

## THE DEVELOPMENT OF A CONCEPT

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When, in 1945, I started to study biology at Leiden University, population dynamics were dominated by the ideas of Nicholson (1933). From 1953 onwards, when I became an assistant of Dr. D.J. Kuenen, the first Professor of Ecology in the Netherlands, I was involved in population dynamics and had to form an opinion about the ideas of Nicholson. In the summary of his paper Nicholson stated (1933: 176): "2. The densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments. 3. For balance, it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way." I had great difficulties with these and related ideas of Nicholson, which were deeply discussed in evening meetings at Don Kuenen's home.

In this introduction I will try to explain my doubts and to describe how in successive steps my thoughts about an alternative for regulation and the expected survival of populations developed. The papers resulting from this development and from the associated investigations on the survival of populations are successively mentioned in the following sections and the most important ones are reprinted in following chapters.

### **Objections against regulation of animal numbers**

My field experiences as an active member of the Netherlands Youth Association for the Study of Nature (NJN) did not support the idea that animal populations would be 'in a state of balance with their environments'. I struggled with questions like "what are these 'environments'"; "do weather conditions also belong to the environment, and can populations ever be 'in balance' with conditions that change from day to day?" At first, it was explained to me that weather conditions are not part of the environment, but disturb the 'balance' between population and environment. 'Competition' would be the governing factor that tends to bring density back to its 'steady state' value. But how would density be kept in balance when there is no competition, because no resource is in short supply? Then, I was told, density would increase until the 'carrying capacity' of the environment was reached and the animals had to compete for one or more

resources. This competition would decrease density, which would then return to its equilibrium value or even lower. I was not sure that without competition, density would always increase. For instance, weather conditions could prevent a return to the steady state density. And how could density, which is an abstraction, (i.e. the mean number of animals per unit of surface or volume) result in a state of balance? In the natural environments that I observed, individuals of most animal species are clustered to varying degrees in small parts of the total habitat of the population; so, what is the reactive density? And what does 'population' mean? To be regulated it must be a small group of animals, for otherwise the individuals cannot directly compete for a resource in short supply. Does Nicholson have such small groups of animals in mind? Strictly speaking, only closed populations can be 'regulated', and how many local populations in nature are closed? In short, as long as nobody could convincingly show me how such a 'regulation of animal numbers' could come about, I stayed sceptical.

#### **The book of Andrewartha and Birch**

During the discussions at Kuenen's home about 'regulation of animal numbers' the book of Andrewartha & Birch 'The distribution and abundance of animals' (1954) appeared, and at the discussion evenings I had to explain why these Australian ecologists had

similar doubts about the ideas of their fellow-countryman Nicholson as I had. On the one hand, this book supported my scepticism, but on the other, because of the way in which criticisms were formulated by the authors, I realised that the controversies would never disappear if an alternative hypothesis for the relative stability over time of many populations could not be proposed and tested. Therefore, from that time on I thought about an alternative for 'regulation of animal numbers'. The population ecologists I knew at that time, all studied only single populations of one species, e.g. Varley & Gradwell a single 'population' of the winter moth near Oxford, Herman Klomp a single 'population' of the pine looper at 'Hoge Veluwe', etc. Such studies might render it difficult to discriminate between general and exceptional causes of density fluctuations. Hence, I concluded that a **comparative** investigation into the fluctuations of numbers in several well-defined populations might provide the best possibility to discover both the general causes of these fluctuations and their effects on the survival of the groups of animals concerned.

In 1953 we (the biologists of the Zoological Department of Leiden University) started an investigation to follow the effects of an artificial change of environmental conditions, brought about by inundation of certain dune valleys in Meijendel near The Hague. I decided to compare the fluctuations of numbers of

different species of carabid beetles in different habitats. Carabid beetles seemed to me very suitable for comparative investigations, because individuals of all species moving around in a certain habitat could be caught in the same set of pitfalls. To get the necessary data we put pitfalls in many structurally different habitats.

In 1958 I got the opportunity to organise my own comparative investigations at the Biological Station in Wijster, a Department of Wageningen Agricultural University. Hence, in 1959 I placed pitfalls in many habitats around the Biological Station, and compared the fluctuations of population numbers of about 60 carabid species in a considerable variety of habitat over as many years as possible.

Meanwhile, by letter, I continued the discussions about competition with Kees Bakker, who had finished a thorough experimental study about competition between *Drosophila*-larvae (1961), and, with Herman Klomp, who was a ardent defender of the ideas of Nicholson about regulation of animal numbers. These correspondences, which helped me to develop my thoughts, were a follow-up of discussions started in Leiden.

