

Carabid beetles, a master model for population dynamics

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Abstract. To contribute to solving the controversies regarding the **regulation of insect numbers** in 1958 the author started a **comparative investigation** on the fluctuations of numbers of 64 Carabid species in the surroundings of the Biological Station Wijster (Drenthe, the Netherlands). Year-catches of Carabid species in standard sets of pitfalls appeared to give accurate relative estimates of local densities, i.e. of the density of the population (interaction group) around the set of pitfalls.

Net reproduction (**R**) values are characteristic for the species and not for the conditions at the sample site, so that R-values could be put together per species. For each species a log-normal distribution (**LND**) could be fitted to the collection of R-values from the year-catches. Data over more than 30 years were available. With the LND of each species density fluctuations of interaction groups could be simulated and compared with the field fluctuations. In almost all species the bounds between which densities were fluctuating (Logarithmic Range, **LR**) were wider than expected for random fluctuations according to the specific LND. Contrary to the expectation for a regulated population in all cases tested (not only for carabids) **LR** increased in time.

Survival times of Carabid populations around Wijster could be estimated from the simulations: a few years in **T**-species (in ephemeral habitats, high dispersal power), a number of decades in **L**-species (in old habitats, low dispersal), and appeared to correlate significantly (DPS) with dispersal power. Carabid beetles are excellent indicators of the quality of the environment, especially for that of the soil in which the larvae have to grow up. Therefore, Carabid beetles not only form a master model for population dynamics – as expounded in this paper – but these dynamics also give a accurate picture of the degree of degradation of natural environments, so that Carabid beetles are essential indicators for Nature Protection and the planning of sustainable forestry and other kinds of land use.

When, immediately after the second world war, I studied biology at Leiden University, as a field biologist I got involved into population dynamics, at that time the leading branch of the new science of ecology. Therefore, I had to define my position concerning the ‘**regulation of animal numbers**’, as it was introduced by Nicholson (1933, 1937). Nicholson claimed that insect numbers would be kept within positive limits by density-dependent processes, especially by intra-specific competition. Numbers would thus be kept fluctuating, i.e. ‘regulated’, around an equilibrium level determined by the local environmental conditions. This

hypothesis was opposed by Uvarov (1931) and Thompson (1929, 1939), who stated that the varying physical conditions, i.e. density-independent processes, eventually would quantitatively overrule the expected effects of possible density-dependent processes. My field experiences were in line with the ideas of Uvarov and Thompson, and were later supported by the book of Andrewartha & Birch (1954). Apart from a few remarks at relevant places in this paper I will not deal with this not yet completely resolved controversy (see Dempster & McLean 1998); my arguments against regulation can be found in my book with Hans Reddingius (Den Boer & Reddingius 1996).

Here I will emphasize that most ecologists who tried to show the regulating effect of density-dependent processes only studied a single insect population (e.g. Varley & Gradwell 1960, 1968; a population of the winter moth and Klomp 1958, 1966; a population of the pine looper). If regulation would be a general mechanism in animal populations it would dominate the fluctuation patterns of all insect populations. If so, a **comparative study** of fluctuation patterns would be the best strategy to show whether or not such a 'mechanism' would indeed keep insect numbers within positive bounds. Hence, I planned to start a comparative study into the fluctuation patterns of some group of easily sampled insects.

The sampling of carabid beetles

From my field work I knew that carabid beetles can be sampled with pitfalls, and that beetles of many species are sampled at the same time with the same pitfalls. Hence, I decided to set up a comparative investigation into the fluctuation patterns of a group of carabid species, and to find out what are the dominating features of such patterns.

In 1958 I accepted a research job at the Biological Station Wijster, where I could realize my plan. In 1959 I placed standard sets of pitfalls in most semi-natural areas around Wijster. After some years it became clear that 64 carabid species were caught in sufficiently high numbers to study the patterns of fluctuating numbers over years: Den Boer (1977).

The interaction group

First, I had to establish, for each species, the quantitative relationship between the number of beetles caught and the local density. As the amount of activity of carabid beetles will be largely determined by physical factors, especially temperature, catches over short periods, e.g. one or two weeks, will be highly affected by the degree of activity and thus not be a reliable estimate of local density (Briggs 1961; Greenslade 1964). However, I assumed that in catches in a set of pitfalls over much longer periods, e.g. the entire reproductive period of the

species or the whole year, the differences in activity between periods with different kinds of weather conditions would be levelled out sufficiently to let the summed catches over that longer period be a reasonable estimate of mean local density. With extensive mark-recapture experiments I could show that catches of unmarked beetles summed over a whole year (year-catches) give almost perfect ($r = 0.927$) relative estimates of mean local density (Den Boer 1971, 1979: Fig. 2). This question was more directly tackled by Baars. He marked the individuals of two species radioactively, traced these beetles each day with a sensitive scintillation detector, and thus reconstructed the walking pattern in day-distances (Baars 1979a). These patterns appeared to consist of random day-distances in arbitrary directions. These walking patterns were simulated in the computer, so that both the walking pattern and pitfall catches could be reconstructed for thousands of beetles. At the same time he enclosed some areas before the activities started and caught all beetles out, thus establishing density within the enclosure. These direct density values as well as the simulated year-catches were compared with the actual year-catches in neighbouring sets of pitfalls. Again, the relationship was nearly perfect (Baars 1979b): Figure 1. Hence, year-catches of carabid species in standard sets of pitfalls (Den Boer 1977: 1c) are reliable – though relative – estimates of local density, and thus also are a sound base for comparing patterns of fluctuating numbers of carabid beetles.

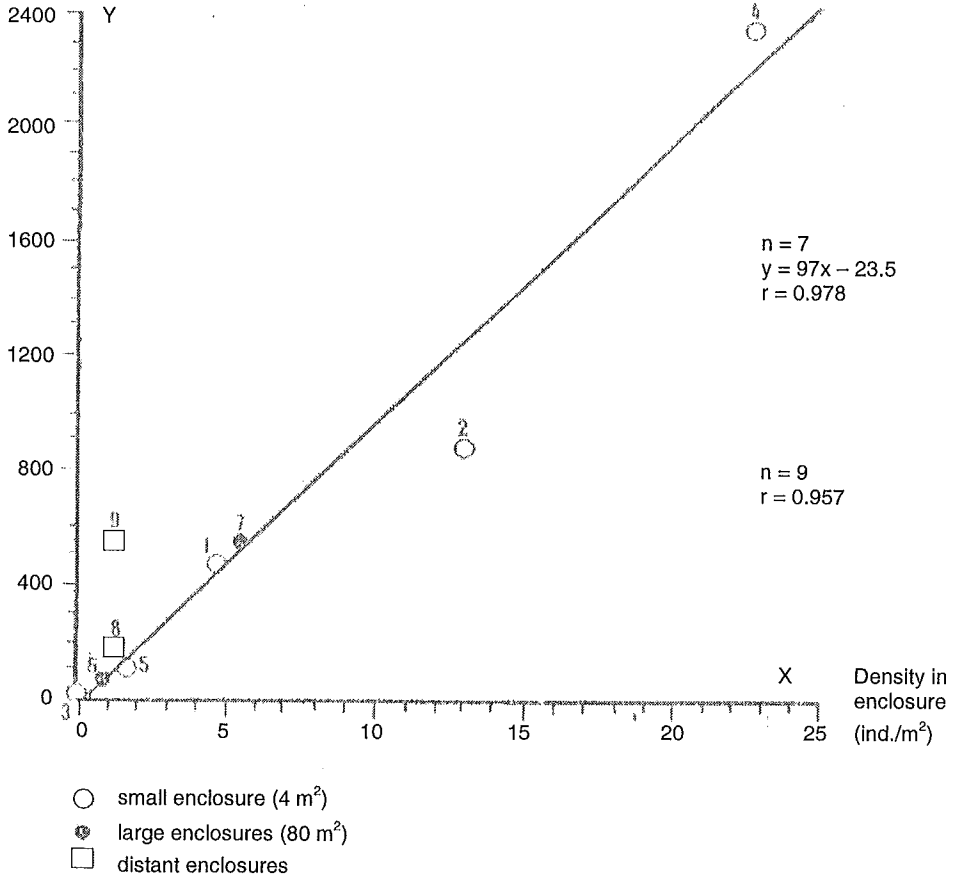
The walking patterns studied by Baars (1979a) enabled us to estimate the area from which 90% of the beetles were caught. This group of beetles which are able to meet both with the pitfalls and with each other, was called an **interaction group** (Den Boer 1977: 1.3; 1981). Two examples are given here: Figures 2 and 3. As density-dependent processes, especially intra-specific competition (Nicholson 1937), calls for interactions between the members of the population concerned I considered an interaction group of carabid beetles to be the best **unit of population** when studying fluctuation patterns. Hence, the year-catches of the 64 carabid species mentioned above are reliable estimates of mean local density, i.e. of the relative density of the interaction group sampled by the standard set of pitfalls concerned. By estimating the year-catches of these species over many years the desired patterns of fluctuating numbers were obtained and could be compared.

A year-catch of some carabid species in a standard set of pitfalls varies between 0.01% and 1% of the interaction group and is characteristic for the species (depends on dispersal power and the way of moving over the soil: Den Boer 1977).

For instance, an interaction group of *Calathus melanocephalus* lives on a surface of 1–2 ha of heath around a set of pitfalls and contains 10,000 to more than 200,000 beetles. An interaction group of *Pterostichus versicolor* lives on 7–13 ha of heath around a set of pitfalls and consists of about 30,000 to 130,000 beetles (Den Boer 1986a).

