

# The role of density-independent processes in the stabilization of insect populations

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## 3.1 REGULATION AND NATURAL CONTROL

When I became involved in population dynamics in the 1950s, two concepts concerning the fluctuations of insect numbers dominated the literature: the hypothesis of regulation or governing of numbers introduced by Nicholson (1933), and the idea of natural control advanced by Thompson (1929, 1939). Nicholson supposed insect populations to be in a state of balance with the environment, i.e. special processes – later recognized as feedback processes (e.g. Wilbert, 1962, 1971; Bakker, 1964, 1971) – would return the density to an equilibrium which was determined by the average environmental conditions vital to the species. Thompson, who was an applied entomologist acquainted with biological control of insect pests, supposed insect numbers to be kept down by predators and parasitoids. This idea of natural control was clearly inspired by successes in the biological control of pest insects which had been inadvertently introduced into the USA. By introducing specific predator or parasitoid species from the pests' areas of origin, it appeared possible in some cases to keep such pests below the level where they cause serious damage to the relevant crops.

Hence, natural control, as a generalization derived from biological control, gave a possible explanation for the phenomenon that, under natural conditions, outbreaks of insect species are the exception rather than the rule. The balance of animal numbers, however, was entirely theoretical,

although illustrated by Nicholson (1957) with the help of laboratory experiments with blowflies. How can one show, for instance, that there is an equilibrium density in a natural insect population? And is such a supposed equilibrium density a constant, or, as supposed by Wilbert (1962), a variable equilibrium level that changes with changing environmental conditions? How can one estimate the values of such a variable equilibrium level in a natural population (see e.g. Wolda, 1989, 1991)? It is often assumed that the existence of an equilibrium level of density is a logical necessity when numbers are kept within positive limits over a long period of time by density-dependent processes. Nicholson (1933) probably had this in mind when stating (page 133) that "Populations must exist in a state of balance for they are otherwise inexplicable".

Although I consider the few successful cases of biological control to be legitimate field experiments supporting the hypothesis of the occurrence of natural control, I am also aware of the counter-arguments. Outbreaks of insect pests occur in spite of the presence of specific predators and/or parasitoids (and not only in crops, orchards and forest plantations). Added to this, difficulties in biological control arise if introduced enemies are so successful as to almost eradicate the prey species, thus causing the extinction of the controlling agent, so that it must be repeatedly reintroduced (e.g. Van Lenteren and Woets, 1988). In my opinion, these counter-arguments illustrate not only that biological control does not always succeed, but also that natural control is less self-evident than was initially believed. The lesson to be learnt from biological control, therefore, is not that insect populations are naturally controlled, but that predators and parasitoids are often, but not always, able to reduce high densities of prey species for a period of time. However, this does not prevent outbreaks or local extinctions. Although natural control is not a general principle, it gives a realistic explanation for the often effective reduction of high densities of many natural insect populations. However, at the same time, such a reduction in density increases the chance of a population reaching dangerously low densities in the future (underpopulation: Andrewartha and Birch, 1954; Den Boer, 1968), and may ultimately cause extinction.

### 3.2 RETURN FROM LOW DENSITIES

The hypothesis that insect numbers are in a state of balance with environmental conditions (Nicholson, 1933) requires not only that high densities return to some mean (equilibrium) level, but also that low densities return to the same level. Nicholson (1937) thought that a return of population density to the equilibrium level from either above or below was brought about by intraspecific competition: at high densities, competition would be so severe that mortality increased and reproduction decreased, thus the density would be lowered until a level without significant com-

petition was reached. At low densities, the animals would profit from the absence of competition by more easily obtaining enough of their necessary resources (in the first instance, food) to reduce mortality and increase reproduction, so that density would increase until a level of significant competition was reached again. Milne (1957b, 1962) assumed that intraspecific competition would operate only at high densities, when one individual obtaining its needs reduces the chances of others doing likewise. At lower densities, numbers would be determined by density-independent and/or imperfectly density-dependent processes. Milne claimed that density dependence is restricted to intraspecific competition at high densities, a view that stemmed from the observation that specific predators and parasitoids can keep down an increase in the density of their prey only after they have produced a new generation of adults. This delay in the response of specific enemies to a change of prey density causes the fluctuations in their number to lag behind those of their prey. In the deterministic regulation models of Nicholson and Bailey (1935), this resulted in the fluctuations in prey numbers showing an ever-increasing amplitude, i.e. the opposite of regulation. Nicholson (1937) supposed that intraspecific competition would not show this lag in a numerical response, at least not so far as mortality from competition was concerned. Later it was found, for example by East (1974), that generalist predators can also react without a time lag.

In view of the undeniably great effects of changes in physical conditions, especially weather, on insect numbers (e.g. Uvarov, 1931; Andrewartha and Birch, 1954), I considered that these theoretical discussions about a possible regulating mechanism were not very fruitful. I would expect physical conditions to be able to change insect numbers at least as vigorously as density-dependent processes, i.e. density-independent processes would determine the greater part of the variation in numbers. Moreover, I doubted whether, at low densities, environmental conditions will always be favourable, i.e. allow numbers to return to some mean (equilibrium?) density. To test the latter hypothesis, I checked for three species whether the mean egg production per female was always high enough to return low densities to the geometric mean (which is often considered to give a reasonable indication of the expected value of the equilibrium density). These species were selected because their population density was claimed to be regulated by a clearly indicated mechanism, and densities had been estimated for more than 10 years. It was evident that, in all three populations at the majority of densities below the geometric mean, egg production per female was too low to return density to this level in one generation (Figs 3.1-3.3). Indeed, in many years egg production per female would have needed to be many times higher than the maximum possible fecundity of the females; see section 2.3.7 of Den Boer and Reddingius (1996).

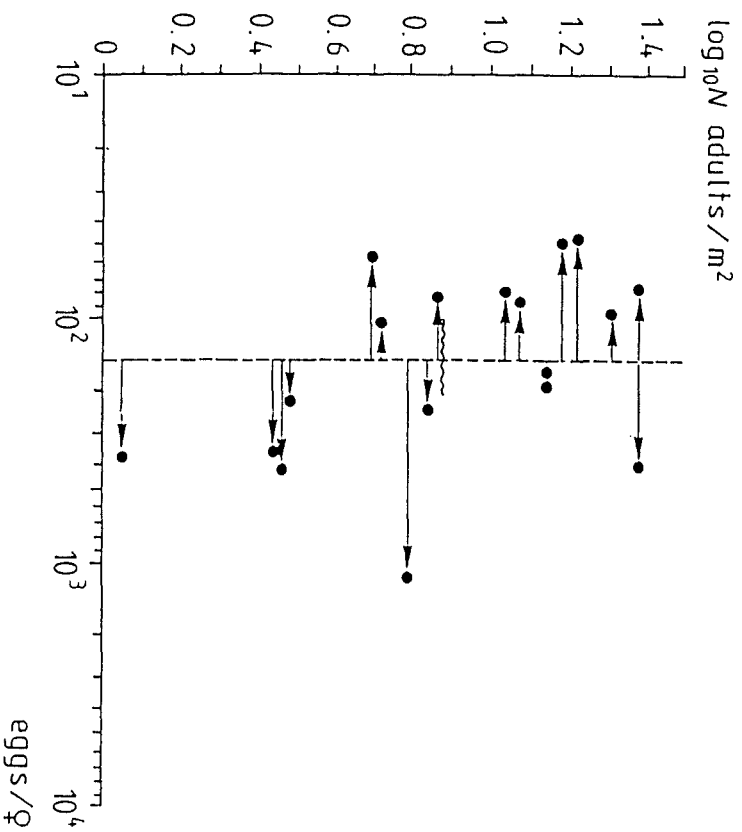


Fig. 3.1 Egg production (averaged per female) of winter moth (*Operophtera brumata*) in Wytham Wood, Oxford, in the period 1950–68, that would have been needed in each generation to compensate for total generation mortality (black dots), plotted against density of reproducing adults. The required egg production would return density to its supposed equilibrium value (the geometric mean); the geometric mean of density over these 18 years is 7.6 adults/m<sup>2</sup> canopy ( $\log_{10} = 0.88$ , horizontal wavy line). Sex ratio is assumed to be 1:1. Vertical broken line represents actual egg production per female, assumed to be about constant at 150 eggs. Data from Varley *et al.* (1973).

