

# SPREADING OF RISK AND STABILIZATION OF ANIMAL NUMBERS

by

**P. J. DEN BOER**

(Biological Station <sup>1)</sup> of the Laboratory for Plant Taxonomy and Plant Geography,  
Agricultural University, Wageningen, The Netherlands)

(Received 26. IV. 1968; Revised 30. IX. 1968)

(Communication no. 136 of the Biological Station, Wijster)

## I. INTRODUCTION

In 1959 I started a field investigation into the most important factors governing the distribution of carabid beetles over a number of localities in the neighbourhood of Wijster (prov. of Drenthe, The Netherlands).

The daily contact with data from the field soon showed that change and variation predominate in the natural situation, and that my original assumption that populations of carabid beetles would be found to fit nicely to some definite habitat definable in terms of important ecological factors was too simple.

Since the intensity of important environmental factors varies from place to place and also in time (especially meteorological and biotic factors), and the sensitivity and behaviour (tolerance, preference, ability to search to hide, etc.) of the individuals in a population varies between individuals, and also for each particular animal in time (e.g.: age classes or developmental stages), the essential problem became: How do the phenotypic and developmental variations of populations in space and time interact with the spatio-temporal variation of the habitat? This is clearly a question that should be tackled along statistical lines; it cannot be treated typologically (cf. MAYR, 1963: 5-6).

After some time, I realized that heterogeneity and instability must not be considered as just a drawback of field data to be neglected ("averaged away" or "seen through by intuition") or circumvented by re-treating into the laboratory because they are mere deviations from the "typical" or "representative" case (or even "noise"). On the contrary, heterogeneity and/or instability must be recognized as fundamental features of a natural situation. The chance of survival of a population

---

1) Address: Kampsweg 27, Wijster (Drenthe), The Netherlands.

may even be increased, because the variation within the population makes it possible to cope with the variation in space and time of the habitat.

This possibility led me to formulate the concept "spreading of risk".

## II. "SPREADING OF RISK"

It is known that in times of rapid economic change an industry producing only one specialized article runs a greater risk of failing than one manufacturing a number of different articles; the latter industry has spread and thereby diminished its risk, which gives it a better chance of surviving an unstable period. The insurance business in particular is founded on the relation between spreading of risk and "chance of survival".

In a comparable way, variation within natural populations as well as in their environments may result in a spreading (diminution) of the risk of extinction these populations run under the influence of any drastical changes in environmental factors.

That is, the effects of "factors" that influence the chance to survive and reproduce are spread over individuals differing in various respects, and, as will be shown below, this often favourably influences the chance of survival of the population as a whole. During my investigation on carabid beetles I encountered a number of interesting examples of the different ways in which the risk may be spread. These examples will be published separately. In the present paper I shall deal only with the general phenomenon and its consequences, illustrated briefly by a few examples.

### II. 1. *Spreading of risk by phenotypic variation*

Most of the individuals constituting a natural population<sup>1)</sup> show some degree of divergence in their tolerance, preference, behaviour, etc. with respect to a number of environmental factors, so that the chances

---

1) Under natural population is understood a group of individuals of one species living in a specified locality whose limits are spatially determined by natural barriers or are arbitrarily set by the ecologist (or a group of individuals that moves: migrating birds, herd). Such a population can be sampled to collect information about certain quantitative properties of the group (e.g.: relative density, activity rate, sex ratio, mortality rate, birth rate, age distribution, frequency of phenotypes). Hence, a natural population is an ecological working-unit (compare: the statistical working-unit "population") and is not considered an entity. The quantitative properties of a population, which we estimate by taking samples from it, are nothing but added-up properties (statistics) of the individuals in the samples (MILNE, 1957, 1962 and ANDREWARTHA, 1957).

of surviving and reproducing must vary between individuals, even if the environment were spatially and temporally homogeneous—which never occurs in nature.

Since the chances of surviving and reproducing differ in different phenotypes, within a given population the selective advantages in a fluctuating environment (e.g. unstable weather) will shift continually from one phenotype to another.

For each generation in turn, the range of tolerance of a population is thus increased by phenotypic variation and this range is therefore much wider than that of the individual animals. This is important, since future variation of the environment is hardly predictable. In other words: the effect of fluctuating environmental factors on the population is continuously damped to some degree by the phenotypic variation within the population: fluctuations in animal numbers in one phenotypic group will be more or less levelled out by fluctuations in other such groups.

Consequently, this spreading of the risk by phenotypic variation will result in a relative reduction in the amplitude of fluctuations of animal numbers in the population as a whole (cf. III. 1: Stabilization) as compared to the numerical fluctuations in a hypothetical homogeneous population under similar circumstances. Since within a population every phenotypic difference in the chances of surviving and reproducing may contribute to the spreading of risk, the influence of these differences on the numerical fluctuations of natural populations will have general significance in nature (see II. 6).

Especially for natural populations living in highly unstable environments (e.g. variable weather), a high phenotypic variation resulting in a wide range of tolerance of the population as a whole will have survival value.

Therefore, a high phenotypic variation may be relatively favoured and thus preserved by varying selection that continually shifts between individuals. Hence, spreading of risk is the statistical outcome of selection varying from generation to generation within a heterogeneous population, i.e. selection of individuals<sup>1)</sup>. Migration between populations will increase

---

1) Although spreading of the risk evidently enhances the chance of survival of the population, it depends on selection of individuals; it is therefore unnecessary to postulate some kind of "group selection" (cf. WILLIAMS, 1966: 92-124). Since this kind of spreading of risk results from the extent to which the quantitative aspects of the frequency distribution of phenotypic variation—irrespective of the nature of the phenotypes—fits into that of the environment, it evolves little or not at all. The extent of fitting can only vary in magnitude, and this also holds for its result: i.e. the spreading of risk, which, consequently, has always existed to some degree.

phenotypic and genetic heterogeneity, and thus will contribute to the spreading of risk (compare II. 3.).

If the phenotypic variation in ecologically important features is in some way connected with an (indifferent?) morphological feature, the eventually resulting spreading of the risk may become apparent in changes in the frequencies of the different morphs in the population when they follow the fluctuations of the selecting environmental factor(s) closely. A clear example of this situation is described by TIMOFÉEFF-RESSOVSKY (1940), who recorded the seasonal fluctuation of the proportions of black and red morphs in *Adalia bipunctata* L. over a number of years. The black morphs always appeared to be less numerous than the red ones in April and more numerous in October. Obviously, one group of morphs (red) was relatively favoured during hibernation and the other group (black) during the summer.

In this way the range of tolerance is increased because of the simultaneous occurrence of these two groups of morphs, making the population as a whole able to cope with unfavourable conditions during both summer and winter: spreading of the risk (see also DOBZHANSKY 1951, Ch. V).

A similar situation was found in the carabid beetle *Pterostichus oblongopunctatus* F., where the morphs with up to 5 pits on the elytra are relatively favoured in dry summers and the morphs with 6 pits or more in wet summers (DEN BOER, in preparation). In this case the sensitivity of the larvae for the moisture content of the substrate seems to be associated with the number of pits on the elytra of the adult.

Morphological variation within a population may also result directly in spreading of the risk, e.g. when the different morphs have a different predation risk (see III. 5). Since phenotypic variation in natural populations often reflects genetic variation at least partially, spreading of risk by phenotypic variation generally means spreading of risk by genetic variation as well. An example of spreading of risk by genetic variation is provided by BAND's observations (1963) in a population of *Drosophila melanogaster* Mg: "The results indicate that different heterozygotes have different adaptive values and adaptive potentials, by which the population can continuously readjust its genetic composition in relation to the changing environments."

MAYR also (1963: 165) points to the advantages of the genetic variation of a population for survival under temporal change, and it is clear that he sees the phenomena of heterosis and polymorphism in the same way (pp. 228, 250-251).