Calathus melanocephalus

Number of ind. caught
in a standard set of pitfalls



Distance between enclosure and pitfalls

year			year		
1	1973	20 m	6	1974	69 m
2	1973	25 m	7	1974	85 m
3	1973	34 m	8	1974	165 m
4	1973	55 m	9	1974	285 m
5	1973	58 m			

FIGURE 1. Relationship between year-catches of *Calathus melanocephalus* (at the ordinate) and direct measures of local density by catching out nearby enclosures

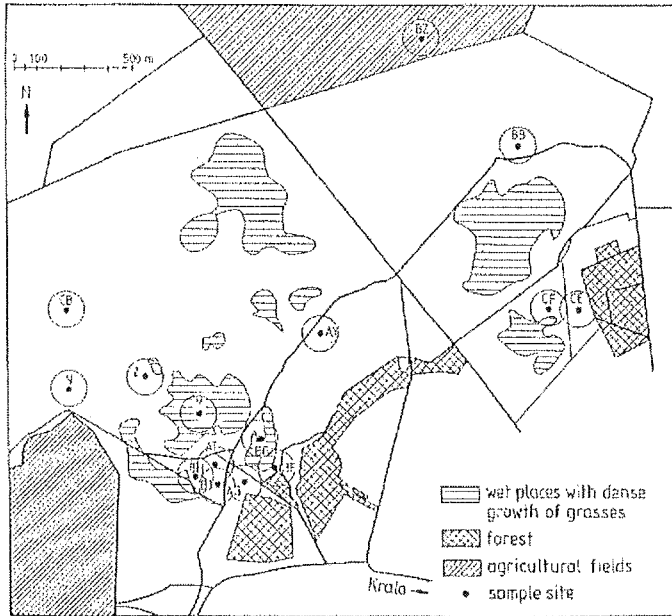


FIGURE 2. Interaction groups (about 2 ha) of *Calathus melanocephalus* around standard sets of pitfalls at Kralo Heath. Compare Figure 5

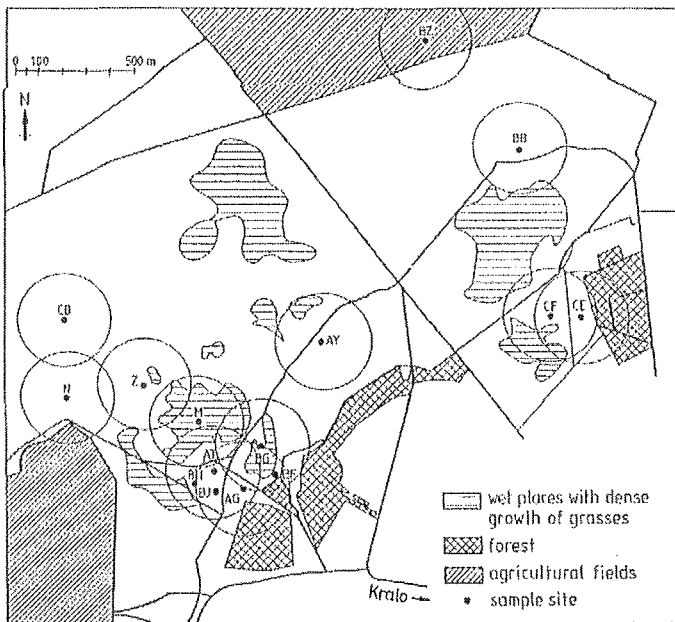


FIGURE 3. Interaction groups (about 12 ha) of *Pterostichus versicolor* around standard sets of pitfalls (the same as in Fig. 2) at Kralo Heath. Compare Figure 4

Defining 'population' as a group of interacting individuals restricts this concept to a fixed location (where 90% of the individuals are expected to interact). This means that the surface of some habitats of the species will be smaller than the area of a single interaction group and that of other habitats larger. Certain habitat-areas may even contain a number of more or less independent interaction groups. Figure 2 shows such possibly independent interaction groups at the Heath of Kralo for *Calathus melanocephalus*, and Figure 3 partly overlapping interaction groups for *Pterostichus versicolor*. But even the overlapping interaction groups in Figure 3 are sufficiently independent of each other to show a differing pattern of numbers over years. Only some of the beetles of both groups – i.e. in the overlapping area – are able to interact (Fig. 4, e.g. AG and BG). In general, the patterns of fluctuation of numbers over years of this species differ between sampling sites: Figure 4. As this species occupies the entire heath area of about 1200 ha, all interaction groups, whether or not defined at a fixed site by a standard set of pitfalls, are interconnected; they form what is called by Andrewartha & Birch (1984: 9.1) a '**multipartite population**'. In spite of the fact that *Calathus melanocephalus* also inhabits the entire heath area, and therefore also forms a 'multipartite population' the patterns of fluctuating numbers over years occur synchronously between sites: Figure 5. Van Dijk & Den Boer (1992) showed that this is because the larvae of *Calathus melanocephalus* grow up in winter when soil conditions are similar (moist and cold) everywhere in the heath area, while the larvae of *Pterostichus versicolor* grow up in spring when there are great local differences in soil moisture and temperature.

Spreading of risk

If in a large habitat-area interaction groups of some carabid species are interconnected and so form a **multipartite population**, because of the largely random movements, beetles from groups with high numbers will enter interaction groups with lower numbers more often than the other way round. In this way extreme fluctuations of numbers in some groups will be more or less levelled, so that the fluctuations of numbers in the entire multipartite population may be levelled down to a high degree (see Fig. 4 upper graph). I called this phenomenon '**spreading of risk**' and put it forward as an alternative for '**regulation of numbers**' to explain the often remarkably stable numerical fluctuations of some populations (Den Boer 1968, 1971, 1981, 1986a, 1998, 1999; Reddingius & Den Boer 1970; Reddingius 1971). Most entomologists will sample multipartite populations without realizing that the samples are heterogeneous, because these are taken from different, but not recognized, interaction groups, and are put together as being a single sample from a supposedly homogeneous population.

Therefore, patterns of fluctuating numbers from such samples may be stabilized by **spreading of risk** to an extent as in the upper graph of Figure 4, and thus thought to be **'regulated'** in some way. Two examples of such unconsciously sampled multipartite populations (Schwerdtfeger 1941) are given here in Figure 6.

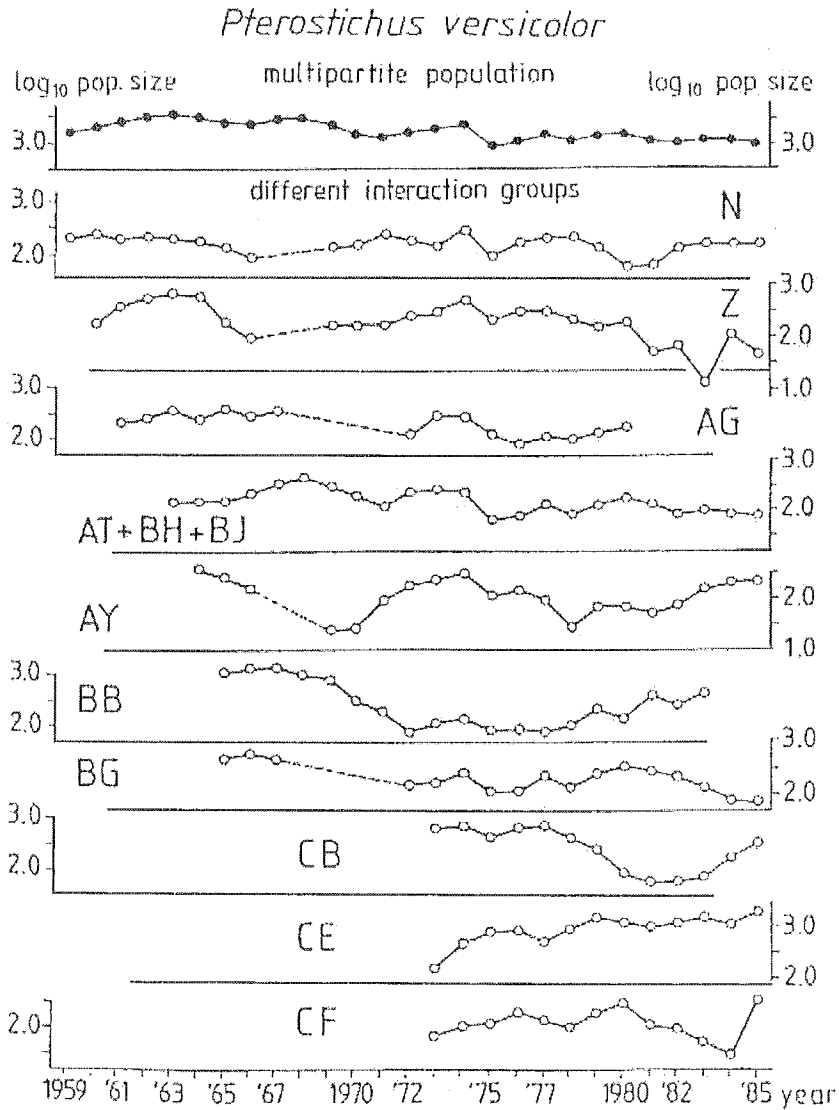


FIGURE 4. Fluctuations of local density (year-catches) of *Pterostichus versicolor* between 1959 and 1985 in 10 interaction groups (compare Fig. 3) at Kralo Heath, as compared with the expected fluctuations of density in the multipartite population composed of these 10 local groups (at the top)