It may be objected that density might return to its mean level after some delay, i.e. not always in the next year, but after 2 or 3 years. I also checked this possibility (Table 2.2 of Den Boer and Reddingius, 1996) and, indeed, after an average of 3 years, decreasing densities turned into increasing ones, or *vice versa*. However, this delayed density dependence is exactly similar to what would be expected if densities fluctuated randomly (e.g. Cole, 1951, 1954). In addition, the supposed delayed density-dependent reactions tended to destabilize the fluctuations by increasing their amplitude, as is demonstrated in the time series of Fig. 3.4. In these

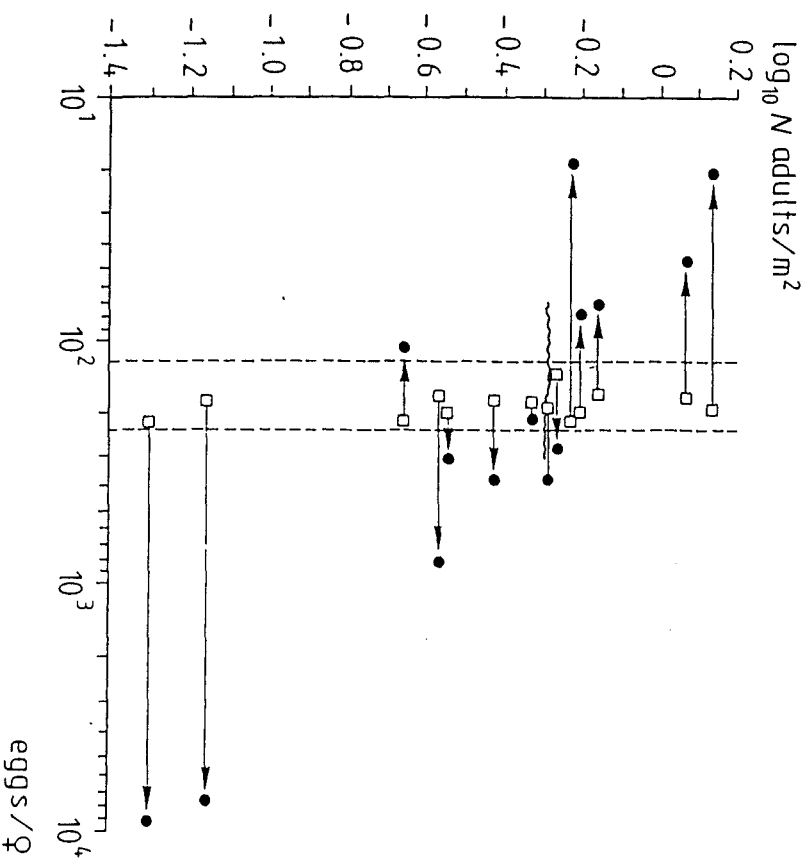


Fig. 3.2 Egg production (averaged per female) of pine looper (*Bupalus piniarius*) at Hoge Veluwe, the Netherlands, in the period 1950–63; relationship plotted as in Fig. 3.1. The geometric mean of density over these 14 years was 0.52 adults/m<sup>2</sup> canopy ( $\log_{10} = -0.28$ , horizontal wavy line). Sex ratio is assumed to be 1:1. Open squares between two vertical broken lines represent actual mean egg production per female as estimated by Klomp (1966) for each generation. A weak correlation ( $r_s = -0.20$ , NS) between density and mean egg production did not compensate for generation mortality. See caption to Fig. 3.1. Data from Klomp (1966).

field data the difference between highest and lowest density ( $\log$ -range) was greater (by the permutation test of Reddingius and Den Boer, 1989) than could be expected in more than 5–10% of the time series in which the same net reproduction values succeed each other randomly (except for larvae in August of the pine looper of Klomp, 1966) (Den Boer and Reddingius, 1989; but see also Den Boer, 1990a). Apparently, random walks of densities resulting from net reproduction values of the same magnitude, but in a different order (i.e. independent of the preceding

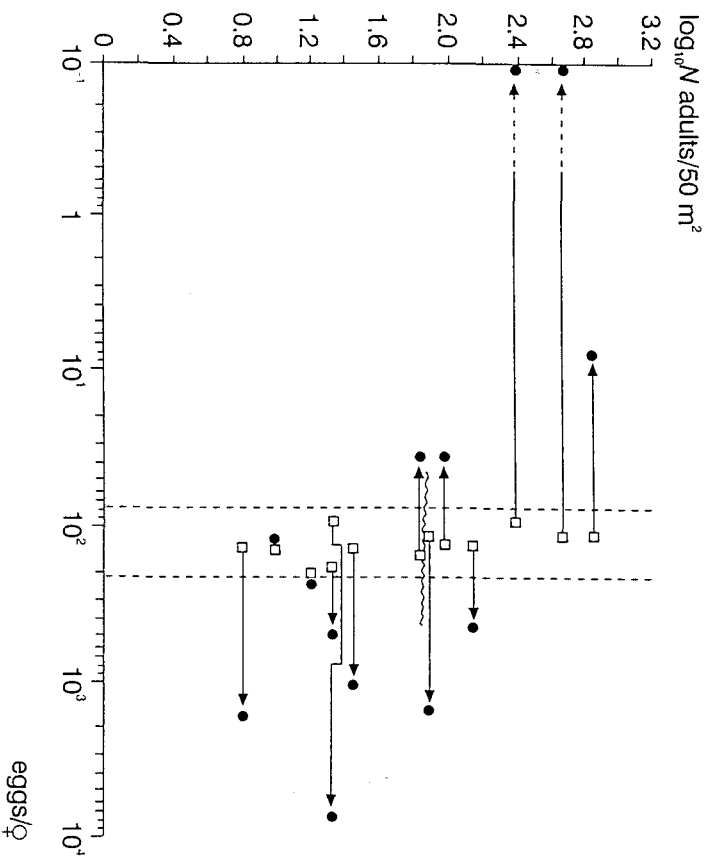


Fig. 3.3 Egg production (averaged per female) of the carabid beetle *Calathus melanocephalus* at Dwingelder Veld, Drenthe, the Netherlands between 1965 and 1978; relationship plotted as in Figs 3.1 and 3.2. Black dots show egg production per female needed to maintain density at the geometric mean over these 13 years: 75.9 adults per 50 m<sup>2</sup> heath ( $\log_{10} = 1.88$ , horizontal wavy line). Open squares between two vertical broken lines represent actual egg production in the field as derived from relationship between eggs in ovaries and eggs laid according to Table 3 of Van Dijk (1986). Significant correlation ( $r_s = -0.54$ ,  $P = 0.05$ ) between density and egg production did not compensate for generation mortality. Note that at two of the higher densities of adults, the number of old adults surviving from the preceding year is sufficiently high to maintain density at its mean level, so that no egg production would have been necessary. See further captions to Figs 3.1 and 3.2. Data from Baars and Van Dijk (1984).

densities) may often be more stable than time series observed in the field (see also Den Boer, 1991), because in random walks the delayed density-dependent effects are removed. As stated above, this destabilizing effect of delayed density dependence was evident in the deterministic models of Nicholson and Bailey (1935), and can also be expected to play some part in the more stochastic situation of field populations.

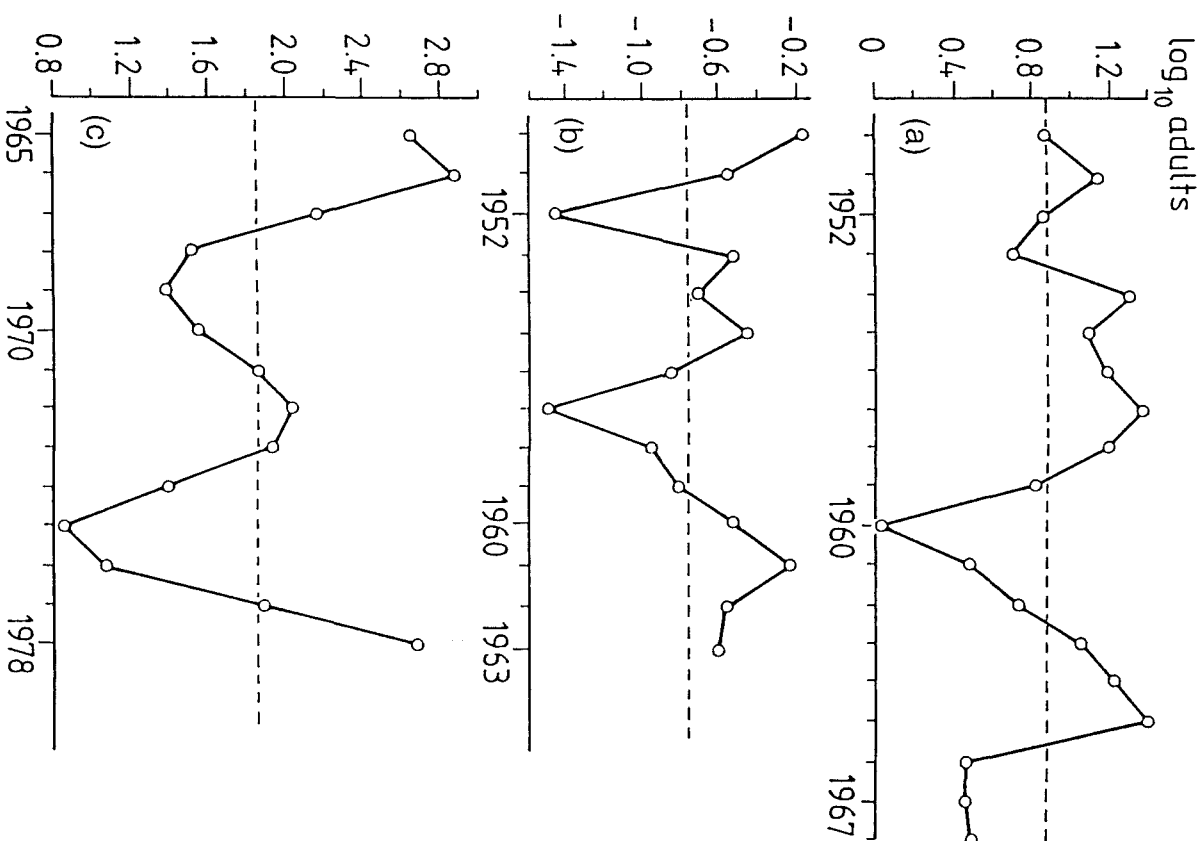


Fig. 3.4 Adult density ( $\log_{10}$ ) in a number of succeeding years in (a) winter moth in Wytham Woods, Oxford (Varley *et al.*, 1973); (b) pine looper at Hoge Veluwe, the Netherlands (Klomp, 1966),  $\log_{10}$  reproducing adults; (c) carabid beetle *Calathus melanocephalus* at Kralo Heath, Dwingelder Veld, the Netherlands (Baars and Van Dijk, 1984).