## II. 2 *Spreading of risk in time*

A natural population includes not only a number of different phenotypes but also a number of different developmental stages or age classes generally showing differences in tolerance, preference, and behaviour, and consequently differences in chance of survival. If there is a high variation in the rate of development or time of reproduction or both, individuals of the same developmental stage (age class) will be exposed to different environmental factors at different times of the year. Hence, within the same stage the risk of dying and the chance of survival may be spread over a variety of environmental conditions and consequently the chance to reproduce may also be spread: spreading of the risk in time. An important consequence of this is that the risk may be spread during periods with almost unpredictable conditions (e.g. during the winter in Western Europe) over a number of different stages with different tolerances. It will be evident that temporal spreading of risk like the spreading of risk by phenotypic variation, will result in a relative reduction in the amplitude of fluctuations of animal numbers and will thereby contribute to a relative stability of the population size (see III. 1).

The quantitative influences of these ways of spreading of the risk—both of which are dependent on the heterogeneity of the population—will be intricate.

In my opinion, variation in the rate of development and time of reproduction is probably very common in all kinds of animal populations (but see II. 6). Most carabid species caught in the surroundings of Wijster for intensive study show some form of developmental variation: e.g. hibernation in the larval as well as in the adult stage of *Calathus melanocephalus* L. and *Calathus erratus* Sahlb.; a second reproduction in the next season occurring at the same time as the first reproduction of the young females of *Calathus melanocephalus* L. (VLIJM & VAN DIJK, 1967), *Calathus erratus* Sahlb., *Pterostichus oblongopunctatus* F., and *Pterostichus coerulescens* L.; and reproduction in two seasons of the same year by *Calathus erratus* and *C. melanocephalus*.

In many of these cases the developmental variation can be expected to result in spreading of the risk in time (see the examples given in II. 1). Investigations concerning this point are in progress.

MURDOCH (1966) came to a similar conclusion. He discovered that the survival of adult females of the carabids *Agonum fuliginosum* Panz. and *Agonum thoreyi* Dej. from the end of one breeding season to the

beginning of the next (with a second reproduction in the next season) is inversely proportional to the amount of reproduction in the first breeding season (the number of eggs developed).

I am convinced that these phenomena are not restricted to carabid beetles (cf.: DANILEVSKII, 1965: Chs. VI, VII).

### II. 3. *Spreading of risk in space*

The effective environments of natural populations <sup>1)</sup> are very heterogeneous.

Their habitats generally consist of mosaics of which all the component parts differ in structure and, therefore, in microweather, food, natural enemies, etc. Therefore, the chances of surviving and reproducing must be different in these different places. This means for the population as a whole that the effect of extreme conditions in one place will be damped to some degree by the effect of less extreme conditions in others. In other words: the risk of wide fluctuation in animal numbers is spread unequally over a number of subpopulations <sup>2)</sup> living in different micro-environments.

Moreover, a place showing extreme conditions in one year is often quite normal in another, and vice versa. Therefore, fluctuations in animal numbers in different places must quite often be different. The fluctuation of animal numbers in the population as a whole will be the resultant of the numerical fluctuations in the different places (subpopulations). The consequence of this spreading of the risk in space will be a relative reduction in the amplitude of fluctuations of animal numbers in the entire population (see III. 1: Stabilization).

Since natural habitats generally show a complex structural heterogeneity on a small as well as on a large scale, it may be expected that spreading of the risk in space is a widespread phenomenon that contri-

1) Under effective environment of a natural population is understood that subset of its environment whose components have a measurable influence on the statistics of the population at some time; see note to II. 1 and ANDREWARTHA & BIRCH (1954).

2) Under subpopulation is understood a group of individuals within a natural population living in a place with some spatial limitation (see note to II. 1). Hence, the difference between subpopulation and (natural) population is only a practical one: a subpopulation is smaller and less limited than a (natural) population. If this difference is immaterial to the subject, the term "local group" is used (II. 3). Hence, a local group may be the individuals in one mushroom, on one tree, etc., as well as the individuals in one wood, in part of a wood, on one island, in one district, etc., depending only on the problem under consideration.

butes significantly to the relative stability of population size; see II. 6.

Migration between different subpopulations will generally contribute to the stabilizing tendency of spatial heterogeneity, since in this way extreme effects of some places will be levelled out more thoroughly. Hence, migration will improve the outcome of spreading of the risk in space.

Migration will not only be beneficial within populations but also between populations. Since the amount of spatial heterogeneity (number of micro-environments) generally increases with area, it may be expected that its influence in terms of spreading of the risk in space will be the greater the larger the area and the larger the number of (sub)populations living there. This relation is important with regard to the chances of survival in small and large areas, particularly for sparse populations. Spatial heterogeneity combined with migration and heterogeneity within the population (II. 1 and II. 2) will be intricate, so that a heterogeneous (natural) population within a heterogeneous (natural) environment may be expected to experience an appreciable reduction of numerical fluctuations through spreading of the risk. An illustration of the effects of spatial heterogeneity is given by populations of the ground-beetles *Calathus melanocephalus* L. and *C. erratus* Sahlb. inhabiting a number of dissimilar places within one and the same locality. The survival in winter of larval stages and adults is divergent both in these places and in different years (DEN BOER, in preparation).

Fluctuations in animal numbers must sometimes end in the extinction of a local group ((sub)population). If other groups of the same species are present in the neighbourhood, there is a good chance that migration will eventually lead to the establishment of another group in the vacant place.

Frequent migration between the groups would not only decrease the chance of extinction of a local group, but also increase the chance of starting a new one in a vacant place. The greater the number of individuals and the greater the dispersive capacity of the animals, the greater the chance that a vacant place will become filled again in due time. Hence, the risk of extinction of a population or a species as a whole is spread over a number of local groups: a kind of spatial spreading of the risk, the success of which depends on the number of local groups and on the degree of migration between the groups. In exactly the same way the risk of reaching too high a number is spread over a number of local groups. This form of spreading of risk in space is implicit in the "general theory" of ANDREWARTHA & BIRCH (1954). A very clear example of a

population composed of local groups is presented by *Cactoblastis cactorum* (See: NICHOLSON 1957). In this case local groups either die out, are started, or reach too high a number in an irregular spatial sequence which shifts again in time. In my opinion, the risk of extinction as well as the risk of reaching too high a number (resulting in wastage of the food supply, in this case of the prickly pear, *Opuntia*) of the entire population is here obviously spread effectively over a large number of local groups with an adequate amount of migration between them (see also BIRCH 1957).

Since in general the number of local groups must be relatively <sup>1)</sup> greater in a large area than in a small one, this form of spatial spreading of risk would be most effective in populations or species inhabiting relatively large areas. Hence, the risk of extinction of a species (or population) inhabiting a relatively small area must generally be greater (spread over a smaller number of groups) than that of a species inhabiting a relatively large area and, conversely, per unit of surface a smaller number of species may be expected to live in a small area (e.g. a small island) than would be found in a comparable large one. An example of this phenomenon is given by DARLINGTON (1943) in a discussion of the numbers of carabid species in the four Greater Antilles. More examples regarding many kinds of animals and plants are given by DARLINGTON (1957) and by PRESTON (1962). (See also MAYR 1942: 224).

#### II. 4 *Spreading of risk and relations to other species*

The heterogeneity of the environment also includes food and other species (see note to II. 3). The size of a population of a monophagous predator often depends on the amount of available prey, and consequently follows the fluctuations in numbers of the latter. Because of the high degree of interdependence, the fluctuations in numbers of the predator contributes in turn to the numerical fluctuations of the prey. Since there will always be a time-lag between a numerical change in one of the species and the numerical response of the other, when very homogeneous conditions prevail (e.g. in a laboratory experiment or a plantation) the above-mentioned phenomenon may even lead to oscillations with an ever-increasing amplitude, ultimately with the risk of self-destruction of the system (NICHOLSON & BAILEY, 1935; HUTCHINSON, 1954).