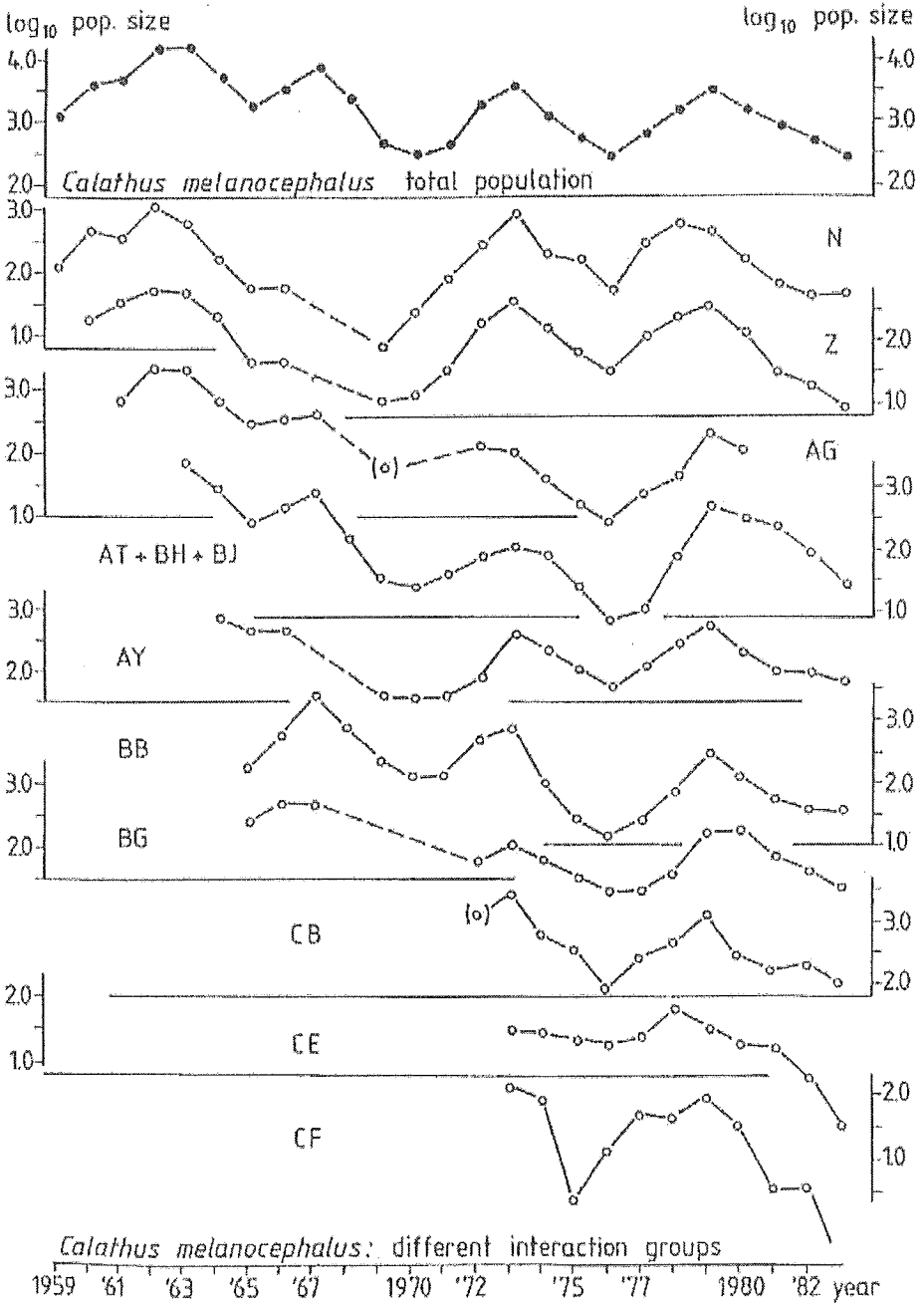


FIGURE 5. The same as in Figure 4 for *Calathus melanocephalus* between 1959 and 1982 (compare Fig. 2)

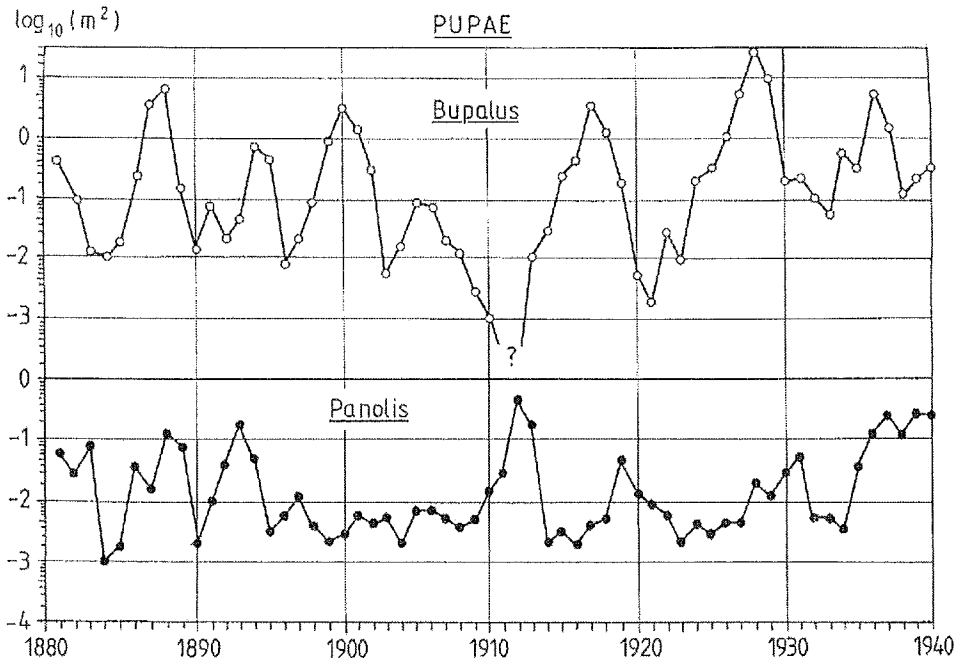


FIGURE 6. Yearly fluctuations of the numbers of pupae per m^2 of soil of two forest pests (*Bupalus piniarius* and *Panolis flammea*) in large areas of pine forest near Letzingen (at present in West Poland). Data from Schwerdtfeger (1941). Note, in 1911 and 1912 numbers of *Bupalus*-pupae were too low to be trustable, i.e. the ? does not point to extinction

As not only interaction groups in a multipartite population may show different patterns of fluctuating numbers, but also individuals of most species show a different genetic make-up, the chances to reproduce and survive will also be spread over individuals with a different genetic make-up, by which fluctuations of numbers may be levelled down (Den Boer et al. 1993; Den Boer, 1999; Den Boer & Reddingius 1996; Andrewartha & Birch 1984: 11). Spreading of risk does not only lead to a better understanding of population dynamics, but might also contribute to a more sophisticated nature and forest management (as in the case of Szyszko 1990).

How to quantify patterns of fluctuation?

To be able to compare patterns of fluctuating numbers it is necessary to quantify such a pattern. Fluctuations occur when numbers (or mean density) change from one year to the next, so that a direct measure of such a change is the **net rate of reproduction (R)**, i.e. density in year t divided by density in year $t-1$ ($R = N_t/N_{t-1}$), and the pattern will be characterized by **Variance (R)**. However, the

pattern will also depend on the sequence in which these R-values are realized: a succession of high or low R-values gives greater fluctuations of numbers than alternating high and low R-values.

Therefore, the difference between the logarithms of the highest and the lowest density (or year-catch) over a number of years, **Logarithmic Range LR = ln (highest N) – ln (lowest N)**, gives an estimate of the range over which density has been fluctuating during that number of years. Of course, only the LR-values of the same number of years can be compared directly. The overall trend of density over time (downward or upward) is characterized by the average logarithm of R (= logarithm of the geometric mean of R), **mean lnR** (we prefer to use natural logarithms (ln) in such cases). For m generations this simply is $1/m[\ln N_m - \ln N_0]$. The longer an interaction group is observed to persist the closer mean lnR will be to zero. Note: this has nothing to do with regulation, it is a statistical truism (compare Fig. 6). See Reddingius & Den Boer (1970) and Den Boer (1971). Also, note that the above quantities to characterize patterns of fluctuating numbers are not affected by the level of the actual densities. Therefore, the relative densities as reliably estimated by the year-catches of carabid beetles in pitfalls are just what we need to compare patterns of fluctuating numbers! Now we are in a position to answer some questions about patterns of fluctuating numbers.

The quantitative effects of spreading of risk

The most important question I would like to answer now is: what are the quantitative effects of **spreading of risk** for the survival time of populations? In the present case: what is the survival value of the interconnection of interaction groups and the expected levelling of fluctuations in density that may result if the **multipartite population** is composed of these interaction groups. This effect is pictured in the upper graph of Figure 4. A similar effect was found in other abundant carabid species that occupy the entire heath area, for instance in *Pterostichus lepidus* (Fig. 7), in *Pterostichus diligens* (Den Boer 1998: Fig. 3.8), and in many other species. It will be evident that the range of fluctuations in density (LR) in the multipartite population (as in the upper graphs of Figs. 4 and 7) is much narrower than in any of the local interaction groups that are part of it. Den Boer (1982: Tab. 1) showed that LR of the multipartite population of *Pterostichus versicolor* has about half the value of the mean LR of the interaction groups composing it. Most probably this will also hold true in many less abundant species at Kralo Heath. Because of low densities year-catches of interaction groups of the latter species are zero in some years, making it difficult to estimate the effect of risk spreading quantitatively. A good example of such a species is *Agonum ericeti* (De Vries & Den Boer 1990). Figure 8 shows that also in this species different

interaction groups fluctuated asynchronously, just as in the abundant species pictured earlier (in Figs. 4 and 7). Of course, these effects of spreading of risk are not restricted to carabid beetles. It will occur in every multipartite population where interaction groups are not recognized and many samples are put together as being inaccurate values of the same population density. This occurred in the two noxious moth species of extensive pine plantations pictured in Figure 6 (Den Boer 1990a).