If insect populations were regulated by some feedback mechanism, density would fluctuate (after some initial period after founding) between constant limits, i.e. the log-range (log highest density minus log lowest density) would not increase with time (Fig. 4.13 of Den Boer and Reddingius, 1996). Den Boer (1991) showed that in all time series longer than 10 years, including those claimed to be regulated, the log-range increased over time to the same degree as in random walks of density. Hence, in none of these was density kept within limits, as could have been expected with densities in a state of balance with environmental conditions.

Nevertheless, regulation of density is not impossible in field populations. If in each generation, both the production of reproducing adults is sufficiently high to compensate for the losses in the preceding generation, and high densities are effectively controlled, such a population might be considered regulated. Kluuyver (1971) convincingly showed that a population of great tits on the isle of Vlieland was regulated according to these criteria. Even taking away 40% of the eggs or young did not disturb the stability of this population, where density was effectively restricted by territorial behaviour in each generation. It was a pity, however, that the situation studied by Kluuyver was artificial, insofar as the birds were breeding in nest boxes, in which survival of eggs and young is much better than in natural tree holes (see further Den Boer and Reddingius, 1996). Nonetheless, the possibility cannot be excluded that natural populations of some territorial species might be regulated if the production of reproducing adults is always high enough to compensate for losses in the preceding generation, and if the exchange of individuals with other groups of the same species, i.e. the turnover of individuals, is not greater than the changes of the number of autochthonous individuals. It would be worthwhile to check populations of territorial vertebrates for these conditions, but I do not expect insect populations will be found that can be considered regulated according to these criteria.

It must be noted that the tests developed in recent decades for overall density dependence in time-series data (Reddingius, 1971; Bulmer, 1975; Pollard *et al.*, 1987; Dennis and Taper, 1994) indicate only the occurrence of statistical density dependence; they do not tell us anything about the biological processes that may be involved. Although density dependence is a necessary condition for regulation to occur, it is not a sufficient condition. Den Boer (1990a) gives some examples of the application of such tests producing significant results without the operation of a density-dependent mechanism. For instance, after a sudden drop in density, Bulmer's (1975) first test often gives a significant result. Sometimes random walks of density give significant results in tests for density dependence, if by chance they do not show a clear trend for a large number of generations. Long series of unreliable estimates of density may give sig-

nificant results with the test of Dennis and Taper (1994), e.g. data from light traps (Wolda and Dennis, 1993; section 6.5.3 in Den Boer and Reddingius, 1996). Averaged estimates from large and heterogeneous areas in long time series may give significant results with almost all of these tests; compare the *Pimplis* data over 60 years in Den Boer (1990a). Hence, application of these tests gives an indication that some interesting processes might have been operating in the population concerned, but a careful analysis is required to decide whether or not these processes have anything to do with regulation of numbers, or even with some kind of overall density dependence. For instance, many correlations with density may be indirect or even chance events.

### 3.3 OVERALL QUANTITATIVE EFFECTS OF DENSITY-INDEPENDENT FACTORS

Although I do not deny the possibility of the occurrence of natural control over a period of some decades, and once a regulated population in the sense of Nicholson (1933) is actually found, I will not deny it, I am sure that density-independent forces have played a decisive role in the dynamics of the majority of insect populations observed by ecologists. In other words, I believe that neither natural control nor regulation of numbers gives a sufficiently general theoretical base for the explanation of the fluctuating patterns of insect numbers observed in field populations. In particular, physical factors (weather) will significantly influence insect numbers (Uvarov, 1931). Some examples are given below.

Because of an extreme drought in the summer and autumn of 1959, many populations of the caddis fly *Ecnoclyta pusilla* became extinct in drier parts of the Netherlands (Van der Drift, 1963). In a moist forest that I sampled with pitfalls, the catches of full-grown larvae of this caddis fly fell from about 11 000 in the spring of 1959 to seven in the spring of 1960, because of the almost total mortality of young larvae in the exceptionally dry September–October of 1959. In a much wetter forest, numbers fell from about 3400 to 50 (section 2.3.6 of Den Boer and Reddingius, 1996). In a moist winter, more than 95% of the over-wintering larvae of *Calathus melanocephalus* (and most probably of other autumn-breeding carabid beetles) become infected by fungi and die (Van Dijk and Den Boer, 1992), dramatically decreasing the number of reproducing adults in the next year. On the other hand, after a dry winter the number of reproducing adults usually increases. For a period of 17 years (1971–87), both the yearly increases and decreases in the number of reproducing adults fitted the alternation (with a period of about 3 years) of moist and dry winters, respectively (Van Dijk and Den Boer, 1992). Because insects are poikilothermic, all of their activities and processes are highly dependent on temperature. For instance, in *C. melanocephalus* (and most probably in other

carabid species), four times more eggs are laid at 19 °C than at 8.5 °C (Van Dijk, 1979, 1982). See Uvarov (1931) for more examples.

After the severe winter of 1995–96, I observed a spectacular example of the phenomenon, well-known among entomologists, of the increase in numbers of many insect pests, most probably because over-wintering larvae and pupae did not die from fungal disease. In spring 1996, all around Wijster enormous outbreaks of winter moth, *Tortrix viridana*, a number of miners and some other moths occurred, which resulted in local defoliation of trees in many sites. Density-independent changes in the quality of the food, especially nitrogen content, can cause both outbreaks and crashes of insect numbers (Van Dijk, 1996; White, 1993).

In general, the variation between years of many density-independent factors affecting insect numbers may be much greater (sometimes even many times greater) than the variation of density-dependent processes, so that the effects of the latter are overwhelmed and cannot regulate numbers. An example of this is given by Den Boer (1986a). In the carabid *C. melanocephalus*, the effect on numbers of the density-dependent egg production is completely overwhelmed by the much greater variation in larval mortality, over years. In order to regulate numbers, the variation of density-dependent processes must be at least as great as the variation of all density-independent forces.

As we cannot make science by merely piling up examples, I will not give more examples of the huge impacts that density-independent factors may have on insect numbers. Instead, I will discuss the effects of heterogeneity in both populations and environment on insect numbers, which gives an alternative explanation for the often surprising stability over time of some insect populations.

### 3.4 THE INTERACTION GROUP AS A UNIT OF POPULATION

When I was first confronted with the hypothesis of the regulation of animal numbers, I realized that this idea stemmed from a mechanistic view of natural processes. I have no objections to mechanistic and deterministic hypotheses about natural processes, but I doubt whether such hypotheses can successfully explain the apparently restricted fluctuations of insect numbers over time. One can argue that a balance of animal numbers can be supposed to exist only if the individual animals either all have the same chance of survival and reproduction, or show a stable frequency distribution of the critical properties, e.g. a stable age distribution and/or a stable frequency distribution of reproductive rates. The population area should also be homogeneous, so that the individual animals can be distributed uniformly in space, and be affected to the same degree everywhere by relevant environmental factors. Although these necessary conditions can be relaxed somewhat without completely abolishing the

possibility of population regulation, rapid and disorderly local changes of environmental conditions and the composition of populations, in my opinion, are not compatible with a balance of animal numbers over long periods of time.

My field experiences have convinced me that even in a seemingly homogeneous environment such as a uniform heathland, relevant environmental factors, e.g. temperature, can change over short distances (e.g. Den Boer and Sanders, 1970). Therefore, the environment of a natural population will consist of many microhabitats in which the fate of individual animals may be very different, and usually difficult to predict. Moreover, among iteroparous carabid populations studied in the field, we observed neither a stable age distribution (see e.g. Den Boer, 1979; Baars and Van Dijk, 1984), nor a stable frequency distribution of genotypes (e.g. Den Boer *et al.*, 1993); frequencies of both changed from year to year in a disorderly manner. Therefore, I did not see a rosy future for the application of the regulation hypothesis to natural insect populations, and this led me to think about possible alternative explanations for the relative stability of some insect populations. Such an alternative should incorporate the natural variability in the composition of field populations and in their environments.

Heterogeneity and variability should not be considered as just drawbacks of field data, to be averaged away in order to discover the underlying more deterministic rules of nature. They should be recognized as fundamental features of a natural situation. The chance of survival of a population may even be increased if variations between individuals within that population make it possible for them to cope with the variations in environmental conditions in space and time (Den Boer, 1968). For instance, in cold periods and at cold sites in their habitat, cold-resistant individuals will have a better chance of survival than more sensitive individuals. The same applies to heat-resistant individuals during warm periods and at hot sites in the habitat. In other words, the risk of dying from lethal temperatures is spread over individuals with different tolerances to extreme temperatures. The number of victims of such temperatures will be restricted to the unlucky sensitive ones, that were at the wrong site at the wrong time. This relationship between spreading of risk and chance to survive is the *raison d'être* of the insurance business.

In almost every natural population there will be sufficient genetic and/or phenotypic variability in sensitivity to relevant environmental variables to simulate a degree of risk spreading that resembles the situation met by an insurance company: the reduction of extreme losses, so that the fluctuation of losses over time is more or less stabilized around a certain value. Note that this value is not an equilibrium value, but a simple mean, because there is no mechanism operating that tends to return deviations from this mean, either in the payments of the insurance com-

pany, or in the losses from natural populations. In both cases, the time series result from a succession of chance realizations.

Reddingius and Den Boer (1970), Reddingius (1971) and section 4.3 of Den Boer and Reddingius (1996) demonstrated that stabilization of animal numbers by spreading of risk might occur when variability and/or heterogeneity of reproduction and/or mortality are introduced in otherwise unspecified simulation models. This suggests that this kind of stabilization may be quite general in field populations. To test this supposition, I sampled field populations in such a way that the degree of variability and/or heterogeneity in reproduction and mortality can be estimated and compared under different conditions. I decided first to concentrate upon the effects of heterogeneity in space, to see whether the fluctuations of numbers over time, in subpopulations at different sites of the same habitat, may differ as a result of differences in the reproduction and mortality of individuals.