On the other hand, the risk of self-destruction will be decreased when

---

<sup>1)</sup> Relative to the kind of animal: a local group of some carabid species inhabits a many times smaller locality than a local group of e.g. rabbit or hare.



the environment of the prey-predator system is sufficiently heterogeneous to provide some spreading of the risk in space (see II.3) and thus a reduction in the amplitude of numerical fluctuations (see SCHNEIDER, 1939; NICHOLSON, 1957; VARLEY & GRADWELL, 1958; TINBERGEN & KLOMP, 1960; BAILEY, NICHOLSON & WILLIAMS, 1962; see also: III. 3).

In my opinion, the risk is also decreased when the population(s) includes enough heterogeneity to give rise to spreading of the risk by phenotypic variation (see II. 1) or spreading of the risk in time (see II. 2).

The risk is reduced ultimately when the predator is not monophagous but polyphagous, the risk of starvation then being spread over a number of different prey-species (see NICHOLSON, 1933; SCHNEIDER, 1939; VOÛTE, 1946, 1964; and TINBERGEN, 1960).

This argument, of course, also applies to monophagous versus polyphagous parasites and their hosts, and something similar probably takes place in all other species that are mutually dependent, e.g. as symbionts or commensals, and even as competitors. The prey (host) population too may profit if the risk of being consumed, or killed in some other way, is spread over a number of different predator or parasite species (see also III. 5). Furthermore, less obvious relations between species (e.g. holes of mice and moles, which increase shelter heterogeneity for many arthropods; activities of phytophagous animals which facilitate or hamper the feeding and/or dwelling activities of other animals) may contribute to some degree to the spreading of risk due to relations with other species and/or to those in space. Hence, these forms of heterogeneity, too, may contribute to a relative reduction in the amplitude of fluctuations of animal numbers in the populations concerned (see III. 1: Stabilization). The influence of heterogeneity in the relations with other species will also be integrated with the influences of heterogeneity within the populations concerned (see II. 1 and II. 2) and with those of the spatial heterogeneity in their environments (see II. 3).

## II. 5 "*Balance of nature*"

It is evident from the preceding paragraphs of this section that the relative reduction in the amplitude of numerical fluctuations increases in importance the greater the number of groups (phenotypes, developmental stages (age classes)), micro-environments, (sub)populations, species) over which the risk is spread. That is why the simultaneous occurrence of different kinds of heterogeneity can be expected to increase the spreading of risk. Every natural population includes different phenotypes (genotypes) as well as developmental stages and groups

in micro-environments with migration between them, and every natural population will also show quantitative relations with other populations of the same and of different species. In general, the greater the number of species living together in the same place the more likely that spreading of risk in the relations with other species will play an important part: the number of different preys of a polyphagous predator will increase, the number of different predators and/or parasites of a phytophagous insect will increase, as will the number of potential competitors, etc. (see III. 5).

Moreover, the manifold activities of a large number of species living in the same place increase the structural heterogeneity of the environment and therefore may make an important contribution to spatial spreading of the risk (see II. 3), and, conversely, an increased environmental heterogeneity will offer appropriate conditions for an increased number of species. Hence, a biocoenosis<sup>1)</sup> rich in species may be expected to be more stable (provided with more intricate spreading of the risk) than one with few species (see II. 6).

This important feature of the so-called "balance of nature", of which every biologist and layman has some vague notion, is therefore the result of a complex and highly intricate "system" of spreading of the risk within populations and between populations of the same and especially of different species (see III. 5). Hence, the "balance of nature" is not a balance but rather a relatively high degree of stability.

It should be noted that there is no question here of fixed and specific relations between pairs of species; on the contrary, I consider changeable (spread) relations between differing numbers of species to be much more important, because only the latter can result in the necessary variation in the chances of surviving and reproducing within the populations involved. Since most species in a natural biocoenosis show some quantitative relationships with a number of other species, it seems to me that the *number* of species in a community will often be more important for its stability than the taxonomic identity of the species (see III. 5).

A somewhat similar idea is expressed by MACARTHUR (1955), who discussed the distribution of energy entering a community and concluded:

---

1) Under biocoenosis (community) is understood a group of populations of different species living in a spatially more or less limited locality. Such a group of populations can be sampled to study its species composition, the frequency distribution of individuals over species (WILLIAMS, 1964), and statistics of the separate populations and of their eventual interrelations. A biocoenosis is an ecological working-unit (a compound population). To consider a biocoenosis an entity is an extrapolation of analogues (MULLER, 1958). (See note to II. 1.)

“the amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community”. Hence, the more prey species to a predator and the more predator species to a prey, the more stable the community. HUTCHINSON (1959) stated: “. . . because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the average population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree. In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuation in a way that can be advantageous to both species”. Both authors are evidently aware of the existence of spreading of risk. From the above, it will be clear that the activities of man in nature often result in an increase in the amplitude of numerical fluctuations of some species, leading ultimately either to catastrophically high numbers or to extinction (“disturbance of the balance of nature”) by:

- a. direct or indirect eradication of one or more species, which decreases the degree of spreading of risk in the relation to other species (see II. 4);
- b. levelling down of the structural heterogeneity, which decreases the degree of spatial spreading of the risk (see II. 3), whereby for some species the appropriate conditions will often disappear too (compare a);
- c. reduction and breaking up of the surfaces occupied by natural environments, which will often decrease the degree of spreading of the risk of extinction (see II. 3).

On the other hand, small-scale activities of man in nature may contribute, like most of the activities of other animals, to environmental heterogeneity and so to an increase of population stability and even to faunal enrichment. The extreme of b is reached in plantations and other monocultures, resulting in a drastic reduction of the number of species and in periodic numerical outbursts of some of the remaining species (SCHNEIDER, 1939; VOÛTE, 1946, 1964).

## II. 6 *The effect of extreme weather conditions*

In regions with very pronounced meteorological differences between seasons (e.g.: in arctic and boreal regions) there will be, in most populations, no important spreading of the risk in time (see II. 2), since often

only one developmental stage will be able to survive the most severe conditions (e.g. the winter in these regions) and the life cycle of most species will therefore be appreciably synchronized with the course of the seasons. Moreover, communities will be relatively poor in species in such regions as a consequence of the extreme conditions, and therefore spreading of risk in the relations to other species (see II. 4) will be relatively decreased. Perhaps even spatial spreading of the risk (see II. 3) is relatively decreased under such extreme conditions, since the vegetation will also be poor in species, and will therefore often be rather monotonously structured. On the basis of these considerations we may expect to find that the reduction in the amplitude of numerical fluctuations by spreading of the risk will generally be smaller the more extreme the climatic conditions, in particular with regard to great differences between the seasons <sup>1</sup>).

Hence, natural populations will fluctuate more heavily in numbers in arctic regions than in the tropics (see e.g. THOMPSON, 1929; SOLOMON, 1949; MACARTHUR, 1955; HUTCHINSON, 1959).

Theoretically, in temperate regions numerical fluctuations can be expected to be smaller in the long run in areas with unstable and thus relatively unpredictable weather conditions and sometimes rather unpronounced differences between the seasons (e.g. The Netherlands) than in areas with more predictable and thus more stable weather conditions and generally more pronounced (and stable) differences between the seasons (e.g. in Central Europe), although complications may enter into the picture in this case (e.g. greater spatial heterogeneity—e.g. due to differences in altitude—in some of the latter regions than in some of the former).