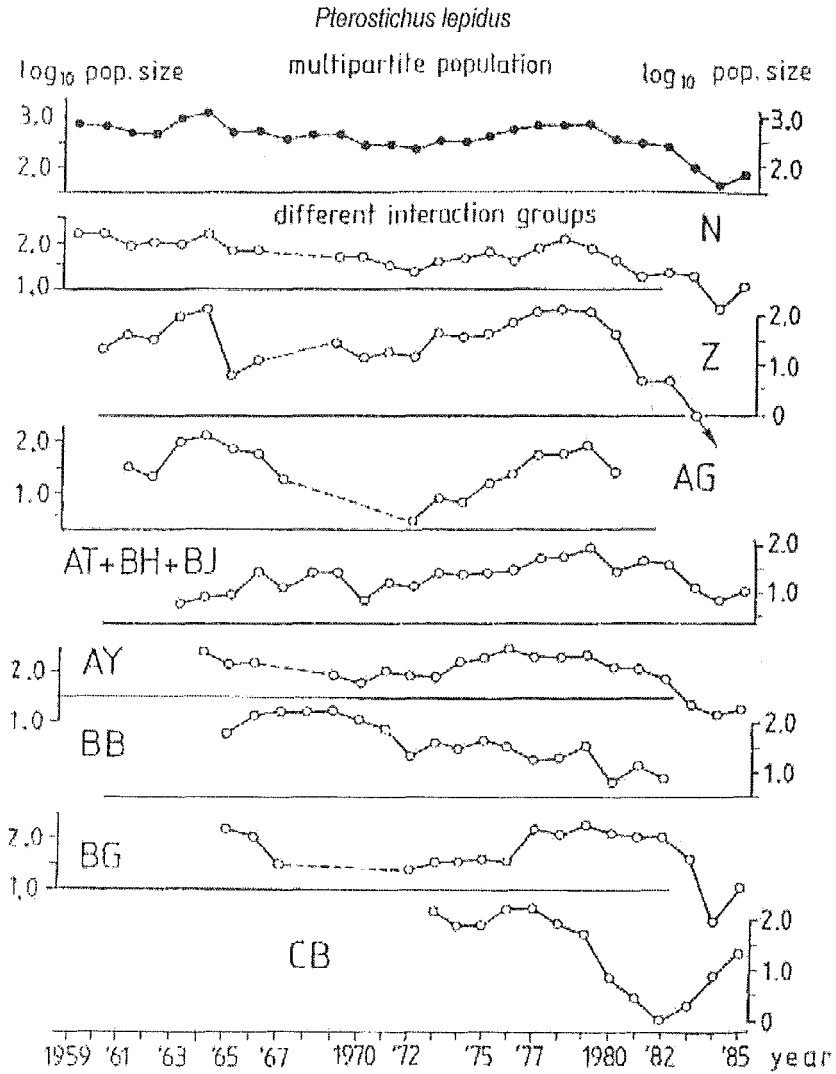


FIGURE 7. The same as in Figure 4 for *Pterostichus lepidus* for 8 interaction groups and the multipartite population composed of these 8 local groups (interaction groups as in Fig. 3)

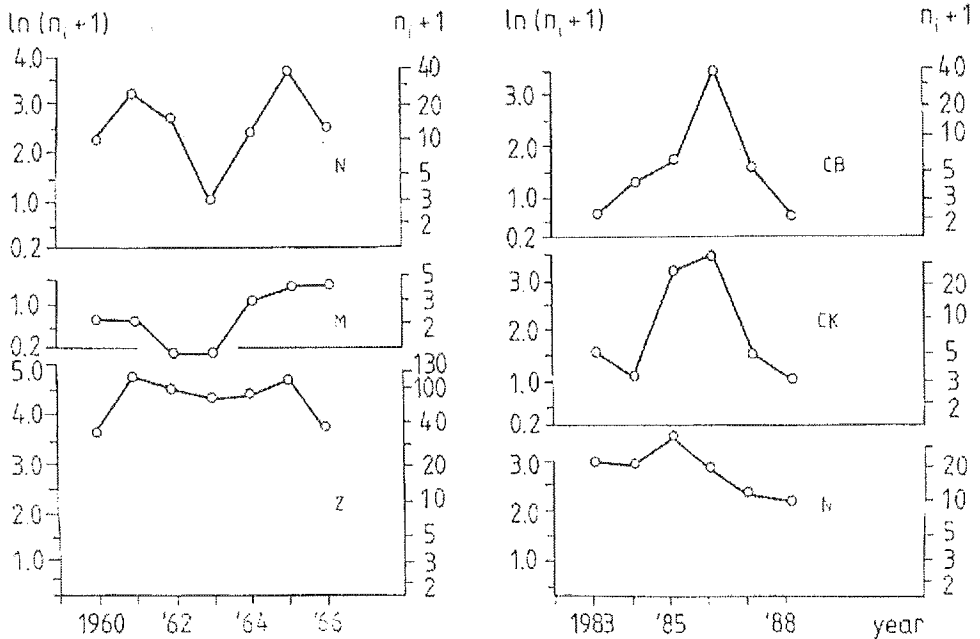


FIGURE 8. Uninterrupted year-catches of *Agomum ericeti* in standard sets of pitfalls at Kralo Heath; usually the numbers fluctuated asynchronously: W (coefficient of concordance) = 0.59 for N, M, Z in 1960–1966 and $W = 0.65$ for CB, CK, N in 1983–1988. This means that the fluctuations were asynchronous for 35–41%, which will give effective spreading of risk. I added 1 to the year-catches to avoid $\ln(1) = 0$ (two years in M)

A more quantitative method seems to be: comparing the variance of $\ln R$ per interaction group over years averaged for all interaction groups sampled with the variance per year over the sampled interaction groups averaged for all sampling years: Den Boer (1971: Tab. 3). In *Pterostichus versicolor* (= *P. coerulescens*) the mean variance of $\ln R$ per site for the 11 sampling years appeared to be of about the same value as the mean variance of $\ln R$ per year for the 11 sampling sites. This indicates that the fluctuations of numbers over years in the 11 interaction groups at Kralo Heath are sufficiently asynchronous to considerably level down the pattern of fluctuating numbers in the multipartite population (Figs. 4 and 7) and thus to significantly increase the survival time of the multipartite population concerned. Den Boer & Reddingius (1996: Tables 4.5 and 4.6) calculated this anew for 26 years and 16 sites at Kralo Heath with similar results. I (Den Boer 1981) tried to evaluate this situation with the help of simulation experiments. For 19 years and 15 sites at the Heath of Kralo I concluded that the survival time of the multipartite population with the asynchronously fluctuating interaction groups found in the field (Fig. 4) could be expected to survive 10–15 times longer than a comparable multipartite population with synchronously fluctuating interaction groups, i.e.

without any spreading of risk over sites. A similar effect can be expected for many other species – and not only carabid species – at Kralo Heath (and elsewhere), e.g. in *Pterostichus lepidus* (Fig. 7).

To show that the above results should indeed be attributed to the effects of spreading of risk the same calculations were applied to *Calathus melanocephalus*, where the different interaction groups (sampled in the same sets of pitfalls, at the same sites and in the same years as for *P. versicolor*) fluctuated about in parallel over years: Figure 5. Both Den Boer (1971: Tab. 4) and Den Boer & Reddingius (1996: Tables 4.3 and 4.4) showed that for this species mean variance lnR per site over years is much higher (1.7 to 3.1 times) than mean variance lnR per year over sites, so that there can hardly be any spreading of risk over sampling sites. This was confirmed by Den Boer (1981) concerning expected survival times of the multipartite population with synchronously or asynchronously fluctuating interaction groups. It is also confirmed by Den Boer (1982: Tab. 1), who showed that LR of the multipartite population of *C. melanocephalus* does not differ from mean LR of its interaction groups (compare *Pterostichus versicolor* above).

Almost all carabid species in our area reproduce only once a year, but in many of these species an important proportion of the adults survive winter and may reproduce again in a following year (Den Boer 1971: Tab. 2; Den Boer 1979: Tab. 1). This means that two groups of reproducing beetles exists: young beetles that reproduce for the first time and old beetles that reproduce in a second or third year. If a population exists of more groups of differently reproducing individuals this can be expected to relatively level down the density fluctuations from year to year. In other words, the chances to reproduce and survive are spread over more groups of individuals: **spreading of risk**: Figure 9; Den Boer (1998: Fig. 3.13).

Den Boer & Reddingius (1970) showed that spreading of risk is a general phenomenon occurring everywhere when more factors or processes result in a single quantity such as the number of individuals in a population: **multicausal processes** (Hilborn & Stearns 1982). See also Den Boer (1971). Therefore, not only the genetic and/or phenotypic heterogeneity of natural populations, but also physical and/or chemical differences between sites within the environment of a population (Fig. 6), different properties of individuals of different ages (Fig. 9), individuals that use different kinds of food because of differing local conditions, etc., **may spread the risks over different ages, genotypes, or other groups, and so contribute to stabilization of patterns of fluctuating numbers, thus relatively increasing the survival time of the population.**

An interesting example of spreading of risk is shown by the two populations of *Callosobruchus chinensis* bred by Utida (1957) during 68 generations, one culture with a single parasitoid species and the other with two parasitoid species. The population with two parasitoid species fluctuated between much narrower

bounds than the population with a single parasitoid species (Den Boer 1971: Fig. 8; Den Boer 1982: Tab. 2).