The first problem to solve was: how to define a subpopulation as an adequate unit of population, i.e. as a group of individuals the composition (and local environmental conditions) of which differ from those of other subpopulations within the same population area. As we were working on the dynamics of carabid beetles, we already knew that both eggs production and mortality are significantly determined by physical factors, such as temperature (e.g. Van Dijk, 1982). We also knew that the relevant physical factors are affected to a high degree by the structure of the vegetation (e.g. Den Boer and Sanders, 1970). Hence, we decided to sample differently structured sites within the same heathland, the Heath of Kralo (part of the National Park Dwingelder Veld) in the Netherlands. However, in this large heath area it was difficult to determine which individuals may be considered to belong together, i.e. to form a subpopulation that differs from other subpopulations.

This problem was attacked and solved by Martien Baars. Individual carabid beetles of two heathland species were radioactively marked and tracked with a sensitive scintillation detector. The directions of movement appeared to be arbitrary, and the distances covered fell into two classes, short distances, called random walks, and long distances in a more or less fixed, but arbitrary, direction, called directed walks. From the frequency distributions of directions and of the two groups of distances, the pattern of movement could be simulated in a computer programme. With this computer programme, the movements of a thousand individuals of two species, *Calathus melanocephalus* and *Pterostichus versicolor*, could be simulated, and the area covered by these movements estimated (Baars, 1979a). Using a thousand brand-marked beetles, released in small groups in the field and recaptured at different distances, the results of the simulations could be checked and were found to be sufficiently close to reality. At the same time, Baars (1979b) showed that year-catches in standard sets of pit-

falls give reliable estimates of local densities. This was confirmed by Den Boer (1979) for four other species, with the help of extensive mark-recapture experiments in a small forest. The correlation between actual mean densities and year-catches in all cases tested is almost unity.

Ninety percent of the individuals of *C. melanocephalus* caught during a year (year-catch) in a standard set of pitfalls appeared to have moved around an area of about 2 ha. Such a group of beetles of the same species is called an interaction group, because these individuals are readily able to meet and interact. The other 10% of the year-catch are considered directed movers that had covered greater distances, i.e. had moved in from outside the interaction group and were thus connecting different interaction groups by exchange of individuals. To give some idea of the size of an interaction group: at the Heath of Kralo, an interaction group of *C. melanocephalus* consists of about 10 000 to 200 000 beetles, of which about 30 to 900 will be caught in a standard set of pitfalls in a year-catch (Fig. 2.2 of Den Boer and Reddingius, 1996). In the same way, it was established that the individuals in an interaction group of *P. versicolor*, the adults of which are twice the length of those of *C. melanocephalus*, move around an area of about 12 ha and at the Heath of Kralo will consist of about 30 000 to 130 000 individuals, of which about 250 to 1000 will be caught in a year-catch (Fig. 2.12 of Den Boer and Reddingius, 1996). An interaction group of the related *Pterostichus lepidus* lives in about the same area of 12 ha, but will consist of fewer individuals at most sites. Small beetles will tend to move over small areas and big beetles over large areas; for instance, an interaction group of *Carabus cancellatus*, another heathland species with individuals of about four times the length of *C. melanocephalus*, will cover an area of more than 700 ha.

### 3.5 SPREADING OF RISK IN SPACE

What are the results of comparing the patterns of fluctuation in numbers in different interaction groups over years, to test whether they are the best population units for studying the dynamics of carabid beetles? Our standard pitfall sampling enabled us, over many years, to estimate the annual relative densities (year-catches) of some carabid species occupying differently structured sites in the entire Heath of Kralo. Taken together, the interaction groups of each species can be considered a random sample of all interaction groups of that species covering the whole area and thus forming a multipartite population, i.e. a population that consists of a continuum of mutually merging interaction groups (section 9.2 of Andrewartha and Birch, 1984).

Let us take *Pterostichus versicolor* as an example (see Fig. 3.5 for details). Figure 3.6 shows the fluctuations in numbers over years of 10 interaction groups, and of the total (multipartite) population that can be considered

to be composed of these 10 interaction groups. Section 4.4.3 of Den Boer and Reddingius (1996) showed that the limits between which the density was fluctuating ( $\log\text{-range} = LR$ ) in the multipartite population (consisting of six of these interaction groups sampled for at least 25 years) was reduced to 58% of that of an average interaction group (with mean  $LR$  values). Such an increased range stability for a multipartite population, as compared to an isolated interaction group, results in an increase in its expected survival time under stationary conditions, in the present case, an increase by a factor of  $> 10$  (see Den Boer, 1981).

For students who like to draw conclusions from the application of the current density dependence tests, it might be interesting to mention that

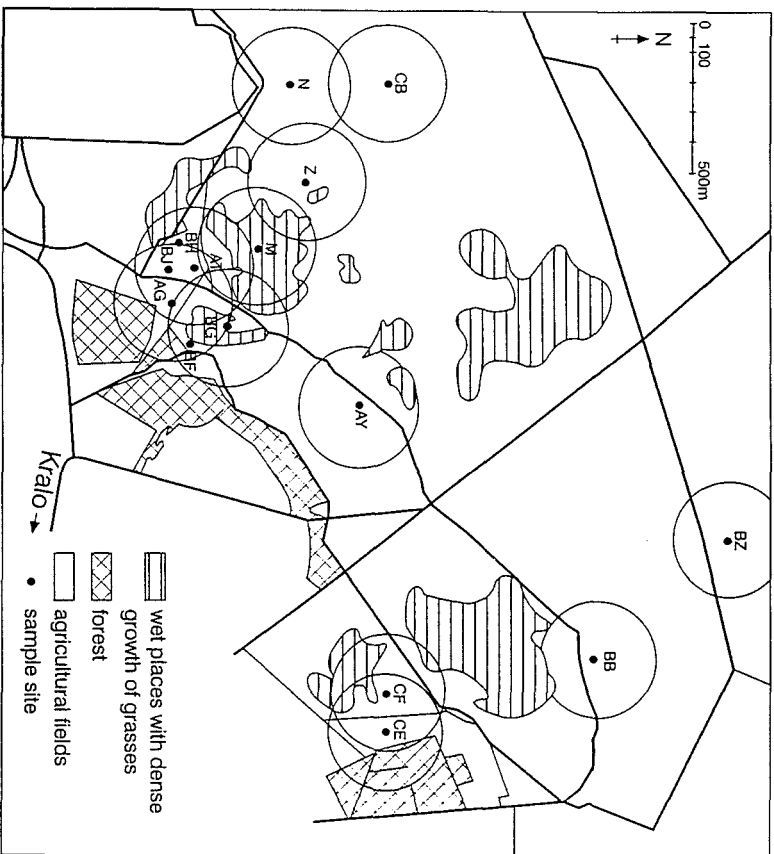


Fig. 3.5 Some interaction groups of the carabid beetle *Pterostichus versicolor* occupying areas of about 12 ha each (circles) around a standard set of pitfalls at Krato Heath, Dwingelder Veld, the Netherlands. The heath area is uninterruptedly populated by this species. Radioactively marked beetles of this species cover about 180–190 m during a year (as the crow flies). For the carabid beetle *P. lepidus* these interaction groups will cover about the same areas.

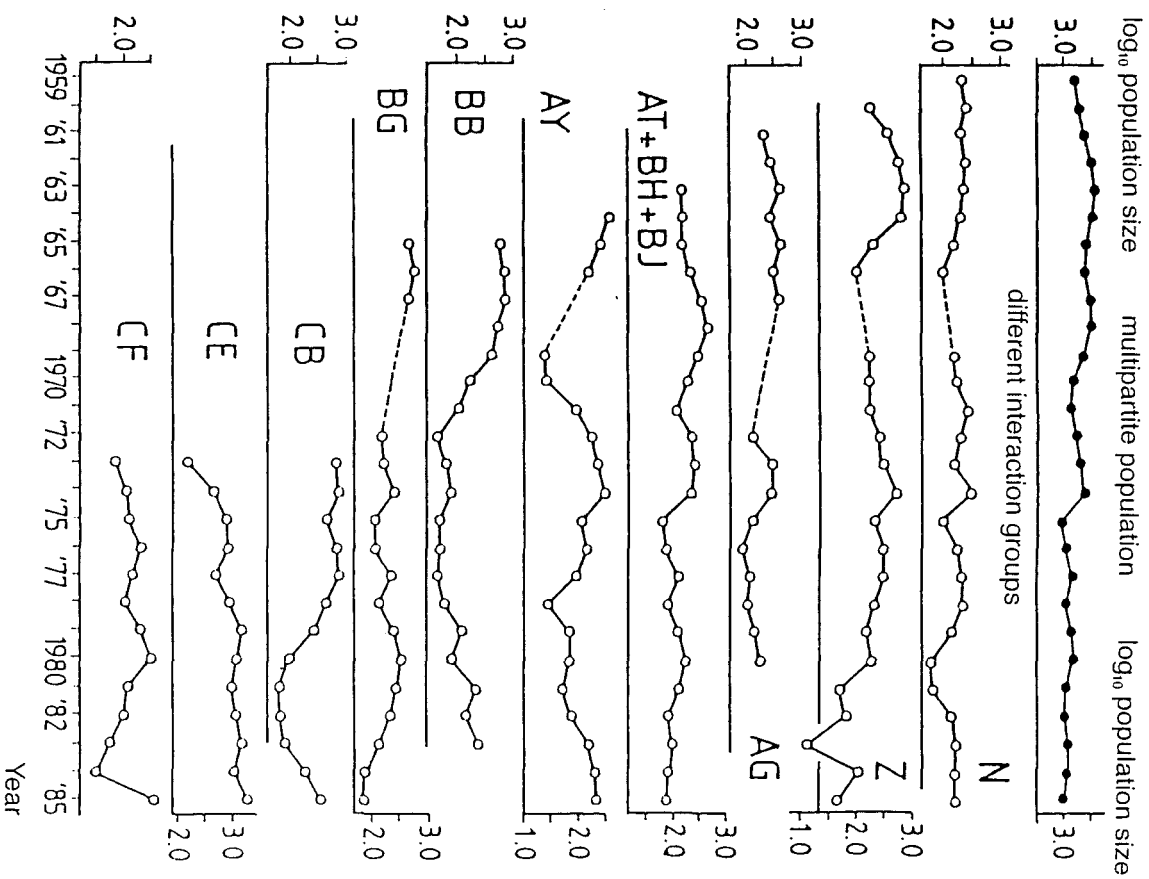


Fig. 3.6 Fluctuations of year-catches in standard sets of pitfalls in different interaction groups (subpopulations) of the carabid beetle *Pterostichus versicolor* at Krato Heath, Dwingelder Veld, the Netherlands. At top, fluctuations in the multipartite population composed of these interaction groups. Capital letters indicate different sample sites pictured in Fig. 3.5. Data from Van Dijk and Den Boer (1992).