#### **The influence of climate and weather on animal numbers**

In 1961 Klomp presented a paper on the influence of weather and climate on the mean density level and the fluctuations and

regulation of density in animal populations. In this lecture, delivered for the Dutch Zoological Society, he stated that climate was responsible for the mean density level of animal populations, and that weather conditions resulted in fluctuations of numbers around this mean density. As weather conditions may cause heavy fluctuations of numbers, populations can only persist if there is some 'mechanism' that 'regulates' their numbers, i.e. a mechanism that returns numbers to the mean density level. In the discussion after the presentation, I proposed an idea contrary to Klomp's view. I suggested that different weather conditions of variable intensities might partly compensate each others' effects so that change of numbers (net rate of reproduction) may be smaller than expected from the weather conditions considered separately. I brought this into the discussion because, for a long time, I had been thinking about the effect on net reproduction of a number of variables influencing numbers, and about the possibility of what I initially formulated as '**compensation of risks**' and later as '**risk distribution**'.

The discussion with Herman Klomp did not lead to a satisfactory conclusion, so that by letter he tried to convince me that I was wrong. As I was not convinced by his arguments we corresponded about this and related subjects over a number of years, but we never came to a joint conclusion. Because of that,

in his publication in Archives Néerlandaises de Zoologie of 1962 on this subject my opinion was represented as follows (p. 93): "It has been argued by one of my colleagues in Holland (Dr. P.J. den Boer, in letters to the present author) that most animal populations fluctuate at random within relatively narrow limits due to weather influences, density related factors only coming into operation at extremely high (and perhaps low) densities. This would especially be the case if the net rate of reproduction is determined by a high number of factors." In his paper, he argued why such a 'mechanism' does not work. This paper (Klomp 1962) stimulated me to find ways to convincingly show the compensating effects that a number of factors together may have on the net rate of reproduction of an animal population.

**A model on the levelling effects of the number of weather factors on fluctuations of population numbers**

In 1963 I planned to develop a sufficiently realistic model in which the net rate of reproduction in a population is determined by one, two, etc., until ten weather variables acting simultaneously upon the population. As I had no access at that time to a computer I had to do all calculations with my slide rule. To avoid spending much time doing calculations, which were based on a mathematically inefficient model, I went to the Institute of Theoretical Biology in Leiden to get an opinion

about the mathematics of my model. There I met Hans Reddingius, who was immediately highly interested in my project, because he was preparing a thesis about mathematical problems associated with 'regulation of animal numbers'. He liked the structure of my model, and during the following period of modelling we corresponded about details and more general aspects of what I called ~~sation~~ 'stabilisation of animal numbers'; stabilisation brought about by a number of variables determining the frequency distribution of net reproduction values of a population. After many evenings, spread over a period of two years (during the day I worked at the Biological Station at Wijster), of sliding with my slide rule I could show that with an increasing number of weather variables determining the frequency distribution of net reproduction values, usually a population would become more stable; i.e. densities would fluctuate between narrower limits and periods with decreasing and increasing densities respectively would become shorter (Den Boer 1966).

#### **Spreading of risk**

In order not to interfere with the preparation of Hans Reddingius' thesis we agreed to separately write down our opinions about regulation and stabilisation. I promised to provoke reactions from my colleagues to a preliminary paper about my model, which I presented to the ~~d~~ discussion group on

Population Dynamics, founded by Herman Klomp and Huib Kluyver. This discussion occurred early in 1966. Among my colleagues, especially Henk Wolda, who proposed to call the phenomenon I proposed 'spreading of risk', and Kees Bakker, who had just published a paper about the controversies surrounding population theories (Bakker 1964), were interested in the results of my model. Next, Hans Reddingius asked me to prepare a paper about my ideas on 'the stabilisation of animal numbers by spreading of risk' (Den Boer 1968), so that he could refer to it in his thesis. Meanwhile Reddingius had transferred to the Groningen University, where he had access to a relatively fast computer, for which he wrote a computer programme to simulate a more sophisticated version of my model, which corroborated my theories. Together we published the results (Reddingius & Den Boer 1970) and added simulation results obtained by Reddingius at Leiden for a model with subpopulations and exchanges between them.