In short: I am sure that **spreading of risk in nature** is much more general and possibly also much more important for the survival of populations than the sometimes (but not always and everywhere) also occurring density-dependent processes.

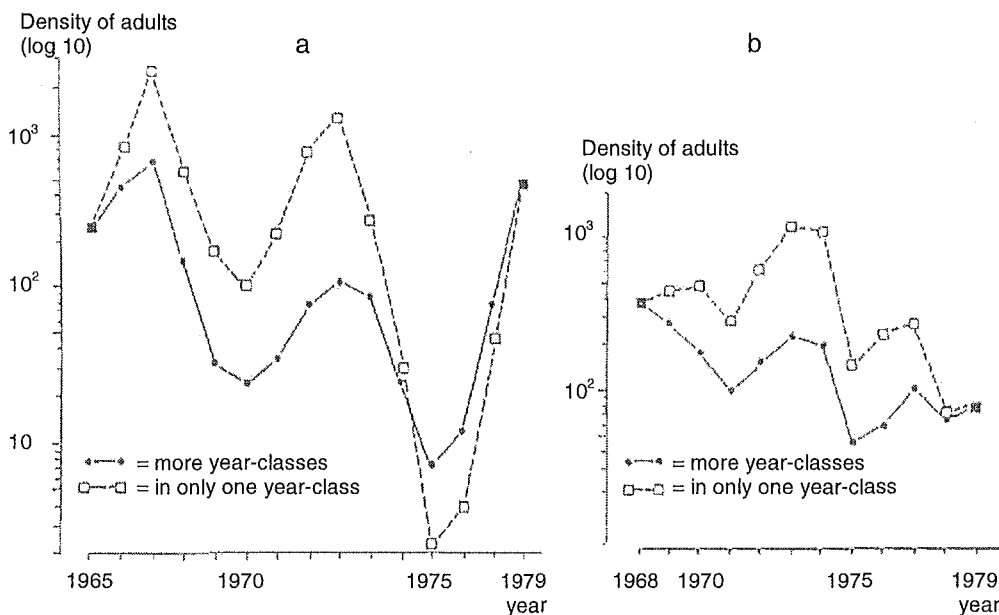


FIGURE 9. Density fluctuations (year-catches) in interaction group AT,BH,BJ (compare Figs. 2 and 3) if different age-groups the field situation participate in reproduction (black dots), as compared with the situation if only a single year-class had reproduced (open squares) in such a way that mean net reproduction stayed the same. a. *Calathus melanocephalus*; b. *Pterostichus versicolor*. Data from Baars & Van Dijk (1984, Appendix)

The frequency distribution of $\ln R$

Another interesting question is: Is the pattern of density fluctuations characteristic for the species or for the local environment? As we sampled in different sites during many years, for each carabid species I could compare the R -values realized in different interaction groups with the test of Mann-Whitney. It then appeared that for each species separately the R -values realized in different interaction groups during 6–8 or more years all belonged to the same frequency distribution of $\ln R$.

Hence, the fluctuation patterns (R -values) found are characteristic for the species and **not** for the environmental conditions – at least within the same

climatological region, i.e. central Drenthe around Wijster – so that for each species sampled I could put together all $\ln R$ -values from all habitats sampled into a common frequency distribution of $\ln R$ -values. For each of the 64 carabid species studied (during more than 30 years) I could show that such a frequency distribution does not differ significantly (X^2 -test) from the **log-normal distribution of R-values**, that could be fitted to it (see Appendix by J. Reddingius to Den Boer 1985): some examples are shown in Figure 10. See also Den Boer & Reddingius (1996: 2.3.8 and Table 2.3). If M and V are Mean and Variance respectively of the set of $\ln R$ -values estimated from the field data of some species, then $\text{mean}(Y) = 2 \cdot \ln M - \frac{1}{2} \cdot \ln(V^2 + M^2)$ and $\text{Var}(Y) = \ln(V^2 + M^2) - 2 \cdot \ln M$ are **mean** and **variance** respectively of the $\ln R$ -values of the **fitted log-normal distribution (LND)** of these R-values: Den Boer (1990b: Tab. 1).

What does it mean that the $\ln R$ -values of some species (not only carabid species: Den Boer 1990c) put together from a number of separate interaction groups within the same climatological region form a pseudo-normal distribution? Apparently, the processes, factors and incidents that affect both egg production per female, mortality of eggs, larvae in different stages and adults, are – although fundamentally determined by genetical properties of the individuals – so highly variable from place to place and from year to year that the resulting $\ln R$ -values almost simulate random variables. Note, the $\ln R$ -values **are not random variables**, because at least some of the underlying processes can be formulated deterministically if the necessary information was available, e.g. egg production per female, which is determined by genotype and age of the female (and male?), temperature, quality and quantity of the food (Van Dijk 1979, 1994, 1996), so that with sufficient data it might be predicted. That is why many entomologists do not like to study the dynamics of a population by estimating the distribution of successive R-values, but prefer to analyse the causal processes and factors as well as possible and put together this knowledge in computer models, hoping to be able to predict successive R-values. To keep such models manageable, however, it is necessary to simplify the field data to a high degree, e.g. to suppose that all individuals are equal, that the environment is homogeneous and constant, that weather conditions do not play a significant part, etc. I thought this unwarranted, since such generalizations are always wrong. The chances of development, survival and reproduction of each individual are unique, both because in sexual species each individual has a unique genetic make-up (except in identical twins, of course), as well as because the individual's course through life is uniquely affected by local structural and micrometeorological variables. Furthermore, in my opinion it will never be possible to predict local weather conditions – let alone microweather conditions for individual animals – a year ahead, which would be necessary to predict density in the following year. Moreover, however urgent protection of

certain populations may be, the money and time to keep the genetic composition of such a population up to date will rarely be available. Therefore, the approach of population dynamics expounded in this paper seems the only realistic one.

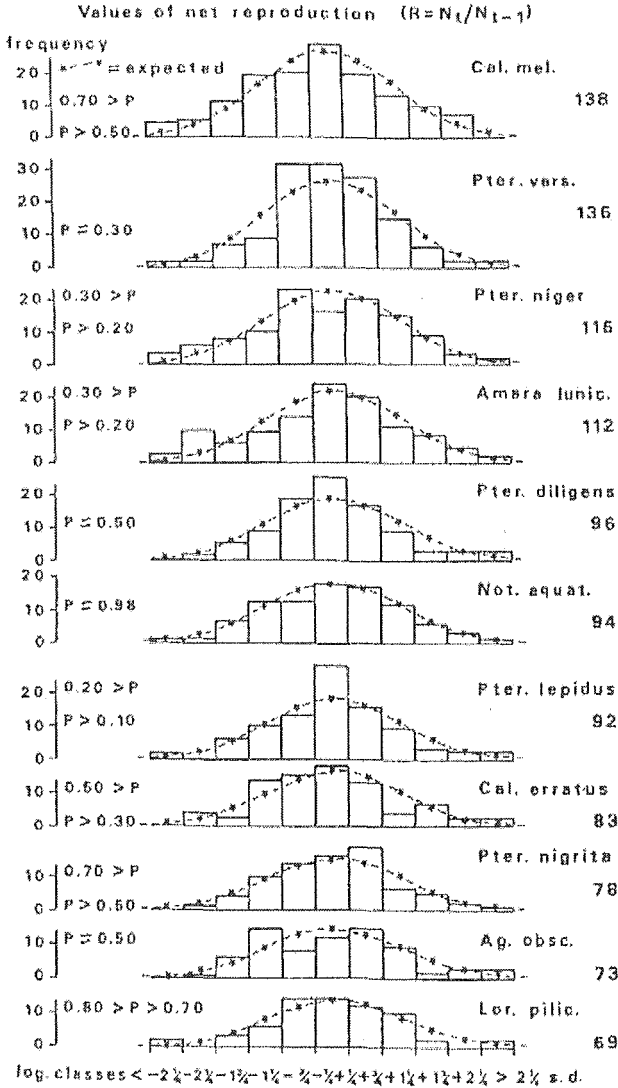


FIGURE 10. Frequency distribution of net reproduction (R) values on a logarithmic scale (below) of the 11 most abundant carabid species around Wijster, as compared with the fitted lognormal (specific LND: broken line between stars). Class-width = $\frac{1}{2}$ standard deviation (below). At left: probability (from χ^2) that the differences between the two distributions are due to chance deviations only. At right: number of R-values from field-samplings per species. Cal = *Calathus*, Pter = *Pterostichus*, Not = *Notiophilus*, Ag = *Agonum*, Lor = *Loricera*, mel = *melanocephalus*, vers = *versicolor*, lunic = *lunicollis*, aquat = *aquatius*, obsc = *obscurum*, pilic = *pilicornis*

Estimating survival times of interaction groups

The favourable property of $\ln R$ -values of reliably sampled carabid species forming a pseudo-normal distribution enabled me to simulate computer-populations of each of the 64 more abundant species [with the specific mean(Y) and the square root of $\text{var}(Y)$ of the fitted LND, **random-range method**: Den Boer 1985, 1990b]. Starting from a reasonable estimate of local mean density and comparing actual LR-values from the field with simulated ones, I could estimate the expected survival time of an interaction group of that species under stationary conditions (i.e. if the changes of critical environmental conditions in future years vary according to the same distributions as in past years). By repeating these simulations for each species 500 times I could select the simulated series with the same or lower LR as the field series and so establish most probable averages: Den Boer (1990b): Table 1.