In a summer which is extremely hot and dry it will also be hot and dry in most micro-environments, in spite of the important differences in degree. Hence, extreme weather conditions will have an overwhelming influence on the effects of spatial heterogeneity, as a result of which numerical fluctuations in different places will be similar, although there may be important differences in amplitude. On the other hand, in a less extreme summer numerical fluctuations will often differ in different micro-environments, and under such conditions spatial spreading of the risk has its maximal effect. To summarize: Climatic conditions (favourable in the tropics and unfavourable in arctic and desert regions), and

---

<sup>1</sup>) In fact, the most important feature of such climates is that the annual return of great differences between seasons can be safely predicted.

even, incidentally, extreme weather conditions, will influence the degree of spreading of the risk resulting from heterogeneity within populations, spatial heterogeneity, and heterogeneity in the relations to other species (communities poor or rich in species). Under extreme climatic conditions, heterogeneity within the population will hardly be "preserved" by natural selection (see II. 1) and thus will be relatively small.

### III. STABILIZATION OF ANIMAL NUMBERS

During the last thirty or forty years the problem of the apparently long-term existence of insect populations has intrigued a large number of ecologists. Many authors have put forward "general theories" ranging from the maintainance of some "balance" or "equilibrium value" by a rigid "regulation mechanism" by density governing factors (e.g. NICHOLSON, 1933; NICHOLSON & BAILEY, 1935) or by a negative feed-back mechanism (PIMENTEL, 1961; WILBERT, 1962), through more or less compromising "theories" (e.g. SOLOMON, 1949; MILNE, 1957, 1962; BODENHEIMER, 1958), to a chance determination of numbers in each generation (BODENHEIMER, 1928, 1930; THOMPSON, 1929, 1939, 1956; ANDREWARTHA & BIRCH, 1954).

For a number of years I have had the impression than an insect population may be subject to only restricted density fluctuations, and may exist for a long time by spreading the risk of becoming extinct over a large *number* of "factors" (or groups within the population).

In Section II, I have discussed the relative reduction of the amplitude of numerical fluctuations resulting from various ways in which the risk may be spread. In Section III, I shall try to apply the concept of spreading of risk to the problem of the long-term survival of (insect) populations.

#### III. 1. *Stabilization*

Most population ecologists agree that the fluctuations of animal numbers in natural populations are somehow restricted to some extent. On theoretical grounds, some ecologists expect either extinction or an increase to such high numbers that exhaustion of the resources, ending ultimately with the death of all individuals, to be the fate of most animal populations within the course of a certain number of generations. To describe the simple fact that such catastrophes do not always happen in nature, we need some theoretically neutral term. For this purpose I propose the use of the word "stabilization" under which is meant that, despite theoretical expectations of relatively rapid extinction or explo-

sive growth, density fluctuations in natural populations prove to be more restricted, more stable.

This term does not imply any cause or "mechanism" and does not exclude the possibility that density fluctuations in natural populations can become stabilized by stochastic processes (i.e. by chance). We are now able to pose a hypothesis: density fluctuations in natural populations are stabilized to some degree by spreading of risk, which, of course, does not exclude the possibility of additional stabilization by some "regulatory (governing) mechanism" in many or only in a few cases. However, it will be evident from Section II that, although we still have little or no exact knowledge of its quantitative influence, spreading of the risk must be at work sufficiently universally in natural populations to rule out the logical necessity for an exclusive "regulation" of animal numbers by "density-dependent (governing) factors".

In each particular case it will be necessary to investigate how much is contributed to population stability by spreading of the risk and how much by density-governing processes (see also III. 3 and III. 4). As long as we do not know the quantitative outcome of stabilization resulting from the many intricate ways by which the risk may be spread, we cannot interpret the fluctuations of animal numbers observed in natural populations or predict how long a population that is "only" stabilized by spreading of the risk (i.e. by chance) is likely to survive (see also Section 4).

### III. 2. *The importance of the number of "factors" influencing animal numbers*

In Section II, the relatively stabilizing influence of heterogeneity within populations (II. 1 and II. 2) and of spatial heterogeneity within the habitat (II. 3) was discussed. These heterogeneities enable natural populations to cope to some extent with the vagaries of weather. We did not discuss, however, the fact that the variation of weather conditions in time may itself contribute to the relative stability of population numbers. Unfavourable weather conditions in one part of the year may be compensated for to some degree by more favourable conditions at other times.

By using numerical data concerning various meteorological factors (taken from Tables prepared by the Meteorological Institute, De Bilt, Holland) in annual sequence and attributing to them arbitrary influences on the net rate of reproduction of model populations, it could be demonstrated that increase of the *number* of meteorological factors may have a favourable influence on the relative stabilization of numer-

ical fluctuations (spreading of the risk). These models will not be discussed here. The results of these models will be published separately (REDDINGIUS and DEN BOER, in press).

Within the scope of the present paper it will suffice to note that if the risk of reaching excessively high or low densities is spread over a number of (meteorological) factors, density fluctuations will be relatively stabilized and the survival chance of the population will be increased. This special aspect of spreading of the risk was not discussed separately in Section II, since, in my opinion, its occurrence in natural populations will not be self-evident to every ecologist and its demonstration requires a model with special premises. However, the assumed influence of the number of meteorological factors has been an important subject of discussion in the literature (see KLOMP, 1962 and WILBERT, 1962).

The conclusion given above is not confined to spreading of the risk over a number of meteorological factors. A model demonstrating the influence of an increasing number of predator and/or parasite-species would have shown the same stabilizing tendencies upon density fluctuations of a prey-species.

A model demonstrating the influence of an increasing number of phenotypes, stages of development, subpopulations in different micro-environments, migration between subpopulations, etc. within the population would also have indicated comparable stabilizing influences. In general, the number of "factors", i.e. the amount of variation and heterogeneity, tends to have a levelling effect on extremes and trends. If we imagine a population composed of two sexes, a number of phenotypes, and a number of developmental stages (or age-classes), divided into a number of subpopulations with migration between them, living in different micro-environments with different microweather varying in time, consuming different kinds of food, influenced by a number of different predators, parasites, and other animals, we can form some idea of the immense number of interacting "factors" (amount of heterogeneity and variation) influencing animal numbers in nature and obtain an impression of the probable stabilization resulting from it.

The view that the very existence of a large number of factors influencing density has an important restricting influence on density fluctuations is encountered in various forms in the literature (e.g. THOMPSON, 1929, 1939, 1956; ANDREWARTHA & BIRCH, 1954; GLEN, 1954; MILNE, 1957, 1962; REYNOLDS, 1957). A very clear statement is made by RICHARDS (1961): "Most of this excess stability in the population can be accounted for by the homeostatic effect of overlapping causes of death,

so that individuals that in any particular year escape one source of mortality merely survive to encounter one of the others. No other arrangement could account for the relative stability of many populations in most years; adjustments by density-dependent factors are usually too slow and in many cases actually observed to be absent". After discussing a number of experiments with marbles, SCHWERDTFEGER (1958) concludes: "In nature, there are regularly numerous and varying factors influencing the population. They are partly dependent on the changing abundance, partly independent; they take effect on the population density partly in a promoting, partly in a checking manner. The greater the number of independent factors that influence the population, the higher is the possibility that promoting and checking factors compensate for some time, that the abundance remains in balance".

But a number of authors are sceptical, including KLOMP (1962: 3.2.4: 93), WILBERT (1962: 588), and SOLOMON (1957) who says: "It may be that, in some way at present unknown, the heterogeneity of environments in space and time can independently bring about natural control, but I cannot see a logical basis for this and shall remain unconvinced unless someone can demonstrate how it works out (or at least, for a start, how it could do so)".

In this paper I have attempted to give such a logical basis (see also REDDINGIUS, 1968).