#### **Gambling for existence**

In his thesis Reddingius (1971: 38), after having discussed deterministic population theory in mathematical terms, and having pointed out that the applicability of this theory met with serious difficulties, he concluded: **"A realistic population theory will have to be framed in terms of probabilities, averages**

and similar statistical concepts." Next, he tried to translate the deterministic concepts of 'regulation theory' into probabilistic terms and concluded (1971: 77/78): "**Deterministic theory in population ecology seems to be of little help in providing a framework for probabilistic theory. We had better not adhere too much to our deterministic concepts and ideas, but start afresh.**"

Reddingius then discussed a number of 'admissible hypotheses' in population theory, which led him to the opinion (1971: 98):

"Therefore I think it an attractive idea to replace the metaphor 'struggle for existence' by the other metaphor '**gambling for existence**'. This gambling may be prolonged to a considerable extent by distributing one's stakes over different adversaries and different occasions."

"What is true for species on a geological time scale should be true a fortiori for populations as studied by ecologists. I think admissible hypotheses in population ecology can best be formulated in the light of Den Boer's (1968) theory of the stabilisation of animal numbers by 'spreading of risk'".

### **Natural selection and risk spreading**

It seems that Charles Darwin (1859) realised that 'natural selection' is not a 'mechanism' but a blind force, the results of

which do not depend on the future. Some individuals in a population benefit from the results of natural selection as long as the circumstances allow. As soon as environmental conditions change natural selection also changes direction. Hence, this really is 'gambling for existence', and in this 'gamble' some or many individuals may benefit from certain forms of risk spreading, and these survive certain adverse conditions to meet the same or other adverse conditions in the future. \*. Certain individuals are thought to be favoured because the risk of becoming extinct is 'spread' over a number of categories (individuals of different ages, with different properties, under different circumstances, and the like), thus diminishing the risk. Individuals with special properties or those that are exposed to certain circumstances will suffer from some adverse conditions. But not all individuals in the population will suffer, and thus the fluctuations of numbers may be levelled. In general, the greater heterogeneity in both population and environment, the higher the chance that the risk of extinction is sufficiently spread and

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\* Note that, like natural selection, spreading of risk is a passive force. Individual animals neither select themselves, nor actively spread their risks.

'gambling' is continued, i.e. the population will survive for some time.

**The Advanced Study Institute on Dynamics of Numbers in Populations**

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In 1970, and international congress on population dynamics 74  
united all important population ecologists of the Netherlands and many colleagues from abroad in the 'Bilderberg' in Oosterbeek, thanks to financial support by NATO. For me it was the first opportunity to present and debate my ideas on 'stabilisation of animal numbers by means of risk spreading' (Den Boer 1971) to to an international group of colleagues. While 'regulation of animal numbers' was no longer the dominant topic at the congress (Den Boer & Gradwell 1971) as it was in Cold Spring Harbor in 1957, I presented my paper with the first examples of risk spreading in real populations, which aroused great interest from Andrewartha and Birch.

**The interaction group as a population unit**

To be able to compare the fluctuations in the density of a number of carabid species, which are sampled with standard sets of pitfalls, it is necessary, of course, to know the quantitative

relationship between pitfall catches and actual density. During the first years of my investigations at the Wijster Biological Station, it had become clear that for all 'normal' activities (feeding, looking for a mate, laying eggs, etc.) carabid beetles move about randomly on the ground. As the degree of activity is greatly affected by weather conditions, the numbers of individuals caught in a set of pitfalls can only show some stable relationship with local density if summarized over a sufficiently long period, i.e. a period in which all kinds of weather conditions will have occurred frequently enough to average special effects. Also it became clear that carabid beetles' wings and flight muscles are only used to disperse, i.e. to leave the local population (Den Boer 1970). With the help of mark-recapture experiments it was established that the pitfall catches, summed over the entire activity period, or the whole year (year-catch), represent a reliable relative estimate of mean density in the vicinity of the set of pitfalls. The first results of such mark-recapture experiments are given in Den Boer (1971).

The carabid beetles of the same species caught in a particular set of pitfalls, and which form a representative sample of local density, were able to interact with each other. Hence, they are a sample of the local 'interaction group', which I considered to be the most relevant unit of local population (Den Boer 1977). But what is the size of such an interaction group and over what

surface does it occur?