over many years the densities in one, but only one, of the interaction groups (group N in Fig. 3.6) scored significantly with Bulmer's (1975) first test, and almost significantly ( $P=0.054$ ) with the test of Pollard *et al.* (1987). In my opinion, this was not because this interaction group, and none of the others, had been regulated by some density-dependent process(es), but because, by chance, the numbers of adults did not show a distinct trend during these 25 years. This suggests that density has in some way been kept between limits. From our work with this species, no indications of stabilizing density-dependent effects were found. On the contrary, both larvae and adults are polyphagous predators, individually hunting all kinds of available arthropods, so that intraspecific competition for food does not seem a very probable option, the more so because a number of carabid species of about the same size are living in the same sites and are hunting the same kinds of arthropods (Hengeveld, 1980).

The significant negative correlation between mean density and the mean number of eggs in the ovaries, as found in another interaction group (AG) by Baars and Van Dijk (1984), was an indirect one, and most probably resulted from changes in food quality which are known to have a strong effect on the egg production of carabid beetles (Van Dijk, 1996; personal communication), and which by chance might have been correlated with changes in density (see also Den Boer, 1986a). Intraspecific competition for food is not a very probable hypothesis in this case, because many kinds of potential prey species were found in this site (to judge from other arthropods both caught in these pitfalls and found as remnants in the intestines of *P. versicolor*; Hengeveld, 1980). Also, the density of *P. versicolor* in AG was relatively low as compared with that in other interaction groups sampled (Fig. 3.6).

It must be noted that the multipartite population of this species scored nearly significantly ( $P=0.062$ ) with the permutation test of Reddingius and Den Boer (1989). As the multipartite population is heterogeneously composed of a number of different interaction groups, this will not result from the succession of net reproduction values being favoured by some density-dependent process(es). We should realize that the multipartite population shown is a rather arbitrary collection of interaction groups, but this is only used to illustrate the possible effects of spreading of risk in space. Hence, by chance, the combination of some interaction groups may have resulted in a relatively favourable succession of net reproduction values. However, this spreading of risk is not optimal, for the fluctuations of numbers in the different interaction groups are not independent: the coefficient of concordance (W of Kendall, 1955) being 0.22 ( $P\approx 0.01$ ). Strictly speaking, we cannot exclude the possibility that density-dependent processes, which affect the course of numbers over time, are also operating in some interaction groups, but we would not expect a significant stabilizing effect from such processes; see also Wolda and Dennis (1993), Wolda *et al.* (1994).

Figures 3.7 and 3.8 show that in the species *Pterostichus lepidus* (with interaction groups occupying about the same area as *P. versicolor*) and *Pterostichus diligens* (with interaction groups covering much smaller areas), the spreading of risk in space over interaction groups has similar results as in *P. versicolor* (33 and 40% reduction of LR, respectively, in the multipartite population). In these three species, the variation of net reproduction within interaction groups over years is about the same as the variation of net reproduction within years over interaction groups, and therefore the latter variation can approximately compensate for the former, provided there is sufficient exchange of individuals between interaction groups; see also section 4.4.3 and Table 4.6 of Den Boer and Reddingius (1996). The exchange of individuals between adjacent interaction groups is not known exactly, but is estimated to be between 5 and 20% of the individuals (see Den Boer, 1991), which is sufficient to level out differences in density fluctuations between adjacent interaction groups.

Although the above examples of spreading of risk in space were established by studying a number of interaction groups, similar results would have been found by studying habitat patches (e.g. Hassell, 1987) or subpopulations of a metapopulation (e.g. Hanski, 1991), or some other grouping in which individuals are expected to interact. The only necessary condition is that there is sufficient exchange of individuals between asynchronously fluctuating groups to contribute a certain degree of spreading of risk, by levelling out fluctuations of density and in preventing local extinctions (compare Den Boer, 1991). In fact, the subpopulation model of Reddingius and Den Boer (1970) is a general model, illustrating spreading of risk in space by exchange of individuals between groups, whether these groups are patches, interaction groups or subpopulations of a metapopulation. Note that, as shown by simulations, the degree of spreading of risk, i.e. the reduction of fluctuations in the total population by exchange of individuals, is not affected significantly by whether the exchange is density-dependent or density-independent.

In the species *Annina lunicollis* (Fig. 3.9) and *Galathus melanocephalus* (Figs 3.10 and 3.11) the resulting stability of the multipartite population is much smaller (15 and 23% reduction of LR, respectively), because the variation of net reproduction values within interaction groups over years is much greater than the variation within years over interaction groups, so that the latter variation cannot compensate for the former. In particular, in *C. melanocephalus* the different interaction groups fluctuate almost in parallel and have a coefficient of concordance (W) of 0.65 ( $P < < 0.001$ ). For an explanation of these synchronous fluctuations in different interaction groups, rarely observed among carabid beetles, see Van Dijk and Den Boer (1992).

In spite of the significant negative correlation between mean density and numbers of eggs in ovaries found by Baars and Van Dijk (1984) in

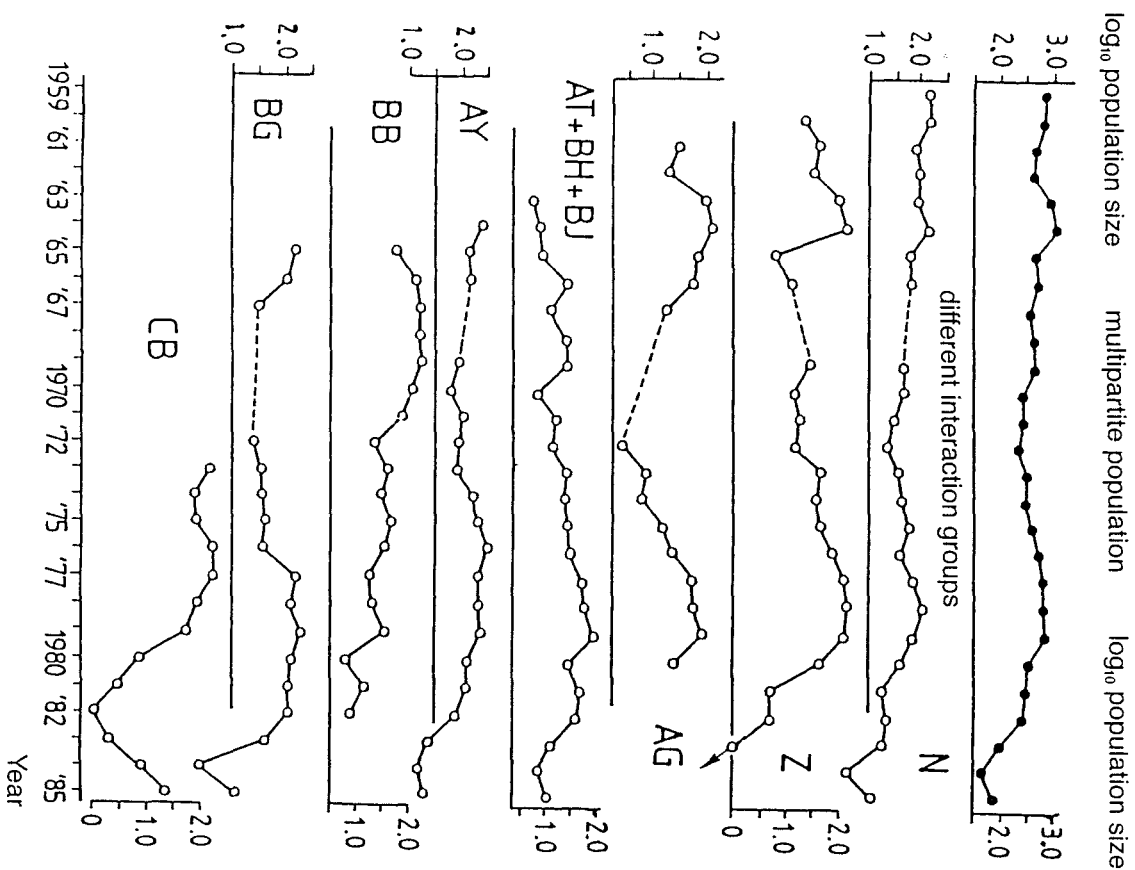


Fig. 3.7 As in Fig. 3.6, for the carabid beetle *Pterostichus lepidus* at Kralo Heath, Dwingelder Veld, the Netherlands. Areas of interaction groups are pictured in Fig. 3.5.