### III. 3. *Spreading of the risk brought about by density-dependent factors*

A high degree of dependence between the densities of prey and predator (or parasite and host) may lead to oscillations of increasing amplitude leading in turn to self-destruction of the system (see II. 4). A number of authors conclude that when the environment of the prey-predator system is somewhat heterogeneous, the risk of self-destruction will be reduced; in my opinion, this holds because in such a case the risk arising from the density-dependent factors (to be abbreviated as: risk from d.d.f.) is spread over a number of micro-environments. In other words: the determinant of this risk—the high degree of dependence between the densities of prey and predator—is spread unequally over a number of micro-environments and is thereby diminished: a high degree of dependence in some places is levelled out by a low degree or absence of dependence in other places. Migration between the different places will increase this "levelling out" and thereby decrease the general degree of dependence (see II. 3).

The same result is reached when in different places the prey-predator cycles are not synchronized, e.g.: *Opuntia* and *Cactoblastis cactorum*



(NICHOLSON, 1957; see also II. 3). Spreading of the risk from d.d.f. is improved not only by spatial heterogeneity, but also by temporal heterogeneity (many weather factors), heterogeneous age-distribution, phenotypic variation (both in the prey and in the predator), polyphagy in the predator, more than one predator (parasite) species to the prey, hyperpredation (hyperparasitism), influences of other animals, and so forth. Moreover, not only is the prey-predator (host-parasite) relation influenced by spreading of the risk from d.d.f., but the same is to some extent true for all kinds of density dependence. For example: the result of intraspecific competition cannot be considered to be "perfectly density-dependent" as it is thought to be by MILNE (1957, 1962), since the "risk" from this kind of d.d.f. is spread by phenotypic variation (e.g. differences in sensitivity to competition), developmental variation, spatial heterogeneity combined with variable clustering of individuals and migration between these clusters, changing weather (e.g.: temperature, which directly influences the degree of activity in poikilotherms), etc.

Apart from these theoretical difficulties, there is a technical problem: the existence of competition can only be assessed by direct observation, but it is almost impossible to measure, and cannot be inferred from mere density measurements. Spreading of the risk from d.d.f. is only a special form of spreading of risk: any given numerical influence within one group of animals at a certain time is levelled out to some extent by other numerical influences within the same and/or other groups at the same and/or other time(s). That is why I do not expect that significant negative density-dependent influences <sup>1)</sup> will generally be found in a heterogeneous (natural) population in a heterogeneous (natural) environment. And if an example of a measurable density-dependent influence in one period of a generation cycle (e.g. in one season) is found, there will be a chance that it would be levelled out by other quantitative influences during other periods of the cycle.

In my opinion, significant density-dependent influences are to be expected mainly under rather homogeneous conditions (homogeneous, of course, as far as the kind of animal is concerned), e.g. in plantations and especially in the laboratory. This does not mean, however, that a heterogeneous population in a heterogeneous environment would always

---

1) Under negative density-dependent influence is understood an influence of an ecological factor that on the average tends to depress the net rate of reproduction the more severely the higher the density. However, "on the average" is a statistical concept and allowance must be made for the probability that large deviations from the average can occur frequently.

be exclusively stabilized by spreading of the risk (see III. 4). It only means that the greater heterogeneity (the greater spreading of the risk) the smaller the effect of density-dependent processes will be and the smaller the significance of such influences on the stabilization of animal numbers. Moreover, many supposed density-dependent factors may often appear to be density-independent, and vice versa (cf. ANDREWARTHA, 1957). I agree with ANDREWARTHA that the density fluctuations of natural populations can only be adequately simulated with a stochastic model: unless we incorporate into our population models some of the most conspicuous features of nature—heterogeneity and instability—we have not even attempted to simulate nature (see also REDDINGIUS, 1968).

On the other hand, we must keep in mind that under rather homogeneous conditions (e.g. in plantations), density-dependent influences may play a significant part in the stabilization of animal numbers, since under such conditions specific influences often will not be levelled out completely.

#### III. 4. *Limitation of density*

No matter which theory concerning the factors that determine the size of populations one advocates, it remains obvious that no population can continue to increase in numbers in a limited environment. Sooner or later, the capacity of the environment will be approached or even reached, and further growth will only increase the mortality.

Since, by definition, full exploitation of the capacity of an environment is accompanied by an exhaustion of resources (e.g. the food supply), the result will be a more or less conspicuous reduction of animal numbers or even extinction. Whether such a reduction in numbers is called density-dependent or not may be of theoretical interest, but the only thing of importance to the population will be the reduction or extinction itself.

In my opinion, it is of no more value to state that "population density is regulated by the capacity of the environment" than it is to state that "the density of passengers is regulated by the carrying-capacity of a ship". In both cases the capacity is simply the maximum number that can be supported (see also WILLIAMS, 1966: 236). It must not be forgotten that the attainment of the capacity of the environment is not always conspicuous, as it is, for example, in case of defoliation; if only a particular stage or part of the food can be consumed, cases of food scarcity may be difficult to detect. Moreover, in many cases the factor that limits density is not the available amount of suitable food itself but rather the amount of suitable food that can be found per unit of time (c.f. III. 5 and AN-

DREWARTHA & BIRCH, 1954, Ch. II). Matters may be still more complicated, since the "environmental resistance" may be affected by the increase of density when its capacity is approached.

Polyphagous predators and parasites may react to a large increase of density of one of their preys by specialization to that prey or, just the reverse, by avoidance of that prey (TINBERGEN, 1960); more or less monophagous predators and parasites may show a gradual increase in numbers, and may thus contribute to the "environmental resistance" of a growing prey-population, for instance if such an increase of the numbers of enemies is not too slow (VOÛTE, 1946, 1964). In general, a relatively dense population will influence its environment unfavourably, which will decrease its chance of survival especially during "outbreaks" (VOÛTE, 1964). In a number of animals some kind of intolerant behaviour (contest) may limit density effectively.

I have the impression that the "regulation of numbers" is thought by many authors to consist of these forms of limitation of density, i.e. by "environmental resistance" and/or by resistance from the members of the population themselves (cf. NICHOLSON, 1957). Although such density-limiting influences may be extremely important, I do not like to use the term "regulation" in these cases where only limitation of density (cf. FRANZ, 1962) is meant. This does not imply that I would deny the possible importance of such kinds of density-limitation. On the contrary, intolerant behaviour (territoriality, cannibalism) and the total action of a great number of predators and parasites may sometimes limit density very effectively (see III. 5) and contribute significantly to the stability of natural communities (see II. 5). But, in my opinion, it is not so much the degree to which the limitation or decrease is density-dependent that is quantitatively important in these cases, but the limitation or decrease itself (of which the degree of density-dependence generally will be immaterial to the degree of stabilization) and/or the degree of spreading of the risk in the relations to other species (see II. 4 and III. 5; REDDINGIUS and DEN BOER, in press). Moreover, for many animal populations—especially sparse insect populations—there are no indications that limitation of density ever plays any part; it is exactly the long-term existence of sparse populations that must be seen as the crux of the problem. Spreading of the risk is not greatly influenced by density, and will always be at work in sparse as well as in dense populations (especially the risks concerning space, food, and relations with other species), but it has an important restricting influence on the fluctuations of density (cf. III. 2). On the other hand, its incidental occurrence

brings about that limitation of density need not necessarily influence the magnitude of density fluctuations. Moreover, each limitation of density after one or more generations will necessarily be followed by an accordingly low trough, by which the chance the population runs of becoming extinct may be increased: if, after a limitation of density, environmental factors (e.g. the weather) were to result in an  $R$  value of, for instance, 0.1, density would be decreased more than if limitation had been absent in the preceding generation (other things being equal). To summarize, not only different ways of spreading of risk but also different kinds of density limitation may determine the "stabilization of animal numbers" (cf. III. 1) and the survival chance of animal populations. Mere limitation of density cannot be responsible for a "stabilization of animal numbers", because it does not prevent extinction but may only prevent the occurrence of excessively high numbers. Spreading of risk, on the contrary, has the same levelling influence on high as on low densities.