These questions were investigated and answered by Martien Baars. By marking some beetles radioactively, and recording the place of recovery each day with a sensitive scintillation detector, Baars (1979a) could reconstruct the walking pattern in day-distances over the entire reproductive season for two species of carabid beetles. By simulating these day-distances from the frequency distribution found in the field, and letting the simulated beetles "walk" in the computer, he could estimate the area covered during one or more activity seasons by beetles belonging to the same interaction group. With these walking patterns Baars (1979b) simulated my pitfall-catches with a group of 1000 computer-beetles released at the same site and recaptured at different distances. He then executed this experiment in the field with 1000 brand-marked beetles to show that his simulations closely resemble the field situation. By catching all beetles early in the activity period within enclosures of different sizes and comparing these direct measures of density with the year-catches in nearby standard sets of pitfalls, Baars (1979b) was able to translate year-catches into local densities. The correlation between year-catch and local density was almost identical. *perfect.*

The above results of Martien Baars' investigations together with those of my mark-recapture experiments (Den Boer 1979) enabled me to compare the actual density fluctuations over 21 years of two carabid species living in several interaction groups in the same heath area of about 800 ha with the fluctuations in the population consisting of the combined fluctuations of all the interaction groups (Den Boer 1981).

#### **Little change of opinion among population ecologists**

In 1980 Theo van Dijk, my colleague at the Biological Station, and I, presented our findings from the Station at a symposium on 'Biological Systems theory' at the University of Bremen. I demonstrated that a population couldn't be considered a 'system', because most populations cannot be objectively bounded and are heterogeneously structured. Most natural populations consist of local subpopulations, living under local conditions and thus showing fluctuations of numbers that may differ from that of other subpopulations. I gave examples of subpopulations of two carabid species at Kralo Heath and demonstrated that this heterogeneous structure results in spreading the risk of extinction over differently fluctuating subpopulations (Den Boer 1982). Theo van Dijk gave examples of individual variability in egg production and age within subpopulations of two carabid species. He especially emphasized the effect of temperature and

food quantity and quality on the amount of eggs produced, and tried to indicate to what degree both a heterogeneous egg production and age composition in a subpopulation may contribute to levelling of density fluctuations (Van Dijk 1982). Especially Steve Stearns was impressed by the content of our papers, and went with us to Wijster to learn more about our research.

Meanwhile, discussions on 'regulation of animal numbers' continued. Strong (1986) tried to take a compromising view by introducing 'density-vague processes'. Hassell (1985) tried to explain how spatial heterogeneity within generations can 'regulate' population numbers, i.e. can result in temporal density dependence. This view was countered by Dempster & Pollard (1986). Nevertheless, Hassell (1986) still upholds the view that density dependence within separate patches leads to density-dependent regulation of population numbers, even though it becomes apparent from life-table analyses that environmental stochasticity might prevent this. Den Boer (1987a) tries to show that when density-dependent processes are synchronized over all patches it will also be detected in life tables, and when such a density dependence does not appear from life tables population numbers are not 'regulated' by density-dependent processes, because the effects are asynchronously spread over the patches and thus obliterated. Population processes are 'scale-dependent': What is found to occur in a patch or interaction group as a

result of interactions between individuals, usually differs from what is observed at what is generally considered to be the population level. This is because individuals do not cover the whole area occupied by the 'population' and thus cannot interact with all other individuals; interactions are necessarily local.

Although these and similar discussions deal with the effects of heterogeneity in population and environment no author cites my works on risk spreading. Wellington et al. (1975) and Thompson et al. (1976) convincingly show that the survival of the Western Tent Caterpillar (*Malacosoma californicum pluviale*) at Saanich Peninsula near Vancouver is an evident case of stabilisation by 'spreading of risk' as defined by Den Boer (1968). Andrewartha & Birch (1984) made 'spreading of risk' one of the cornerstones of their new book, and devoted an entire chapter to 'spreading of risk in evolution'. In this chapter, illustrated by many examples from field studies, they especially emphasize the processes, situations and factors that promote genetic diversity, which in turn results in genetic spreading of the risk, further contributing to the maintenance of genetic diversity.

#### **On the survival of interaction groups**

Unfortunately, the second book of Andrewartha & Birch (1984) did not provoke the excitement and discussions of their first book. Many ecologists merely considered it 'more of the same'.

Therefore, I tried to model the fluctuations of numbers I observed in long-term studies of field populations of carabid beetles as random walks of densities, and to predict what we might expect for the survival time of interaction groups from such patterns. These modelled survival times appeared to vary between four years for species living as nomades and more than hundred years for species of old, deciduous forest (Den Boer 1985a).