two interaction groups of *C. melanocephalus* (AG and [AT+BH+BJ], Fig. 3.10), neither the separate fluctuation patterns of any of the interaction groups sampled, nor that of the multipartite population, scored significantly with any of the tests for overall density dependence proposed in

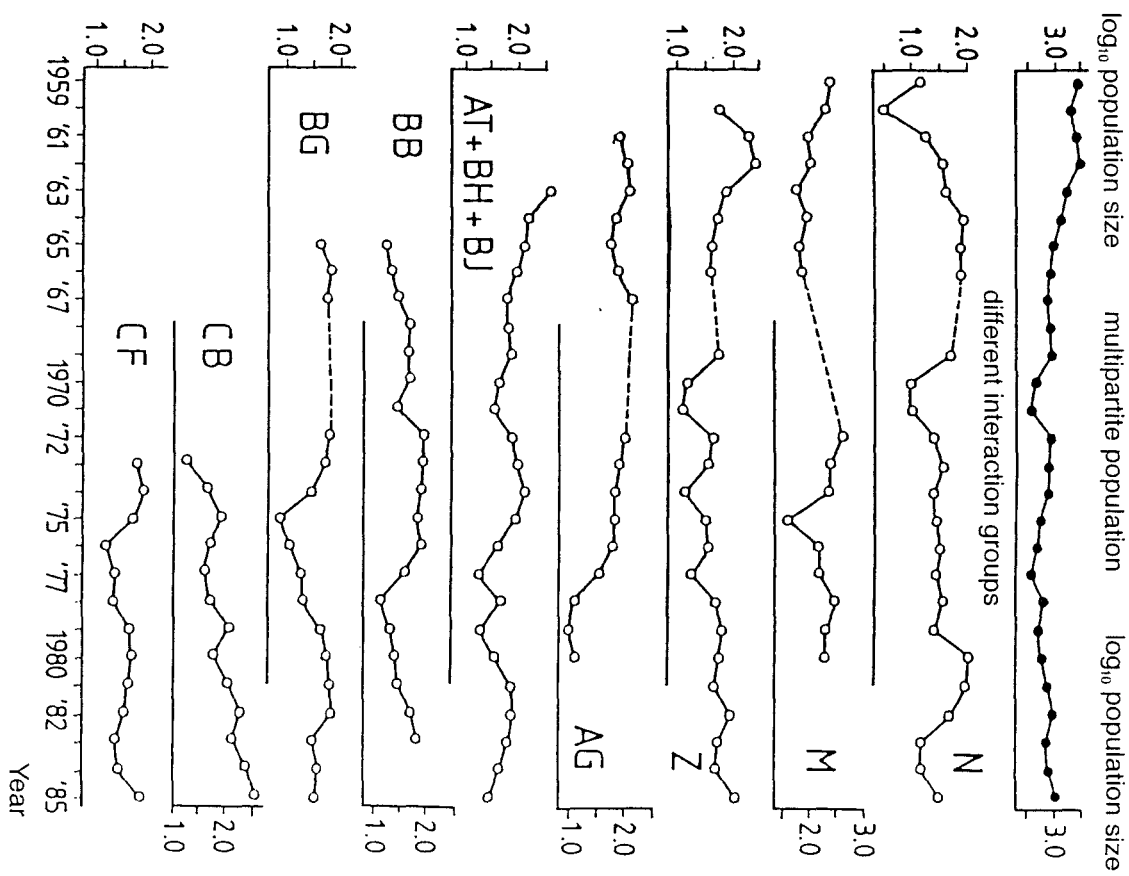


Fig. 3.8 As in Fig. 3.6, for the carabid beetle *Pterostichus diligens* at Kralo Heath, Dwingelder Veld, the Netherlands. Areas of interaction groups will be about as pictured in Fig. 3.10.

the literature in recent decades. As expounded by Den Boer (1986a), this lack of density dependence in the fluctuation patterns of this species must be caused by the variation in survival of larvae over years being many times greater than the variation in size of egg production over

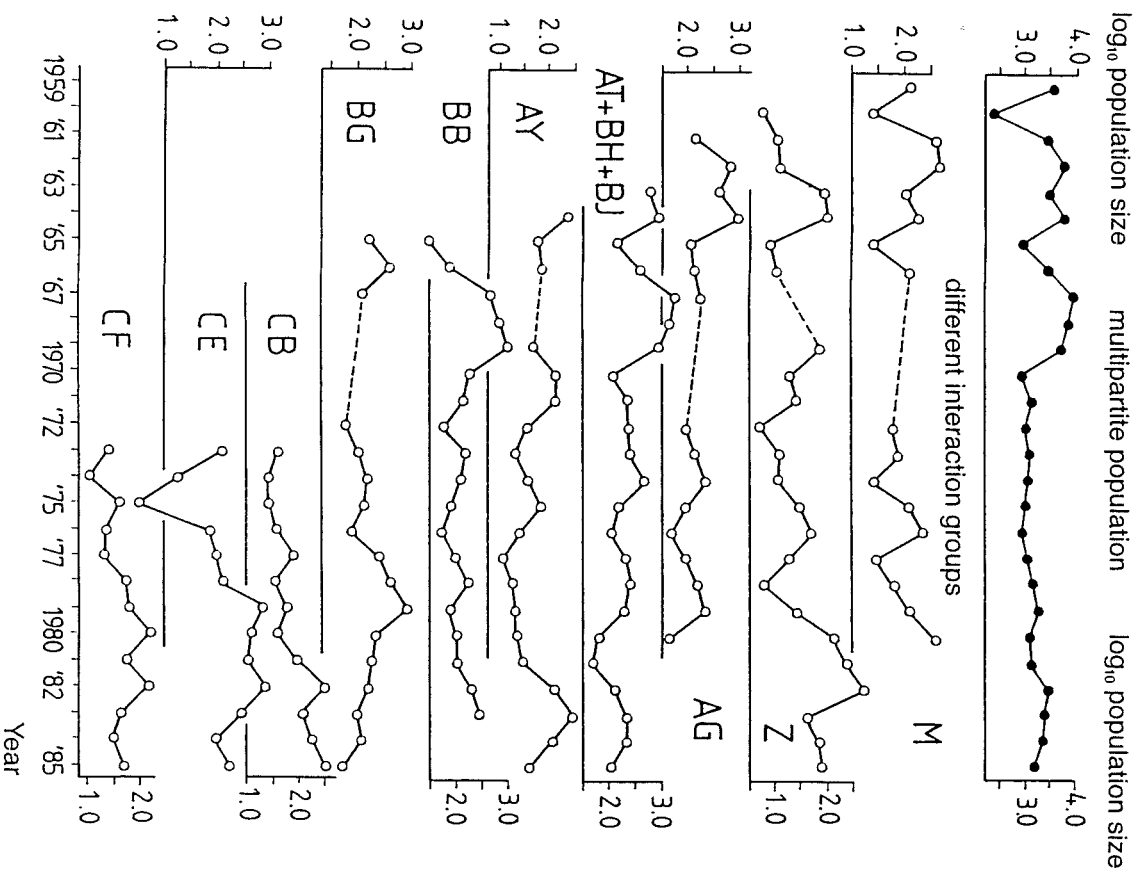


Fig. 3.9 As in Fig. 3.6 for the carabid beetle *Amara luricollis* at Kralo Heath, Dwingelder Veld, the Netherlands. Areas of interaction groups are not exactly known for this species.

years, so that the latter variation is almost completely overwhelmed by the former. Just as expected in *P. versicolor* (see above), the density-dependent egg production in this species probably results from changes in the quality of food species.

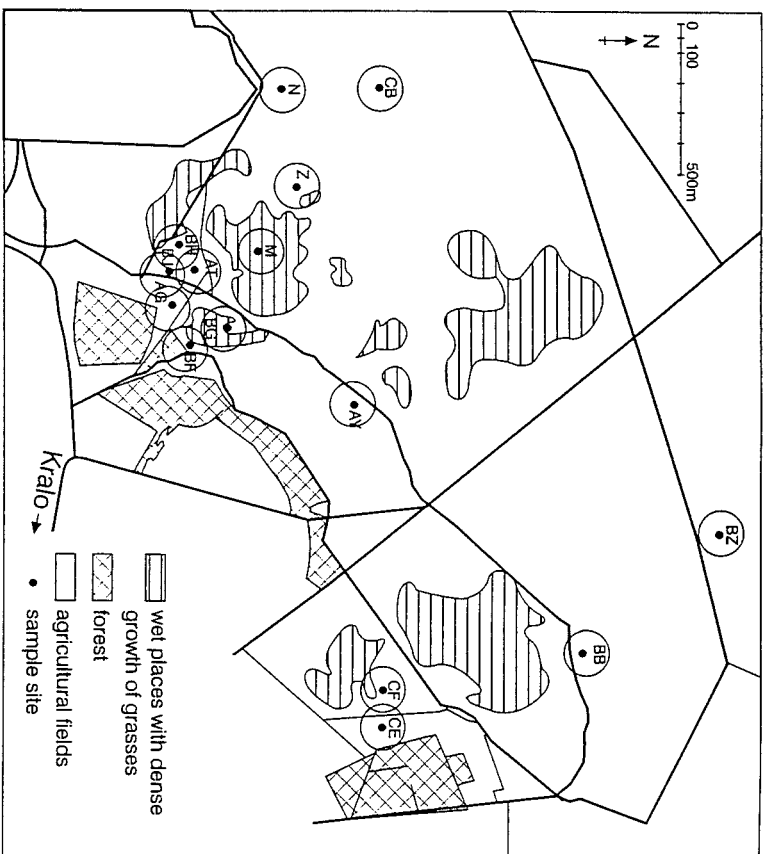


Fig. 3.10 Some interaction groups of the carabid beetle *Calathus melanocephalus* at Kralo Heath, Dwingelder Veld, the Netherlands. Each interaction group occupies an area of about 2 ha, circles with a radius of 80 m around a standard set of pitfalls.