### III. 5 *The influence of polyphagous predators and parasites*

In natural environments most arthropod species are attacked by a number of different predators and/or parasites, most of which are polyphagous. This means that in spite of their being very important mortality factors, the influence of polyphagous predators and parasites in general will hardly be density-dependent. The amount of predation by a polyphagous predator will depend not so much on the density of a particular prey as on the ratio between the "risk index" (TINBERGEN, 1960) of that prey and those of alternative preys: the amount of predation of the prey in question may be altered considerably by a simple change in the densities of some alternative prey species. Hence, the density of a particular prey species is not only influenced directly by the densities of a number of predators and parasites but also indirectly by the densities of a great number of other species that are alternative preys of these predators. It will be evident that as a result of this situation the spreading of risk in the relations with other species (cf. II. 4) will be greatly improved, and in my opinion it may also be the crux of the "balance of nature" (cf. II. 5). In these and in many comparable cases, spreading of the risk will be much more important to the stabilization of animal numbers than any small density-dependent influences that may be discovered, since the latter will be highly liable to spreading of the "risk" from d.d.f., at least in heterogeneous environments (cf. III. 3).

For some predators, the amount of available prey will depend mainly on the chance of encounters; for others, however, it will be greatly

affected by "specific searching images" of the predator itself (TINBERGEN, 1960: the Great Tit). Some predators or parasites search by eye, others react to noises or chemical agents, so that the cryptic or mimetic properties of a prey will have a different quantitative influence with respect to different enemies. These and many other differences in the searching abilities of predators and/or the hiding abilities of preys introduce considerable heterogeneity into the quantitative relations between species, which again will contribute to the general spreading of risk.

Another result of the amount of predation experienced by a particular prey species—which is partially dependent on the densities of alternative preys—is the low predation risk run by relatively sparse prey species; this will be especially apparent when the predator is able to develop "searching images" (TINBERGEN, 1960) or when the prey shows Batesian mimicry (cf. COTT, 1940). In these ways, a number of relatively sparse species may experience some "protection" from severe predation in the midst of a dense population of an alternative prey. Perhaps this is one of the possible "explanations" of the relative commonness of sparse (rare) species (cf. WILLIAMS, 1964). Within one and the same population different morphs—for example, those having differences in cryptic or mimetic properties—may run a different predation risk, due to differences in morph frequency, which will be especially effective when this situation influences the readiness for the development of "searching images" in the predator. Changes in morph frequency may thus result in a shift of the predation risk from one morph to another (cf. II. 1: spreading of risk by phenotypic variation).

Since generally, under natural conditions, no prey population will be attacked by only one predator or parasite species, the quantitative relation between a particular predator (even when it is monophagous) and (one of) its prey(s) can hardly be expected to be governed by density-dependent factors (compare: II. 4), especially because the amount of predation will depend not so much on the number of prey individuals present as on the chance of an encounter with a prey individual. This chance of an encounter is influenced not only by the densities of both prey and predator, but also by the pattern of distribution of the prey (cf. KLOMP, 1966), its hiding abilities, cryptic properties etc., the searching abilities of the predator, the structure of the habitat, weather conditions, etc. Since, under natural conditions, a number of different predator and/or parasite species will take a toll of the same prey population in some way, the quantitative influence of one particular predator species will generally be rather small. Moreover, there must be a favourable

relation between the energy spent in searching for a prey and the energy ingested from that prey. Consequently, the amount of food available to a particular predator species may have an important density-limiting influence without being "regulating" and even without the food supply itself being affected appreciably. This situation may, for instance, merely determine the amount of reproduction made possible by the net amount of energy ingested from preys during the reproductive season (cf. MURDOCH, 1966). If the net amount of this ingested energy is barely sufficient to maintain life, reproduction may even be delayed until a following reproductive season (cf. LACK, 1966, Ch. 8).

In this section I have tried to give some impression of the high degree of complexity and intricacy of some of the relations between species. In spite of the fact that these relations generally will not result in significant density-dependence, they may bring about an important limitation of density and will contribute to the stabilization of numerical fluctuations brought about by several forms of spreading of the risk. Therefore, the contribution of such relations to the "balance of nature" cannot, in my opinion, be overestimated. But once again: a "balance of nature" results not from a number of separate specific relations (interdependences) between pairs of species, but, on the contrary, from the intricate interaction of a great number of "spread" and changeable relations between differing numbers of species. In such a "system", the "role" of one species is readily taken over by another (especially in a biocoenosis having many species) and therefore the *number* of species seems to be more important than their individual taxonomic identity if enough different "ecological life-forms" are present to fill up the most important "niches" (e.g.: phytophage, predator, parasite, saprophage, etc.) and to give the necessary variations in the chances to survive and to reproduce (cf. II. 5). ELTON (1966: 377) takes the same view: "If this proposition is true the fact of complexity would seem to carry with it some stabilizing property. It is reasonable to suggest, though it cannot be proved yet, that the interlocking of biotic connections right through a terrestrial ecosystem is one of the chief reasons for this property. In turn, if this is really the case, the girder system (interlocking of community units) must have some effect either in controlling numbers or at any rate in damping down fluctuations or slowing down deviations from the norm".

## II. 6. *Invasions*

The stabilizing influence on density fluctuations of a large number of factors affecting density (cf. III. 2) is based on the assumption that there

are factors that increase and factors that decrease density, besides factors whose effect is at times increasing and then again decreasing, and that a quantitative preponderance of one of these groups will only be temporarily. This assumption seems the more plausible the greater the number of factors involved, i.e. the greater the spreading of risk. Although I am convinced that the picture developed in this paper represents the general case under natural conditions, it may be postulated that a quantitative preponderance of density-increasing or -decreasing factors is maintained over many successive generations, i.e. that the environment continues to be too "favourable" or too "unfavourable" (ANDREWARTHA & BIRCH, 1954).

This may be especially the case with respect to new invaders of an area (ELTON, 1958), since the chance that an environment new to a species will consist of a quantitatively rather unbalanced set of density-increasing and -decreasing factors may generally be high. If the new environment of an invader is too "unfavourable", the invasion will not succeed or will fail quite soon: the invaders encounter a high "environmental resistance". Although they will generally escape attention completely, the number of such cases must be enormous (see: MAYR, 1965). Sometimes, invaders fit themselves into a new environment without attaining very high numbers. Such cases, in which there is apparently no prolonged preponderance of density-increasing or -decreasing factors, must be more numerous than is generally expected (see e.g. ELTON, 1958: 123). Every specialist concerned with a group of animals or plants knows examples of species that extend their area of distribution rather rapidly without reaching extremely high numbers in their new environments (BIRCH, 1957 and MAYR, 1965; for examples concerning carabid beetles, see LINDROTH, 1949: 621).

If the new environment of an invader is too "favourable", density will have a rising trend resulting ultimately in exhaustion of resources. Such catastrophes may happen several times in the same and/or other localities unless extinction, irreversible changes in the (genetic) composition of the population or in its environment, or an increase of "environmental resistance" intervenes. At first, an invader will experience only few biotic mortality factors; predators and parasites will generally not react adequately to the strange stimuli. In the course of time, however, a number of predator and/or parasite species may make increasing use of the new, abundant food supply, and "environmental resistance" will increase. This will not only bring about a growing limitation of the density (III. 4) but also an increasing spreading of risk in the relations

with other species (II. 4, II. 5, and III. 5), resulting in a reduction of density fluctuations and in a lowering of the risk of reaching excessively high or low densities. Moreover, if the invader takes live food, the growing pressure on the food population will mean a vigorous selection, which may ultimately result in the development of some means of defense (increase of "environmental resistance").