TABLE 1. Numbers of sampling runs that show narrower (na) respectively wider (wi) density ranges than the mean Logarithmic Ranges (LR) under the assumption of randomly succeeding R-values as compared with the expected numbers of deviations according to these random - range models

Species	In the field		Expected		X^2 of comparison	Comment on field range:
	na	wi	na	wi		
1	2	3	4	5	6	7
<i>Notiophilus aquaticus</i> L.	41	20	45.6	15.4	1.838	
<i>Trichocellus cognatus</i> Gyll.	18	17	25.1	9.9	7.100***	too wide
<i>Bradycellus ruficollis</i> Steph.	25	12	26.9	10.1	0.492	
<i>Loricera pilicornis</i> F.	24	13	28.9	8.1	3.795*	too wide
<i>Dyschirius globosus</i> Herbst	22	16	27.7	10.9	3.346*	too wide
<i>Amara lunicollis</i> Schidte	50	29	54.4	26.6	1.084	
<i>Bradycellus harpalinus</i> Serv.	22	16	30.6	7.4	12.417***	too wide
<i>Metabletus foveatus</i> Fourcr.	7	13	13.6	6.4	10.010***	too wide
<i>Calathus erratus</i> Sahlberg	35	17	34.8	17.2	0.004	
<i>Nebria brevicollis</i> F.	23	13	24.5	11.5	0.288	
<i>Amara plebeja</i> Gyll.	24	30	34.7	19.3	9.232***	too wide
<i>Agonum obscurum</i> Herbst	34	20	37.5	16.5	1.069	
<i>Calathus melanocephalus</i> L.	49	48	60.9	36.1	6.248**	too wide
<i>Amara communis</i> Panz.	22	25	30.0	17.0	5.898**	too wide
<i>Notiophilus biguttatus</i> F.	21	12	21.8	11.2	0.087	
<i>Clivina fossor</i> L.	15	20	23.3	11.7	8.845***	too wide
<i>Pterostichus lepidus</i> Leske	39	25	43.1	20.9	1.194	
<i>Pterostichus nigrita</i> Payk.	43	9	41.5	10.5	0.269	
<i>Pterostichus niger</i> Schaller	41	41	57.3	24.7	15.394	too wide

Table 1. (continued)

1	2	3	4	5	6	7
<i>Olisthopus rotundatus</i> Payk.	23	8	21.9	9.1	0.188	
<i>Pterostichus diligens</i> Sturm	37	23	40.4	19.6	0.876	
<i>Pterostichus versicolor</i> Sturm	68	28	60.8	35.2	2.325	
<i>Carabus problematicus</i> Herbst	30	8	24.8	13.2	3.139*	too narrow
<i>Harpalus latus</i> L.	36	9	29.8	15.2	3.819*	too narrow
<i>Pterostichus oblongopunctatus</i> F.	20	25	26.6	18.4	4.005*	too wide

*= 0.10 > p > 0.05, **= 0.05 > p > 0.01, ***p < 0.01, in all other cases p > 0.10

As actual local densities of most species were not available from all sampling sites, I also developed another method to estimate expected survival times of interaction groups. This method was based on the number of times **zero year-catches** were found in the sampling series of each species. These zero year-catches could point either to local extinction or to such low densities that not even a single specimen was caught during an entire year: **pseudo-turnover**. By simulating the actual field-level of year-catches, by sampling from a computer population that would survive the actual sampling period at that site, it was possible to discriminate between pseudo-turnover and real (and generally temporary) local extinction. By correcting gross turnover (total of all zero year-catches) from the field data of that species for pseudo-turnover, I could estimate actual turnover – extinction and (re)founding – by comparing the percentage corrected turnover with the number of positive year-catches from all sampling series of that species (Den Boer 1985: Tab. 2; 1990b: Tab. 2).

Although the results of both of these methods to estimate mean survival times of interaction groups of carabid species did not contradict or significantly differ from each other, I preferred the latter method (with correction for pseudo-turnover). Because not only were values of real local densities not required, but also because the few trustable guesses of survival times from other (e.g. historical) data agreed remarkably well with the estimates from the latter method. A good example of this is worked out by De Vries & Den Boer (1990) for *Agonum ericeti*.

Among the 64 more abundant carabid species in our area there were – as could be expected – both species with a high turnover of local populations (interaction groups), called **T-species** (from high TURNOVER and high dispersal power), and species with a low turnover of interaction groups, called **L-species** (from LOW turnover and low dispersal power), and intermediate ones: Figure 11. This difference in turnover is mainly connected with **dispersal power**, which was extensively studied by Lindroth (1945), Den Boer (1970, 1977, 1990b) and Den Boer et al. (1980).

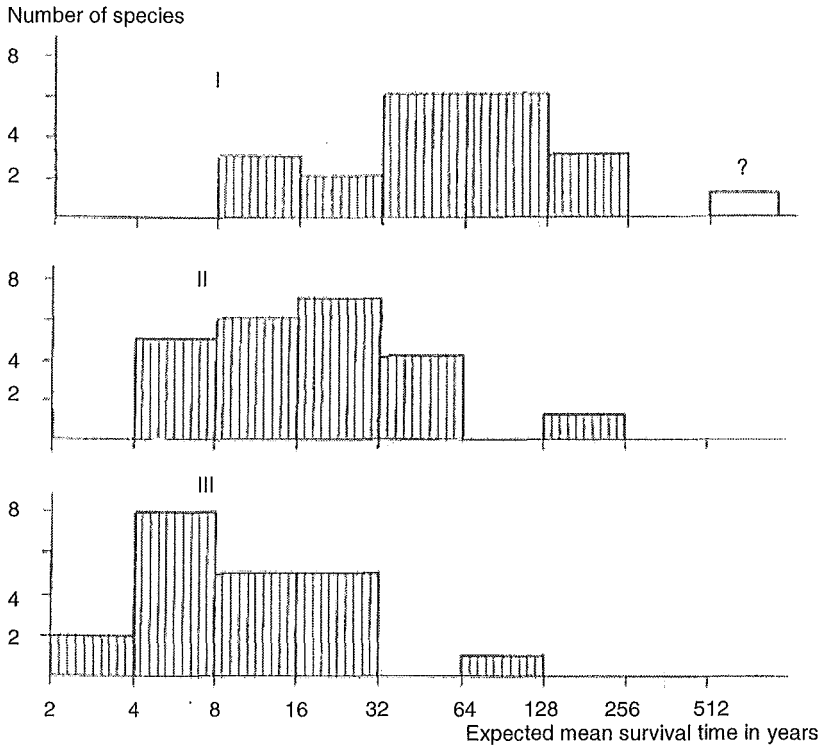


FIGURE 11. Frequency distribution of estimates of expected survival times of local populations (interaction groups) of 64 carabid species sampled around Wijster (Drenthe, the Netherlands), divided in three groups with different powers of dispersal: **I**. Poorly dispersing (**L**) species; **II**. intermediate or locally different powers of dispersal; **III**. well dispersing (**T**) species

Fluctuation bounds in time in field populations

Nicholson (1933) and followers, who expect that natural populations are **'regulated'**, claim that densities are kept within positive bounds by **density-dependent** processes. This would mean that if we have studied some natural population for many years, the Logarithmic Range (**LR**) during the first 5 years (say) would not differ significantly from the LR of longer periods. In other words: the fluctuations of density would be kept within about the same limits during our period of observation. In the practice of field studies this would mean: after a founding period in a **regulated** population the bounds of density fluctuations (LR-values) would stay about the same in the course of time, whereas in a **non-regulated** population these bounds would become wider (growing LR-values) in the course of time. Den Boer (1991: Tab. 1; Fig. 1) showed that in all the interaction groups of carabid species that survived 20 years of observation LR increased in time, i.e. there was no indication of **'regulation'** of numbers by some

density-dependent process, as was supposed by Baars & Van Dijk (1984) for some of the interaction groups of *Calathus melanocephalus* and *Pterostichus versicolor*; but see also Den Boer (1986b). Not only among carabid species, but also among animal populations generally supposed to be 'regulated' LR-values increased in time: Den Boer (1991: Tab. 2; Fig. 2).

If populations would be 'regulated' we should not only expect LR not to increase significantly in time, i.e. density to be kept between positive bounds, but also that R-values would succeed each other in such a way that density would be kept fluctuating around the supposed 'equilibrium value'. This means that the order in which R-values are realized in the pertinent population would be a special one by which LR can be kept low. To test this hypothesis Reddingius & Den Boer (1989) developed the permutation test: when permuting the R-values of the pertinent population 500 times (say) it was expected that the LR-value of the field population tested would be smaller than at least 95 (or 99)% of the LR-values of the permuted populations. None of the populations tested – both carabid populations and populations claimed in literature to be "regulated" – could be considered to be "regulated" according to this criterion (Den Boer & Reddingius 1989; Den Boer 1990a). The same can be concluded from the application of other tests suggested in literature (Den Boer & Reddingius 1996: Ch. 6; Rothery 1998).

Random walks or bounded fluctuations of density?