The importance of food quality is indicated by Fig. 3.12, which shows that low numbers of eggs in the ovaries not only coincide with high densities of adults, but also with outbreaks of the heather beetle (*Lochmaea suturalis*). These outbreaks severely damage the heather and result in low quality food for other phytophages on the heather (Den Boer, 1986b). As such phytophages (especially larvae) are important prey species for *C. melanocephalus*, the adults of this species necessarily consume low quality prey. In addition, the abundant larvae of the heather beetle are of little value, because these are more or less toxic to the adults of *C. melanocephalus*. Although they do not prefer the larvae of the heather beetle, adults can hardly avoid eating them, because they actively crawl in high numbers on the soil surface in search of undamaged heather plants. Consumption of these larvae results in almost complete cessation of egg production and sometimes even in premature death (section 5.5.4 of Den Boer and Reddingius, 1996).

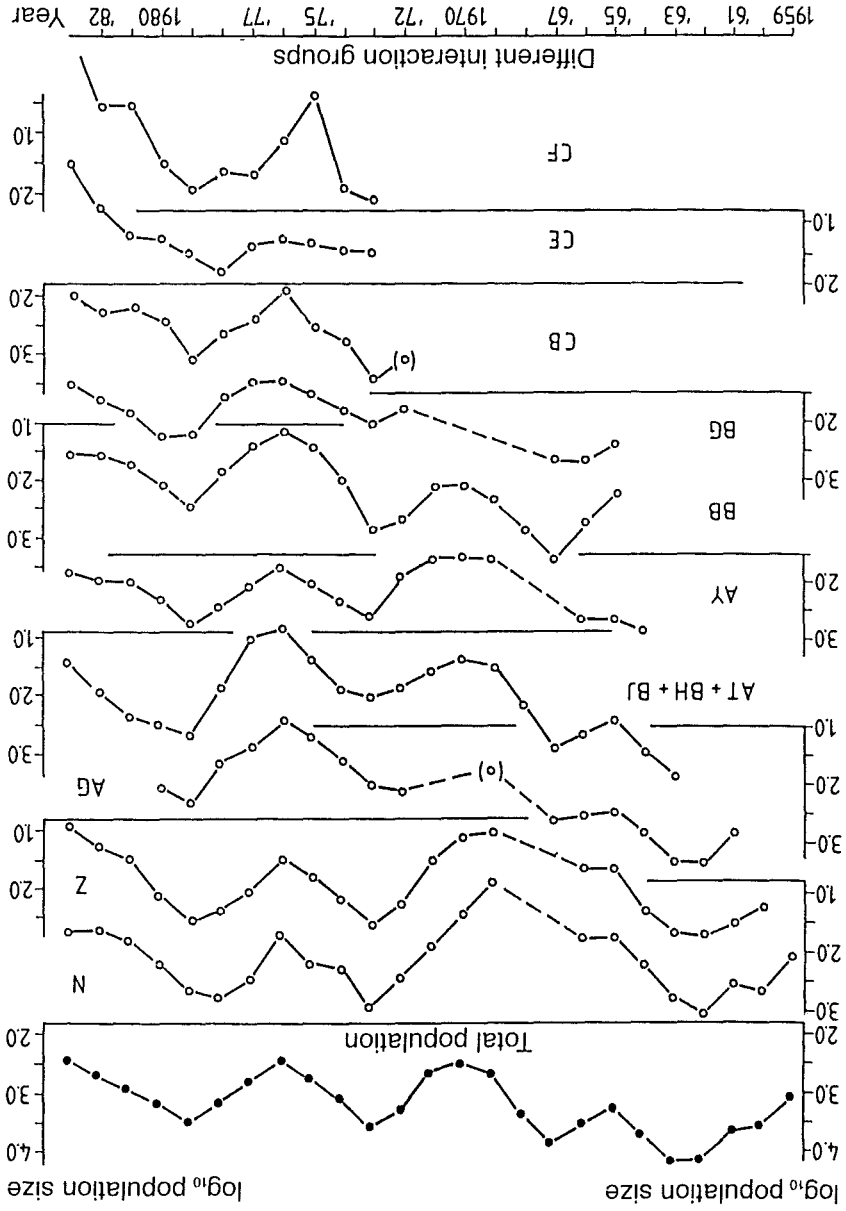


Fig. 3.11 As in Fig. 3.6 for the carabid beetle *Calathus melanocephalus* at Kralo Heath, Dwingelder veld, the Netherlands. Areas of interaction groups are pictured in Fig. 3.10.

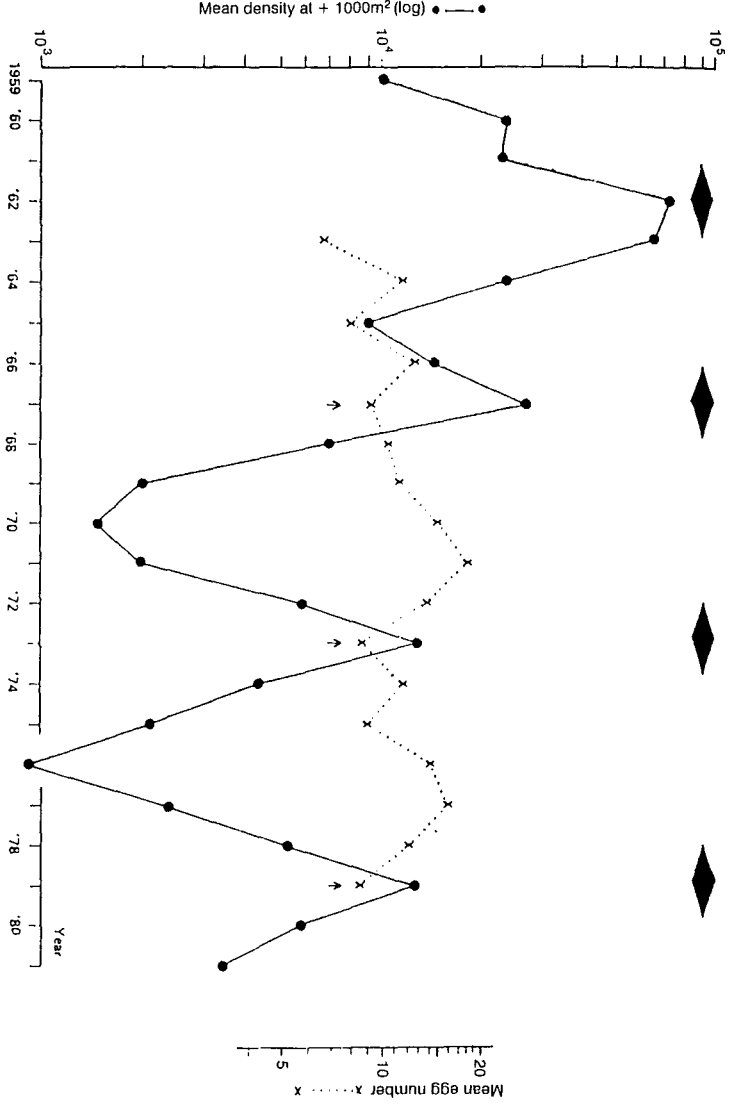


Fig. 3.12 Relationship between the occurrence of pest densities of the heather beetle *Lochmaea suturalis* (black diamonds above the graph), densities (year-catches; black dots), and mean numbers of eggs in ovaries in the carabid beetle *Calathus melanocephalus* (crosses) at Kralo Heath, Dwingelder veld, the Netherlands. Mean density (year-catch) is significantly correlated with mean number of eggs in ovaries ( $r_s = -0.667$ ,  $P = 0.0076$ ). Model II regression (Bartlett) eggs/female =  $13.2117 - 0.16297$  density/m<sup>2</sup>.

The fact that a natural population is composed of subpopulations (interaction groups) with differing frequencies of genotypes and age classes, living under different conditions, suggests that the fluctuations of a natural population cannot be satisfactorily represented by large-number models, neither deterministic nor stochastic (pseudodeterministic); see section 2.2.4 of Den Boer and Reddingius (1996). Thus, the argument sometimes advanced in favour of the use of large-number approximations, that the variation of the sum of random variables is the sum of the variances of those variables plus twice the sum of all covariances, does not apply to interaction groups of a multipartite population, because the changes in numbers in such groups are a mixture of additions and multiplications (section 2.2.5 of Den Boer and Reddingius, 1996). Partly due to this, we preferred to work with variances of net reproduction values, in the way demonstrated in Tables 4.4 and 4.6 of Den Boer and Reddingius (1996).

I realize very well that my work with interaction groups was more or less imposed on me by the sampling technique (pitfalls) used. In many other animal species it will not be easy to recognize the best units of population to study, i.e. interaction groups of individuals largely averaging the effects of small local differences in conditions by their normal mobility, such as occurs in carabid beetles. Nevertheless, with sufficient knowledge of the behaviour of the animals to be studied, it should be possible to find the right scale of population units for studies of population dynamics. In cases of doubt, such units of population are better too small (e.g. patches) than too large. Concerning the latter, it must be noted that many subpopulations of a metapopulation (Hanski, Chapter 1 in this volume) may be multipartite populations covering a number of interaction groups. Considering the combined changes in numbers of differently fluctuating interaction groups as the fluctuation pattern of such a subpopulation may lead one either to overlook the most important stabilizing processes (spreading of risk), or to attribute this pattern wrongly to other (e.g. density-dependent) processes. Combining changes in numbers of some almost identical, or largely overlapping, interaction groups (as occurred in *P. versicolor* in Fig. 3.5) may, in the worst case, result in too pessimistic an impression of the stability of the multipartite population. Since we will not usually be able to study all units of a natural population that can be distinguished, our impression of the stability of the multipartite population will in any case be too pessimistic. Hence, in these discussions we have tended to underestimate the effect of spreading of risk on the stability of natural populations.