The best-known examples (and perhaps also the most numerous ones) of invaders finding a too "favourable" environment concern insects noxious to some crop (in agriculture, forestry, fruit-growing, etc.). In these cases, in which man has created a food supply for these insects that is "superfavourable" in many respects (quality, quantity, density, etc.), he will try to increase "environmental resistance", for instance by applying insecticides or importing predators, parasites, pathogens, etc. The application of insecticides must be continuous, of course, since it prevents other kinds of "environmental resistance" from developing or even abolishes them. The importation of enemies may initially result in the limitation of density, but since the spreading of risk in space and in the relations with other species will generally be very small in these rather homogeneous environments having few animal species, a high risk of great density fluctuations will remain (VOÛTE, 1964).

#### IV. CONCLUSION

When considering the problem of the long-term survival of populations we may wonder which characteristics of the population will give the most reliable information for an estimate of its chance of survival. It may be argued that a dense population will have a lower risk of extinction than a sparse one. But a high density has little insurance value, because it can be transformed into a low density within a very short time. I have, for example, seen two dense populations of the caddisfly *Enoicyla pusilla* Burm. decrease in one generation to about 1/60th and 1/1600th of their larval numbers, after which they remained at these low density levels throughout the next seven years during which these populations were observed. Furthermore, a sparse population can be transformed into a dense one in a very short time, a phenomenon seen in many noxious insect species. Therefore, density itself does not give reliable information for evaluation of the chance of survival. It is the way in which and the degree to which density fluctuates during a number of generations that determines the chance of reaching high or low numbers.

It will be evident that the less frequently the density approaches



extreme values, the greater will be the population's chance of survival (see also: WILLIAMS, 1966: 107). Most population ecologists agree that the amplitude of density fluctuations is determined to a great extent by density-independent factors (e.g. weather factors in temperate regions). Thus, the more effectively density is influenced by density-limiting factors, which decrease the possibilities for further growth of the population, the greater is the chance that the population will be exterminated in the course of time by the influence of density-independent factors (other things being equal). Limitation of density has little influence on the magnitude of density fluctuations; it usually only shifts them to a lower density level, thus increasing the risk of extinction (cf. III. 4). Hence, our problem is not "How is density limited?" but "*How is density-fluctuation restricted?*" The most reliable information for an evaluation of the chance of survival of a population should be sought in those statistics that characterize pattern and magnitude of density fluctuations (REDDINGIUS and DEN BOER, in press). The discussion in Section 2 suggests that these statistics are strongly influenced by the degree of variation in population and environment, since the different ways of spreading of the risk all have one and the same result: a relative reduction in the amplitude of fluctuations of animal numbers. Consequently, a population with a good chance of survival must be a population showing a high degree of phenotypic (cf. II. 1) and developmental (cf. II. 2) heterogeneity, inhabiting a large and heterogeneous locality (cf. II. 3), showing many and "spread" relations with many other species (cf. II. 4 and II. 5), and with a density fluctuating at a relatively high level but otherwise low enough to reduce the chance of excessive demands on the capacity of the environment, to which one or more forms of density-limitation (cf. III. 4 and III. 5) may contribute incidentally. Movement within the population and migration between populations of the same species have a favourable influence on the chance of survival.

Although such a population would have a high chance of survival, there can be no doubt that it will ultimately become extinct. In my opinion, this is not questionable at all (compare: ANDREWARTHA & BIRCH, 1954: 663 and BIRCH, 1957), since the extinction of populations and even of species is a common event, not only in a geological time scale. The only relevant point of discussion is how extinction can be delayed for some time: *extinction is only a matter of the realization of chance in the course of time.* An individual animal does not live very long; a subpopulation will persist much longer, especially if the spreading of the risk between individuals is considerable; a population will have a still

greater chance of survival, especially when the spreading of the risk of extinction between subpopulations is considerable (cf. II. 3); a species generally will have a very high chance of survival because of spreading of the risk of extinction between populations, and so on. After all, the question of the life-span necessary to maintain populations or species in nature should be considered in relation to the probable time-scale of changes in the environment, such as climatic changes, succession in the vegetation, diversion of rivers, etc., by which their habitats disappear, or in relation to the probability of major changes in their gene pool causing a principal alteration in the relations with their habitats. As a general conclusion, we may state that the chance of survival of a population depends on the pattern and magnitude of its density fluctuations, and, in turn, that these depend on the amount of spreading of the risk. In each particular case it will be necessary to investigate how much is contributed to population-stability by spreading of the risk and how much by limitation of density. Since the number of possible and even of realized combinations of kinds of populations with kinds of environments will be astronomically large, all kinds of more or less complicated and intricate combinations may be expected to exist. Hence, I am sure that any ecologist putting forward a sensible hypothesis on animal numbers will be able to find examples in nature that more or less confirm his ideas; and if he does not immediately succeed in finding such an example or does not care to seek a natural one, he may, with enough skill, "create" it in the laboratory. However, any "general theory" on animal numbers should take into account the enormous amount of variation in nature.

Since spreading of the risk may result from many kinds of variation, its occurrence in nature will be sufficiently universal to provide any of the most general "principles". But the last word will be spoken by the fieldworker, who is the only who can tell us what actually happens in nature.

#### V. ACKNOWLEDGEMENTS

I am greatly indebted to a number of Dutch population ecologists, since extensive correspondence and many discussions with them over the last seven years enabled me to mature my thoughts. Special thanks are due to Dr. J. REDDINGIUS and Dr. H. WOLDA (Groningen) for the many and very valuable improvements they proposed in the text of this paper. I am also grateful to Prof. Dr. H. KLOMP (Wageningen) for keeping a highly productive discussion open even though our opinions are in conflict in many respects.

I wish, too, to acknowledge the stimulating discussions and correspondence with Dr. K. BAKKER (Leiden) and Dr. A. D. VOÛTE (Arnhem).

Every part of the text has been discussed several times with my friend Mr. R. HENGEVELD (Wijster), and I am very grateful for his encouraging interest, valuable criticism, and productive exchange of ideas. Many thanks are also extended to Prof. Dr. H. J. VENEMA (Wageningen) for giving me full scope in my investigations at the Biological Station, Wijster. I want to thank Mrs. N. E. NANNENGA-BREMEKAMP (Doorwerth) and Mrs. I. SEEGER-WOLF (Leiden) for correcting the English text.

## VI. SUMMARY

Variation within natural populations as well as in their environments may result naturally in a spreading (diminution) of the risk of extinction to which these populations are exposed under the influence of variable environmental factors. Different ways of spreading of the risk can be distinguished:

1. Spreading of risk by phenotypic variation.
2. Spreading of risk in time: variation between individuals in time and rate of development and/or reproduction.
3. Spreading of risk in space: the effect of extreme conditions in one place will be levelled out to some degree by less extreme conditions in others. Migration can contribute to the levelling influence of spatial heterogeneity. The smaller the area inhabited by a population or species the lower the spatial heterogeneity and the greater the risk of extinction will be.
4. Spreading of risk in relations with other species: e.g. polyphagy, more than one predator (parasite) species to a prey, hyperpredation, hyperparasitism, phenotypic and developmental variation in preys and enemies, and spatial heterogeneity in their environments.

The different ways in which the risk is spread are intricate, and may contribute to a relative reduction in the amplitude of fluctuations in animal numbers. The chance of survival of a population is determined by the pattern and magnitude of its fluctuations. On this basis, a hypothesis is posed: density fluctuations in natural populations are stabilized to some degree by spreading of risk, or, in other words, by the number of factors influencing density. In a natural (heterogeneous) population in a natural (heterogeneous) environment, density-dependent and other

specific influences will be spread (levelled out) to a high degree. Hence, significant density-dependent influences can be expected mainly under rather homogeneous conditions. No population can continue to increase in numbers in a limited environment. Such limitation of density does not necessarily influence the magnitude of density fluctuations but mainly shifts them to a lower density level, thus increasing the risk of extinction. Spreading of the risk, on the contrary, has the same levelling influence on high as on low densities, and can be operative in sparse as well as in dense populations.