But then Hassell et al. (1989) stated: "Most studies in which populations have been monitored over several generations show fluctuations in population size around some characteristic level of abundance, quite unlike unbounded population growth or any 'random walk' inevitably meandering to extinction. Clearly, some kind of negative feedback process acting for at least some of the time on at least part of the population, must be involved in the dynamics of such populations (...)",

I realised that most population ecologists will find it difficult to distinguish interaction groups for the animals under study. However, if populations, defined in a different way or not at all, but are sampled continuously according to the same method during many generations, net reproduction values will fit a log-normal distribution too. In an effort to explain the concept, I compared random walks of densities with the patterns of fluctuations of the density of natural populations, which have

been monitored long enough to show a pattern. This demonstrated that the numbers of many natural populations - including those that are claimed to be 'regulated'- do not fluctuate between narrower limits than comparable random walks of densities. Sometimes they fluctuate between even wider limits. It was especially significant that both in field populations and in random walks of densities, the limits between which densities fluctuate (Log-Range) increase in time to about the same extent. In 'regulated' populations, however, one would expect these limits to stay the same in the course of time (Den Boer 1991). It could even be shown that these methods enable us to make realistic estimates of the survival time of populations (De Vries & Den Boer 1990). See also Den Boer & Reddingius (1996: 4.3, 4.5).

In 1997, I was invited to speak about the effects of density-independent processes on the stability and survival of insect populations at a symposium of the Royal Entomological Society in the University of Newcastle (Den Boer 1998);

### **Spreading of risk and evolution**

As 'spreading of risk' may influence the survival of all groups of animals it also has consequences for our ideas about evolution. From the first moment I realised that 'spreading of risk' is a reality in nature I was convinced that it must also

affect evolutionary processes. I formulated this conviction as follows: "Moreover, in the course of time, in the field natural selection has appeared usually to be a very complicated and often elusive process, that in many cases seems to be more properly described as 'the non-survival of the non-fit' than as 'the survival of the fittest'. This slogan has to be understood as: sufficient survival and reproduction in many cases can be reached from a number of quite different combinations of properties and/or conditions, by which in many -if not most- cases the more persevering changes of the gene-pool on average might appear mainly to result from selecting away of the overall 'non-fit', thus leaving intact a great reserve of genetic variability enabling the population to cope with many different situations (spreading of risk: Den Boer 1968; Andrewartha and Birch 1984: Ch. 11)" (Den Boer 1985b: 260).

#### **Genetic spreading of risk**

In order to be able to distinguish *P. oblongopunctatus* from the closely related *P. quadrifoveolatus* (= *P. angustatus*) I had to inspect the pattern and number of pits on the elytra. From the very start of my investigations in 1959, it struck me that in *P. oblongopunctatus* the number of pits varies greatly, ranging from 4(3) or 5(6) to a maximum of 12. By determining for each site sampled the frequency distribution of pit numbers it became clear

that there are two groups: 'low-pitters' with 4 or 5 pits, which dominate under rather dry conditions, and 'high-pitters' with 6 or more pits, which dominate under moist conditions of soil and litter. Some crossing experiments in the field showed that the difference between these two groups of pit numbers has a genetic base, though not a simple one. I hypothesized that larvae of 'high-pitters' survive better under moist conditions and those of 'low-pitters' under dryer conditions. In spite of some field experiments to test this hypothesis and a lot of circumstantial evidence confirming the existence of this 'genetic spreading of risk', a convincing proof was not obtained. Therefore, for many years this evidence stayed in my desk. But when in the 1980's one of my doctoral students and my Polish colleague Jan Szyszko found new circumstantial evidence confirming my hypothesis I decided to publish all evidence we had so far (Den Boer et al. 1993).

#### **Regulation versus spreading of risk**

In a series of publications (Den Boer 1986, 1987b, 1988), I tried to demonstrate, that populations which are supposed to be 'regulated' by density-dependent processes fluctuate between wider limits with than without these density-dependent effects; together with Hans Reddingius, I showed that the design of tests for density dependence is bound by some necessary restrictions (Reddingius & Den Boer 1989; Den Boer & Reddingius 1989; Den Boer

1990). In 1996 Hans Reddingius and I authored a book in which the whole story around the 'regulation' versus 'stabilisation' of animal numbers has been brought together (Den Boer and Reddingius 1996). In this book all arguments and data favouring the belief of an overall 'regulation of animal numbers' by density-dependent processes are critically discussed. We showed that though density dependence is a necessary condition for 'regulation' to occur, it is not at all a sufficient condition. 'Regulation of numbers' in natural populations is not impossible, but a convincing example of a 'regulated' field population under natural conditions has still to be found.

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