### 3.6 SPREADING THE RISK OVER INDIVIDUALS

It will be evident that differences between the fates of individuals of the same group may have a stabilizing effect on the changes in numbers of

such a group, because the risk is spread over individuals with different chances of death and/or reproduction. It is difficult, however, to illustrate this effect in a natural interaction group, because we do not have long series of reliable data on changes in the frequencies of genotypes or age classes in insect populations, comparable with the statistics on which insurance premiums are based. A first step in this direction was taken by Den Boer *et al.* (1993) by recording the changes in frequencies of two phenotypes (with a genetic basis) in interaction groups of the carabid beetle *Pterostichus oblongopunctatus*, but it appeared impossible to show directly the stabilizing effect of these changes, because the time series was too short to allow an analysis like that in Tables 4.4 and 4.6 of Den Boer and Reddingius (1996).

From Van Dijk (1979, 1982) we know that egg production of females of *P. versicolor*, and other carabid species, differs with age (see also section 2.3.9 of Den Boer and Reddingius, 1996), older beetles laying significantly more eggs on average than young beetles. Therefore, changes in age composition over years may affect the numbers of eggs laid, although it will not be easy to show such effects under field conditions. Even the fact that some of the first-year beetles survive the winter and reproduce again in the next year (iteroparity) must have a stabilizing effect on adult numbers. We can demonstrate this effect in two carabid species, in which old beetles were distinguished from young beetles (see Baars and Van Dijk, 1984), by simulating the situation in which no old beetles survived the first year's reproduction, i.e. are semelparous. Of course, the production of young beetles will be lower if the contribution of old beetles is neglected, so we had to compensate for these losses, as described in section 4.4.2 of Den Boer and Reddingius (1996), in order to keep simulated numbers comparable to those observed in the field. The results of these simulations are shown in Fig. 3.13: both LR and VarInR in the one age-class simulation are about twice those of the values estimated in the field series (see Table 4.2 of Den Boer and Reddingius, 1996).

As natural populations usually show high genetic variability and natural environments are heterogeneous in many respects, the stabilizing effects of spreading the risk over individuals can hardly be overestimated, despite the fact that these effects are less easy to demonstrate than those shown by insurers for human populations. This kind of risk spreading must be very general, and together with the effects of spreading of risk in space, it could well have given many entomologists the impression that natural insect populations must be regulated. It should be noted that under certain conditions, iteroparity may result in statistical density dependence because of the transfer of quantitative effects from one generation to following ones. Therefore, Den Boer and Reddingius (1989) restricted tests to time series of species that are both univoltine and semelparous. I hope I have shown that, even without the assumption of a

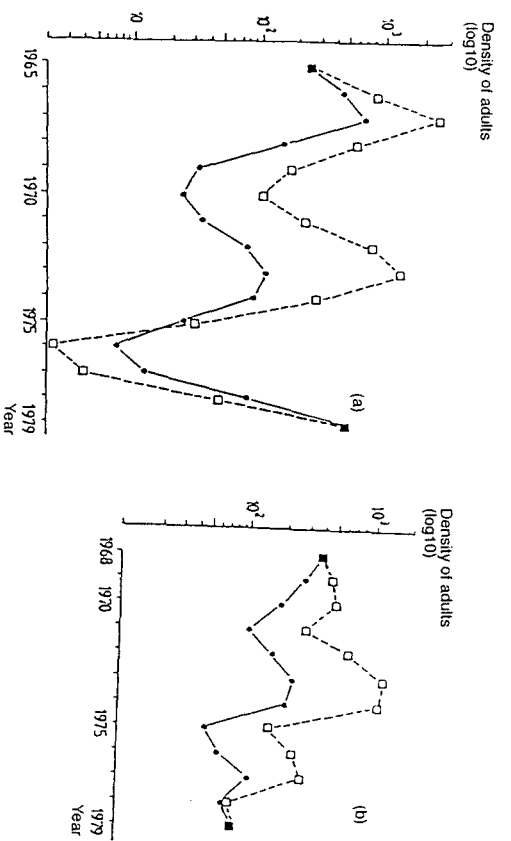


Fig. 3.13 Density fluctuations (year-catches) in field populations (interaction group 'grassy field', [AT, BH, BJ], see Figs 3.5 and 3.10) of two carabid beetles in which more than one year-class participates in reproduction (black dots), as compared with the fluctuations if only a single year-class had reproduced in such a way that mean net reproduction stayed the same (open squares). (a) *Calathus melanoccephalus* (Figs 3.10 and 3.11); (b) *Pterostichus versicolor* (Figs 3.5 and 3.6). Data from Appendix of Baars and Van Dijk (1984).

general occurrence of regulation, stability of insect populations is not inapplicable (Nicholson, 1933).

Apart from spreading the risk over individuals, the risk of large changes in numbers may also be spread in other ways. For instance, a polyphagous predator spreads risk over different prey species, so reducing the chance of food shortage. The price for this is, of course, that a polyphagous predator cannot be expected to develop a highly specialized hunting behaviour. Something similar will apply to generalized feeders at all trophic levels.

### 3.7 THE STABILITY OF THE FLUCTUATIONS OF INSECT NUMBERS

Now we have seen that, apart from the remote possibility of strict regulation of numbers, other situations and processes may contribute to a certain degree of stability in numbers over time, we should ask ourselves "How stable are insect numbers in general?". As I have intensively studied mainly carabid populations, I can answer this question only for a number of carabid species in Drenthe. However, there are no reasons why carabid beetles

should be so special as not to be representative of many other insect groups. Therefore, I believe my findings for carabid beetles may apply to insect species in general and possibly also to many other animal species.

In the course of 30 years, I have been able to follow the fluctuations in numbers for interaction groups of 64 of the more abundant carabid species in the province of Drenthe (Den Boer, 1985, 1990b). First of all, I established that the coefficients of net reproduction, estimated from different interaction groups of the same species, cover the same ranges of values (Mann-Whitney test), so that these values could be put together as a frequency distribution specific for the species. For none of the 64 species did the frequency distribution of net reproduction values differ significantly ( $\chi^2$  test) from the fitted log-normal (see Reddingius's Appendix to Den Boer, 1985). Therefore, the pattern of fluctuation of each of these species could be characterized by mean  $\ln R$  and  $\text{sd } \ln R$  of the fitted log-normal (examples given by Den Boer, 1990b). These data enabled me to simulate random walks of densities of the same lengths as those observed in the field for each of the 64 species, and compare the  $LR$  found in the field with the mean  $LR$  value of 500 simulated random walks of density of the same number of years, for each interaction group of that species.

In 38 of these species, the  $LR$  values of interaction groups, observed in the field during 8 years or longer, did not differ from the values expected when the numbers had fluctuated from year to year, as in random walks of densities (examples given by Den Boer, 1990b). In 22 other species, the numbers fluctuated significantly between even wider limits than expected with random walks of densities, and in only four species were the fluctuations in numbers in the field smaller than those in relevant random walks of densities, a result that could almost have been expected by chance ( $P=0.06$ ).

From these data, I concluded that the extent of fluctuations of density in interaction groups of carabid species either are similar to, or greater than, those of random walks of densities of the species concerned. I conclude from this that interaction groups of carabid beetles, and most probably of other insect species, are not kept within limits (stabilized) by density-dependent (regulating) processes, but largely fluctuate under the influence of density-independent forces. As stated earlier, this does not mean that density-dependent processes, such as density-dependent egg production (Baars and Van Dijk, 1984), do not occur. I merely believe such processes usually do not contribute significantly to keeping density within limits (Varley *et al.*, 1973), i.e. they are taken up in the general fluctuation pattern that is dominated by density-independent processes.

If density-independent processes dominate, it would be expected that increases in the range of densities in time ( $IR$ ) in random walks and in time series of densities from field populations would be similar. If one

compares the LR value of the first 5 years of observation with that after 18 years (i.e.  $LR = (LR_{18} - LR_5)/LR_5$ ), the increase of IR in time, for 13 random walks of densities, appears to vary between 0.34 and 2.446 (Den Boer, 1991). This variation is smaller, but not significantly so (Mann-Whitney,  $P=0.082$ ), than for interaction groups of carabid beetles observed in the field (Den Boer, 1991). For a number of other time series from the literature, including other kinds of insects, and populations claimed to be regulated such as winter moth, pine looper, great tit, muskrat, bobwhite quail, etc. (Den Boer, 1991), IR increased in time at a rate similar to that in random walks (Mann-Whitney,  $P=0.58$ ). The lowest IR value found so far was in the great tit population studied by Kluwyer (1951): a value of 0.03, a population that might be considered regulated in a broad sense, i.e. each year sufficient young reproducing birds are produced (in nest boxes) to compensate for the losses in the current generation, and density is efficiently reduced by territorial behaviour.

In summary, I conclude that regulation of numbers in the sense of keeping density within limits (Varley *et al.*, 1973), if it exists, must be an exceptional phenomenon, particularly for insect populations which, being poikilothermic, are always strongly affected by density-independent forces (Uvarov, 1931). On the other hand, there are many generally occurring phenomena that can be considered aspects of heterogeneity in both population and environment, which might result in a smaller or greater stabilization of numbers over time, but these stabilizing forces are not connected in any way with an equilibrium density. Further arguments and data are given by Den Boer and Reddingius (1996).

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