It is supposed that the stabilization of animal numbers in natural populations is established by spreading of the risk, incidentally supplemented by some kind of density limitation. The "balance of nature" must be the result of a complex and highly intricate "system" of spreading of the risk within populations and between populations of the same and especially of different species.

#### VII. REFERENCES

- ANDREWARTHA, H. G. (1957). The use of conceptual models in population ecology. Cold Spring Harb. Symp. quant. Biol., 22: 219-236.
- & L. C. BIRCH (1954). The distribution and abundance of animals. Chicago.
- BAILEY, V. A., A. J. NICHOLSON and E. J. WILLIAMS (1962). Interaction between hosts and parasites when some host individuals are more difficult to find than others. J. theor. Biol., 3: 1-18.
- BAND, H. T. (1963). Genetic structure of populations. II. Variabilities and variances of heterozygotes in constant and fluctuating environments. Evolution, 17: 307-319.
- BIRCH, L. C. (1957). The role of weather in determining the distribution and abundance of animals. Cold Spring Harb. Symp. quant. Biol., 22: 203-218.
- BODENHEIMER, F. S. (1928). Welche Faktoren regulieren die Individuen-Zahl einer Insektenart in der Natur? Biol. Zbl., 48: 714-739.
- (1930). Ueber die Grundlagen einer allgemeinen Epidemiologie der Insektenkalamitäten. Z. angew. Ent., 16: 433-450.
- (1958). Animal ecology to-day. Den Haag.
- COTT, H. B. (1940). Adaptive coloration in animals. London.
- DANILEVSKII, A. S. (1956). Photoperiodism and seasonal development of Insects. London.
- DARLINGTON, P. J. (1943). Carabidae of mountains and islands. Ecol. Monogr., 13: 37-61.
- (1957). Zoogeography. New York.
- DOBZHANSKY, TH. (1951). Genetics and the origin of species. 3rd ed. New York.
- ELTON, CH. S. (1958). The ecology of invasions by animals and plants. London.
- (1966). The pattern of animal communities. London.
- FRANZ, J. M. (1962). Definitions in biological control. Verh. XI. int. Kongr. Ent. (Wien, 1960), 2: 670-674.
- GLEN, R. (1954). Factors that affect insect abundance. J. Econ. Ent., 47: 398-405.

- HUTCHINSON, G. E. (1954). Theoretical notes on oscillatory populations. *J. Wildl. Mgmt.*, 18: 107-109.
- (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Naturalist*, 93: 145-149.
- KLOMP, H. (1962). The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal numbers. *Arch. Néerl. Zool.*, XV: 69-109.
- (1966). The dynamics of a field population of the Pine Looper, *Bupalus piniarius* L. (Lep., Geom.). *Adv. ecol. Res.*, 3: 207-305.
- LACK, D. (1966). Population studies of birds. Oxford.
- LINDROTH, CH. (1949). Die fennoskandischen Carabidae. III. Göteborgs Kgl. Vetensk. Handl., 4 (3): 1-911.
- MACARTHUR, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology*, 36: 533-536.
- MAYR, E. (1942). Systematics and the origin of species. New York. Dover Publ. Inc., 1964.
- (1963). Animal species and evolution. University of Harvard Press.
- (1965). The nature of colonizations in birds. (H. G. Bakker & G. C. Stebbens, The genetics of colonizing species). Acad. Press.
- MILNE, A. (1957). Theories on natural control of insect populations. Cold Spring Harb. Symp. quant. Biol., 22: 253-271.
- (1962). A theory of natural control of insect populations. *J. theor. Biol.*, 3: 19-50.
- MULLER, C. H. (1958). Science and philosophy of the community concept. *Am. Scientist*, 46: 294-308.
- MURDOCH, W. W. (1966). Population stability and life history phenomena. *Am. Naturalist*, 100: 5-11.
- NICHOLSON, A. J. (1933). The balance of animal populations. *J. Anim. Ecol.*, 11: 132-178.
- (1957). The self-adjustment of populations to change. Cold Spring Harb. Symp. quant. Biol., 22: 153-173.
- & V. A. BAILEY (1935). The balance of animal populations. *Proc. zool. Soc., Lond.*, 3: 551-598.
- PIMENTEL, D. (1961). Animal population regulation by the genetic feed-back mechanism. *Am. Naturalist*, 95: 65-79.
- PRESTON, F. W. (1962). The canonical distribution of commonness and rarity. *Ecology*, 43: 185-215, 410-432.
- REDDINGIUS, J. (1968). Gambling for existence. *Acta Biotheor.* (In press).
- & P. J. DEN BOER (1969). Computational models illustrating stabilization of animal numbers by spreading of risk. *Acta Biotheor.* (In press).
- REYNOLDS, T. B. (1957). Population fluctuations in *Urceolaria mitra* (Peritricha) and *Enchytraeus albidus* (Oligochaeta) and their bearing on regulation. Cold Spring Harb. Symp. quant. Biol., 22: 313-327.
- RICHARDS, O. W. (1961). The theoretical and practical study of natural insect populations. *Ann. rev. ent.*, 6: 147-162.
- SCHNEIDER, F. (1939). Ein Vergleich von Urwald und Monokultur in Bezug auf ihre Gefährdung durch phytophage Insekten auf Grund einiger Beobachtungen an der Ostküste von Sumatra. *Schweiz. Z. Forstwesen*, 2 u. 3 (22 pp.).
- SCHWERTFEGER, F. (1958). Is the density of animal populations regulated by mechanisms or by chance? *Proc. X. int. Congr. Ent.*, 1956, 4: 115-122.
- SOLOMON, M. E. (1949). The natural control of animal populations. *J. Anim. Ecol.*, 18: 1-35.
- (1957). Dynamics of insect populations. *Ann. Rev. ent.*, 2: 121-142.

- THOMPSON, W. R. (1929). On natural control. *Parasitology*, 21: 269-281.
- (1939). Biological control and the theories of the interactions of populations. *Parasitology*, 31: 299-388.
- (1956). The fundamental theory of natural and biological control. *Ann. Rev. ent.*, 1: 397-402.
- TIMOFÉEFF-RESSOVSKY, N. W. (1940). Zur Analyse der Polymorphismus bei *Adalia bipunctata*. *Biol. Zbl.*, 60: 130-137.
- TINBERGEN, L. (1960). The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. *Arch. Néerl. Zool.*, XIII: 265-336.
- and H. KLOMP (1960). The natural control of insects in pine woods. II. Conditions for damping of Nicholson oscillations in parasite-host systems. *Arch. Néerl. Zool.*, XIII: 344-379.
- VARLEY, G. C. and G. R. GRADWELL (1958). Balance in insect populations. *Proc. X. int. Congr. Ent.*, 1956, 2: 619-624.
- VLIJM, L. and TH. S. VAN DIJK (1967). Ecological studies in Carabid beetles. II. General pattern of population structure in *Calathus melanocephalus* (Linn.) at Schiermonnikoog. *Z. Morph. Ökol. Tiere*, 58: 396-404.
- VOÛTE, A. D. (1946). Regulation of the density of the insect populations in virgin forests and cultivated woods. *Arch. Néerl. Zool.*, VII: 435-470.
- (1964). Harmonious control of forest insects. *Int. Rev. Forest. Res.*, 1: 325-383.
- WILBERT, H. (1962). Ueber Festlegung und Einhaltung der mittleren Dichte von Insektenpopulationen. *Z. Morph. Ökol. Tiere*, 50: 576-615.
- WILLIAMS, C. B. (1964). *Patterns in the balance of nature*. London.
- WILLIAMS, G. C. (1966). *Adaption and natural selection*. University of Princeton Press.