pattern of Fig. 3H? It is therefore not surprising that none of the statistical tests applied to the pattern of Fig. 2K gave significant results (Den Boer and Reddingius 1989: Tables 2 and 3). Of course, we cannot make good science by just offering some well-selected examples, but neither can we do that by stating that "most studies ...show fluctuations around some characteristic level of abundance, quite unlike unbounded population growth or any 'random walk'..." (Hassell et al. 1989) without presenting the relevant data or literature which should support this remarkable conclusion.

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