"If density fluctuations were not bounded in some way populations would rapidly either become extinct or grow above all bounds", as is argued by Nicholson and his followers, e.g. by Hassell et al. (1989). Den Boer (1991) demonstrated that this argument was false, and originated from a wrong conception of 'random walk of densities'. Animals will never realize the theoretical capacity of reproduction, both because the amount of progeny produced is restricted, and because under natural conditions only a fraction of the young will survive to reproductive age. In other words, the R-values of a species are restricted, which does not mean that the densities reached would always be restricted: theoretically a long series of high R-values (> 1.0) may increase density above all bounds, and a long series of low R-values (< 1.0) may decrease even a very high density to zero. Therefore, a more realistic notion of "random walk of densities" will restrict R-values to the known possibilities of the pertinent species within the climatological area to which it is adapted. A better concept of 'random walk of densities' will start from Mean and Variance of the LND fitted to all densities available from the study area, by which all R-values are included that may be realized there (see above). I (Den Boer 1990b) applied this concept to the 64 most abundant carabid species around Wijster: for each species and for each uninterrupted sampling run at some site

(during 4, 5, 6 and so on years). I separately simulated 500 sets of random density fluctuations with the specific LND and calculated mean LR for each collection of 500 sets and the averaged value per species. Next I established in how many cases these mean LR's from the simulations were wider or narrower than the LR's from the pertinent field series. It appeared that in 38 of the 64 species the numbers of narrower and wider LR's of the field runs fitted the expectations from these random-range models. In 22 species in the field runs there were significantly more LR's wider than predicted by the models, and in only 4 species in the field runs there were significantly more LR's narrower than expected. This means: the hypothesis that in these 64 carabid species densities would fluctuate at random ($X^2 = 25,45; v = 2, P \ll 0.001$), or even better (i.e. between narrower bounds than random), must be rejected in favour of the hypothesis that interaction groups of these carabid species fluctuate more heavily (i.e. between wider bounds) than at random. In Den Boer (1990b: Tab. 3) the data for the 25 most abundant species are given: Table 1, and in Figure 12 the results for 7 abundant species of heath are pictured.

The above unexpected result of my **comparative investigations** of carabid populations, which also seems to apply to other insect species – but which cannot be strictly proven because of a lack of comparative studies in other insect groups – indicates that a 'random walk of densities' might be the best '**survival strategy**' of field populations (interaction groups). Therefore, the idea of a **biological equilibrium** that could be disturbed by irresponsible actions of humans, is wrong, because there is no equilibrium, neither in population numbers (Wolda 1989, 1991), nor in the numerical relations between populations.

Nevertheless, the above discussion shows that – at least for carabid beetles – for a fixed number of sampling years LR must give a useful indication about the survival times that might be expected for the pertinent interaction group. Figure 13 gives such expected survival times for LR-values from sampling runs of 8 years. As was remarked earlier Figure 13 demonstrates that in general interaction groups of L-species survive longer than those of T-species.

Does the absence of a biological equilibrium mean that the activities of people in nature, such as the cutting of forests, do not have an important impact on the survival of species and on the relations between species? Of course, our activities have such an impact, but these are **not** destructive because of '**disturbing the biological equilibrium**', but because of too drastically changing the numerical relations among species and that between population numbers and environment. For, in spite of population densities not fluctuating around an equilibrium level by density-dependent processes, there are uncountable quantitative relations between species and quantitative effects of changing environmental conditions. These highly vulnerable interactions can easily be irreparably disturbed or even completely destroyed by thoughtless people, who are merely interested in personal gain.



FIGURE 12. Logarithmic Ranges (LR), i.e. $\ln(\text{highest year-catch}) - \ln(\text{lowest year-catch})$ of interaction groups of the seven most abundant carabid species sampled during a fixed number of years (at abscis) in standard sets of pitfalls at Kralo Heath (Drenthe, the Netherlands): black columns = LR-values of field groups; open columns = mean LR-values of 500 simulations of these groups from the specific LND of that species. The location of the standard sets of pitfalls (indicated by capitals: at top) is given in Figures 2 and 3. C = *Calathus*, P = *Pterostichus*, A = *Agonum*, H = *Harpalus*

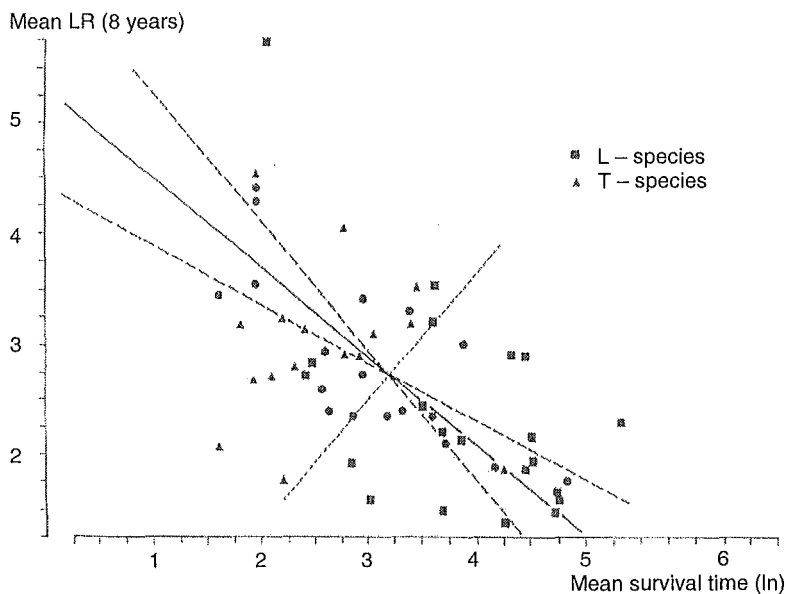


FIGURE 13. Relationship between mean LR (compare text to Fig. 12) over 8 year periods and natural logarithms (\ln) of mean survival times of interaction groups of 55 (of 64; in 9 species 8 year periods were not available) carabid species of Drenthe (the Netherlands) estimated from simulations with the zero year-catches model (Den Boer 1985). The continuous line is the first principal axis with the equation $Y = 6.5491 - 1.2337X$ (Y = mean survival time; X = mean LR). The 95% confidence limits for the slope of this relation (broken lines) have equations $Y_1 = 8.26645 - 1.865X$ and $Y_2 = 5.4873 - 0.8434X$. The second principal axis (stippled line) has the equation $Y = 0.9877 + 0.8106X$, and separates most T-species (at left) from most L-species (at right); filled circles are intermediate between L- and T-species (compare text to Fig. 11). Mean LR and mean \ln (survival time) are significantly correlated, r (Pearson) = -0.567 ($P \ll 0.001$), r (Spearman) = -0.593 ($P < 0.000035$)

However, such interactions do not have fixed values, they change continuously under the influence of both changing numbers of interrelated species, and of changing environmental conditions. Although these numerical changes are difficult to predict, because of lack of knowledge about these highly complicated and interwoven relations, the activities of humans in nature usually are more or less destructive by endangering the survival of some or even many species. Many ecologists suppose these interwoven relations form 'ecosystems', i.e. complicated networks of interrelations that are connected and kept together by feedbacks (e.g. Berryman 1987, 1990). Although feedbacks undoubtedly occur in the relations between populations coexisting at some site, there are no indications that an 'ecosystem' really would be a 'system' in the technical sense, such as the financial system of a bank, or the system of fiscal taxes of a country.

Carabid beetles and nature protection

From the first days of my studies of carabid beetles I noted that most species seem to show rather restricted needs of habitat conditions. Each carabidologist knows examples of closely related species living under quite different habitat conditions, e.g. one species in deciduous forest and the other in heath areas, or one species in young forest and the other in old forest, etc. Therefore, I thought the occurrence of special carabid species indicated special environmental conditions that might be of vital importance for many other species too: Den Boer (1977); see also Lindroth (1945) and Thiele (1977).

Although the effect of humans on nature reached almost catastrophic dimensions during the second half of the 20th century, it had already been going on for many centuries. Therefore, Turin & Den Boer (1988) could show that many changes in the carabid fauna of the Netherlands occurred during the last 100 years: some species disappeared completely (e.g. *Carabus intricatus*), the distribution of many species dwindled remarkably, whereas that of others (especially agricultural and nitrogen-loving species) increased.

As the models discussed in earlier sections were based on the hypothesis that environmental conditions were stationary, it was necessary to check to what extent this assumption could be validated. Especially the growing awareness in the sixties of possible effects of air pollution, which caused acidification and fertilization of the soil, alarmed us, because carabid larvae have to grow up in the soil. Therefore, Den Boer & Van Dijk (1994) checked whether stenotopic carabid species of heath areas (as indicated by Turin et al. 1991 as A1-species) had decreased in the Dwingelder Veld. Indeed, the year-catches of most A1-species became smaller in the seventies, whereas some eurotopic species had kept about the same numbers: Table 2. This means that the expected survival times of interaction groups of stenotopic heath species as discussed in earlier sections were too optimistic.

Following a preliminary atlas by Turin et al. (1977), this phenomenon was especially worked out by Turin et al. (1991). On the basis of hundreds of years of pitfall samplings all over the Netherlands, they showed that 33 types of habitat are characterized by the occurrence of special carabid species. In 665 pages Turin (2000) summarized our knowledge of the Dutch Carabid species: their distribution in the past (changes during about a century) and present; and their ecology, biology, choice of habitat and value as indicators for Nature Management.

Because of the enormous amount of knowledge brought together by a group of Dutch carabidologists, these easily sampled beetles, which can be found in sufficient numbers of species in each kind of habitat are excellent indicators of the quality of soil conditions. And since all organisms in some way (directly or indirectly) depend on soil conditions, carabid beetles indicate the quality of natural processes in general around the site of sampling.

TABLE 2. Estimates of the course of numbers in time of some characteristic carabid species at the Heath of Kralo of "Dwingelder Veld" (The Netherlands). All values are recalculated in such a way that they represent the summarized year-catches from 10 interaction groups (multipartite populations)

Species	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
AI – species																
<i>Carabus cancellatus</i>	18	10	12	14	13	25	23	11	12	4	3	2	–	1	2	–
<i>Carabus nitens</i>	24	20	6	8	15	12	17	12	14	–	2	2	–	–	–	–
<i>Harpalus solitarius</i>	–	–	35	26	30	34	32	89	43	12	8	–	–	18	–	2
<i>Amara infima</i>	–	–	10	30	22	58	42	65	32	14	18	193	143	72	33	32
<i>Cymindis vaporariorum</i>	24	32	34	18	16	12	9	21	23	13	15	10	38	15	27	15
<i>Agonum sexpunctatum</i>	5	7	3	3	4	12	8	6	10	8	4	7	2	4	6	6
<i>Amara equestris</i>	239	225	169	247	185	270	115	284	337	176	207	173	247	140	114	105
<i>Agonum ericeti</i>	93	51	148	117	86	96	158	64	85	77	55	20	45	84	56	42
<i>Olisthopus rotundatus</i>	12	30	72	79	35	48	59	42	–	–	3	7	11	15	59	61
<i>Bradycellus ruficollis</i>	415	1140	548	373	268	343	246	585	428	–	56	159	394	335	132	151
<i>Trichocellus cognatus</i>	267	426	199	262	297	604	179	173	313	27	88	418	491	1176	493	318
<i>Carabus arvensis</i>	112	123	43	50	66	92	66	143	164	59	29	14	5	3	–	–
<i>Pterostichus lepidus</i>	1073	1066	755	713	1393	2064	877	970	552	645	670	411	453	308	461	462
<i>Harpalus latus</i>	235	576	946	1060	958	1014	441	517	437	298	360	238	148	191	296	238
<i>Pterostichus diligens</i>	2322	1599	1905	2484	1443	1003	728	667	571	620	691	365	266	914	776	783
BI – species																
<i>Notiophilus germinyi</i>	15	14	30	20	28	9	25	26	42	6	3	5	4	2	25	23
<i>Bembidion nigricorne</i>	80	75	105	370	110	68	60	96	30	10	8	54	115	361	321	272
<i>Cymindis macularis</i>	–	–	–	–	10	9	21	14	65	38	21	12	9	2	9	9
Eurytopic species																
<i>Syntomus foveatus</i>	12	17	21	52	22	29	51	76	168	6	12	31	42	46	234	67
<i>Calathus erratus</i>	3075	1650	768	1245	2001	3412	1346	1754	1162	1216	483	427	925	995	1505	1057

Table 2. (continued)

Species	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
<i>C. melanocephalus</i>	2607	6056	5788	17630	15691	5492	2142	3302	6599	2375	660	479	651	1368	2626	1107
<i>P. versicolor</i>	1525	1859	2453	3179	3649	3154	2484	2368	2887	3043	2019	1432	1269	1556	1810	2382
<i>Amara lunicollis</i>	4152	284	3388	6728	3370	6408	799	2637	8242	6943	5148	892	1327	1001	1238	1118
Species	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	
A1 – species																
<i>Carabus cancellatus</i>	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	
<i>Carabus nitens</i>	–	–	–	–	–	–	–	1	1	1	1	–	–	8	34	
<i>Harpalus solitarius</i>	4	2	–	–	–	–	–	–	–	–	2	2	–	–	–	
<i>Amara infima</i>	91	114	43	15	22	17	6	3	–	–	3	–	–	–	–	
<i>Cymindis vaporariorum</i>	22	38	30	22	7	2	4	2	12	6	5	7	2	8	1	
<i>Agonum sexpunctatum</i>	5	–	2	–	3	2	3	–	–	21	33	80	30	57	38	
<i>Amara equestris</i>	211	334	403	181	87	28	43	17	14	3	16	21	44	71	9	
<i>Agonum ericeti</i>	28	15	14	8	–	6	3	14	29	35	68	186	29	25	36	
<i>Olisthopus rotundatus</i>	35	17	19	8	13	13	2	–	1	5	11	6	10	94	22	
<i>Bradycellus ruficollis</i>	117	179	169	118	92	94	84	79	94	98	82	156	5	30	155	
<i>Trichocellus cognatus</i>	138	182	134	89	93	34	27	45	37	57	33	51	12	46	149	
<i>Carabus arvensis</i>	–	4	18	12	12	480	335	156	143	95	97	52	70	102	199	
<i>Pterostichus lepidus</i>	554	791	993	920	1128	495	449	400	153	53	101	146	119	147	244	
<i>Harpalus latus</i>	100	81	100	83	86	75	96	75	96	108	174	276	163	132	161	
<i>Pterostichus diligens</i>	491	470	338	573	413	553	751	855	623	720	951	766	453	471	378	
B1 – species																
<i>Notiophilus germinyi</i>	13	10	–	–	3	3	–	–	–	–	3	–	1	3	2	
<i>Bembidion nigricorne</i>	59	14	6	29	–	2	–	2	1	14	3	4	–	1	34	

Table 2. (continued)

Species	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
<i>Cymindis macularis</i>	2	2	-	-	-	-	-	-	6	-	-	2	5	6	18
Eurytopic species															
<i>Syntomus foveatus</i>	70	13	6	9	2	3	-	1	8	10	52	10	33	102	66
<i>Calathus erratus</i>	635	317	397	510	459	137	74	78	147	74	43	273	536	653	727
<i>C. melanocephalus</i>	506	167	645	1529	3700	2011	1198	600	320	184	269	1289	1589	1333	978
<i>P. versicolor</i>	838	1034	1324	988	1178	1356	1063	964	1115	1072	967	900	827	528	419
<i>Amara lunicollis</i>	984	806	1051	1537	1847	1162	1050	2431	1955	1996	1682	2452	1060	1482	1884

Al – species are species of peaty soils and/or oligotrophic sandy soils

Bl – species are species of non-oligotrophic sandy soils with sparse vegetation (*Corynephorum*, and poor grassland)

The eurytopic species prefer peaty and/or sandy soils

These categories are described in Turin et al. (1991): Tables 2, 3 and 8.

In years with (-) not a single specimen of that species was caught in any of the sampling series.

Conclusions

This paper tries to show why carabid beetles are ideal indicators of the quality of natural processes, because:

1. In each kind of habitat you can expect **10–40 species** to occur in sufficient numbers to get a more or less **quantitative indication** of the quality of the soil, and therefore of the environmental conditions necessary for survival and reproduction of most animal and plant species at the site.

2. Carabid species occurring at some habitat-sites are easy to sample with a standard set of pitfalls, by which a **comparative study of the dynamics** of these species is possible.

3. A **year-catch** of some carabid species from continuous sampling with a standard set of pitfalls is a reliable relative estimate of **local density**, by which both year-catches from different populations of the same species, and successive year-catches at the same locality can be safely compared.

4. From successive year-catches of some local carabid population the **dynamics over years** can be followed as a series of **net reproduction values**.

5. Net reproduction values of populations of each species in the same climatological region form a **pseudo-lognormal distribution (LND)**, with which realistic random fluctuations of numbers can be simulated.

6. If the **Logarithmic Range (LR)** of some field population is compared with the LR's of **random walks of densities from the LND** of the species field populations appear to fluctuate between wider bounds than the simulated random walks.

7. Statements 4–6 enable us to estimate **expected survival times** of interaction groups under the assumption of stationary conditions; especially estimates with the model for **pseudo-turnover** seem to fit field values.

8. Survival times of interaction groups of carabid species depend on dispersal power: **T-species** (high dispersal) have short survival times, **L-species** (low dispersal) have longer survival times of local populations.

9. **Asynchronously fluctuating subpopulations spread the risk of extinction over these groups** and thus **increase the survival time of the multipartite population**.

10. **Different age classes and different genetic groups** in a population **spread the risk of extinction over these groups** and so **increase the survival time** of the population.

These statements also apply to other insect groups, because there is nothing special in the dynamics of carabid beetles. With the assumption that they – contrary to many other animal species – move randomly over the surface of the soil, many species can be accurately sampled with the same set of pitfalls. The

dynamics of a number of species can thus be compared directly. Therefore, carabid beetles can be a **master model for population dynamics**.

Just at the moment that the carabidologists working at the Biological Station were so far and were planning how our knowledge on these important indicators could be used in Nature Management the Agricultural University at Wageningen closed the Biological Station. The only thing we, my last Ph.D. student Rikjan Vermeulen and I, could do to save this kind of research for Nature protection was forming a Foundation, The Willem Beijerinck Biological Station (WBBS) and trying to get subsidised the necessary investigations. Together with Groningen University the first studies would have been started this year, but the outburst of 'foot-and-mouth-disease prevented entering our research areas'. We will start this next year.

Acknowledgements

During the more than 30 years I worked on the dynamics of carabid beetles I have had much help from coworkers, students and Ph.D. students. Most of them were acknowledged in the Communications of the Biological Station Wijster. Therefore, here I will mention the help I had from other colleagues to develop the ideas I presented in this paper. I am especially grateful to my Polish friend Jan Szyszko, who was one of the very few, who immediately understood what is the impact and importance of spreading of risk in nature. I am grateful that Hans Turin was able to bring together all information about the Dutch carabid species, by which he could emphasize the use of carabid species as excellent indicators. I have also to mention the fruitful contacts with my late friend Carl Lindroth and with late Hans-Ulrich Thiele.

I thank my friend Tom White (Adelaide) for correcting my continental English.

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